# THE PRINCIPLES

OF

# BIOLOGY.

BY

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# PREFACE.

The aim of this work is to set forth the general truths of Biology, as illustrative of, and as interpreted by, the laws of Evolution: the special truths being introduced only so far as is needful for elucidation of the general truths.

For aid in executing it, I owe many thanks to Prof. Huxley and Dr Hooker. They have supplied me with information where my own was deficient;* and, in looking through the proof-sheets, have pointed out errors of detail into which I had fallen. By having kindly rendered me this valuable assistance, they must not, however, be held committed to any of the enunciated doctrines that are not among the recognized truths of Biology.

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* Gross misrepresentations of this statement, which have been from time to time made, oblige me, much against my will, to add here an explanation of it. The last of these perversions, uttered in a lecture delivered at Belfast by the Rev. Professor Watts, D.D., is reported in the *Belfast Witness* of December 18, 1874; just while a third impression of this work is being

printed from the plates. The report commences as follows :—" Dr. Watts, after showing that on his own confession Spencer was indebted for his facts to Huxley and Hooker, who," &c., &c.

Wishing in this, as in other cases, to acknowledge indebtedness when conscious of it, I introduced the words referred to, in recognition of the fact that I had repeatedly questioned the distinguished specialists named, on matters beyond my knowledge, which were not dealt with in the books at my command. Forgetting the habits of antagonists, and especially theological antagonists, it never occurred to me that my expression of thanks to my friends for "information where my own was deficient," would be turned into the sweeping statement that I was indebted to them for my facts.

Had Professor Watts looked at the preface to the second volume (the two having been published separately, as the prefaces imply), he would have seen a second expression of my indebtedness "for their valuable criticisms, and for the trouble they have taken in *checking* the numerous statements of fact on which the arguments proceed"—no further indebtedness being named. A moment's comparison of the two volumes in respect of their accumulations of facts, would have shown him what kind of warrant there was for his interpretation.

Doubtless the Rev. Professor was prompted to make this assertion by the desire to discredit the work he was attacking; and having so good an end in view, thought it needless to be particular about the means. In the art of dealing with the language of opponents, Dr. Watts might give lessons to Monsignor Capel and Archbishop Manning.

*December 28th*, 1874.

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# PART I.

## THE DATA OF BIOLOGY.

# CHAPTER I.

## ORGANIC MATTER.

§ 1. Of the four chief elements which, in various combinations, make up living bodies, three are gaseous. While carbon is known only as a solid, oxygen, hydrogen, and nitrogen are known only in the aeriform state. Under pressures great enough to reduce them almost to the density of liquids these elements have still defied all efforts to liquefy them. There is a certain significance in this. When we remember how those re-distributions of Matter and Motion which constitute Evolution, structural and functional, imply motions in the units that are re-distributed; we shall see a probable meaning in the fact that organic bodies, which exhibit the phenomena of Evolution in so high a degree, are mainly composed of ultimate units having extreme mobility. The properties of substances, though destroyed to sense by combination, are not destroyed in reality: it follows from the persistence of force, that the properties of a compound are *resultants* of the properties of its components—*resultants* in which the properties of the components are severally in full action, though greatly obscured by each other. One of the leading properties of each substance is its degree of molecular mobility; and its degree of molecular mobility more or less sensibly affects the molecular mobilities of the various compounds into which it enters. Hence we may infer some relation between the gaseous form of three out of the four chief organic elements, and that comparative readiness displayed by organic matters to undergo those changes in the arrangement of parts which we call development, and those transformations of motion which we call function.

Considering them chemically instead of physically, it is to be remarked that three out of these four main components of organic matter, have affinities which are narrow in their range and low in their intensity. Hydrogen combines with comparatively few other elements; and such chemical energy as it does show, is scarcely at all shown within the limits of the organic temperatures. Of carbon it may similarly be said that it is totally inert at ordinary heats; that the number of substances with which it unites is not great; and that in most cases its tendency to unite with them is but feeble. Lastly, this chemical indifference is shown in the highest degree by nitrogen—an element which, as we shall hereafter see, plays the leading part in organic changes.

Among the organic elements, including under the title not only the four chief ones, but also the less conspicuous remainder, that capability of assuming different states, called allotropism, is frequent. Carbon presents itself in the three unlike conditions of diamond, graphite, and charcoal. Under certain circumstances, oxygen takes on the form in which it is called ozone. Sulphur and phosphorus (both, in small proportions, essential constituents of organic matter) have allotropic modifications. Silicon, too, is allotropic; while its oxide, silica, which is an indispensable constituent of many lower organisms, exhibits the analogue of allotropism—isomerism. And even of the iron which plays an active part in higher organisms, and a passive part in some lower ones, it may be said that though not known to be itself allotropic, yet isomerism characterizes those compounds of it that are found in living bodies. Allotropism being interpretable as some change of molecular arrangement, this frequency of its occurrence among the components of organic matter, is significant as implying a further kind of molecular mobility.

One more fact, that is here of great interest for us, must be set down. These four elements of which organisms are almost wholly composed, present us with certain extreme antitheses. While between two of them we have an unsurpassed contrast in chemical activity; between one of them and the other three, we have an unsurpassed contrast in molecular mobility. While carbon, by successfully resisting fusion and volatilization at the highest temperatures that can be produced, shows us a degree of atomic cohesion greater than that of any other known element, hydrogen, oxygen, and nitrogen, show the least atomic cohesion of all elements. And while oxygen displays, alike in the range and intensity of its affinities, a chemical energy exceeding that of any other substance (unless fluorine be considered an exception), nitrogen displays the greatest chemical inactivity. Now on calling to mind one of the general truths arrived at when analyzing the process of Evolution, the probable significance of this double difference will be seen. It was shown (*First Principles*, § 123) that, other things equal, unlike units are more easily separated by incident forces than like units are—that an incident force falling on units that are but little dissimilar does not readily segregate them; but that it readily segregates them if they are widely dissimilar. Thus, these two extreme contrasts, the one between physical mobilities, and the other between chemical activities, fulfil, in the highest degree, a certain further condition to facility of differentiation and integration.

§ 2. Among the binary combinations of these four chief organic elements, we find a molecular mobility much less than that of these elements themselves; at the same time that it is much greater than that of binary compounds in general. Of the two products formed by the union of oxygen with carbon, the first, called carbonic oxide, which contains one atom of carbon to one of oxygen (expressed by the symbol C O), is an incondensible gas; and the second carbonic acid, containing an additional atom of oxygen ($C O_2$) assumes a liquid form only under a pressure of nearly forty atmospheres. The several compounds of oxygen with nitrogen, present us with an instructive gradation. Protoxide of nitrogen, which contains one atom of each element ($N O$), is a gas condensible only under a pressure of some fifty atmospheres; deutoxide of nitrogen ($N O_2$) is a gas hitherto uncondensed (the molecular mobility remaining undiminished in consequence of the volume of the united gases remaining unchanged); nitrous acid ($N O_3$) is gaseous at ordinary temperatures, but condenses into a very volatile liquid at the zero of Fahrenheit; peroxide of nitrogen ($N O_4$) is gaseous at 71°, liquid between that and 16°, and becomes solid at a temperature below this; while nitric acid ($N O_5$) may be obtained in crystals which melt at 85° and boil at 113°. In this series we see, though not with complete uniformity, a decrease of molecular mobility as the weights of the compound molecules are increased. The hydro-carbons illustrate the same general truth still better. One series of them will suffice. Marsh gas ($C_2 H_4$) is permanently gaseous. Olefiant gas ($C_4 H_4$) may be liquefied by pressure. Oil gas, which is identical with olefiant gas in the proportions of its constituents but has double the atomic weight, ($C_8 H_8$), becomes liquid without pressure at the zero of Fahrenheit. Amylene ($C_{10}H_{10}$) is a liquid which boils to 102°. And the successively higher multiples, caproylene ($C_{12} H_{12}$), caprylene ($C_{16} H_{16}$), elaene ($C_{18} H_{18}$) and paramylene ($C_{20} H_{20}$), are liquids which boil respectively at 102°, 131°, 257°, 230°, and 329°. Cetylene ($C_{32} H_{32}$) is a liquid which boils at 527°; while paraffine ($C_{54} H_{54}$) and mylene ($C_{60} H_{60}$) are solids. Only one compound of hydrogen with nitrogen has been obtained in a free state—ammonia ($H_3 N$); and this, which is gaseous, is liquefiable by pressure, or by reducing its temperature to —40° F. In cyanogen, which is composed of nitrogen and carbon ($N C_2$), we have a gas that becomes liquid at a pressure of four atmospheres and solid at —30° F. And, in paracyanogen, formed of the same proportions of these elements in higher multiples ($N_3$ $C_6$), we have a solid which does not fuse or volatilize at ordinary temperatures. Lastly, in the most important member of this group, water, (H O or else as many chemists now think $H_2$ $O_2$) we have a compound of two incondensible gases which assumes both the fluid state and the solid state within ordinary ranges of temperature; while its molecular mobility is still such that its fluid or solid masses are continually passing into the form of vapour, though not with great rapidity until the temperature is raised to 212°.*

Considering them chemically, it is to be remarked of these binary compounds of the four chief organic elements, that they are, on the average, less stable than binary compounds in general. Water, carbonic oxide, and carbonic acid, are, it is true, difficult to decompose. But omitting these, the usual strength of union among the elements of the above-named substances is low considering the simplicity

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* This immense loss of molecular mobility which oxygen and hydrogen undergo on uniting to form water—a loss far greater than that seen in other binary compounds of analogous composition—suggests the conclusion that the atom of water is a multiple atom. Thinking that if this conclusion be true, some evidence of the fact must be afforded by the heat-absorbing power of aqueous vapour, I lately put the question to Prof. Tyndall, whether it resulted from his experiments that the vapour of water absorbs more heat than the supposed simplicity of its atom would lead him to expect. I learned from him that it *has* an excessive absorbent power—an absorbent power more like that of the complex-atomed vapours than like that of the simple-atomed vapours—an absorbent power that therefore harmonizes with the supposition that its atom is a multiple one. Besides this anomalous loss of molecular mobility and this anomalous heat-absorbing power, there are other facts which countenance the supposition. The unparalleled evolution of heat during the combination of oxygen and hydrogen is one. Another is that exceptional property which water possesses, of beginning to expand when its temperature is lowered below 40°; since this exceptional property is explicable only on the assumption of some change of molecular arrangement—a change which is comprehensible if the molecules are multiple ones. And yet a further confirmatory fact is the ability of water to assume a colloid condition; for as this implies a capacity in its atoms for aggregating into high multiples, it suggests, by analogy with known cases, that they have a capacity for aggregating into lower multiples.

of the substances. With the exception of acetylene, the various hydro-carbons are not producible by directly combining their elements; and the elements of most of them are readily separated by heat without the aid of any antagonistic affinity. Nitrogen and hydrogen do not unite with each other immediately; and the ammonia which results from their mediate union, though it resists heat, yields to the electric spark. Cyanogen is stable: not being resolved into its components at a red heat, unless in iron vessels. Much less stable however are the several oxides of nitrogen. The protoxide, it is true, does not yield up its elements below a red heat; but nitrous acid cannot exist if water be added to it; hypo-nitric acid is decomposed both by water and by contact with the various bases; and nitric acid not only readily parts with its oxygen to many metals, but when anhydrous, spontaneously decomposes. Here it will be well to note, as having a bearing on what is to follow, how characteristic of most nitrogenous compounds is this special instability. In all the familiar cases of sudden and violent decomposition, the change is due to the presence of nitrogen. The explosion of gunpowder results from the readiness with which the nitrogen contained in the nitrate of potash, yields up the oxygen combined with it. The explosion of gun-cotton, which also contains nitric acid, is a substantially parallel phenomenon. The various fulminating salts are all formed by the union with metals, of a certain nitrogenous acid called fulminic acid; which is so unstable that it cannot be obtained in a separate state. Explosiveness is a property of nitro-mannite, and also of nitro-glycerin. Iodide of nitrogen detonates on the slightest touch, and often without any assignable cause. Percussion produces detonation in sulphide of nitrogen. And the body which explodes with the most tremendous violence of any that is known, is the chloride of nitrogen. Thus these easy and rapid decompositions, due to the chemical indifference of nitrogen, are characteristic. When we come hereafter to observe the part which nitrogen plays in organic actions, we shall see the significance of this extreme readiness shown by its compounds to undergo change. Returning from these facts parenthetically introduced, we have next to note that though among these binary compounds of the four chief organic elements, there are a few active ones, yet the majority of them display a smaller degree of chemical energy than the average of binary compounds. Water is the most neutral of bodies: usually producing little chemical alteration in the substances with which it combines; and being expelled from most of its combinations by a moderate heat. Carbonic acid is a relatively feeble acid: the carbonates being decomposed by the majority of other acids and by ignition. The various hydro-carbons are but narrow in the range of their comparatively weak affinities. The compounds formed by ammonia have not much stability: they are readily destroyed by heat, and by the other alkalies. The affinities of cyanogen are tolerably strong; though they yield to those of the chief acids. Of the several oxides of nitrogen it is to be remarked, that while those containing the smaller proportions of oxygen are chemically inert, that containing the greatest proportion of oxygen (nitric acid) though chemically active, in consequence of the readiness with which one part of it gives up its oxygen to oxidize a base with which the rest combines, is nevertheless driven from all its combinations by a red heat.

These binary compounds, like their elements, are to a considerable degree characterized by the prevalence among them of allotropism; or, as it is more usually called when displayed by compound bodies—isomerism. Professor Graham finds reason for thinking that a change in atomic arrangement of this nature, takes place in water, at or near the melting point of ice. The relation between cyanogen and paracyanogen is, as we saw, an isomeric one. In the above-named series of hydro-carbons, differing from each other only in the multiples in which the elements are united, we find isomerism becoming what is distinguished as polymerism.

The like is still more conspicuous in other groups of the hydro-carbons, as in the essential oils: sixteen to twenty of which are severally isomeric with essential oil of turpentine. Here the particular kind of molecular mobility implied by these metamorphoses, is well shown: essential oil of turpentine being converted into a mixture of several of these polymerides, by simple exposure to a heat of 460°.

There is one further fact respecting these binary compounds of the four chief organic elements, which must not be overlooked. Those of them which form parts of the living tissues of plants and animals (excluding water which has a mechanical function, and carbonic acid which is a product of decomposition) are confined to one group—the hydro-carbons. And of this group, which is on the average characterized by comparative instability and inertness, these hydro-carbons found in living tissues, are among the most unstable and inert.

§ 3. Passing now to the substances which contain three of these chief organic elements, we have first to note that along with the greater atomic weight which mostly accompanies their increased complexity, there is, on the average, a further marked decrease of molecular mobility. Scarcely any of them maintain a gaseous state at ordinary temperatures. One class of them only, the alcohols and their derivatives, evaporate under the usual atmospheric pressure; but not rapidly unless heated. The fixed oils, though they show that molecular mobility implied by an habitually liquid state, show this in a lower degree than the alcoholic compounds; and they cannot be reduced to the gaseous state without decomposition. In their allies, the fats, which are solid unless heated, the loss of molecular mobility is still more marked. And throughout the whole series of the fatty acids, in which to a fixed proportion of oxygen there are successively added higher equimultiples of carbon and hydrogen, we see how the molecular mobility decreases with the increasing sizes of the atoms. In the amylaceous and saccharine group of compounds, solidity is the habitual state: such of them as can assume the liquid form, doing so only when heated to 300° or 400° F.; and decomposing when further heated, rather than become gaseous. Resins and gums exhibit general physical properties of like character and meaning.

In chemical stability these ternary compounds, considered as a group, are in a marked degree below the binary ones. The various sugars and kindred bodies, decompose at no very high temperatures. The oils and fats are also readily carbonized by heat. Resinous and gummy substances are easily made to render up some of their constituents. And the alcohols with their allies, have no great power of resisting decomposition. These bodies, formed by the union of oxygen, hydrogen and carbon, are also, as a class, chemically inactive. The formic and acetic are doubtless energetic acids; but the higher members of the fatty-acid series are easily separated from the bases with which they combine. Saccharic acid, too, is an acid of considerable power; and sundry of the vegetal acids possess a certain activity, though an activity far less than that of the mineral acids. But throughout the rest of the group, there is shown but a small tendency to combine with other bodies; and such combinations as are formed have usually little permanence.

The phenomena of isomerism and polymerism are of frequent occurrence in these ternary compounds. Starch and dextrine are isomeric. Fruit sugar, starch sugar, eucalyn, sorbin, and inosite, are polymeric. Sundry of the vegetal acids exhibit similar modifications. And among the resins and gums, with their derivatives, molecular re-arrangements of this kind are not uncommon.

One further fact respecting these compounds of carbon, oxygen and hydrogen, should be mentioned; namely, that they are divisible into two classes—the one consisting of substances that result from the destructive decomposition of organic matter, and the other consisting of substances that exist as such in organic matter. These two classes of substances exhibit in different degrees, the properties to which we have been directing our attention. The lower alcohols, their allies and derivatives, which possess greater molecular mobility and chemical stability than the rest of these ternary compounds, are not found in animal or vegetal bodies. While the sugars and amylaceous substances, the fixed oils and fats, the gums and resins, which have all of them much less molecular mobility, and are, chemically considered, more unstable and inert, are components of the living tissues of plants and animals.

§ 4. Among compounds containing all the four chief organic elements, a division analogous to that just named may be made. There are some which result from the decomposition of living tissues; there are others which make parts of living tissues in their state of integrity; and these two groups are contrasted in their properties in the same way as are the parallel groups of ternary compounds.

Of the first division, certain products found in the animal excretions are the most important, and the only ones that need be noted; such, namely, as urea, kreatine, kreatinine. These animal bases exhibit much less molecular mobility than the average of the substances treated of in the last section: being solid at ordinary temperatures, fusing, where fusible at all, at temperatures above that of boiling water, and having no power to assume a gaseous state. Chemically considered, their stability is low, and their activity but small, in comparison with the stabilities and activities of the simpler compounds.

It is, however, the nitrogenous constituents of living tissues, that display most markedly, those characteristics of which we have been tracing the growth. Albumen, fibrin, casein, and their allies, are bodies in which that molecular mobility exhibited by three of their components in so high a degree, is reduced to a minimum. These substances are known only in the solid state: that is to say, when deprived of the water usually mixed with them, they do not admit of fusion, much less of volatilization. To which add, that they have not even that molecular mobility which solution in water implies; since, though they form viscid mixtures with water, they do not dissolve in the same perfect way as do inorganic compounds. The chemical characteristics of these substances, are instability and inertness carried to the extreme. How rapidly albumenoid matters decompose under ordinary conditions, is daily seen: the difficulty of every house-wife being to prevent them from decomposing. It is true that when desiccated and kept from contact with air, they may be preserved unchanged for a long period; but the fact that they can only be thus preserved, proves their great instability. It is true, also, that these most complex nitrogenous principles are not absolutely inert; since they enter into combinations with some bases; but their unions are very feeble.

It should be noted, too, of these bodies, that though they exhibit in the lowest degree that kind of molecular mobility, which implies facile vibration of the atoms as wholes, they exhibit in a high degree that kind of molecular mobility resulting in isomerism, which implies permanent changes in the positions of adjacent atoms with respect to each other. Each of them has a soluble and insoluble form. In some cases there are indications of more than two such forms. And it appears that their metamorphoses take place under very slight changes of conditions.

In these most unstable and inert organic compounds, we find that the atomic complexity reaches a maximum: not only since the four chief organic elements are here united with small proportions of sulphur and phosphorus; but also since they are united in high multiples. The peculiarity which we found characterized even binary compounds of the organic elements, that their atoms are formed not of single equivalents of each component, but of two, three, four and more equivalents, is carried to the greatest extreme in these compounds, that take the leading part in organic actions, According to Mulder, the formula of albumen is $10\,(C^{40}\,H^{31}\,N^{5}\,O^{12}) + S^{2}\,P$. That is to say, with the sulphur and phosphorus there are united ten equivalents of a compound atom containing forty atoms of carbon, thirty-one of hydrogen, five of nitrogen, and twelve of oxygen: the atom being thus made up of nearly nine hundred ultimate atoms.

§ 5. Did space permit, it would be useful here to consider in detail, the interpretations that may be given of the peculiarities we have been tracing: bringing to their solution, those general mechanical principles which are now found to hold true of molecules as of masses. But it must suffice briefly to indicate the conclusions that such an inquiry promises to bring out.

Proceeding on mechanical principles, it may be argued that the molecular mobility of a substance must depend partly on the inertia of its molecules; partly on the intensity of their mutual polarities; partly on their mutual pressure, as determined by the density of their aggregation, and (where the molecules are compound) partly on the molecular mobilities of their component molecules. Whence it is to be inferred that any three of these remaining constant, the molecular mobility will vary as the fourth. Other things equal, therefore, the molecular mobility of atoms must decrease as their masses increase; and so there must result that general progression we have traced, from the high molecular mobility of the uncombined organic elements, to the low molecular mobility of those large-atomed substances into which they are ultimately compounded.

Applying to atoms the mechanical law which holds of masses, that since inertia and gravity increase as the cubes of the dimensions while cohesion increases as their squares, the self-sustaining power of a body becomes relatively smaller as its bulk becomes greater; it might be argued that these large, aggregate atoms which constitute organic substance, are mechanically weak—are less able than simpler atoms to bear, without alteration, the forces falling on them. That very massiveness which renders them less mobile, enables the physical forces acting on them more readily to change the relative positions of their component atoms; and so to produce what we know as re-arrangements and decompositions.

Further, it seems a not improbable conclusion, that this formation of large aggregates of elementary atoms, and resulting diminution of self-sustaining power, must be accompanied by a decrease of those contrasts of dimension to which polarity is ascribable. A sphere is the figure of equilibrium which any aggregate of units tends to assume, under the influence of simple mutual attraction. Where the number of units is small and their mutual polarities are decided, this proclivity towards spherical grouping will be overcome by the tendency towards some more special form, determined by their mutual polarities. But it is manifest that in proportion as an aggregate atom becomes larger, the effects of simple mutual attraction must become relatively greater; and so must tend to mask the effects of polar attraction. There will consequently be apt to result in highly compound atoms like these organic ones containing nine hundred elementary atoms, such approximation to the spherical form as must involve a less distinct polarity than in simpler atoms. If this inference be correct, it supplies us with an explanation both of the chemical inertness of these most complex organic substances, and of their inability to crystallize.

§ 6. Here we are naturally introduced to another aspect of our subject—an aspect of great interest. Professor Graham has recently published a series of important researches, which promise to throw much light on the constitution and changes of organic matter. He shows that solid substances exist under two forms of aggregation—the *colloid* or jelly-like, and the *crystalloid* or crystal-like. Examples of the last are too familiar to need specifying. Of the first may be named such instances as "hydrated silicic acid, hydrated alumina, and other metallic peroxides of the aluminous class, when they exist in the soluble form; with starch, dextrine and the gums, caramel, tannin, albumen, gelatine, vegetable and animal extractive matters." Describing the properties of colloids, Professor Graham says:—"Although often largely soluble in water, they are held in solution by a most feeble force. They appear singularly inert in the capacity of acids and bases, and in all the ordinary chemical relations." * * * "Although chemically inert in the ordinary sense, colloids possess a compensating activity of their own arising out of their physical properties. While the rigidity of the crystalline structure shuts out external impressions, the softness of the gelatinous colloid partakes of fluidity, and enables the colloid to become a medium of liquid diffusion, like water itself." * * * "Hence a wide sensibility on the part of colloids to external agents. Another and eminently characteristic quality of colloids is their mutability." * * * "The solution of hydrated silicic acid, for instance, is easily obtained in a state of purity, but it cannot be preserved. It may remain fluid for days or weeks in a sealed tube, but is sure to gelatinize and become insoluble at last. Nor does the change of this colloid appear to stop at that point; for the mineral forms of silicic acid, deposited from water, such as flint, are often found to have passed, during the geological ages of their existence, from the vitreous or colloidal into the crystalline condition (H. Rose). The colloid is, in fact, a dynamical state of matter, the crystalloidal being the statical condition. The colloid possesses *energia*. It may be looked upon as the primary source of the force appearing in the phenomena of vitality. To the gradual manner in which colloidal changes take place (for they always demand time as an element) may the characteristic protraction of chemico-organic changes also be referred."

The class of colloids includes not only all those most complex nitrogeneous compounds characteristic of organic tissue, and sundry of the oxy-hydro-carbons found along with them; but, significantly enough, it includes several of those substances classed as inorganic, which enter into organized structures. Thus silica, which is a component of many plants, and constitutes the spicules of sponges as well as the shells of many foraminifera and infusoria, has a colloid, as well as a crystalloid, condition. A solution of hydrated silicic acid, passes in the course of a few days into a solid jelly that is no longer soluble in water; and it may be suddenly thus coagulated by a minute portion of an alkaline carbonate, as well as by gelatine, alumina, and peroxide of iron. This last-named substance, too—peroxide of iron—which is an ingredient in the blood of mammals and composes the shells of certain protozoa, has a colloid condition. "Water containing about one per cent. of hydrated peroxide of iron in solution, has the dark red colour of venous blood." * * * "The red solution is coagulated in the cold by traces of sulphuric acid, alkalies, alkaline carbonates, sulphates, and neutral salts in general." * * * "The coagulum is a deep red-coloured jelly, resembling the clot of blood but more transparent. Indeed, the coagulum of this colloid is highly suggestive of that of blood, from the feeble agencies which suffice to effect the change in question, as well as from the appearance of the product." The jelly thus formed soon becomes, like the last, insoluble in water. Lime also, which is so important a mineral element in living bodies, animal and vegetal, enters into a compound belonging to this class. "The well-known solution of lime in sugar, forms a solid coagulum when heated. It is probably, at a high temperature, entirely colloidal."

Generalizing some of the facts which he gives, Professor Graham says—"The equivalent of a colloid appears to be always high, although the ratio between the elements of the substance may be simple. Gummic acid, for instance, may be represented by $C^{12} H^{11} O^{11}$; but, judging from the small proportions of lime and potash which suffice to neutralize this acid, the true numbers of its formula must be several times greater. It is difficult to avoid associating the inertness of colloids with their high equivalents, particularly where the high number appears to be attained by the repetition of a small number. The inquiry suggests itself whether the colloid molecule may not be constituted by the grouping together of a number of smaller crystalloid molecules, and whether the basis of colloidality may not really be this composite character of the molecule."

§ 7. A further contrast between colloids and crystalloids, is equally significant in its relations to vital phenomena. Professor Graham points out that the marked differences in volatility displayed by different bodies, are paralleled by differences in the rates of diffusion of different bodies through liquids. As alcohol and ether at ordinary temperatures, and various other substances at higher temperatures, diffuse themselves in a gaseous form through the air; so, a substance in aqueous solution, when placed in contact with a mass of water (in such way as to avoid mixture by circulating currents) diffuses itself through this mass of water. And just as there are various degrees of rapidity in evaporation, so there are various degrees of rapidity in diffusion: "the range also in the degree of diffusive mobility exhibited by different substances appears to be as wide as the scale of vapour-tensions." This parallelism is what might have been looked for; since the tendency to assume a gaseous state, and the tendency to spread in solution through a liquid, are both consequences of molecular mobility. It also turns out, as was to be expected, that diffusibility, like volatility, has, other things equal, a relation to atomic weight—(other things equal, we must say, because molecular mobility must, as pointed out in § 5, be affected by other properties of atoms, besides their inertia). Thus the substance most rapidly diffused of any on which Professor Graham experimented, was hydro-chloric acid—a compound which is of low atomic weight, is gaseous save under a pressure of forty atmospheres, and ordinarily exists as a liquid, only in combination with water. Again, "hydrate of potash may be said to possess double the velocity of diffusion of sulphate of potash, and sulphate of potash again double the velocity of sugar, alcohol, and sulphate of magnesia,"—differences which have a general correspondence with differences in the massiveness of the atoms.

But the fact of chief interest to us here, is that the relatively small-atomed crystalloids have immensely greater diffusive power than the relatively large-atomed colloids. Among the crystalloids themselves, there are marked differences of diffusibility; and among the colloids themselves, there are parallel differences, though less marked ones. But these differences are small compared with that between the diffusibility of the crystalloids as a class, and the diffusibility of the colloids as a class. Hydro-chloric acid is seven times as diffusible as sulphate of magnesia; but it is fifty times as diffusible as albumen, and a hundred times as diffusible as caramel.

These differences of diffusibility manifest themselves with nearly equal distinctness, when a permeable septum is placed between the solution and the water. And the result is, that when a solution contains substances of different diffusibilities, the process of dialysis, as Professor Graham calls it, becomes a means of separating the mixed substances: especially when such mixed substances are partly crystalloids and partly colloids. The bearing of this fact on organic processes will be obvious. Still more obvious will its bearing be, on joining it with the remarkable fact, that while crystalloids can diffuse themselves through colloids nearly as rapidly as through water, colloids can scarcely diffuse themselves at all through other colloids. From a mass of jelly containing salt, into an adjoining mass of jelly containing no salt, the salt spread more in eight days than it spread through water in seven days; while the spread of "caramel through the jelly appeared scarcely to have begun after eight days had elapsed." So that we must regard the colloidal compounds of which organisms are built, as having by their physical nature, the ability to separate colloids from crystalloids, and to let the crystalloids pass through them with scarcely any resistance.

One other result of these researches on the relative diffusibilities of different substances, has a meaning for us. Professor Graham finds, that not only does there take place by dialysis, a separation of *mixed* substances which are unlike in their molecular mobilities; but also that *combined* substances between which the affinity is feeble, will separate on the dialyzer, if their molecular mobilities are strongly contrasted. Speaking of the hydro-chlorate of peroxide of iron, he says, "such a compound possesses an element of instability in the extremely unequal diffusibility of its constituents;" and he points out that when dialyzed, the hydro-chloric acid gradually diffuses away, leaving the colloidal peroxide of iron behind. Similarly, he remarks of the peracetate of iron, that it "may be made a source of soluble peroxide, as the salt referred to is itself decomposed to a great extent by diffusion on the dialyzer." Now this tendency to separate displayed by substances that differ widely in their molecular mobilities, though usually so far antagonized by their affinities as not to produce spontaneous decomposition, must, in all cases, induce a certain readiness to change which would not else exist. The unequal mobilities of the combined atoms, must give disturbing forces a greater power to work transformations than they would otherwise have. Hence the probable significance of a fact named at the outset, that while three of the chief organic elements have the greatest atomic mobilities of any elements known, the fourth, carbon, has the least atomic mobility of known elements. Though, in its simple compounds, the affinities of carbon for the rest are strong enough to prevent the effects of this great difference from clearly showing themselves; yet there seems reason to think, that in those complex compounds composing organic bodies—compounds in which there are various cross affinities leading to a state of chemical tension—this extreme difference in the molecular mobilities must be an important aid to molecular re-arrangements. In short, we are here led by concrete evidence to the conclusion which we before drew from first principles, that this great unlikeness among the combined units must facilitate differentiations.

§ 8. A portion of organic matter in a state to exhibit those phenomena which the biologist deals with, is, however, something far more complex than the separate organic matters we have been studying; since a portion of organic matter in its integrity, contains several of these.

In the first place, no one of those colloids which make up the mass of a living body, appears capable of carrying on vital changes by itself: it is always associated with other colloids. A portion of animal-tissue, however minute, almost always contains more than one form of protein-substance: different chemical modifications of albumen and gelatine are present together, as well as, probably, a soluble and insoluble modification of each; and there is usually more or less of fatty matter. In a single vegetal cell, the minute quantity of nitrogenous colloid present, is imbedded in colloids of the non-nitrogenous class. The microscope makes it at once manifest, that even the smallest and simplest organic forms are not absolutely homogeneous.

Further, we have to contemplate organic tissue, formed of mingled colloids in both soluble and insoluble states, as permeated throughout by crystalloids. Some of these crystalloids, as oxygen,* water, and perhaps certain salts, are agents of decomposition; some, as the saccharine and fatty

* It will perhaps seem strange to class oxygen as a crystalloid. But inasmuch as the crystalloids are distinguished from the colloids by their atomic simplicity, and inasmuch as sundry gases are reducible to a crystalline state, we are justified in so classing it.

matters, are probably materials for decomposition; and some, as carbonic acid, water, urea, kreatine, and kreatinine, are products of decomposition. Into the mass of mingled colloids, mostly insoluble and where soluble of very low molecular mobility or diffusive power, we have constantly passing, crystalloids of high molecular mobility or diffusive power, that are capable of decomposing these complex colloids; and from these complex colloids, so decomposed, there result other crystalloids (the two chief ones extremely simple and mobile, and the rest comparatively so) which diffuse away as rapidly as they are formed.

And now we may clearly see the necessity for that peculiar composition which we find in organic matter. On the one hand, were it not for the extreme molecular mobility possessed by three of its chief elements out of the four; and were it not for the consequently high molecular mobility of their simpler compounds; there could not be this quick escape of the waste products of organic action; and there could not be that continuously active change of matter which vitality implies. On the other hand, were it not for the union of these extremely mobile elements into immensely complex compounds, having relatively vast atoms that are made comparatively immobile by their inertia, there could not result that mechanical fixity which prevents the components of living tissue from diffusing away along with the effete matters produced by the decomposition of tissue.

§ 9. Thus in the substances of which organisms are composed, the conditions necessary to that re-distribution of Matter and Motion which constitutes Evolution, are fulfilled in a far higher degree than at first appears.

The mutual affinities of the chief organic elements are not active within the limits of those temperatures at which organic actions take place; and one of these elements is especially characterized by its chemical indifference. The compounds formed by these elements in ascending grades of complexity, become progressively less stable. And those most complex compounds into which all these four elements enter, together with small proportions of two other elements that very readily oxidize, have an instability so great that decomposition ensues under ordinary atmospheric conditions.

Among these elements out of which living bodies are built, there is an unusual tendency to unite in multiples; and so to form groups of products which have the same chemical components, but, being different in their modes of aggregation, possess different properties. This prevalence among them of isomerism and polymerism, shows, in another way, the special fitness of organic substances for undergoing re-distributions.

In those most complex compounds that are instrumental to vital actions, there exists a kind and degree of molecular mobility which constitutes the plastic quality fitting them for organization. Instead of the extreme molecular mobility possessed by three out of the four organic elements in their separate states—instead of the diminished, but still great, molecular mobility possessed by their simpler combinations, the gaseous and liquid characters of which unfit them for showing to any extent the process of Evolution—instead of the properties of their less simple combinations, which, when not made unduly mobile by heat, assume the unduly rigid form of crystals; we have in these colloids, of which organisms are mainly composed, just the required compromise between fluidity and solidity. They cannot be reduced to the unduly mobile conditions of liquid and gas; and yet they do not assume the unduly fixed condition usually characterizing solids. The absence of power to unite together in polar arrangement, leaves their atoms with a certain freedom of relative movement which makes them sensitive to small forces, and produces plasticity in the aggregates composed of them.

While the relatively great inertia of these large and complex organic atoms, renders them comparatively incapable of being set in motion by the ethereal undulations, and so reduced to less coherent forms of aggregation; there is reason to think that this same inertia facilitates changes of arrangement among their constituent atoms; since, in proportion as an incident force impresses but little motion on a mass, it is the better able to impress motion on the parts of the mass in relation to each other. And it is further probable that the extreme contrasts in molecular mobilities among the components of these highly complex atoms, aid in producing modifiability of arrangement among them.

Lastly, the great difference in diffusibility between colloids and crystalloids, makes possible in the tissues of organisms, a specially rapid re-distribution of matter and motion; both because colloids, being easily permeable by crystalloids, can be chemically acted on throughout their whole mass, instead of only on their surfaces; and because the products of decomposition, being also crystalloids, can escape as fast as they are produced, leaving room for further like transformations. So that while the composite atoms of which organic tissues are built up, possess that low molecular mobility fitting them for plastic purposes, it results from the extreme molecular mobilities of their ultimate constituents, that the waste products of vital activity escape as fast as they are formed.

To all which add, that the state of warmth, or increased molecular vibration, in which all the higher organisms are kept, increases these various facilities for re-distribution: not only as aiding chemical changes, but as accelerating the diffusion of crystalloid substances.

# CHAPTER II.

## THE ACTIONS OF FORCES ON ORGANIC MATTER.

§ 10. To some extent, the parts of every body are changed in their arrangement by any incident mechanical force. But in organic bodies, the changes of arrangement produced by mechanical forces are usually conspicuous. It is a distinctive mark of colloids, that they yield with great readiness to pressures and tensions; and that they yet recover, more or less completely, their original shapes, when the pressures or tensions cease. It is clear that without this pliability and elasticity, most organic actions would be impossible. Not only temporary but permanent alterations of form are facilitated by this colloid character of organic matter. Continued pressure on living tissue, by modifying the processes going on in it, (perhaps retarding the absorption of new material to replace the old that has decomposed and diffused away,) gradually diminishes and finally destroys its power of resuming the outline it had at first. Thus the matter of which organisms are built up, is modifiable by arrested momentum or by continuous strain, in a far greater degree than is ordinary matter.

§ 11. Sensitiveness to certain forces that are quasi-mechanical, if not mechanical in the usual sense, is seen in two closely-related peculiarities displayed by organic matter as well as other matter that assumes the same state of molecular aggregation.

Colloids take up by a power that has been called "capillary affinity," a large quantity of water: undergoing at the same time great increase of bulk with change of form. Conversely, with like readiness, they give up this water by evaporation: resuming more or less completely their original states. Whether resulting from capillarity, or from the relatively great diffusibility of water, or from both; these changes are to be here noted as showing another mode in which the arrangement of parts in organic bodies, is affected by mechanical forces.

In what is called osmose, we have a further mode of allied kind. When on opposite sides of a permeable septum, and especially a septum of colloidal substance, are placed miscible solutions of different densities, a double transfer takes place: a large quantity of the less dense solution finds its way through the septum into the more dense solution; and a small quantity of the more dense finds its way into the less dense—one result being a considerable increase in the bulk of the more dense at the expense of the less dense. This process, which appears to depend on several conditions, is not yet fully understood. But be the explanation what it may, the process is one that tends continually to work alterations in organic bodies. Through the surfaces of plants and animals, transfers of this kind are ever taking place. Very many of the conspicuous changes of form undergone by organic germs, are due mainly to the permeation of their limiting membranes by the surrounding liquids.

It should be added that besides the direct alterations which the imbibition and transmission of water and watery solutions by colloids produce in organic matter, they produce indirect alterations. Being instrumental in conveying into the tissues the agents of chemical change, and conveying out of them the products of chemical change, they aid in carrying on other re-distributions.

§ 12. As elsewhere shown (*First Principles*, § 103) Heat, or a raised state of molecular vibration, enables incident forces more easily to produce changes of molecular arrangement in organic matter. But besides this, it conduces to certain vital changes in so direct a way as to become their chief cause.

The power of the organic colloids to imbibe water, and to bring along with it into their substance the materials which work transformations, would not be continuously operative if the water imbibed were to remain. It is because it escapes, and is replaced by more containing more materials, that the succession of changes is maintained. Among the higher animals and higher plants its escape is facilitated by evaporation. And the rate of evaporation is, other things equal, determined by heat. Though the current of sap in a tree is mainly caused by some action, probably osmotic, that is at work in the roots; yet the loss of water from the surfaces of the leaves, and the consequent absorption of more sap into the leaves by capillary attraction, must largely aid the circulation. The drooping of a plant when exposed to the sunshine while the earth round its roots is dry, shows us how evaporation empties the sap-vessels; and the quickness with which a withered slip revives on being placed in water, shows us the part which capillary action plays. In so far then, as the evaporation from a plant's surface helps to produce currents of sap through the plant, we must regard the heat which produces this evaporation as a part-cause of those re-distributions of matter which these currents effect. In terrestrial animals, heat similarly aids the changes that are going on. The exhalation of vapour from the lungs and the surface of the skin, forming the chief escape of the water that is swallowed, conduces to the maintenance of those currents through the tissues, without which the functions would cease. For though the vascular system distributes nutritive fluids in ramified channels through the body; yet the absorption of these fluids into tissues, partly depends on the escape of fluids which the tissues already contain. Hence, to the extent that such escape is facilitated by evaporation, and this evaporation facilitated by heat, heat becomes an agent of re-distribution in the animal organism.

§ 13. Light, which is now known to modify many inorganic compounds—which works those chemical changes utilized in photography, causes the combinations of certain gases, alters the molecular arrangements of many crystals, and leaves traces of its action even on substances that are extremely stable,—may be expected to produce marked effects on substances so complex and unstable as those which make up organic bodies. It does produce such marked effects; and some of them are among the most important that organic matter undergoes.

The molecular changes wrought by light in animals, are but of secondary moment. There is the darkening of the skin that follows exposure to the sun's rays. There are those alterations in the retina which cause in us sensations of colours. And on certain eyeless creatures that are semi-transparent, the light permeating their substance works some effect evinced by movement. But speaking generally, the opacity of animals limits the action of light to their surfaces; and so renders its direct physiological influence but small.* On plants, however, the solar rays that produce in us the impression of yellow, are the immediate agents of those molecular changes through which are hourly accumulated the materials for further growth. Experiments have shown that when the sun shines on living leaves, they begin to exhale oxygen and to accumulate carbon and hydrogen—results which are traced to the decomposition by the solar rays, of the carbonic acid and water absorbed. It is now an accepted conclusion that, by the help of certain

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* The increase of respiration found to result from the presence of light, is probably an *indirect* effect. It is most likely due to the reception of more vivid impressions through the eyes, and to the consequent nervous stimulation.

classes of the ethereal undulations penetrating their leaves, plants are enabled to separate from the associated oxygen, those two elements of which their tissues are chiefly built up.

This transformation of ethereal undulations into certain molecular re-arrangements of an unstable kind, on the overthrow of which the stored-up forces are liberated in new forms, is a process that underlies all organic phenomena. It will therefore be well, if we pause a moment to consider whether any proximate interpretation of it is possible. Certain recent researches in molecular physics, give us some clue to its nature.

The elements of the problem are these:—The atoms of several ponderable matters exist in combination: those that are combined having strong affinities, but having also affinities less strong for some of the surrounding atoms that are otherwise combined. The atoms thus united, and thus mixed among others with which they are capable of uniting, are exposed to the undulations of a medium that is relatively so rare as to seem imponderable. These undulations are of numerous kinds: they differ greatly in their lengths, or in the frequency with which they recur at any given point. And under the influence of undulations of a certain frequency, some of these atoms are transferred from atoms for which they have a stronger affinity, to atoms for which they have a weaker affinity. That is to say, particular orders of waves of a relatively imponderable matter, remove particular atoms of ponderable matter from their attachments, and carry them within reach of other attachments. Now the discoveries of Bunsen and Kirchoff respecting the absorption of particular luminiferous undulations by the vapours of particular substances, joined with Prof. Tyndall's discoveries respecting the absorption of heat by gases, show very clearly that the atoms of each substance have a rate of vibration in harmony with ethereal waves of a certain length, or rapidity of recurrence. Every special kind of atom can be made to oscillate by a special order of ethereal waves, which are absorbed in producing its oscillations; and can by its oscillations generate this same order of ethereal waves. Whence it appears that immense as is the difference in density between ether and ponderable matter, the waves of the one can set the atoms of the other in motion, when the successive impacts of the waves are so timed as to correspond with the oscillations of the atoms. The effects of the waves are, in such case, cumulative; and each atom gradually acquires a momentum made up of countless infinitesimal momenta. Note further, that unless the members of a chemically-compound atom are so bound up as to be incapable of any relative movements (a supposition at variance with the conceptions of modern science) we must conceive them as severally able to vibrate in unison or harmony with those same classes of ethereal waves that affect them in their uncombined states. While the compound atom as a whole, will have some new rate of oscillation determined by its attributes as a whole; its components will retain their original rates of oscillation, subject only to modifications by mutual influence. Such being the circumstances of the case, we may partially understand how the sun's rays can effect chemical decompositions. If the members of a binary atom stand so related to the undulations falling on them, that one is thrown into a state of increased oscillation and the other not; it is manifest that there must arise a tendency towards the dislocation of the two—a tendency which may or may not take effect, according to the weakness or strength of their union, and according to the presence or absence of collateral affinities. This inference is in harmony with several significant facts. Dr Draper remarks that " among metallic substances (compounds) those first detected to be changed by light, such as silver, gold, mercury, lead, have all high atomic weights; and such as sodium and potassium, the atomic weights of which are low, appeared to be less changeable." As here interpreted, the fact specified amounts to this; that the compounds most readily decomposed by light, are those in which there is a marked contrast between the atomic weights of the constituents, and probably therefore a marked contrast between the rapidities of their vibrations. The circumstance, too, that different chemical compounds are decomposed or modified in different parts of the spectrum, implies that there is a relation between special orders of undulations and special orders of composite atoms—doubtless a correspondence between the rates of these undulations and the rates of oscillation which some of the components of such atoms will assume. Strong confirmation of this view may be drawn from the decomposing actions of those longer ethereal waves which we perceive as heat. On contemplating the whole series of binary compounds, we see that the elements which are most remote in their atomic weights, as hydrogen and the noble metals, will not combine at all: their vibrations are so unlike that they cannot keep together under any conditions of temperature. If again we look at a smaller group, as the metallic oxides, we see that whereas those metals that have atoms nearest in weight to the atoms of oxygen, cannot be separated from oxygen by heat, even when it is joined by a powerful collateral affinity; those metals which differ more widely from oxygen in their atomic weights, can be de-oxidized by carbon at high temperatures; and those which differ from it most widely, combine with it very reluctantly, and yield it up if exposed to thermal undulations of moderate intensity. And here indeed, remembering the relations among the atomic weights in the two cases, may we not suspect a close analogy between the de-oxidation of a metallic oxide by carbon under the influence of the longer ethereal waves, and the de-carbonization of carbonic acid by hydrogen under the influence of the shorter ethereal waves?

These conceptions help us to some dim notion of the mode in which changes are wrought by light in the leaves of plants. Among the several elements concerned, there are wide differences in molecular mobility, and probably in the rates of molecular vibration. Each is combined with one of the others; but is capable of forming various combinations with the rest. And they are severally in presence of a complex compound into which they all enter, and which is ready to assimilate with itself the new compound atoms that they form. Certain of the ethereal waves falling on them when thus arranged, there results a detachment of some of the combined atoms and a union of the rest. And the conclusion suggested is, that the induced vibrations among the various atoms as at first arranged, are so incongruous as to produce instability; and to give collateral affinities the power to work a rearrangement, which, though less stable under other conditions, is more stable in the presence of these particular undulations. There seems, indeed, no choice but to conceive the matter thus. An atom united with one for which it has a strong affinity, has to be transferred to another for which it has a weaker affinity. This transfer implies motion. The motion is given by the waves of a medium that is relatively imponderable. No one wave of this imponderable medium can give the requisite motion to this atom of ponderable matter: especially as the atom is held by a positive force besides its inertia. The motion required can hence be given only by successive waves; and that these may not destroy each other's effects, it is needful that each shall strike the atom just when it has completed that recoil produced by the impact of previous ones. That is, the ethereal undulations must coincide in rate with the oscillations of the atom, determined by its inertia and the forces acting on it. It is also requisite that the rate of oscillation of the atom to be detached, shall differ from that of the atom with which it is united; since if the two oscillated in unison, the ethereal waves would not tend to separate them. And, finally, the successive impacts of the ethereal waves must be accumulated, until the resulting oscillations have become so wide in their sweep as greatly to weaken the cohesion of the united atoms, at the same time that they bring one of them within reach of other atoms with which it will combine. In this way only does it seem possible for such a force to produce such a transfer. Moreover, while we are thus enabled to conceive how light may work these molecular changes; we also gain an insight into the method by which the insensible motions propagated to us from the sun, are treasured up in such way as afterwards to generate sensible motions. By the accumulation of infinitesimal impacts, atoms of ponderable matter are made to oscillate. The quantity of motion which each of them eventually acquires, effects its transfer to a position of unstable equilibrium, from which it can afterwards be readily dislodged. And when so dislodged, along with other atoms similarly and simultaneously affected, there is suddenly given out all the motion which had been before impressed on it.

Speculation aside, however, that which it concerns us to notice, is the broad fact that light is an all-important agent of molecular changes in organic substances. It is not here necessary for us to ascertain *how* light produces these compositions and decompositions: it is necessary only for us to observe that it *does* produce them. That the characteristic matter called chlorophyll, which gives the green colour to leaves, makes its appearance whenever the blanched shoots of plants are exposed to the sun; that the petals of flowers, uncoloured while in the bud, acquire their bright tints as they unfold; and that on the outer surfaces of animals, analogous changes are induced; are wide inductions which are enough for our present purpose.

§ 14. We come next to the agency of chief importance among those that work changes in organic matter; namely, chemical affinity. How readily vegetal and animal substances are modified by other substances put in contact with them, we see daily illustrated. Besides the many compounds which cause the death of an organism into which they are put, we have the much greater number of compounds which work those milder effects termed medicinal—effects implying, like the others, molecular re-arrangements. Indeed, nearly all soluble chemical compounds, natural and artificial, produce, when taken into the body, alterations that are more or less conspicuous in their results.

After what was shown in the last chapter, it will be manifest that this extreme modifiability of organic matter by chemical agencies, is the chief cause of that active molecular re-arrangement which organisms, and especially animal organisms, display. In the two fundamental functions of nutrition and respiration, we have the means by which the supply of materials for this active molecular re-arrangement is maintained.

Thus the process of animal nutrition consists in the absorption, partly of those complex substances that are thus highly capable of being chemically altered, and partly in the absorption of simpler substances capable of chemically altering them. The tissues always contain small quantities of alkaline and earthy salts, which enter the system in one form and are excreted in another. Though we do not know specifically the parts which these salts play, yet from their universal presence, and from the transformations which they undergo in the body, it may be safely inferred that their chemical affinities are instrumental in working some of the metamorphoses ever going on.

The inorganic substance, however, on which mainly depend these metamorphoses in organic matter, is not swallowed along with the solid and liquid food, but is absorbed from the surrounding medium—air or water, as the case may be. Whether the oxygen taken in, either, as by the lowest animals, through the general surface, or, as by the higher animals, through respiratory organs, is the immediate cause of those molecular changes that are ever going on throughout the living tissues; or whether the oxygen, playing the part of scavenger, merely aids these changes by carrying away the products of decompositions otherwise caused; it equally remains true, that these changes are maintained by its instrumentality. Whether the oxygen absorbed and diffused through the system, effects a direct oxidation of the organic colloids which it permeates; or whether it first leads to the formation of simpler and more oxidized compounds, that are afterwards further oxidized and reduced to still simpler forms; matters not, in so far as the general result is concerned. In any case it holds good, that the substances of which the animal body is built up, enter it in a but slightly oxidized and highly unstable state; while the great mass of them leave it in a fully oxidized and stable state. It follows, therefore, that whatever the special changes gone through, the general process is a falling from a state of unstable chemical equilibrium, to a state of stable chemical equilibrium. Whether this process be direct or indirect, the total molecular re-arrangement and the total motion given out in effecting it, must be the same.

§ 15. There is another species of re-distribution among the component units of organisms, which is not immediately effected by the affinities of the units concerned, but is mediately effected by other affinities; and there is reason to think that the re-distribution thus caused, is important in amount, if not indeed the most important. In ordinary cases of chemical action, the two or more substances concerned, themselves undergo changes of molecular arrangement; and the changes are confined to the substances themselves. But there are other cases in which the chemical action going on, does not end with the substances at first concerned; but sets going chemical actions, or changes of molecular arrangement, among surrounding substances that would else remain quiescent. And there are yet further cases in which mere contact with a substance that is itself quiescent, will cause other substances to undergo rapid metamorphoses. In what we call fermentation, the first species of this communicated chemical action is exemplified. One part of yeast, while itself undergoing molecular changes, will convert 100 parts of sugar into alcohol and carbonic acid; and during its own decomposition, one part of diastase "is able to effect the transformation of more than 1000 times its weight of starch into sugar." As illustrations of the second species, may be mentioned those changes which are suddenly produced in many colloids by minute portions of various substances added to them—substances that are not undergoing any manifest transformation, and suffer no appreciable effect from the contact. The nature of the first of these two kinds of communicated molecular change, which here chiefly concerns us, may be rudely represented by certain visible changes that are communicated from mass to mass, when a series of masses has been arranged in a special way. The simplest example is that furnished by the child's play of setting bricks on end in a row, in such positions that when the first is overthrown it overthrows the second; the second, the third; the third, the fourth; and so on to the end of the row. Here we have a number of units severally placed in unstable equilibrium, and in such relative positions that each, while falling into a state of stable equilibrium, gives an impulse to the next, sufficient to make the next, also, fall from unstable to stable equilibrium. Now since among mingled compound atoms, no one can undergo change in the arrangement of its parts without a molecular motion that must cause some disturbance all around; and since an adjacent atom disturbed by this communicated motion, may have the arrangement of its constituent molecules altered, if it is not a stable arrangement; and since we know, both that the atoms which are changed by this so-called catalysis *are* unstable, and that the atoms resulting from their change are *more* stable; it seems probable that the transformation is really analogous, in principle, to the familiar one named. Whether thus interpretable or not, however, there is great reason for thinking that to this kind of action, is due a large amount of vital metamorphosis. Let us contemplate the several groups of facts which point to this conclusion.

In the last chapter (§ 2) we incidentally noted the extreme instability of nitrogenous compounds in general. We saw that sundry of them are liable to explode on the slightest incentive—sometimes without any apparent cause; and that of the rest, the great majority are very easily decomposed by heat, and by other substances. We shall perceive much significance in this general characteristic, when we join it with the fact, that the substances capable of initiating extensive molecular changes in the manner above described, are all nitrogenous ones. Yeast consists of vegetal cells containing nitrogen,—cells that grow by assimilating the nitrogenous matter contained in wort. Similarly, the "vinegar-plant," which so greatly facilitates the formation of acetic acid from alcohol, is a fungoid growth, that is doubtless, like others of its class, rich in nitrogenous compounds. Diastase, by which the transformation of starch into sugar is effected, during the process of malting, is also a nitrogenous body. So too is a substance called synaptase—an albumenous principle contained in almonds, that has the power of working several metamorphoses in the matters associated with it. These nitrogenized compounds, like the rest of their family, are remarkable for the rapidity with which they decompose; and the extensive changes produced by them in the accompanying oxy-hydro-carbons, are found to vary in their kinds according as the decompositions of the ferments vary in their stages. We have next to note, as having here a meaning for us, the chemical contrasts between those organisms which carry on their functions by the help of external forces, and those which carry on their functions by forces evolved from within. If we compare animals and plants, we see that whereas plants, characterized as a class by containing but little nitrogen, are dependent on the solar rays for their vital activities; animals, the vital activities of which are not thus dependent, mainly consist of nitrogenous substances. There is one marked exception to this broad distinction, however; and this exception is specially instructive. Among plants, there is a considerable group—the Fungi—many members of which, if not all, can live and grow in the dark; and it is their peculiarity that they are very much more nitrogenous than other plants. Yet a third class of facts of like significance, is disclosed when we compare different portions of the same organisms. The seed of a plant contains nitrogenous substance in a far higher ratio than the rest of the plant; and the seed differs from the rest of the plant in its ability to initiate, in the absence of light, extensive vital changes—the changes constituting germination. Similarly in the bodies of animals, those parts which carry on active functions are nitrogenous; while parts that are non-nitrogenous—as the deposits of fat—carry on no active functions. And we even find that the appearance of non-nitrogenous matter, throughout tissues normally composed almost wholly of nitrogenous matter, is accompanied by loss of activity: what is called fatty degeneration, being the concomitant of failing vitality. One more fact which serves to make still clearer the meaning of the foregoing ones, still remains—the fact, namely, that in no part of any organism where vital changes are going on, is nitrogenous matter wholly absent. It is common to speak of plants—or at least all parts of plants but the seeds—as non-nitrogenous. But they are only relatively so; not absolutely. The quantity of albumenoid substance contained in the tissues of plants, is extremely small compared with the quantity contained in the tissues of animals; but all plant-tissues which are discharging active functions, contain some albumenoid substance. In every living vegetal cell there is a certain part that contains nitrogen. This part initiates those changes which constitute the development of the cell. And if it cannot be said that the *primordial utricle*, as this nitrogenous part is called, is the worker of all subsequent changes undergone by the cell, it nevertheless continues to be the part in which the independent activity is most marked.

Looking at the evidence thus brought together, do we not get an insight into the part played by nitrogenous matter in organic changes? We see that nitrogenous compounds in general, are extremely prone to decompose: their decomposition often involving a sudden and great evolution of force. We see that the substances classed as ferments, which, during their own molecular changes, set up molecular changes in the accompanying oxy-hydro-carbons, are all nitrogenous. We see that among classes of organisms, and among the parts of each organism, there is a relation between the amount of nitrogenous matter present and the amount of independent activity. And we see that even in organisms and parts of organisms where the activity is least, such changes as do take place are initiated by a substance containing nitrogen. Does it not seem probable, then, that these extremely unstable compounds, have everywhere the effect of communicating to the less unstable compounds associated with them, molecular movements towards a stable state, like those they are themselves undergoing? The changes which we thus suppose nitrogenous matter to produce in a body, are clearly analogous to those which we see it produce out of the body. Out of the body, certain oxy-hydro-carbons in continued contact with nitrogenous matter, are transformed into carbonic acid and alcohol, and unless prevented the alcohol is transformed into acetic acid: the substances formed being thus more highly oxidized and more stable than the substances destroyed. In the body, these same oxy-hydro-carbons together with some hydro-carbons, in continued contact with nitrogenous matter, are transformed into carbonic acid and water: substances which are also more highly oxidized and more stable than those from which they result. And since acetic acid is itself resolved by further oxidation into carbonic acid and water; we see that the chief difference between the two cases, is, that the process is more completely effected in the body, than it is out of the body.* Thus, to carry further the simile used above, the atoms of hydro-carbons and oxy-hydro-carbons contained in the tissues, are, like bricks on end, not in the stablest equilibrium, but still in an equilibrium so stable, that they cannot be overthrown by the chemical and thermal forces which the body brings to bear on them. On the other hand, being like similarly-placed bricks that have very narrow ends, the nitrogenous atoms contained in the tissues are in so unstable an equilibrium that they cannot withstand these forces. And when these delicately-poised nitrogenous atoms fall into stable arrangements, they give impulses to the more firmly-poised non-nitrogenous atoms, which cause them also to fall into stable arrangements. It is a curious and significant fact, that in the arts, we not only utilize this same principle of initiating extensive changes among comparatively stable compounds, by the help of compounds much less stable; but we employ for the purpose compounds of the same general class. Our modern method of firing a gun, is to place in close proximity with the gunpowder which we wish to decompose or explode, a small portion of fulminating powder, which is decomposed or exploded with extreme facility; and which, on decomposing, communicates the consequent molecular disturbance to the less-easily decomposed gunpowder. When we ask what this fulminating powder is composed of, we find that it is a nitrogenous salt.

Thus various evidences point to the conclusion, that besides the molecular re-arrangements produced in organic matter by direct chemical action, there are others of kindred importance produced by indirect chemical action. Indeed, the inference

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* May it not be well to inquire whether alcohol is not, in a greater or less measure, transformed in the body into acetic acid? If, when in contact with changing nitrogenous matter, in presence of oxygen, alcohol undergoes this transformation out of the body, it seems not improbable that it does so in the body—especially as the raised temperature which aids the change in the one case exists in the other. It would be out of place here to set down the sundry facts which countenance this hypothesis. I may say, however, that it apparently removes some of the difficulties which at present perplex the question.

that some of the leading transformations occurring in the animal organism, are due to this so-called catalysis, appears necessitated by the general aspect of the facts; apart from any such detailed interpretations as the foregoing. We know that various amylaceous and saccharine matters taken as food, are decomposed in their course through the body. We know that these matters do not become components of the tissues, but only of the fluids circulating through them; and that thus their metamorphosis is not an immediate result of the organic activities. We know that their stability is such that the thermal and chemical forces to which they are exposed in the body, cannot alone decompose them. The only explanation open to us, therefore, is that the transformation of these oxy-hydro-carbons, into carbonic acid and water, is due to communicated chemical action.

§ 16. This chapter will have served its purpose if it has given a conception of the extreme modifiability of organic matter by surrounding agencies. Even did space permit, it would be needless to describe in detail the immensely varied and complicated changes which the forces from moment to moment acting on them, work in living bodies. Dealing with biology in its general principles, it concerns us only to notice how specially sensitive are the substances of which organisms are built up, to the varied influences that act upon organisms. And their special sensitiveness has been made sufficiently manifest, in the several foregoing sections.

# CHAPTER III.

## THE RE-ACTIONS OF ORGANIC MATTER ON FORCES.

§ 17. Re-distributions of Matter, imply concomitant re-distributions of Motion. That which under one of its aspects we contemplate as an alteration of arrangement among the parts of a body, is, under a correlative aspect, an alteration of arrangement among certain momenta whereby these parts are impelled to their new positions. At the same time that a force, acting differently on the different units of an aggregate, changes their relations to each other; these units, re-acting differently on the different parts of the force, work equivalent changes in the relations of these to one another. Inseparably connected as they are, these two orders of phenomena are liable to be confounded together. It is very needful, however, to distinguish between them. In the last chapter, we took a rapid survey of the re-distributions which forces produce in organic matter; and here we must take a like survey of the simultaneous re-distributions undergone by the forces.

At the outset we are met by a difficulty. The parts of an inorganic mass undergoing re-arrangement by an incident force, are, in most cases, passive—do not complicate those necessary re-actions that result from their inertia, by other forces which they originate. But in organic matter, the re-arranged parts do not re-act in virtue of their inertia only: they are so constituted that the incident force usually sets up in them, other actions which are much more important. Indeed, what we may call the indirect re-actions thus caused, are so great in their amounts compared with the direct re-actions, that they quite obscure them.

In strictness, these two kinds of re-action should not be dealt with together. The impossibility of separating them, however, compels us to disregard the distinction between them. Under the above general title, we must include both the immediate re-actions and those re-actions mediately produced, which are among the most conspicuous of vital phenomena.

§ 18. From organic matter, as from all other matter, incident forces call forth that re-action which we know as heat. More or less of molecular vibration almost necessarily results, when, to the forces at work among the molecules of any aggregate, other forces are added. Experiment abundantly demonstrates this in the case of inorganic masses; and it must equally hold in the case of organic masses. In both cases the force which, more markedly than any other, produces this thermal re-action, is that which causes the union of different substances with each other. Though inanimate bodies admit of being greatly heated by pressure and by the electric current, yet the evolutions of heat thus induced, are neither so common, nor in most cases so conspicuous, as those resulting from chemical combination. And though in animate bodies, there are doubtless certain amounts of heat generated by other actions; yet these are all secondary to the heat generated by the action of oxygen on the substances composing the tissues and the substances contained in them. Here, however, we see one of the characteristic distinctions between inanimate and animate bodies. Among the first, there are but few which ordinarily exist in a condition to evolve the heat caused by chemical combination; and such as are in this condition soon cease to be so, when chemical combination and genesis of heat once begin in them. Whereas among the second, there universally exists the ability, more or less decided, thus to evolve heat; and the evolution of heat, in some cases very slight and in no cases very great, continues as long as they remain animate bodies.

The relation between active change of matter and re-active genesis of atomic vibration, is clearly shown by the contrasts between different organisms, and between different states and parts of the same organism. In plants, the genesis of heat is extremely small, in correspondence with their extremely small production of carbonic acid: those portions only, as flowers and germinating seeds, in which considerable oxidation is going on, having a decidedly raised temperature. Among animals, we see that the hot-blooded are those which expend much force and respire actively. We see that though such creatures as insects are scarcely at all warmer than the surrounding air when they are still, they rise several degrees above it when they exert themselves; and that in creatures like ourselves, which habitually maintain a heat much greater than that of their medium, exercise is accompanied by an additional production of heat, often to an inconvenient extent.

This molecular agitation accompanying the molecular re-arrangements that are caused by oxygen taken into the animal organism, must result both from the union of oxygen with those nitrogenous matters of which the tissues are composed, and from its union with those non-nitrogenous matters which are diffused through the tissues. Just as much heat as would be caused by the oxidation of such matters out of the body, must be caused by their oxidation in the body. In the one case as in the other, the heat must be regarded as a concomitant. Whether the distinction made by Liebig between nitrogenous substances as tissue-food, and non-nitrogenous substances as heat-food, be true or not in a narrower sense, it cannot be accepted in the sense that tissue-food is not also heat-food. Indeed he does not himself assert it in this sense. The ability of carnivorous animals to live and generate heat while consuming matter that is almost exclusively nitrogenous, to say nothing of the constant relation above shown between functional activity and the evolution of heat, suffices to prove that the nitrogenous compounds forming the tissues are heat-producers, as well as the non-nitrogenous compounds circulating among and through the tissues. But it is possible that this antithesis is not true even in the more restricted sense. It seems quite an admissible hypothesis that the hydro-carbons and oxy-hydro-carbons which, in traversing the system, are transformed by communicated chemical action, evolve during their transformation, not heat alone, but also other kinds of force. It may be that as the nitrogenous matter, while falling into more stable molecular arrangements, generates both that molecular agitation called heat, and such other molecular movements as are resolved into forces expended by the organism; so, too, does the non-nitrogenous matter. Or perhaps the concomitants of this metamorphosis of non-nitrogenous matter, vary with the conditions. Heat alone may result when it is transformed while in the circulating fluids, but partly heat, and partly another force, when it is transformed in some active tissue that has absorbed it: just as coal, though producing little else but heat as ordinarily burnt, has its heat partially transformed into mechanical motion if burnt in a steam-engine furnace. In such case, the antithesis of Liebig would be reduced to this; —that whereas nitrogenous substance is tissue-food *both* as material for building-up tissue and as material for its function; non-nitrogenous substance is tissue-food *only* as material for function.

There can be no doubt that this thermal re-action which chemical action from moment to moment produces in the body, is from moment to moment an aid to further chemical action. We before saw (*First Principles*, § 103) that a state of raised molecular vibration, is favourable to those re-distributions of matter and motion which constitute Evolution. We saw that in organisms distinguished by the amount and rapidity of such re-distributions, this raised state of molecular vibration is conspicuous. And we here see that this raised state of molecular vibration, is itself a continuous consequence of the continuous molecular re-distributions it facilitates. The heat generated by each increment of chemical change, makes possible the succeeding increment of chemical change. In the body this connexion of phenomena is the same as we see it to be out of the body. Just as in a burning piece of wood, the heat given out by the portion actually combining with oxygen, raises the adjacent portion to a temperature at which it also can combine with oxygen; so, in a living animal, the heat produced by oxidation of each portion of tissue, maintains the temperature at which the unoxidized portions can be readily oxidized.

§ 19. Among the forces called forth from organisms by re-action against the actions to which they are subject, is Light. Phosphorescence is in some few cases displayed by plants—especially by certain fungi. Among animals it is comparatively common. All know that there are several kinds of luminous insects; and many are familiar with the fact that luminosity is a characteristic of various marine creatures.

Most of the evidence goes to show that this evolution of light, as well as the evolution of heat, is consequent on oxidation of the tissues. Light, like heat, is the expression of a raised state of molecular vibration: the difference between them being a difference in the rates of vibration. Hence by chemical action on substances contained in the organism, heat or light may be produced, according to the character of the resulting molecular vibrations. The inference that oxidation is the cause of this luminosity, does not, however, rest only on *à priori* grounds. It is supported by experimental evidence. In phosphorescent insects, the continuance of the light is found to depend on the continuance of respiration; and any exertion which renders respiration more active, increases the brilliancy of the light. Moreover, by separating the luminous matter, Prof. Matteucci has shown that its emission of light is accompanied by absorption of oxygen and escape of carbonic acid. The phosphorescence of marine animals has been referred to other causes than oxidation. In some cases, however, it is, I think, explicable without assuming any more special agency. Considering that in creatures of the genus *Noctiluca*, for example, to which the phosphorescence most commonly seen on our own coasts is due, there is no means of keeping up a constant circulation, we may infer that the movements of aerated fluids through their tissues, must be greatly affected by impulses received from without. Hence it may be that the sparkles visible at night when the waves break gently on the beach, or when an oar is dipped into the water, are called forth from these creatures by the concussion, not because of any unknown influence it excites, but because, being propagated through their delicate tissues, it produces a sudden movement of the fluids and a sudden increase of chemical action. Nevertheless, in other phosphorescent animals inhabiting the sea, as in the *Pyrosoma* and in certain *Annelida*, light seems to be really produced, not by direct re-action on the action of oxygen, but by some indirect re-action involving a transformation of force.

§ 20. The re-distributions of matter in general, are accompanied by electrical disturbances; and there is abundant evidence that electricity is generated during those re-distributions that are ever taking place in organisms. Experiments have shown "that the skin and most of the internal membranes are in opposite electrical states;" and also that between different internal organs, as the liver and the stomach, there are electrical contrasts—such contrasts being greatest where the processes going on in the compared parts are most unlike. It has been proved by M. du Bois-Reymond that when any point in the longitudinal section of a muscle is connected by a conductor with any point in its transverse section, an electric current is established; and further, that like results occur when nerves are substituted for muscles. The special causes of these phenomena have not yet been determined. Considering that the electric contrasts are most marked where active secretions are going on—considering, too, that while they do not exist between external parts which are similarly related to the vascular currents, they do exist between external parts which are dissimilarly related to the vascular currents—and considering also that they are extremely difficult to detect where there are no appreciable movements of fluids; it may be that they are due simply to the friction of heterogeneous substances, which is universally a cause of electric disturbance. But whatever be the interpretation, the fact remains the same, that there is throughout the living organism, an unceasing production of differences between the electric states of different parts; and consequently an unceasing restoration of electric equilibrium by the establishment of currents among these parts.

Besides these general, and not conspicuous, electrical phenomena which appear to be common to all organisms, vegetal as well as animal, there are certain special and strongly marked ones. I refer, of course, to those which have made the *Torpedo* and the *Gymnotus* objects of so much interest. In these creatures we have a genesis of electricity that is not incidental on the performance of their different functions by the different organs; but one which is itself a function, having an organ appropriate to it. The character of this organ in both these fishes, and its largely-developed connexions with the nervous centres, have raised the suspicion, which various experiments have thus far justified, that in it there takes place a transformation of what we call nerve-force into the force known as electricity: this conclusion being more especially supported by the fact, that substances, such as morphia and strychnia, which are known to be powerful nervous stimulants, greatly increase the violence and rapidity of the electric discharges.

But whether general or special, and in whatever manner produced, these evolutions of electricity are among the re-actions of organic matter, called forth by the actions to which it is subject. Though these re-actions are not direct, but seem rather to be remote consequences of those changes wrought by external agencies on the organism, they are yet incidents in that general re-distribution of motion, which these external agencies initiate; and as such must here be noticed.

§ 21. To these known modes of motion, has next to be added an unknown one. Heat, Light, and Electricity are emitted by inorganic matter when undergoing changes, as well as by organic matter. But there is a kind of force manifested in some classes of living bodies, which we cannot identify with any of the forces manifested by bodies that are not alive,—a force which is thus unknown, in the sense that it cannot be assimilated with any otherwise-recognized class. I allude to what is called nerve-force.

This is habitually generated in all animals, save the lowest, by incident forces of every kind. The gentle and violent mechanical contacts, which in ourselves produce sensations of touch and pressure—the additions and abstractions of molecular vibration, which in ourselves produce sensations of heat and cold; produce in all creatures that have nervous systems, certain nervous disturbances — disturbances which, as in ourselves, are either communicated to the chief nervous centre, and there constitute consciousness, or else result in merely physical processes that are set going elsewhere in the organism. In special parts distinguished as organs of sense, other external actions bring about other nervous re-actions; that show themselves either as special sensations, or as excitements which, without the intermediation of consciousness, beget actions in muscles or other organs. Besides neural discharges that follow the direct incidence of external forces, there are others ever being caused by the incidence of forces which, though originally external, have become internal by absorption into the organism of the agents exerting them. For thus may be classed those neural discharges that from moment to moment result from modifications of the tissues, wrought by substances carried to them in the blood. That the unceasing change of matter which oxygen and other agents produce throughout the system, is accompanied by a genesis of nerve-force, is shown by various facts ;—by the fact that nerve-force is no longer generated, if oxygen be withheld, or the blood prevented from circulating ; by the fact that when the chemical transformation is diminished, as during sleep with its slow respiration and circulation, there is a diminution in the quantity of nerve-force ; in the fact that an excessive expenditure of nerve-force, involves excessive respiration and circulation, and excessive waste of tissue. To these proofs that nerve-force is evolved in greater or less quantity, according as the conditions to rapid molecular change throughout the body, are well or ill fulfilled ; may be added proofs that certain special molecular actions, are the causes of these special re-actions. The effects of alcohol, ether, chloroform, and the vegeto-alkalies, put beyond doubt the inference, that the overthrow of molecular equilibrium by chemical affinity, when it occurs at certain places in the body, results in the overthrow of equilibrium in the nerves proceeding from these places—results, that is, in the propagation through these nerves, of the change called a nervous discharge. Indeed, looked at from this point of view, the two classes of nervous changes—the one initiated from without and the other from within—are seen to merge into one class. Both of them may be traced to metamorphosis of tissue. There can be little doubt that the sensations of touch and pressure, are consequent on accelerated changes of matter, produced by mechanical disturbance of the mingled fluids and solids composing the parts affected. There is abundant evidence that the sensation of taste, is due to the chemical actions set up by particles which find their way through the membrane covering the nerves of taste; for, as Prof. Graham points out, sapid substances all belong to the class of crystalloids, which are able rapidly to permeate animal tissue, while colloids, which cannot pass through animal tissue, are all insipid. Similarly with the sense of smell. Substances which excite this sense, are necessarily more or less volatile; and their volatility being the result of their molecular mobility, implies that they have in a high degree, the power of getting at the olfactory nerves by penetrating their mucous investment. Again, the facts which photography has familiarized us with, make it clear that those nervous impressions called colours, are primarily due to certain changes wrought by light in the substance of the retina. And though, in the case of hearing, we cannot so clearly trace the connexion of cause and effect; yet as we see that the auditory apparatus is one fitted to intensify those vibrations constituting sound, and to convey them to a receptacle containing fluid in which nerves are immersed; it can scarcely be doubted that the sensation of sound proximately results from atomic re-arrangements caused in these nerves by the vibrations of the fluid: knowing, as we do, that the re-arrangement of atoms is in all cases aided by agitation. Perhaps, however, the best proof that nerve-force, whether peripheral or central in its origin, results from chemical transformation, lies in the fact that most of the chemical agents which powerfully affect the nervous system, affect it whether applied at the centre or the periphery. Various acids, mineral and vegetal, are tonics—the stronger ones being usually the stronger tonics; and this which we call their acidity, implies a power in them of acting on the nerves of taste, while the tingling or pain that follows their absorption through the skin, implies that the nerves of touch are acted on by them. Similarly with certain vegeto-alkalies which are peculiarly bitter. These by their bitterness, show that they affect the extremities of the nerves; while by their tonic properties, they show that they affect the nervous centres—the most intensely bitter among them, strychnia, being the most powerful nervous stimulant. However true it may be that this relation is not a regular one, since opium, hashish, and some other drugs, which work marked effects on the brain, are not remarkably sapid—however true it may be that there are relations between particular substances and particular parts of the nervous system; yet such instances do but qualify, without negativing, the general proposition. The truth of this proposition can scarcely be doubted when, to the evidence above given, is added the fact that various condiments and aromatic drugs are given as nervous stimulants; and the fact that anæsthetics, besides the general effects they produce when inhaled or swallowed, produce local effects of like kind when absorbed through the skin; and the fact that ammonia, which in consequence of its extreme molecular mobility, so quickly and so violently excites the nerves beneath the skin, as well as those of the tongue and the nose, is a rapidly-acting stimulant when taken internally.

Whether we shall ever know anything more of this nerve-force, than that it is some species of molecular disturbance that is propagated from end to end of a nerve, it is impossible to say. Whether a nerve is merely a conductor, which delivers at one of its extremities an impulse received at the other; or whether, as some now think, it is itself a generator of force which is initiated at one extremity and accumulates in its course to the other extremity; are also questions which cannot yet be answered. All we know is, that forces capable of working molecular changes in nerves, are capable of calling forth from them manifestations of activity—discharges of some force, which, though probably allied to electricity, is not identical with it. And our evidence that nerve-force is thus originated, consists not only of such facts as the above, but also of more conclusive facts established by direct experiments on nerves—experiments which show that nerve-force is generated when the cut end of a nerve is either mechanically irritated, or acted on by some chemical agent, or subject to the galvanic current—experiments which thus prove that nerve-force is liberated by whatever disturbs the molecular equilibrium of nerve-substance. And this is all which it is necessary for us here to understand.

§ 22. The most important of these re-actions called forth from organisms by surrounding actions, remains to be noticed. To the above various forms of insensible motion thus caused, we have to add sensible motion. On the production of this mode of force, more especially depends the possibility of all vital phenomena. It is, indeed, usual to regard the power of generating sensible motion, as confined to one out of the two organic sub-kingdoms; or, at any rate, as possessed by but few members of the other. On looking closer into the matter, however, we see that plant-life as well as animal-life, is universally accompanied by certain manifestations of this power; and that plant-life could not otherwise continue.

Through the humblest, as well as through the highest, vegetal organisms, there are ever going on certain re-distributions of matter. In protophytes the microscope shows us an internal transposition of parts, which when not active enough to be immediately visible, is proved to exist by the changes of arrangement that become manifest in the course of hours and days. In the individual cells of many higher plants, an active movement among the contained granules may be witnessed. And well-developed cryptogams in common with all phanerogams, exhibit this genesis of mechanical motion still more conspicuously in the circulation of sap. It might, indeed, be concluded *à priori*, that through plants displaying much differentiation of parts, an internal movement must be going on; since, without it, the mutual dependence of organs having unlike functions would seem impossible. Besides these motions of fluids kept up internally, plants, especially of the lower orders, are able to move their external parts in relation to each other, and also to move about from place to place. Illustrations in abundance will occur to all students of recent Natural History—such illustrations as the active locomotion of the zoospores of many Algæ, the rhythmical bendings of the *Oscillatoriæ*, the rambling progression of the *Diatomaceæ*. In fact many of these smallest vegetals, and many of the larger ones in their early stages, display a mechanical activity not distinguishable from that of the simplest animals. Among well-organized plants, which are never locomotive in their adult states, we still not unfrequently meet with relative motions of parts. To such familiar cases as those of the Sensitive plant and the Venus' fly-trap, many others may be added. When its base is irritated, the stamen of the Berberry flower leans over and touches the pistil. If the stamens of the common wild *Cistus* be gently brushed with the finger, they spread themselves—bending away from the seed-vessel. And some of the orchid-flowers, as Mr Darwin has recently shown, shoot out masses of pollen on to the entering bee, when its trunk is thrust down in search of honey.

Though the power of moving is not, as we see, a characteristic of animals alone, yet in them, considered as a class, it is manifested to an extent so marked, as practically to become one of their distinctive characters—indeed, we may say, their most distinctive character. For it is by their immensely greater ability to generate mechanical motion, that animals are enabled to perform those actions which constitute their visible lives; and it is by their immensely greater ability to generate mechanical motion, that the higher orders of animals are most obviously distinguished from the lower orders. Though, on remembering the seemingly active movements of infusoria, some will perhaps question this last-named contrast; yet, on comparing the quantities of matter propelled through given spaces in given times, they will see that the momentum evolved is far less in the protozoa than in the teleozoa. These sensible motions of animals are effected by various organs under various stimuli. In the humblest forms, and even in some of the more developed ones which inhabit the water, locomotion results from the vibrations of cilia: the contractility resides in these waving hairs that grow from the surface. Some of the *Acalephæ*, and their allies the Polypes, move when mechanically irritated: the long pendant tentacle of a *Physalia* is suddenly drawn up if touched; and, as well as its tentacles, the whole body of a *Hydra* collapses if roughly handled, or jarred by some shock in its neighbourhood. In all the higher animals however, and to a smaller degree in many of the lower, sensible motion is generated by a special tissue, under the special excitement of a neural discharge. Though it is not strictly true that such animals show no sensible motions otherwise caused; since all of them have certain ciliated membranes, and since the circulation of fluid in them is partially due to osmotic and capillary actions; yet, generally speaking, we may say that their movements are effected only by muscles that contract only through the agency of nerves.

What special transformations of force generate these various mechanical changes, we do not, in most cases, know. Those re-distributions of fluid, with the alterations of form sometimes caused by them, that result from osmose, are not, indeed, quite incomprehensible. Certain motions of plants which, like those of the "animated oat," follow contact with water, are easily interpreted; as are also such other vegetal motions as those of the Touch-me-not, the Squirting Cucumber, and the *Carpobolus*. But we have as yet no clue to the mode in which molecular movement is transformed into the movement of masses, in animals. We cannot refer to known causes the rhythmical action of a Medusa's disc, or that slow decrease of bulk that spreads throughout the mass of an *Alcyonium*, when one of its component individuals has been irritated. Nor are we any better able to say how the insensible motion transmitted through a nerve, gives rise to sensible motion in a muscle. It is true that Science has given to Art, several methods of changing insensible into sensible motion. By applying heat to water we vaporize it; and the movement of its expanding vapour, we transfer to solid matter; but it is clear that the genesis of muscular movement is in no way analogous to this. The force evolved during chemical transformations in a galvanic battery, we communicate to a soft iron magnet through a wire coiled round it; and it would be quite possible, by placing near to each other several magnets thus excited, to obtain, through the attraction of each for its neighbours, an accumulated movement made up of their separate movements, and thus to mechanically imitate a muscular contraction; but from what we know of organic matter, and the structure of muscle, there is no reason to suppose that anything analogous to this takes place in it. We can, however, through one kind of molecular change, produce sensible changes of aggregation such as possibly might, when occurring in organic substance, cause sensible motion in it: I refer to allotropic change. Sulphur, for example, assumes different crystalline and non-crystalline forms at different temperatures; and may be made to pass backwards and forwards from one form to another, by slight variations of temperature: undergoing each time an alteration of bulk. We know that this allotropism, or rather its analogue isomerism, prevails among colloids — inorganic and organic. We also know that some of these metamorphoses among colloids, are accompanied by visible re-arrangements: instance hydrated silicic acid, which, after passing from its soluble state to the state of an insoluble jelly, begins, in a few days, to contract, and to give out part of its contained water. Now, considering that such isomeric changes of organic as well as inorganic colloids, are often very rapidly produced by very slight causes, it seems not impossible that some of the colloids constituting muscle, may be thus changed by a nervous discharge—resuming their previous condition when the discharge ceases. And it is conceivable that by structural arrangements, minute sensible motions so caused, may be accumulated into large sensible motions. There is, however, no evidence to support this supposition.

§ 23. But the truths which it is here our business especially to note, are quite independent of hypotheses or interpretations. It is sufficient for the ends we have in view, to observe that organic matter *does* exhibit these several conspicuous re-actions, when acted on by incident forces: it is not requisite that we should know *how* these re-actions originate.

In the last chapter were set forth the several modes in which incident forces cause re-distributions of organic matter; and in this chapter have been set forth the several modes in which is manifested the motion accompanying this re-distribution. There we contemplated under its several aspects, the general fact, that in consequence of its extreme instability, organic matter undergoes extensive molecular re-arrangements, on very slight changes of conditions. And here we have contemplated under its several aspects, the correlative general fact, that during these extensive molecular re-arrangements, there are necessarily evolved large amounts of force. In the one case the atoms of which organic matter consists, are regarded as changing from positions of unstable equilibrium to positions of stable equilibrium; and in the other case they are regarded as giving out in their falls from unstable to stable equilibrium, certain momenta—momenta that may be manifested as heat, light, electricity, nerve-force or mechanical motion, according as the conditions determine.

I will add only that these evolutions of force are rigorously dependent on these changes of matter. It is a corollary from that primordial truth which, as we have seen, underlies all other truths, (*First Principles*, §§ 76, 141,) that whatever amount of power an organism expends in any shape, is the correlate and equivalent of a power that was taken into it from without. On the one hand, it follows from the persistence of force, that each portion of mechanical or other energy which an organism exerts, implies the transformation of as much organic matter as contained this energy in a latent state. And on the other hand, it follows from the persistence of force that no such transformation of organic matter containing this latent energy can take place, without the energy being in one shape or other manifested.

# CHAPTER IV.*

## PROXIMATE DEFINITION OF LIFE.

§ 24. To those who accept the general doctrine of Evolution, it needs scarcely be pointed out that classifications are subjective conceptions, which have no absolute demarcations in Nature corresponding to them. They are appliances by which we limit and arrange the matters under investigation; and so facilitate our thinking. Consequently, when we attempt to define anything complex, or make a generalization of facts other than the most simple, we can scarcely ever avoid including more than we intended, or leaving out something that should be taken in. Thus it happens that on seeking a definition of Life, we have great difficulty in finding one that is neither more nor less than sufficient. Let us look at a few of the most tenable definitions that have been given. While recognizing the respects in which they are defective, we shall see what requirements a more complete one must fulfil.

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* This chapter and the following two chapters originally appeared in Part III. of the *Principles of Psychology:* forming a preliminary which, though indispensable to the argument there developed, was somewhat parenthetical. Having now to deal with the general science of Biology before the more special one of Psychology, it becomes possible to transfer these chapters to their proper place. They have been carefully revised.

Schelling said that Life is the tendency to individuation. This formula, until studied, conveys little meaning. But it needs only to consider it as illustrated by the facts of development, or by the contrasts between lower and higher forms of life, to recognize its value; especially in respect of comprehensiveness. As before shown, however, (*First Principles*, § 56), it is objectionable, partly on the ground that it refers, not so much to the functional changes constituting Life, as to the structural changes of those aggregations of matter which manifest Life; and partly on the ground that it includes under the idea Life, much that we usually exclude from it: for instance—crystallization.

The definition of Richerand, — "Life is a collection of phenomena which succeed each other during a limited time in an organized body,"—is liable to the fatal criticism, that it equally applies to the decay which goes on after death. For this, too, is "a collection of phenomena which succeed each other during a limited time in an organized body."

"Life," according to De Blainville, "is the two-fold internal movement of composition and decomposition, at once general and continuous." This conception is in some respects too narrow, and in other respects too wide. On the one hand, while it expresses what physiologists distinguish as vegetative life, it excludes those nervous and muscular functions which form the most conspicuous and distinctive classes of vital phenomena. On the other hand, it describes not only the integrating and disintegrating processes going on in a living body, but it equally well describes those going on in a galvanic battery; which also exhibits a "two-fold internal movement of composition and decomposition, at once general and continuous."

Elsewhere, I have myself proposed to define Life as "the co-ordination of actions;"* and I still incline towards this definition as one answering to the facts with tolerable precision.

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* See *Westminster Review* for April, 1852.—Art. IV. "A Theory of Population."

It includes all organic changes, alike of the viscera, the limbs, and the brain. It excludes the great mass of inorganic changes; which display little or no co-ordination. By making co-ordination the specific characteristic of vitality, it involves the truths, that an arrest of co-ordination is death, and that imperfect co-ordination is disease. Moreover, it harmonizes with our ordinary ideas of life in its different gradations: seeing that the organisms which we rank as low in their degree of life, are those which display but little co-ordination of actions; and seeing that from these up to man, the recognized increase in degree of life corresponds with an increase in the extent and complexity of co-ordination. But, like the others, this definition includes too much; for it may be said of the Solar System, with its regularly-recurring movements and its self-balancing perturbations, that it, also, exhibits co-ordination of actions. And however plausibly it may be argued that, in the abstract, the motions of the planets and satellites are as properly comprehended in the idea of life, as the changes going on in a motionless, unsensitive seed; yet, it must be admitted that they are foreign to that idea as commonly received, and as here to be formulated.

It remains to add the definition since suggested by Mr G. H. Lewes—"Life is a series of definite and successive changes, both of structure and composition, which take place within an individual without destroying its identity." The last fact which this statement has the merit of bringing into view—the persistence of a living organism as a whole, in spite of the continuous removal and replacement of its parts—is important. But otherwise it may be argued, that since changes of structure and composition, though probably the *causes* of muscular and nervous actions, are not the muscular and nervous actions themselves, the definition excludes the more visible movements with which our idea of life is most associated; and further, that in describing vital changes as *a series*, it scarcely includes the fact that many of them, as

Nutrition, Circulation, Respiration, and Secretion, in their many subdivisions, go on simultaneously.

Thus, however well each of these definitions expresses the phenomena of life under some of its aspects, no one of them is more than approximately true. It may turn out, that to find a formula which will bear every test is impossible. Meanwhile, it is possible to frame a more adequate formula than any of the foregoing. As we shall presently find, these all omit an essential peculiarity of vital changes in general—a peculiarity which, perhaps more than any other, distinguishes them from non-vital changes. Before specifying this peculiarity, however, it will be well to trace our way, step by step, to as complete an idea of Life as may be reached from our present stand-point: by doing which, we shall both see the necessity for each limitation as it is made, and ultimately be led to feel the need for a further limitation.

And here, as the best mode of determining what are those general characteristics which distinguish vitality from non-vitality, we shall do well to compare the two most unlike kinds of vitality, and see in what they agree. Manifestly, that which is essential to Life must be that which is common to Life of all orders. And manifestly, that which is common to all forms of Life, will most readily be seen on contrasting those forms of Life which have the least in common, or are the most unlike.*

§ 25. Choosing assimilation, then, for our example of bodily life, and reasoning for our example of that life known as intelligence; it is first to be observed, that they are both processes of change. Without change, food cannot be taken into the blood nor transformed into tissue: without

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* This paragraph replaces a sentence that, in *The Principles of Psychology,* referred to a preceding chapter on "Method;" in which the mode of procedure here indicated, was set forth as a mode to be systematically pursued in the choice of hypotheses. Should opportunity ever permit, this chapter on Method will be embodied, along with other matter on the same topic, in a General Introduction to *First Principles.*

change, there can be no getting from premisses to conclusion. And it is this conspicuous manifestation of change, which forms the substratum of our idea of Life in general. Doubtless we see innumerable changes to which no notion of vitality attaches: inorganic bodies are ever undergoing changes of temperature, changes of colour, changes of aggregation. But it will be admitted that the great majority of the phenomena displayed by inorganic bodies, are statical and not dynamical; that the modifications of inorganic bodies are mostly slow and unobtrusive; that on the one hand, when we see sudden movements in inorganic bodies, we are apt to assume living agency, and on the other hand, when we see no movements in organic bodies, we are apt to assume death. From all which considerations it is manifest, that be the requisite qualifications what they may, a definition of Life must be a definition of some kind of change or changes.

On further comparing assimilation and reasoning, with a view of seeing in what respect the change displayed in both differs from non-vital change, we find that it differs in being not simple change, but change made up of *successive* changes. The transformation of food into tissue, involves mastication, deglutition, chymification, chylification, absorption, and those various actions gone through after the lacteal ducts have poured their contents into the blood. Carrying on an argument necessitates a long chain of states of consciousness; each implying a change of the preceding state. Inorganic changes, however, do not in any considerable degree exhibit this peculiarity. It is true that from meteorologic causes, inanimate objects are daily, sometimes hourly, undergoing modifications of temperature, of bulk, of hygrometric and electric condition. Not only, however, do these modifications lack that conspicuousness and that rapidity of succession which vital ones possess, but vital ones form an *additional* series. Living as well as not-living bodies are affected by atmospheric influences; and beyond the changes which these produce, living bodies exhibit other changes, more numerous and more marked. So that though organic change is not rigorously distinguished from inorganic change by presenting successive phases—though some inanimate objects, as watches, display phases of change both quick and numerous—though all objects are ever undergoing change of some kind, visible or invisible—though there is scarcely any object which does not, in the lapse of time, undergo a considerable amount of change that is fairly divisible into phases; yet, vital change so greatly exceeds other change in its display of varying phases, that we may consider this as practically one of its characteristics. Life, then, as thus roughly differentiated, may be regarded as change presenting successive phases; or otherwise, as a series of changes. And it should be observed, as a fact in harmony with this conception, that the higher the life the more conspicuous the variations. On comparing inferior with superior organisms, these last will be seen to display more rapid changes, or a more lengthened series of them, or both.

Contemplating afresh our two typical phenomena, we may see that vital change is further distinguished from non-vital change, by being made up of many *simultaneous* changes. Assimilation is not simply a series of actions, but includes many actions going on together. During mastication the stomach is busy with the food already swallowed; on which it is both pouring out solvent fluids and expending muscular efforts. While the stomach is still active, the intestines are performing their secretive, contractile, and absorbent functions; and at the same time that one meal is being digested, the nutriment obtained from a previous meal is undergoing that transformation into tissue which constitutes the final act of assimilation. So also is it, in a certain sense, with mental changes. Though the states of consciousness which make up an argument occur in series, yet, as each of these states is complex—implies the simultaneous excitement of those many faculties by which the perception of any object or relation has been effected; it is obvious that each such change in consciousness implies many component changes. In this respect too, however, it must be admitted that the distinction between animate and inanimate is not precise. No mass of dead matter can have its temperature altered, without at the same time undergoing an alteration in bulk, and sometimes also in hygrometric state. An inorganic body cannot be oxidized, without being at the same time changed in weight, colour, atomic arrangement, temperature, and electric condition. And in some vast and mobile aggregates like the sea, the simultaneous as well as the successive changes displayed, outnumber those going on in an animal. Nevertheless, speaking generally, a living thing is distinguished from a dead thing, by the multiplicity of the changes at any moment taking place in it. Add to which, that by this peculiarity, as by the previous one, not only is the vital more or less clearly marked off from the non-vital; but creatures possessing high vitality are marked off from those possessing low vitality. It needs but to contrast the many organs co-operating in a mammal, with the few in a polype, to see that the actions which are progressing together in the body of the first, as much exceed in number the actions progressing together in the body of the last, as these do those in a stone. As at present analyzed, then, Life consists of simultaneous and successive changes.

Continuing the comparison, we next find that vital changes, both visceral and cerebral, differ from other changes in their *heterogeneity*. Neither the simultaneous acts nor the serial acts, which together constitute the process of digestion, are at all alike. The states of consciousness comprised in any ratiocination are not repetitions of each other, either in composition or in modes of dependence. Inorganic processes, on the other hand, even when like organic ones in the number of the simultaneous and successive changes they involve, are unlike them in the homogeneity of these changes. In the case of the sea, just referred to, it is observable that countless as are the actions at any moment going on, they are mostly mechanical actions that are to a great degree similar; and in this respect widely differ from the actions at any moment taking place in an organism: which not only belong to the several classes, mechanical, chemical, thermal, electric, but present under each of these classes, innumerable unlike actions. Even where life is nearly simulated, as by the working of a steam-engine, we may see that considerable as is the number of simultaneous changes, and rapid as are the successive ones, the regularity with which they soon recur in the same order and degree, renders them unlike those varied changes exhibited by a living creature. Still, it will be found that this peculiarity, like the foregoing ones, does not divide the two classes of changes with precision; inasmuch as there are inanimate things which exhibit considerable heterogeneity of change: for instance, a cloud. The variations of state which this undergoes, both simultaneous and successive, are many and quick; and they differ widely from each other both in quality and quantity. At the same instant there may occur in a cloud, change of position, change of form, change of size, change of density, change of colour, change of temperature, change of electric state; and these several kinds of change are continuously displayed in different degrees and combinations. Yet notwithstanding this, when we consider that very few inorganic objects manifest heterogeneity of change in a marked manner, while all organic objects manifest it; and further, that in ascending from low to high forms of life, we meet with an increasing variety in the kinds and amounts of changes displayed; we see that there is here a further leading distinction between organic and inorganic actions. According to this modified conception, then, Life is made up of heterogeneous changes both simultaneous and successive.

If now we look for some point of agreement between the assimilative and logical processes, by which they are distinguished from those inorganic processes that are most like them in the heterogeneity of the simultaneous and successive changes they comprise, we discover that they are distinguished by the *combination* subsisting among their constituent changes. The acts that make up digestion are mutually dependent. Those composing a train of reasoning are in close connection. And generally, it is to be remarked of vital changes, that each is made possible by all, and all are affected by each. Respiration, circulation, absorption, secretion, in their many sub-divisions, are bound up together. Muscular contraction involves chemical change, change of temperature, and change in the excretions. Active thought influences the operations of the stomach, of the heart, of the kidneys. But we miss this union among inorganic processes. Life-like as may seem the action of a volcano in respect of the heterogeneity of its many simultaneous and successive changes, it is not life-like in respect of their combination. Though the chemical, mechanical, thermal, and electric phenomena exhibited, have some inter-dependence; yet the emission of stones, mud, lava, flame, ashes, smoke, steam, usually takes place irregularly in quantity, order, intervals, and mode of conjunction. Even here, however, it cannot be said that inanimate things present no parallels to animate ones. A glacier may be instanced as showing nearly as much combination in its changes as a plant of the lowest organization. It is ever growing and ever decaying; and the rates of its composition and decomposition preserve a tolerably constant ratio. It moves; and its motion is in immediate dependence on its thawing. It emits a torrent of water, which, in common with its motion, undergoes annual variations, as plants do. During part of the year the surface melts and freezes alternately; and on these changes are dependent the variations in movement, and in efflux of water. Thus we have growth, decay, changes of temperature, changes of consistence, changes of velocity, changes of excretion, all going on in connexion; and it may be as truly said of a glacier as of an animal, that by ceaseless integration and disintegration it gradually undergoes an entire change of substance without losing its individuality, This exceptional instance, however, will scarcely be held to obscure that broad distinction from inorganic processes, which organic processes derive from the combination among their constituent changes. And the reality of this distinction becomes yet more manifest when we find that, in common with previous ones, it not only marks off the living from the not-living, but also things which live little from things which live much. For while the changes going on in a plant or a zoophyte are so imperfectly combined that they can continue after it has been divided into two or more pieces, the combination among the changes going on in a mammal is so close that no part cut off from the rest can live, and any considerable disturbance of one function causes a cessation of the others. Life, therefore, as we now regard it, is a combination of heterogeneous changes, both simultaneous and successive.

Once more looking for a characteristic common to these two kinds of vital action, we perceive that the combinations of heterogeneous changes which constitute them, differ from the few combinations which they otherwise resemble, in respect of *definiteness*. The associated changes going on in a glacier, admit of indefinite variation. Under a conceivable alteration of climate, its thawing and its progression may be stopped for myriads of years, without disabling it from again displaying these phenomena under appropriate conditions. By a geological convulsion, its motion may be arrested without an arrest of its thawing; or by an increase in the inclination of the surface it slides over, its motion may be accelerated without accelerating its rate of dissolution. Other things remaining the same, a more rapid deposit of snow may cause an indefinite increase of bulk; or, conversely, the accretion may entirely cease, and yet all the other actions continue until the mass disappears. Here, then, the combination has none of that definiteness which, in a plant, marks the mutual dependence of assimilation, respiration, and circulation; much less has it that definiteness seen in the mutual dependence of the chief animal functions: no one of which can be varied without varying the rest: no one of which can go on unless the rest go on. It is this definiteness of combination which distinguishes the changes occurring in a living body from those occurring in a dead one. Decomposition exhibits both simultaneous and successive changes, which are to some extent heterogeneous, and in a sense combined; but they are not combined in a definite manner. They vary according as the surrounding medium is air, water, or earth. They alter in nature with the temperature. If the local conditions are unlike, they progress differently in different parts of the mass, without mutual influence. They may end in producing gases, or adipocire, or the dry substance of which mummies consist. They may occupy a few days, or thousands of years. Thus, neither in their simultaneous nor in their successive changes, do dead bodies display that definiteness of combination which characterizes living ones. It is true that in some inferior creatures the cycle of successive changes admits of a certain indefiniteness—that it may be apparently suspended for a long period by desiccation or freezing; and may afterwards go on as though there had been no breach in its continuity. But the circumstance that only a low order of life permits the cycle of its changes to be thus modified, serves but to suggest that, like the previous characteristics, this characteristic of definiteness in its combined changes, distinguishes high vitality from low vitality, as it distinguishes low vitality from inorganic processes. Hence, our formula as further amended reads thus:—Life is a definite combination of heterogeneous changes, both simultaneous and successive.

Finally, we shall still better express the facts, if, instead of saying *a* definite combination of heterogeneous changes, we say *the* definite combination of heterogeneous changes. As it at present stands, the definition is defective both in allowing that there may be *other* definite combinations of heterogeneous changes, and in directing attention to the heterogeneous changes rather than to the definiteness of their combination. Just as it is not so much its chemical elements which constitute an organism, as it is the arrangement of them into special tissues and organs; so it is not so much its heterogeneous changes which constitute Life, as it is the definite combination of them. Observe what it is that ceases when life ceases. In a dead body there are going on heterogeneous changes, both simultaneous and successive. What then has disappeared? The definite combination has disappeared. Mark, too, that however heterogeneous the simultaneous and successive changes exhibited by an inorganic object, as a volcano, we much less tend to think of it as living, than we do a watch or a steam-engine, which, though displaying homogeneous changes, displays them definitely combined. So dominant an element is this in our idea of Life, that even when an object is motionless, yet, if its parts be definitely combined, we conclude either that it has had life, or has been made by something having life. Thus then, we conclude that Life is—*the* definite combination of heterogeneous changes, both simultaneous and successive.

§ 26. Such is the conception at which we arrive without changing our stand-point. It is, however, an incomplete conception. This ultimate formula (which is to a considerable extent identical with one above given—"the co-ordination of actions;" seeing that "definite combination" is synonymous with "co-ordination," and "changes both simultaneous and successive" are comprehended under the term "actions;" but which differs from it in specifying the fact, that the actions or changes are "heterogeneous")—this ultimate formula, I say, is after all but proximately correct. It is true that it does not fail by including the growth of a crystal; for the successive changes this implies cannot be called heterogeneous. It is true that the action of a galvanic battery is not comprised in it; since here, too, heterogeneity is not exhibited by the successive changes. It is true that by this same qualification the motions of the Solar System are excluded; as are also those of a watch and a steam-engine. It is true, moreover, that while, in virtue of their heterogeneity, the actions going on in a cloud, in a volcano, in a glacier, fulfil the definition; they fall short of it in lacking definiteness of combination. It is further true that this definiteness of combination, distinguishes the changes taking place in an organism during life, from those which commence at death. And beyond all this it is true that, as well as serving to mark off, more or less clearly, organic actions from inorganic actions, each member of the definition serves to mark off the actions constituting high vitality from those constituting low vitality; seeing that life is high in proportion to the number of successive changes occurring between birth and death; in proportion to the number of simultaneous changes; in proportion to the heterogeneity of the changes; in proportion to the combination subsisting among the changes; and in proportion to the definiteness of their combination. Nevertheless, answering though it does to so many requirements, this definition is essentially defective. It does not convey a complete idea of the thing contemplated. *The definite combination of heterogeneous changes, both simultaneous and successive,* is a formula which fails to call up an adequate conception. And it fails from omitting the most distinctive peculiarity — the peculiarity of which we have the most familiar experience, and with which our notion of Life is, more than with any other, associated. It remains now to supplement the definition by the addition of this peculiarity.

# CHAPTER V.

## THE CORRESPONDENCE BETWEEN LIFE AND ITS CIRCUMSTANCES.

§ 27. WE habitually distinguish between a live object and a dead one, by observing whether a change which we make in the surrounding conditions, or one which Nature makes in them, is or is not followed by some perceptible change in the object. By discovering that certain things shrink when touched, or fly away when approached, or start when a noise is made, the child first roughly discriminates between the living and the not-living; and the man when in doubt whether an animal he is looking at is dead or not, stirs it with his stick; or if it be at a distance, shouts, or throws a stone at it. Vegetal and animal life are alike primarily recognized by this process. The tree that puts out leaves when the spring brings a change of temperature, the flower which opens and closes with the rising and setting of the sun, the plant that droops when the soil is dry, and re-erects itself when watered, are considered alive because of these induced changes; in common with the zoophyte which contracts on the passing of a cloud over the sun, the worm that comes to the surface when the ground is continuously shaken, and the hedgehog that rolls itself up when attacked.

Not only, however, do we habitually look for some response when an external stimulus is applied to a living organism, but we perceive a fitness in the response. Dead as well as living things display changes under certain changes of condition: instance, a lump of carbonate of soda that effervesces when dropped into sulphuric acid; a cord that contracts when wetted; a piece of bread that turns brown when held near the fire. But in these cases, we do not see a connexion between the changes undergone, and the preservation of the things that undergo them; or, to avoid any teleological implication—the changes have no apparent relations to future external events which are sure or likely to take place. In vital changes, however, such relations are manifest. Light being necessary to vegetal life, we see in the action of a plant which, when much shaded, grows towards the unshaded side, an appropriateness which we should not see did it grow otherwise. Evidently the proceedings of a spider, which rushes out when its web is gently shaken and stays within when the shaking is violent, conduce better to the obtainment of food and the avoidance of danger than were they reversed. The fact that we feel surprise when, as in the case of a bird fascinated by a snake, the conduct tends towards self-destruction, at once shows how generally we have observed an adaptation of living changes to changes in surrounding circumstances.

Note further the kindred truth, rendered so familiar by infinite repetition that we forget its significance, that there is invariably, and necessarily, a conformity between the vital functions of any organism, and the conditions in which it is placed—between the processes going on inside of it, and the processes going on outside of it. We know that a fish cannot live in air, or a man in water. An oak growing in the ocean, and a seaweed on the top of a hill, are incredible combinations of ideas. We find that every animal is limited to a certain range of climate; every plant to certain zones of latitude and elevation. Of the marine flora and fauna, each species is found exclusively between such and such depths. Some blind creatures flourish only in dark caves; the limpet only where it is alternately covered and uncovered by the tide; the red-snow alga rarely elsewhere than in the arctic regions or among alpine peaks.

Grouping together the cases first named, in which a particular change in the circumstances of an organism is followed by a particular change in it, and the cases last named, in which the constant actions occurring within an organism imply some constant actions occurring without it; we see that in both, the changes or processes displayed by a living body are specially related to the changes or processes in its environment. And here we have the needful supplement to our conception of Life. Adding this all-important characteristic, our conception of Life becomes—The definite combination of heterogeneous changes, both simultaneous and successive, *in correspondence with external co-existences and sequences.* That the full significance of this addition may be seen, it will be necessary to glance at the correspondence under some of its leading aspects.*

§ 28. Neglecting minor requirements, tne actions going

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* Speaking of "the general idea of *life*," M. Comte says:—"Cette idée suppose, en effet, non-seulement celle d'un être organisé de manière à comporter l'état vital, mais aussi celle, non moins indispensable, d'un certain ensemble d'influences extérieure propres à son accomplissement. Une telle harmonie entre l'être vivant et le *milieu* correspondant, caractérise evidemment la condition fondamentale de la vie." Commenting on de Blainville's definition of life, which he adopts, he says:—"Cette lumineuse définition ne me paraît laisser rien d'important à désirer, si ce n'est une indication plus directe et plus explicite de ces deux conditions fondamentales co-relatives, nécessairement inséparables de l'état vivant, un *organisme* determiné et un *milieu* convenable." It is strange that M. Comte should have thus recognized the necessity of a harmony between an organism and its environment, as a *condition* essential to life, and should not have seen that the continuous maintenance of such inner actions as will counterbalance outer actions, *constitutes* life. It is the more strange that he should have been so near this truth and yet missed it, since, besides his wide range of thought, M. Comte is often remarkable for his clear intuitions. Lest by saying this, I should deepen a misconception into which some have fallen, let me take the opportunity of stating, that though I believe some of M. Comte's minor generalizations to be true, and though I recognize the profundity of many incidental observations he makes, I by no means accept his system. Those general doctrines in which I agree with him, are those which he holds in common with sundry other thinkers. With all those general doctrines which are distinctive of his philosophy, I disagree—with all those at least that I have definite knowledge of; for beyond the first half of his "Course of Positive Philosophy," I know his opinions only by hearsay.

on in a plant pre-suppose a surrounding medium containing at least carbonic acid and water, together with a due supply of light and a certain temperature. Within the leaves carbon is being assimilated and oxygen given off; without them, is the gas from which the carbon is abstracted, and the imponderable agents that aid the abstraction. Be the nature of the process what it may, it is clear that there are external elements prone to undergo special re-arrangements under special conditions. It is clear that the plant in sunshine presents these conditions and so effects these re-arrangements. And thus it is clear that the changes which constitute the plant's life, are in correspondence with co-existences in its environment.

If, again, we ask respecting the lowest protozoon, how it lives; the answer is, that while on the one hand its substance is ever undergoing oxidation, it is on the other hand ever absorbing nutriment; and that it may continue to exist, the assimilation must keep pace with, or exceed, the oxidation. If further we ask under what circumstances these combined changes are possible; there is the obvious reply, that the medium in which the protozoon is placed, must contain oxygen and food—oxygen in such quantity as to produce some disintegration; food in such quantity as to permit that disintegration to be made good. In other words—the two antagonistic processes taking place internally, imply the presence externally of materials having affinities that can give rise to these processes.

Leaving those lowest animal forms revealed by the microscope, which simply take in through their surfaces the nutriment and oxygenated fluids coming in contact with them, we pass to those somewhat higher forms which have their tissues partially specialized into assimilative and respiratory. In these we see a correspondence between certain actions in the digestive sac, and the properties of certain surrounding bodies. That a creature of this order may continue to live, it is necessary not only that there be masses of substance in the environment capable of transformation into its own tissue; but that the introduction of these masses into its stomach, shall be followed by the secretion of a solvent fluid that will reduce them to a fit state for absorption. Special outer properties must be met by special inner properties.

When, from the process by which food is digested, we turn to the processes by which it is seized, we perceive the same general truth. The stinging and contractile power of a polype's tentacle, correspond to the sensitiveness and strength of the creatures serving it for prey. Unless that external change which brings one of these creatures in contact with the tentacle, were quickly followed by those internal changes which result in the coiling and drawing up of the tentacle, the polype would die of inanition. The fundamental processes of integration and disintegration within it, would get out of correspondence with the agencies and processes without it; and the life would cease.

Similarly, it may be shown that when the creature becomes so large that its tissue cannot be efficiently supplied with nutriment by mere absorption through its limiting membranes, or duly oxygenated by contact with the fluid that bathes its surface, there arises a necessity for a circulatory system by which nutriment and oxygen may be distributed throughout the mass; and the functions of this system, being subsidiary to the two primary functions, form links in the correspondence between internal and external actions. The like is obviously true of all those subordinate functions, secretory and excretory, that facilitate oxidation and assimilation—functions in which we may trace, both contemporaneous changes answering to co-existences in the environment, and successive changes answering to those changes of composition, of temperature, of light, of moisture, of pressure, which the environment undergoes.

Ascending from the visceral actions to the muscular and nervous actions, we find the correspondence displayed in a manner still more obvious. Every act of locomotion implies the expenditure of certain internal mechanical forces, adapted in amounts and directions to balance or out-balance certain external ones. The recognition of an object is impossible without a harmony between the changes constituting perception, and particular properties co-existing in the environment. Escape from enemies supposes motions within the organism, related in kind and rapidity to motions without it. Destruction of prey requires a particular combination of subjective actions, fitted in degree and succession to overcome a group of objective ones. And so with those countless automatic processes exemplified in works on animal instinct.

In the highest order of vital changes, the same fact is equally manifest. The empirical generalization that guides the farmer in his rotation of crops, serves to bring his actions into concord with certain of the actions going on in plants and soil. The rational deductions of the educated navigator who calculates his position at sea, constitute a series of mental acts by which his proceedings are conformed to surrounding circumstances. Alike in the simplest inferences of the child, and the most complex ones of the man of science, we find a correspondence between simultaneous and successive changes in the organism, and co-existences and sequences in its environment.

§ 29. This general formula, which thus includes the lowest vegetal processes as well as the highest manifestations of human intelligence, will perhaps call forth some criticisms which it is desirable here to meet.

It may be thought that there are still a few inorganic actions included in the definition; as for example that displayed by the mis-named storm-glass. The feathery crystallization which, on a certain change of temperature, takes place in the solution contained by this instrument, and which afterwards dissolves to reappear in new forms under new conditions, may be held to present simultaneous and successive changes that are to some extent heterogeneous, that occur with some definiteness of combination, and, above all, occur in correspondence with external changes. In this case vegetal life is simulated to a considerable extent; but it is *merely* simulated. The relation between the phenomena occurring in the storm-glass and in the atmosphere respectively, is really not a correspondence at all, in the proper sense of the word. Outside there is a certain change; inside there is a change of atomic arrangement. Outside there is another certain change; inside there is another change of atomic arrangement. But subtle as is the dependence of each internal upon each external change, the connexion between them does not, in the abstract, differ from the connexion between the motion of a straw and the motion of the wind that disturbs it. In either case a change produces a change, and there it ends. The alteration wrought by some environing agency on an inanimate object, does not tend to induce in it a secondary alteration, that anticipates some secondary alteration in the environment. But in every living body there is a tendency towards secondary alterations of this nature; and it is in their production that the correspondence consists. The difference may be best expressed by symbols. Let A be a change in the environment; and B some resulting change in an inorganic mass. Then A having produced B, the action ceases. Though the change A in the environment, is followed by some consequent change *a* in it; no parallel sequence in the inorganic mass simultaneously generates in it some change *b* that has reference to the change *a*. But if we take a living body of the requisite organization, and let the change A impress on it some change C; then, while in the environment A is occasioning *a*, in the living body C will be occasioning *c*: of which *a* and *c* will show a certain concord in time, place, or intensity. And while it is *in* the continuous production of such concords or correspondences that Life consists, it is *by* the continuous production of them that Life is maintained.

The further criticism that may be expected, concerns certain verbal imperfections in the definition, which it seems impossible to avoid. It may be fairly urged that the word *correspondence* will not include, without straining, the various relations to be expressed by it. It may be asked :—How can the continuous *processes* of assimilation and respiration, correspond with the *co-existence* of food and oxygen in the environment? or again :—How can the act of secreting some defensive fluid, correspond with some external danger which may never occur? or again :—How can the *dynamical* phenomena constituting perception, correspond with the *statical* phenomena of the solid body perceived? The only reply to these questions, is, that we have no word sufficiently general to comprehend all forms of this relation between the organism and its medium, and yet sufficiently specific to convey an adequate idea of the relation; and that the word *correspondence* seems the least objectionable. The fact to be expressed in all cases, is, that certain changes, continuous or discontinuous, in the organism, are connected after such a manner that, in their amounts, or variations, or periods of occurrence, or modes of succession, they have a reference to external actions, constant or serial, actual or potential—a reference such that a definite relation among any members of the one group, implies a definite relation among certain members of the other group; and the word *correspondence* appears the best fitted to express this fact.

§ 30. The presentation of the phenomena under this general form, suggests how our definition of Life may be reduced to its most abstract shape; and perhaps its best shape. By regarding the respective elements of the definition as relations, we avoid both the circumlocution and the verbal inaccuracy; and that we may so regard them with propriety is obvious. If a creature's rate of assimilation is increased in consequence of a decrease of temperature in the environment; it is that the relation between the food consumed and heat produced, is so re-adjusted by multiplying both its members, that the altered relation in the surrounding medium between the quantity of heat absorbed from, and radiated to, bodies of a given temperature, is counterbalanced. If a sound or a scent wafted to it on the breeze, prompts the stag to dart away from the deer-stalker; it is that there exists in its neighbourhood a relation between a certain sensible property and certain actions dangerous to the stag, while in its organism there exists an adapted relation between the impression this sensible property produces, and the actions by which danger is escaped. If inquiry has led the chemist to a law, enabling him to tell how much of any one element will combine with so much of another; it is that there has been established in him specific mental relations, which accord with specific chemical relations in the things around. Seeing, then, that in all cases we may consider the external phenomena as simply in relation, and the internal phenomena also as simply in relation; the broadest and most complete definition of Life will be—*The continuous adjustment of internal relations to external relations.*[*]

While it is simpler, this modified formula has the further advantage of being somewhat more comprehensive. To say that it includes not only those definite combinations of simultaneous and successive changes in an organism, which correspond to co-existences and sequences in the environment, but also those structural arrangements which *enable* the organism to adapt its actions to actions in the environment, may perhaps be going too far; for though these structural arrangements present internal relations adjusted to external relations, yet the *continuous adjustment* of relations can scarcely be held to include a *fixed adjustment* already made. Clearly, Life, which is made up of *dynamical* phenomena, cannot be defined in terms that shall at the same time define the apparatus manifesting it, which presents only *statical* phenomena. But while this antithesis serves to remind us that the fundamental distinction between the organism and

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[*] In further elucidation of this general doctrine, see *First Principles*, § 25.

its actions, is as wide as that between Matter and Motion, it at the same time draws attention to the fact, that if the structural arrangements of the adult are not properly included in the definition, yet the developmental processes by which those arrangements were established, are included. For that process of evolution during which the organs of the embryo are fitted to their prospective functions, is from beginning to end the gradual or continuous adjustment of internal relations to external relations. Moreover, those structural modifications of the adult organism, which, under change of climate, change of occupation, change of food, slowly bring about some re-arrangement in the organic balance, must similarly be regarded as continuous adjustments of internal relations to external relations. So that not only does the definition, as thus expressed, comprehend all those activities, bodily and mental, which constitute our ordinary idea of Life; but it also comprehends, both those processes of development by which the organism is brought into general fitness for these activities, and those after-processes of adaptation by which it is specially fitted to its special activities.

Nevertheless, superior as it is in simplicity and comprehensiveness, so abstract a formula as this is scarcely fitted for our present purpose. Reserving its terms for such use as occasion may dictate, it will be best commonly to employ its more concrete equivalent—to consider the internal relations as "definite combinations of simultaneous and successive changes;" the external relations as "co-existences and sequences;" and the connexion between them as a "correspondence."

## CHAPTER VI.

### THE DEGREE OF LIFE VARIES AS THE DEGREE OF CORRESPONDENCE.

§ 31. Already it has been shown respecting each other qualification included in the foregoing definition, that the life is high in proportion as that qualification is well fulfilled; and it is now to be remarked, that the same thing is especially true respecting this last qualification—the correspondence between internal and external relations. It is manifest *à priori*, that since changes in the physical state of the environment, as also those mechanical actions and those variations of available food which occur in it, are liable to stop the processes going on in the organism; and since the adaptive changes in the organism have the effects of directly or indirectly counterbalancing these changes in the environment; it follows that the life of the organism will be short or long, low or high, according to the extent to which changes in the environment are met by corresponding changes in the organism. Allowing a margin for perturbations, the life will continue only while the correspondence continues; the completeness of the life will be proportionate to the completeness of the correspondence; and the life will be perfect only when the correspondence is perfect. Not to dwell in general statements, however, let us contemplate this truth under its concrete aspects.

§ 32. In life of the lowest order, we find that only the most prevalent coexistences and sequences in the environment, have any simultaneous and successive changes answering to them in the organism. A plant's vital processes display adjustment solely to the continuous coexistence of certain elements and forces surrounding its roots and leaves; and vary only with the variations produced in these elements and forces by the sun—are unaffected by the countless mechanical and other changes occurring around; save when accidentally arrested by these. The life of a worm is made up of actions referring almost exclusively to the tangible properties of adjacent things. All those visible and audible changes which happen near it, and are connected with other changes that may presently destroy it, pass unrecognized—produce in it no adapted changes: its only adjustment of internal relations to external relations of this order, is seen when it escapes to the surface on feeling the vibrations produced by an approaching mole. Adjusted as are the proceedings of a bird, to a far greater number of coexistences and sequences in the environment, cognizable by sight, hearing, scent, and their combinations; and numerous as are the dangers it shuns and the needs it fulfils, in virtue of this extensive correspondence; it exhibits no such actions as those by which a human being counterbalances variations in temperature and supply of food, consequent on the seasons. And when we see the plant eaten, the worm trodden on, the bird dead from starvation; we see alike that the death is an arrest of such correspondence as existed; that it occurred when there was some change in the environment to which the organism made no answering change; and that thus, both in shortness and simplicity, the life was incomplete in proportion as the correspondence was incomplete. Progress towards more prolonged and higher life, evidently implies an ability to respond to less general coexistences and sequences. Each step upwards must consist in adding to the previously-adjusted relations which the organism exhibits, some further relation parallel to a further relation in the environment. And the greater correspondence thus established, must, other things equal, show itself both in greater complexity of life, and greater length of life—a truth which will be duly realized on remembering that enormous mortality which prevails among lowly-organized creatures, and that gradual increase of longevity and diminution of fertility which we meet with on ascending to creatures of higher and higher development.

It must, however, be remarked, that while length and complexity of life are, to a great extent, associated—while a more extended correspondence in the successive changes, commonly implies increased correspondence in the simultaneous changes; yet it is not uniformly so. Between the two great divisions of life—animal and vegetal—this contrast by no means holds. A tree may live a thousand years, though the simultaneous changes going on in it answer only to the few chemical affinities in the air and the earth, and though its serial changes answer only to those of day and night, of the weather and the seasons. A tortoise, which exhibits in a given time nothing like the number of internal actions adjusted to external ones, that are exhibited by a dog, yet lives far longer. The tree by its massive trunk, and the tortoise by its hard carapace, are saved the necessity of responding to those many surrounding mechanical actions which organisms not thus protected must respond to or die; or rather—the tree and the tortoise display in their structures, certain simple statical relations adapted to meet countless dynamical relations external to them. But notwithstanding the qualifications suggested by such cases, it needs but to compare a microscopic fungus with an oak, an animalcule with a shark, a mouse with a man, to recognize the fact that this increasing correspondence of its changes with those of the environment, which characterizes progressing life, habitually shows itself at the same time in continuity and in complication.

Even were not the connexion between length of life and complexity of life thus conspicuous, it would still be true that the degree of life varies with the degree of correspondence. For if the lengthened existence of a tree be looked upon as tantamount to a considerable degree of life; then it must be admitted that its lengthened display of correspondences is tantamount to a considerable degree of correspondence. If otherwise it be held, that notwithstanding its much shorter existence, a dog must rank above a tortoise in degree of life, because of its superior activity; then it is implied that its life is higher, because its simultaneous and successive changes are more complex and more rapid—because the correspondence is greater. And since we regard as the highest life, that which, like our own, shows great complexity in the correspondences, great rapidity in the succession of them, and great length in the series of them; the equivalence between degree of life and degree of correspondence, is unquestionable.

§ 33. In further elucidation of this general truth, and especially in explanation of the irregularities just referred to, it requires to be observed, that as the life becomes higher the environment itself becomes more complex. Though, literally, the environment means all surrounding space with the coexistences and sequences contained in it; yet, practically, it often means but a small part of this. The environment of an entozoon, can scarcely be said to extend beyond the body of the animal in which the entozoon lives. That of a fresh-water alga is, virtually, limited to the ditch inhabited by the alga. And understanding the term in this restricted sense, we shall see that the superior organisms inhabit the more complicated environments.

Thus, contrasted with that found on land, the lower life is that found in the sea; and it has the simpler environment. Marine creatures are affected by a smaller number of coexistences and sequences than terrestrial ones. Being very nearly of the same specific gravity as the surrounding medium, they have to contend with less various mechanical actions. The zoophyte rooted to a stone, and the acalephe passively borne along in the current, need to undergo no internal changes such as those by which the caterpillar meets the varying effects of gravitation, while creeping over and under the leaves. Again, the sea is liable to none of those extreme and rapid alterations of temperature which the air suffers. Night and day produce no appreciable modifications in it; and it is comparatively little affected by the seasons. Thus its contained fauna show no marked correspondences similar to those by which air-breathing creatures counterbalance thermal changes. Further, in respect to the supply of nutriment the conditions are more simple. The lower tribes of animals inhabiting the water, like the plants inhabiting the air, have their food brought to them. The same current which brings oxygen to the oyster, also brings it the microscopic organisms on which it lives: the disintegrating matter and the matter to be integrated, coexist under the simplest relation. It is otherwise with land animals. The oxygen is everywhere; but that which is needed to neutralize its action is not everywhere: it has to be sought; and the conditions under which it is to be obtained are more or less complex. So too with that liquid by the agency of which the vital processes are carried on. To marine creatures, water is ever present, and by the lowest is passively absorbed; but to most creatures living on the earth and in the air, it is made available only through those nervous changes constituting perception, and those muscular ones by which drinking is effected. Similarly, the contrast might be continued with respect to the electric and hygrometric variations; and the greater multiplicity of optical and acoustic phenomena with which terrestrial life is surrounded. And tracing upwards from the amphibia the widening extent and complexity which the environment, as practically considered, assumes—observing further how increasing heterogeneity in the flora and fauna of the globe, itself progressively complicates the environment of each species of organism—it might finally be shown that the same general truth is displayed in the history of mankind: whose advance in civilization has been simultaneous with their advance from the less varied requirements of the torrid zone to the more varied requirements of the temperate zone; whose chief steps have been made in regions presenting a complicated physical geography; and who, in the course of their progress, have been adding to their physical environment a social environment that has been growing even more involved. Thus, speaking generally, it is clear that those relations in the environment to which relations in the organism must correspond, themselves increase in number and intricacy as the life assumes a higher form.

§ 34. To make yet more manifest the fact, that the degree of life varies as the degree of correspondence, I may here point out, that those other distinctions successively noted when contrasting vital changes with non-vital changes, are all implied in this last distinction—their correspondence with external coexistences and sequences. And to this may be added the supplementary fact, that the increasing fulfilment of those other distinctions which we found to accompany increasing life, is involved in the increasing fulfilment of this last distinction. To descend to particulars:—We saw that living organisms are characterized by successive changes; and that as the life becomes higher, the successive changes become more numerous. Well, the environment is full of successive changes, both positive and relative; and the greater the correspondence, the greater the number of successive changes an organism must display. We saw that life presents simultaneous changes; and that the more elevated it is, the more marked the multiplicity of them. Well, besides countless phenomena of coexistence in the environment, there are often many changes occurring in it at the same moment; and hence increased correspondence with it, supposes an increased display of simultaneous changes in the organism. Similarly with the heterogeneity of the changes. In the environment the relations are very varied in their kinds; and hence, as the organic actions come more and more into correspondence with them, they also must become very varied in their kinds. So again is it, even with definiteness of combination. For though the inorganic bodies of which the environment mainly consists, do not present definitely-combined changes, yet they present definitely-combined properties; and though the minor meteorologic variations of the environment, do not show much definiteness of combination, yet those resulting from day and night and the seasons do. Add to which, that as the environment of each organism comprehends all those other organisms existing within its sphere of life—as the most important and most numerous surrounding changes with which each animal has to deal, are the definitely-combined changes exhibited by other animals, whether prey or enemies; it results that definiteness of combination is a general characteristic of the external changes with which internal ones have to correspond. Hence, increase of correspondence involves increased definiteness of combination. So that throughout, the correspondence of the internal relations with the external ones, is the essential thing; and all the special characteristics of the internal relations, are but the collateral results of this correspondence.

§ 35. As affording the simplest and most conclusive proof that the degree of life varies as the degree of correspondence, it remains to point out that perfect correspondence would be perfect life. Were there no changes in the environment but such as the organism had adapted changes to meet; and were it never to fail in the efficiency with which it met them; there would be eternal existence and universal knowledge. Death by natural decay, occurs because in old age the relations between assimilation, oxidation, and genesis of force going on in the organism, gradually fall out of correspondence with the relations between oxygen and food and absorption of heat by the environment. Death from disease, arises either when the organism is congenitally defective in its power to balance the ordinary external actions by the ordinary internal actions, or when there has taken place some unusual external action to which there was no answering internal action. Death by accident, implies some neighbouring mechanical changes of which the causes are either unobserved from inattention, or are so intricate that their results cannot be foreseen; and consequently certain relations in the organism are not adjusted to the relations in the environment. Manifestly, if, to every outer coexistence and sequence by which it was ever in any degree affected, the organism presented an answering process or act; the simultaneous changes would be indefinitely numerous and complex, and the successive ones endless—the correspondence would be the greatest conceivable, and the life the highest conceivable, both in degree and in length.

§ 36. Before closing the chapter, it will be useful to compare the definition of Life here set forth, with the definition of Evolution set forth in *First Principles.* Living bodies being bodies which display in the highest degree the structural changes constituting Evolution; and Life being made up of the functional changes that accompany these structural changes; we ought to find a certain harmony between the definitions of Evolution and of Life. Such a harmony is not wanting.

The first distinction we noted between the kind of change shown in Life, and other kinds of change, was its serial character: we saw that vital change is substantially unlike non-vital change, in being made up of *successive* changes. Now since organic bodies display in so much higher a degree than inorganic bodies, those continuous differentiations and integrations which constitute Evolution; and since the re-distributions of matter thus carried so far in a comparatively short period, imply concomitant re-distributions of motion; it is clear that in a given time, organic bodies must undergo changes so comparatively numerous as to render the successiveness of their changes a marked characteristic. And it will follow *à priori*, as we found it to do *à posteriori*, that the organisms exhibiting Evolution in the highest degree, exhibit the longest or the most rapid successions of changes, or both. Again, it was shown that vital change is distinguished from non-vital change by being made up of many *simultaneous* changes; and also that creatures possessing high vitality are marked off from those possessing low vitality, by the far greater number of their simultaneous changes. Here too there is entire congruity. In *First Principles*, § 116, we reached the conclusion, that a force falling on any aggregate is divided into several forces; that when the aggregate consists of parts that are unlike, each part becomes a centre of unlike differentiations of the incident force; and that thus the multiplicity of such differentiations must increase with the multiplicity of the unlike parts. It follows necessarily, therefore, that organic aggregates, which as a class are distinguished from inorganic aggregates by the greater number of their unlike parts, must be also distinguished from them by the greater number of simultaneous changes they display; and further that the higher organic aggregates, having more numerous unlike parts than the lower, must undergo more numerous simultaneous changes. We next found that the changes occurring in living bodies, are contrasted with those occurring in other bodies, as being much more *heterogeneous;* and that the changes occurring in the superior living bodies, are similarly contrasted with those occurring in inferior ones. Well, heterogeneity of function is the correlate of heterogeneity of structure; and heterogeneity of structure is the leading distinction between organic and inorganic aggregates, as well as between the more highly organized and the more lowly organized. By reaction, an incident force must be rendered multiform in proportion to the multiformity of the aggregate on which it falls; and hence those most multiform aggregates which display in the highest degree the phenomena of Evolution structurally considered, must at the same time be aggregates which display in the highest degree the multiform actions which constitute Evolution functionally considered. These heterogeneous changes, exhibited simultaneously and in succession by a living organism, prove, on further inquiry, to be distinguished by their *combination* from certain non-vital changes which simulate them. Here, too, the parallelism is maintained. It was shown in § 56 of *First Principles*, that an essential characteristic of Evolution is the integration of parts, which accompanies their differentiation—an integration that is shown both in the consolidation of each part, and in the consolidation of all the parts into a whole. Now, manifestly, combination among the changes going on in different combined parts, must be proportionate to the degree of combination among these parts: the more mutually-dependent the parts, the more mutually-dependent must be their actions. Hence, animate bodies having greater co-ordination of parts than inanimate ones, must exhibit greater co-ordination of changes. And this greater co-ordination of their changes must not only distinguish organic from inorganic aggregates; but must, for the same reason, distinguish higher organisms from lower ones, as we found that it did. Yet once more, it was pointed out that the changes constituting Life, differ from other changes in the *definiteness* of their combination; and that a distinction like in kind, though less in degree, holds between the vital changes of superior creatures and those of inferior creatures. These, also, are contrasts in harmony with the contrasts disclosed by the analysis of Evolution. We saw (*First Principles*, §§ 54, 55) that during Evolution, there is an increase of definiteness as well as an increase of heterogeneity. We saw that the integration accompanying differentiation, has necessarily the effect of increasing the distinctness with which the parts are marked off from each other; and that so, out of the incoherent and indefinite, there arises the coherent and definite. But a coherent whole made up of definite parts definitely combined, must exhibit more definitely combined changes than a whole made up of parts that are neither definite in themselves nor in their combination. Hence, if living bodies display more than other bodies this structural definiteness, then, definiteness of combination must be a characteristic of the changes constituting Life; and must also distinguish the vital changes of higher organisms from those of lower organisms. Finally, however, we discovered that all these peculiarities are subordinate to the one fundamental peculiarity, that vital changes take place in correspondence with external co-existences and sequences; and that the highest possible Life is reached, when there is some inner relation of actions fitted to meet every outer relation of actions by which the organism can be affected. But this conception of the highest possible Life, is in perfect harmony with the conception, before arrived at, of the ultimate limit of Evolution. When treating of equilibration as exhibited in organic phenomena (*First Principles*, §§ 133, 134), it was pointed out, that the continual tendency is towards the establishment of a balance between inner and outer changes. It was shown that "the final structural arrangements must be such as will meet all the forces acting on the aggregate, by equivalent antagonistic forces," and that "the maintenance of such a moving equilibrium" as an organism displays, "requires the habitual genesis of internal forces corresponding in number, directions, and amounts, to the external incident forces—as many inner functions, single or combined, as there are single or combined outer actions to be met." It was shown, too, that the relations among conceptions and ideas, are ever in progress towards a better balance between mental actions and those actions in the environment to which conduct must be adjusted. So that that maintenance of a correspondence between inner and outer relations, which we have here found to constitute Life, and the perfection of which is the perfection of Life, answers completely to that state of organic moving equilibrium which we saw arises in the course of Evolution, and tends ever to become more complete.

There is much significance in this complete parallelism. That two inquiries starting from different points and carried on in different ways, should lead to conclusions so entirely harmonizing with each other, cannot fail further to confirm these conclusions; if further confirmation of them be needed.

# CHAPTER VII.

## THE SCOPE OF BIOLOGY.

§ 37. We are now in a position to map-out the boundaries and divisions of our subject. Grouping together the general results arrived at in the first three chapters, and joining with them the results which the last three chapters have brought us to, we shall be prepared to comprehend the science of Biology as a whole; and to see how its truths may best be classified.

In the chapters treating of Organic Matter, the Actions of Forces on it, and its Reactions on Forces, the generalizations reached were these:—that organic matter is specially sensitive to surrounding agencies; that in consequence of the extreme instability of the compounds it contains, minute disturbances can cause in it large amounts of re-distribution; and that during the fall of its unstably-arranged atoms into stable arrangements, there are given out proportionately large amounts of motion. We saw that organic matter is so constituted, that small incident actions are capable of initiating great reactions—setting up extensive structural modifications, and liberating large quantities of power. In the chapters just concluded, the changes of which Life is made up, were shown to be so adjusted as to balance outer changes. And the general process of the adjustment we found resolves itself into this; that if in the environment there are any related actions, A and B, by which the organism is affected, then if A produces in the organism some change *a*, there follows in the organism some change *b*, fitted in time, direction, and amount to meet the action B—a change which is often required to be much larger than its antecedent. Mark, now, the relation between these two final results. On the one hand, for the maintenance of that correspondence between inner and outer actions which constitutes Life, an organism must be susceptible to small changes from small external forces (as in sensation), and must be able to initiate large changes in opposition to large external forces (as in muscular action). On the other hand, organic matter is at once extremely sensitive to disturbing agencies of all kinds, and is capable of suddenly evolving motion in great amounts. That is to say, the constitution of organic matter specially adapts it to receive and produce the internal changes required to balance external changes.

This being the general character of the vital Functions, and of the Matter in which they are performed, the science of Biology becomes an account of all the phenomena attendant on the performance of such Functions by such Matter—an account of all the conditions, concomitants, and consequences, under the various circumstances fallen into by living bodies. If all the functional phenomena which living bodies present, are, as we have concluded, incidents in the maintenance of a correspondence between inner and outer actions; and if all the structural phenomena which living bodies present, are direct or indirect concomitants of functional phenomena; then the entire Science of Life, must consist in a detailed interpretation of all these functional and structural phenomena in their relations to the phenomena of the environment. Immediately or mediately, proximately or remotely, every trait exhibited by organic bodies, as distinguished from inorganic bodies, must be referable to this continuous adjustment between their actions and the actions going on around them. Such being the extent and nature of our subject-matter, it may be thus divided.

1. An account of the structural phenomena presented by organisms. And this subdivides into:—
   - *a.* The structural phenomena presented by individual organisms.
   - *b.* The structural phenomena presented by successions of organisms.
2. An account of the functional phenomena which organisms present. And this, too, admits of sub-division into:—
   - *a.* The functional phenomena of individual organisms.
   - *b.* The functional phenomena of successions of organisms.
3. An account of the actions of Structure on Function, and the re-actions of Function on Structure. And like the others, this is divisible into:—
   - *a.* The actions and re-actions as exhibited in individual organisms.
   - *b.* The actions and re-actions as exhibited in successions of organisms.
4. An account of the phenomena attending the production of successions of organisms: in other words—the phenomena of Genesis.

There is, indeed, another mode of grouping the facts of Biology, with which all are familiar. According as they are facts of animal or vegetal life, they may be classed under the heads of Zoology and Botany. But this division, though convenient and indeed necessary for practical purposes, is one that does not here concern us. Dealing with organic structures and functions in connexion with their causes, conditions, concomitants, and consequences, Biology cannot divide itself into Animal-Biology and Vegetal-Biology; since the same fundamental classes of phenomena are common to both. Recognizing this familiar distinction only as much as convenience obliges us to do, let us now pass on to consider, more in detail, the classification of biologic phenomena, above set down in its leading outlines.

§ 38. The facts of structure which an individual organism exhibits, are of two chief kinds. In order of conspicuousness, though not in order of time, there come first those ultimate arrangements of parts which characterize the organism in its mature state—an account of which, commonly called Anatomy, is more properly called Morphology. And second, there come those successive modifications through which the organism passes in its development from the germ to the adult form—an account of which is called Embryology.

The facts of structure which any succession of individual organisms exhibits, admit of similar classification. On the one hand, we have those inner and outer differences of shape, that are liable to arise between the adult members of successive generations descended from a common stock—differences which, though usually not marked between adjacent generations, may in course of many generations become great. And on the other hand, we have those developmental modifications through which such modifications of the descended forms are reached.

The interpretation of structure, as exhibited in individual organisms and successions of organisms, is aided by two subsidiary divisions of biologic inquiry, named Comparative Anatomy (properly Comparative Morphology) and Comparative Embryology. These cannot properly be regarded as in themselves parts of Biology; since the facts embraced under them are not substantive phenomena, but are simply incidental to substantive phenomena. All the facts of structural Biology are comprehended under the two foregoing subdivisions; and the comparison of these facts as presented in different classes of organisms, is simply a *method* of interpreting the real relations and dependencies of the facts compared.

Nevertheless, though Comparative Morphology and Comparative Embryology do not disclose additional series of concrete or special facts, they lead to the establishment of certain abstract or general facts. By them it is made manifest that underneath the superficial differences of groups and classes and types of organisms, there are hidden fundamental similarities; and that the courses of development in such groups and classes and types, though in many respects divergent, are in some essential respects, coincident. The wide truths thus disclosed, come under the heads of General Morphology and General Embryology.

By contrasting the structures of organisms, there is also achieved that grouping of the like and separation of the unlike, called Classification. First by observation of external characters; second by observation of internal characters; and third by observation of the phases of development; it is ascertained what organisms are most similar in all particulars; what organisms are like each other in every important attribute; what organisms have common primordial characters. Whence there finally results such an arrangement of organisms, that if certain structural attributes of any one be given, its other structural attributes may be *empirically* predicted; and which prepares the way for that interpretation of their relations and genesis, which forms an important part of *rational* Biology.

§ 39. The second main division of Biology, above described as embracing the functional phenomena of organisms, is that which is in part signified by Physiology: the remainder being what we distinguish as Psychology. Both of these fall into subdivisions that may best be treated separately. That part of Physiology which is concerned with the molecular changes going on in organisms, is known as Organic Chemistry. An account of the modes in which the force generated in organisms by chemical change, is transformed into other forces, and made to work the various organs that carry on the functions of Life, comes under the head of Organic Physics. Psychology, which is mainly concerned with the adjustment of vital actions to actions in the environment (in contrast with Physiology, which is mainly concerned with vital actions apart from actions in the environment) consists of two quite distinct portions. Objective Psychology deals with those functions of the nervo-muscular apparatus by which such organisms as possess it, are enabled to adjust inner to outer relations; and includes also, the study of the same functions as externally manifested in conduct. Subjective Psychology deals with the sensations, perceptions, ideas, emotions, and volitions that are the direct or indirect concomitants of this visible adjustment of inner to outer relations—considers these several kinds of consciousness in their genesis, and their connexions of co-existence and succession. Consciousness under its different modes and forms, being a subject-matter radically distinct in nature from the subject-matter of Biology in general; and the method of self-analysis, by which alone the laws of dependence among changes of consciousness can be found, being a method unparalleled by anything in the rest of Biology; we are obliged to regard Subjective Psychology as a separate study —not absolutely, of course, but relatively to the mind of each student. And since it would be very inconvenient to dissociate Objective Psychology from Subjective Psychology, we are practically compelled to deal with the two as forming an independent sub-science, to be treated apart from the lower divisions of Biology.

Obviously, the functional phenomena presented in successions of organisms, similarly divide into physiological and psychological. Under the physiological, come the modifications of bodily actions that arise in the course of generations, as concomitants of structural modifications; and these may be modifications, qualitative or quantitative, in the molecular changes classed as chemical, or in the organic actions classed as physical, or in both. Under the psychological, come the qualitative and quantitative modifications of instincts, feelings, conceptions, and mental changes in general, that occur in creatures having more or less intelligence, when certain of their conditions are changed. This, like the preceding department of Psychology, has in the abstract two different aspects—the objective and the subjective. Practically, however, the objective, which deals with these mental modifications as exhibited in the changing habits and abilities of successive generations of creatures, is the only one that admits of scientific investigation; since the corresponding alterations in consciousness, cannot be immediately known to any but the subjects of them. Evidently, convenience requires us to class this part of Psychology along with the other parts, in a distinct sub-science.

Light is thrown on functions, as well as on structures, by comparing organisms of different kinds. Comparative Physiology and Comparative Psychology, are the names given to those collections of facts respecting the homologies and analogies, bodily and mental, that are brought to light by this kind of inquiry. These classified observations concerning likenesses and differences of functions, are helpers to interpret functions in their essential natures and relations. Hence Comparative Physiology and Comparative Psychology are names of methods, rather than names of true subdivisions of Biology.

Here, however, as before, the comparison of special truths, besides facilitating their interpretation, brings to light certain general truths. Contrasting bodily and mental functions as exhibited in various orders of organisms, shows that there exists, more or less extensively, a community of processes and methods. Hence result two groups of abstract propositions, constituting General Physiology and General Psychology.

§ 40. In these various divisions and sub-divisions of the first two great departments of Biology, the phenomena of Structure are considered separately from the phenomena of Function, so far as separate treatment of them is possible. The third great department of Biology deals with them in their necessary connexions. It comprehends the determination of functions by structures, and the determination of structures by functions.

As displayed in individual organisms, the action of structures on functions is to be studied, not only in the broad and familiar fact that the general kind of life an organism leads is necessitated by the main characters of its organization, but in the more special and less conspicuous fact, that between members of the same species, minor differences of structure lead to minor differences of power to perform certain kinds of action, and of tendency to perform such kinds of action. Conversely, under the re-actions of function on structure as displayed in individual organisms, come the facts showing that functions, when fulfilled to their normal extents, maintain integrity of structure in their respective organs; and that within certain limits, the increase of functions is followed by such structural changes in their respective organs, as enables the organs to discharge better their extra functions.

Inquiry into the action of structure on function as displayed in successions of organisms, introduces us to such phenomena as Mr Darwin's "Origin of Species" deals with. In this category come all proofs of the general truth, that when an individual is enabled by a certain structural peculiarity, to perform better than others of its species some advantageous action; and when it bequeaths more or less of its structural peculiarity to descendants, among whom those which have it most markedly, are best able to thrive and propagate; there arises through this continuous action of structure on function, a visibly modified type of structure, having a more or less distinct function. In the correlative class of facts, which come under the category of re-actions of function on structure as exhibited in successions of organisms, are to be placed all those modifications of structure which arise in races, when changes of conditions entail changes in the balance of their functions. Here is to be studied the way in which altered function externally necessitated, works, by re-action, altered structure; and how in succeeding generations, this altered structure may be made continually more marked by this altered function. Though logically distinct, these two sub-divisions of biologic inquiry cannot in practice be carried on apart. A speciality of structure which leads to an excess of function in any direction, is, by the perpetual re-action of function, rendered ever more decided. A speciality of function, by calling forth a corresponding speciality of structure, produces an increasingly efficient discharge of such function. Whichever of the two initiates the change, there goes on between them an unceasing action and re-action, producing in them co-ordinate modifications.

§ 41. The fourth great division of Biology, comprehending the phenomena of Genesis, may be conveniently separated into three sub-divisions.

Under the first, comes a description of all the special modes whereby the multiplication of organisms is carried on: which modes range themselves under the two chief heads of sexual and asexual. An account of Sexual Multiplication includes the various methods by which germs and ova are fertilized, and by which, after fertilization, they are furnished with the materials, and maintained in the conditions, needful for their development. An account of Asexual Multiplication includes the various methods by which, from the same fertilized germ or ovum, there are produced many organisms that are partially or totally independent of each other.

The second of these sub-divisions deals with the phenomena of Genesis in the abstract. It takes for its subject-matter, such general questions as—What is the end subserved by the union of sperm-cell and germ-cell? Why cannot all multiplication be carried on after the asexual method? What are the laws of hereditary transmission? What are the causes of variation?

The third sub-division is devoted to still more abstract aspects of the phenomena. Recognizing the general facts of multiplication, without reference to their modes or immediate causes, it concerns itself simply with the different rates of multiplication in different kinds of organisms, and different individuals of the same kind. Generalizing the numerous contrasts and variations of fertility, it seeks a rationale of them in their relations to other organic phenomena.

§ 42. Such appears to be the natural arrangement of divisions and sub-divisions which Biology presents, when regarded from the highest point of view, as the Science of Life—the science which has for its subject-matter, the correspondence of organic relations, with the relations amid which organisms exist. This, however, is a classification of the parts of Biology when fully developed; rather than a classification of the parts of Biology as it now stands. Several of the sub-divisions above named have no recognized existence; and sundry of the others are in quite rudimentary states. It is therefore impossible now to fill in, even in the roughest way, more than a part of the outlines here sketched.

Our course of inquiry being thus in great measure determined by the present state of knowledge, we are compelled to follow an order widely different from this ideal one. It will be necessary first to give an account of those empirical generalizations which naturalists and physiologists have established: arranging them rather with a view to facility of comprehension than to logical sequence; and appending to those which admit of it, such deductive interpretations as *First Principles* furnish us with. Having done this, we shall be the better prepared for dealing with the leading truths of Biology, in connexion with the doctrine of Evolution.

# PART II.

## THE INDUCTIONS OF BIOLOGY.

# CHAPTER I.

## GROWTH.

§ 43. PERHAPS the widest and most familiar induction of Biology, is that organisms grow. While, however, this is a characteristic so habitually and markedly displayed by plants and animals, as to be carelessly thought peculiar to them, it is really not so. Under appropriate conditions, increase of size takes place in inorganic aggregates, as well as in organic aggregates. Crystals grow; and often far more rapidly than living bodies. Where the requisite materials are supplied in the requisite forms, growth may be witnessed in non-crystalline masses: instance the fungus-like accumulation of carbon that takes place on the wick of an unsnuffed candle. On an immensely larger scale, we have growth in geologic formations: the slow accumulation of deposited sediment into a stratum, is not distinguishable from growth in its widest acceptation. And if we go back to the genesis of celestial bodies, assuming them to have arisen by Evolution, these, too, must have gradually passed into their concrete shapes through processes of growth. Growth is indeed a concomitant of Evolution; and if Evolution of one kind or other is universal, growth is universal—universal, that is, in the sense that all aggregates display it in some way at some period.

The essential community of nature between organic growth and inorganic growth, is, however, most clearly seen on observing that they both result in the same way. The segregation of different kinds of detritus from each other, as well as from the water carrying them, and their aggregation into distinct strata, is but an instance of a universal tendency towards the union of like units and the parting of unlike units (*First Principles*, § 123). The deposit of a crystal from a solution, is a differentiation of the previously mixed atoms; and an integration of one class of atoms into a solid body, and the other class into a liquid solvent. Is not the growth of an organism a substantially similar process? Around a plant there exist certain elements that are like the elements which form its substance; and its increase of size is effected by continually integrating these surrounding like elements with itself. Nor does the animal fundamentally differ in this respect from the plant or the crystal. Its food is a portion of the environing matter, that contains some compound atoms like some of the compound atoms constituting its tissues; and either through simple imbibition or through digestion, the animal eventually integrates with itself, units like those of which it is built up, and leaves behind the unlike units. To prevent misconception, it may be well to point out that growth, as here defined, must be distinguished from certain apparent and real augmentations of bulk which simulate it. Thus, the long, white potato-shoots thrown out in the dark, are produced at the expense of the substances which the tuber contains: they illustrate not the accumulation of organic matter, but simply its re-arrangement. Certain animal-embryos, again, during their early stages, increase considerably in size without assimilating any solids from the environment; and they do this by absorbing the surrounding water. Even in the highest organisms, as in children, there appears sometimes to occur a rapid gain in dimensions, that does not truly measure the added quantity of organic matter; but is in part due to changes analogous to those just named. Alterations of this kind must not be confounded with that growth, properly so called, of which we have here to treat.

The next general fact to be noted respecting organic growth, is, that it has limits. Here there appears to be a distinction between organic and inorganic growth; but this distinction is by no means definite. Though that aggregation of inanimate matter which simple attraction produces, may go on without end; yet there appears to be an end to that more definite kind of aggregation which results from polar attraction. Different elements and compounds, habitually form crystals more or less unlike in their sizes; and each seems to have a size that is not usually exceeded without a tendency arising to form new crystals rather than to increase the old. On looking at the organic kingdom as a whole, we see that the limits between which growth ranges, are very wide apart. At the one extreme, we have monads so minute as to be rendered but imperfectly visible by microscopes of the highest power; and at the other extreme, we have trees of 300 feet high, and animals of 100 feet long. It is true that though in one sense this contrast may be legitimately drawn, yet in another sense it may not; since these largest organisms are made by the combination of units that are individually like the smallest. A single plant of the genus *Protococcus*, is of the same structure as one of the many cells united together to form the thallus of some higher Alga, or the leaf of a phænogam. Each separate shoot of a phænogam is usually the bearer of many leaves. And a tree is an assemblage of numerous united shoots. One of these great teleophytes is thus an aggregate of aggregates of aggregates of units, which severally resemble protophytes in their sizes and structures; and a like building up is traceable throughout a considerable part of the animal kingdom. Even, however, when we bear in mind this qualification, and make our comparisons between organisms of the same degree of composition, we still find the limit of growth to have a great range. The smallest branched flowering plant is extremely insignificant by the side of a forest tree; and there is an enormous difference in bulk between the least and the greatest mammal. But on comparing members of the same species, we discover the limit of growth to be much less variable. Among the *Protozoa* and *Protophyta*, each kind has a tolerably constant adult size; and among the most complex organisms, the differences between those of the same kind that have reached maturity, are usually not very great. The compound plants do, indeed, sometimes present marked contrasts between stunted and well-grown individuals; but the higher animals diverge but inconsiderably from the average standards of their species.

On surveying the facts with a view of empirically generalizing the causes of these differences, we are soon made aware that by variously combining and conflicting with each other, these causes produce great irregularities of result. It becomes manifest that no one of them can be traced to its consequences, unqualified by the rest. Hence the several statements contained in the following paragraphs, must be taken as subject to mutual modification.

Let us consider first, the connexion between degree of growth and complexity of structure. This connexion being involved with many others, becomes apparent only on so averaging the comparisons, as to eliminate differences among the rest. Nor does it hold at all where the conditions are radically dissimilar; as between plants and animals. But bearing in mind these qualifications, we shall see that organization has a determining influence on increase of mass. Of plants the lowest, classed as Thallogens, usually attain no considerable size. Lichens, Algæ, and Fungi, count among their numbers but few bulky species: the largest, such as certain Algæ found in antartic seas, not serving greatly to raise the average. Though among Acrogens there are some, as the Tree-ferns, which attain a considerable height, the majority are but of humble growth. The Endogens, including at one extreme small grasses and at the other tall palms, show us an average and a maximum greater than that reached by the Acrogens. And the Endogens are exceeded by the Exogens; among which are found the monarchs of the vegetal kingdom. Passing to animals, we meet the fact that the size attained by *Vertebrata* is usually much greater than the size attained by *Invertebrata.* Of invertebrate animals the smallest, classed as *Protozoa,* are also the simplest; and the largest, belonging to the *Annulosa* and *Mollusca,* are among the most complex of their respective types. Of vertebrate animals we see that the greatest are Mammals; and that though, in past epochs, there were reptiles of vast bulk, their bulk did not equal that of the whale. Between reptiles and birds, and between land-vertebrates and aquatic vertebrates, the relation does not hold: the conditions of existence being in these cases widely different. But among fishes as a class, and among reptiles as a class, it is observable that, speaking generally, the larger species are framed on the higher types. The critical reader, who has mentally checked these statements in passing them, has doubtless already seen that this relation is not a dependence of organization on growth, but a dependence of growth on organization. The majority of Exogens are smaller than some Endogens; many Endogens are exceeded in size by certain Acrogens; and even among Thallogens, the least developed of plants, there are kinds of a size which many plants of the highest order do not reach. Similarly among animals: there are plenty of Crustaceans less than *Actiniæ;* numerous reptiles are smaller than some fish; the majority of mammals are inferior in bulk to the largest reptiles; and in the contrast between a mouse and a well-grown *Medusa,* we see a creature that is elevated in the scale of organization, exceeded in mass by one that is extremely degraded. Clearly then, it cannot be held that high organization is habitually accompanied by great size. The proposition here illustrated is the converse one, that great size is habitually accompanied by high organization. The conspicuous fact that the largest species of both animals and vegetals belong to the highest classes; and that throughout their various sub-classes the higher usually contain the more bulky forms; shows this connexion as clearly as we can expect it to be shown, amid so many modifying causes and conditions.

The relation between growth and supply of available nutriment, is too familiar a relation to need proving. There are, however, some aspects of it that must be contemplated before its implications can be fully appreciated. Among plants, which are all constantly in contact with the gaseous, liquid, and solid matters to be incorporated with their tissues; and which, in the same locality, receive not very unlike amounts of light and heat; differences in the supplies of available nutriment, have but a subordinate connexion with differences of growth. Though in a cluster of herbs springing up from the seeds let fall by a parent, the greater size of some than of others is doubtless due to better nutrition, consequent on accidental advantages; yet no such interpretation can be given of the contrast in size between these herbs and an adjacent tree. Other conditions here come into play: one of the most important probably being, an absence in the one case, and presence in the other, of an ability to secrete such a quantity of ligneous fibre as will produce a stem capable of supporting a large growth. Among animals, however, which (excepting some *Entozoa*) differ from plants in this, that instead of bathing their surfaces, the matters they subsist on are dispersed, and have to be obtained; the relation between available food and growth, is shown with more regularity. The *Protozoa*, living on microscopic fragments of organic matter contained in the surrounding water, are unable, during their brief lives, to accumulate any considerable quantity of nutriment. Polypes and *Molluscoida*, having for food these scarcely visible members of the animal kingdom, are, though large compared with their prey, small as measured by other standards: even when aggregated into groups of many individuals, which severally catch food for the common weal, they are often so inconspicuous as readily to be passed over by the unobservant. And if from this point upwards we survey the successive grades of animals, it becomes manifest that, in proportion as the size is great, the masses of nutriment are either large, or, what is practically the same thing, are so abundant and so grouped as that large quantities may be readily taken in. Though, for example, the greatest of mammals, the arctic whale, feeds on such comparatively small creatures as the acalephes and molluscs floating in the seas it inhabits, its method of gulping in whole shoals of them and filtering away the accompanying water, enables it to secure great quantities of food. We may then with safety say, that, other things equal, the growth of an animal depends on the abundance and sizes of the masses of nutriment which its powers enable it to appropriate. Perhaps it may be needful to add that, in interpreting this statement, the number of competitors must be taken into account. Clearly, not the absolute, but the relative, abundance of fit food is the point; and this relative abundance very much depends on how many individuals are competing for the food. Thus all who have had experience of fishing in Highland lochs, know that where the trout are numerous they are small, and that where they are comparatively large they are comparatively few.

What is the relation between growth and expenditure of force? is a question which next presents itself. Though there is reason to believe such a relation exists, it is not very readily traced: involved as it is with so many other relations. Some contrasts, however, may be pointed out, that appear to give evidence of it. Passing over the vegetal kingdom, throughout which the expenditure of force is too small to allow of such a relation being visible; let us seek in the animal kingdom, some case where classes otherwise allied, are contrasted in their locomotive activities. Let us compare birds on the one hand, with reptiles and mammals on the other. It is an accepted doctrine that birds are organized on a type closely allied to the reptilian type, but superior to it; and though in many respects the organization of birds is inferior to that of mammals, yet in other respects, as in the greater heterogeneity and integration of the skeleton, the more complex development of the respiratory system, and the higher temperature of the blood, it may be held that birds stand above mammals. Hence were growth dependent only on organization, we might infer that the limit of growth among birds should not be much short of that among mammals; and that the bird-type should admit of a larger growth than the reptile-type. Again, we see no manifest disadvantages under which birds labour in obtaining food, but from which reptiles and mammals are free. On the contrary, birds are able to get at food that is fixed beyond the reach of reptiles and mammals; and can catch food that is too swift of movement to be ordinarily caught by reptiles and mammals. Nevertheless, the limit of growth in birds, falls far below that reached by reptiles and mammals. With what other contrast between these classes, is this contrast connected? May we not suspect that it is connected with the contrast between their amounts of locomotive exertion? Whereas mammals (excepting bats, which are small), are during all their movements supported by solid surfaces or dense liquids; and whereas reptiles (excepting the ancient pterodactyles, which were not very large), are similarly restricted in their spheres of movement; the majority of birds move more or less habitually through a rare medium, in which they cannot support themselves without relatively great efforts. The conclusion that there exists this inverse ratio between growth and expenditure of force, is enforced by the significant fact, that those members of the class *Aves*, as the *Dinornis* and *Epiornis*, which approached in size to the larger *Mammalia* and *Reptilia*, were creatures incapable of flight—creatures which did not expend this excess of force in locomotion. Further evidence that there is an antagonism between the increase of bulk and the quantity of motion evolved by an organism, is supplied by the general experience, that human beings and domestic animals, when overworked while growing, are prevented from attaining the ordinary dimensions.

One other general truth concerning degrees of growth, must be set down. It is a rule, having exceptions of no great importance, that large organisms commence their separate existences as masses of organic matter more or less considerable in size, and commonly with organizations more or less advanced; and that throughout each organic sub-kingdom, there is a certain general, though irregular, relation between the initial and the final bulks. Vegetals exhibit this relation much less clearly and constantly than animals. Yet though, among the plants that begin life as minute spores, there are some which, under their special conditions, grow to considerable sizes, the immense majority of them remain small. While, conversely, the great Endogens and Exogens, when thrown off from their parents, have already the formed organs of young plants, to which are attached large stores of highly nutritive matter. That is to say, where the young plant consists merely of a centre of development, the ultimate growth is commonly insignificant; but where the growth is to become great, there exists to start with, a well-developed embryo and a stock of assimilable matter. Throughout the animal kingdom, this relation is tolerably regular. Save among classes that escape the ordinary requirements of animal life, small germs or eggs do not give rise to bulky creatures. Where great bulk is to be reached, the young proceeds from an egg of considerable bulk, or is born of considerable bulk ready-organized and partially active. In the class fishes, for instance, a certain average proportion obtains between the sizes of the ova and the sizes of the adult indidividuals ; and among the highest fishes, as sharks, the eggs are comparatively few and comparatively large. Reptiles have eggs that are smaller in number, and relatively greater in mass, than those of fishes; and throughout this class, too, there is a general ratio between the bulk of the egg and the bulk of the adult creature. As a group, birds show us a further limitation in the number of their eggs, and a further increase in their relative sizes; and from the minute eggs of the humming-bird up to the immense ones of the *Epiornis*, holding several quarts, we see that, speaking generally, the greater the eggs, the greater the birds. Finally, among mammals (omitting the marsupials) the young are born, not only of comparatively large sizes, but with advanced organizations; and throughout this sub-division of the vertebrata, as throughout the others, there is a manifest connexion between the sizes at birth and the sizes at maturity. As having a kindred meaning, there must finally be noted the fact, that the young of these highest animals, besides starting in life with bodies of considerable sizes, almost fully organized, are, during subsequent periods of greater or less length, supplied with nutriment—in birds by feeding, and in mammals by suckling and afterwards by feeding. That is to say, beyond the mass and organization directly bequeathed, a bird or mammal obtains a further large mass at but little cost to itself.

Were an exhaustive treatment of the topic intended, it would be needful to give a paragraph to each of the many incidental circumstances by which growth may be aided or restricted. Such facts as that an entozoon is limited by the size of the creature, or even the organ, in which it thrives; that an epizoon, though getting abundant nutriment without appreciable exertion, is restricted to that small bulk at which it escapes ready detection by the animal it infests; that sometimes, as in the weazel, smallness is a condition to successful pursuit of the animals preyed upon; and that at other times, the advantage of resembling certain other creatures, and so deceiving enemies or prey, becomes an indirect cause of restricted size. But the present purpose is simply to set down those most general relations between growth and other organic phenomena, which induction leads us to. Having done this, let us go on to inquire whether these general relations can be deductively established.

§ 44. That there must exist a certain dependence of growth on organization, may be shown *à priori*. When we consider the phenomena of Life, either by themselves or in their relations to surrounding phenomena, we see that, other things equal, the larger the aggregate the greater is the needful complexity of structure.

In plants, even of the highest type, there is a comparatively small mutual dependence of parts: a gathered flower-bud will unfold and flourish for days, if its stem be immersed in water; and a shoot cut off from its parent-tree and stuck in the ground, will grow. The respective parts having vital activities that are not widely unlike, it is possible for great bulk to be reached without that structural complexity required for combining the actions of parts. Even here, however, we see that for the attainment of great bulk, there requires such a degree of organization as shall co-ordinate the functions of roots and branches—we see that such a size as is reached by trees, is not possible without an efficient vascular system enabling the remote organs to utilize each other's products. And we see that such a co-existence of large growth with low organization, as occurs in some of the marine *Algæ*, occurs where the conditions of existence do not necessitate any considerable mutual dependence of parts—where the near approach of the plant to its medium in specific gravity, precludes the need of a well-developed stem, and where all the materials of growth being derived from the water by each portion of the thallus, there requires no apparatus for transferring materials from part to part. Among animals which, with but few exceptions, are, by the conditions of their existence, required to take in nutriment through one specialized part of the body, it is clear that there must be a means whereby other parts of the body, to be supported by this nutriment, must have it conveyed to them. It is clear that for an equally efficient maintenance of their nutrition, the parts of a large mass must have a more elaborate propelling and conducting apparatus; and that in proportion as these parts undergo greater waste, a yet higher development of the vascular system is necessitated. Similarly with the pre-requisites to those mechanical motions which animals are required to perform. The parts of a mass cannot be made to move, and have their movements so co-ordinated as to produce locomotive and other actions, without certain structural arrangements; and, other things equal, a given amount of such activity requires more involved structural arrangements in a large mass than in a small one. There must at least be a co-ordinating apparatus presenting greater contrasts in its central and peripheral parts.

The qualified dependence of growth on organization, is equally implied when we study it in connexion with that adjustment of inner to outer relations which constitutes Life. In plants this is not conspicuous, because the adjustment of inner to outer relations is but small. Still, it is visible in the fact that the condition on which only a plant can grow to a great size, is, that it shall, by the development of a massive trunk, present inner relations of forces fitted to counterbalance those outer relations of forces, which tend continually and occasionally to overthrow it; and this formation of a core of regularly-arranged woody fibres, is an advance in organization. Throughout the animal kingdom, this connexion of phenomena is manifest. To obtain materials for growth; to avoid injuries, which interfere with growth; and to escape those enemies which bring growth to a sudden end; implies in the organism, the means of fitting its movements to meet numerous external co-existences and sequences—

implies such various structural arrangements as shall make possible these variously-adapted actions. It cannot be questioned that, everything else remaining constant, a more complex animal, capable of adjusting its conduct to a greater number of surrounding contingences, will be the better able to secure food and evade damage, and so to increase bulk. And evidently, without any qualification, we may say that a large animal, living under such complex conditions of existence as everywhere obtain, is not possible without comparatively high organization.

While, then, this relation is traversed and obscured by sundry other relations, it cannot but exist. Deductively we see that it must be modified, as inductively we saw that it is modified, by the circumstances amid which each kind of organism is placed; but that it is always a factor in determining the result.

§ 45. That growth is, *cæteris paribus*, dependent on the supply of assimilable matter, is a proposition so continually illustrated by special experience, as well as so obvious from general experience, that it would scarcely need stating, were it not requisite to notice the qualifications with which it must be taken.

The materials which each organism requires for building itself up, are not of one kind, but of several kinds. As a vehicle for transferring matter through their structures, all organisms require water as well as solid constituents; and however abundant the solid constituents, there can be no growth in the absence of water. Among the solids supplied, there must be a proportion ranging within certain limits. A plant round which carbonic acid, water, and ammonia exist in the right quantities, may yet be arrested in its growth by a deficiency of silica. The total absence of lime from its food, may stop the formation of a mammal's skeleton: thus dwarfing, if not eventually destroying, the mammal; and this, no matter what quantities of other needful colloids and crystalloids are furnished.

Again, the truth that, other things equal, growth varies according to the supply of nutriment, has to be qualified by the condition, that the supply shall not exceed the ability to appropriate it. In the vegetal kingdom, the assimilating surface being external, and admitting of rapid expansion by the formation of new roots, shoots, and leaves, the effect of this limitation is not conspicuous: by artificially supplying plants with those materials which they have usually the most difficulty in obtaining, we can greatly facilitate their growth; and so can produce striking differences of size in the same species. Even here, however, the effect is confined within the limits of the ability to appropriate; since in the absence of that solar light and heat, by the help of which the chief appropriation is carried on, the additional materials of growth are useless. In the animal kingdom this restriction is rigorous. The absorbent surface being, in the great majority of cases, internal; having a comparatively small area, which cannot be greatly enlarged without re-construction of the whole body; and being in connexion with a vascular system, which must also be re-constructed before any considerable increase of nutriment can be made available; it is clear that beyond a certain point, very soon reached, increase of nutriment will not cause increase of growth. On the contrary, if the quantity of nutriment taken in, is greatly beyond the absorbent power, the excess, becoming an obstacle to the regular working of the organism, may retard growth rather than advance it.

While then it is certain, *à priori*, that there cannot be growth in the absence of such substances as those of which an organism consists; and while it is equally certain that the amount of growth must primarily be governed by the supply of these substances; it is not less certain that extra supply will not produce extra growth, beyond a point very soon reached. Deduction shows to be necessary, as induction makes familiar, the truths that, the value of food for purposes of growth depends not on the quantity of the various organizable materials it contains, but on the quantity of the material most needed; that given a right proportion of materials, the pre-existing structure of the organism limits their availability; and that the higher the structure, the sooner is this limit reached.

§ 46. But why should the growth of every organism be finally arrested? Though the rate of increase may, in each case, be necessarily restricted within a narrow range of variation—though the increment that is possible in a given time, cannot exceed a certain amount; yet why should the increments decrease, and finally become insensible? Why should not all organisms, when supplied with sufficient materials, continue to grow as long as they live? To find an answer to this question, we must first revert to the nature and functions of organic matter.

In the first three chapters of Part I., it was shown that plants and animals mainly consist of substances in states of unstable equilibrium—substances which have been raised to this unstable equilibrium by the expenditure of the forces we know as solar radiations, and which give out these forces in other forms, on falling into states of stable equilibrium. Leaving out the water, which serves as a vehicle for these materials and a medium for their changes; and excluding those mineral matters that play either passive or subsidiary parts; organisms are built up of compounds which are stores of force. Those complex colloids and crystalloids which, as united together, form organized bodies, are the same colloids and crystalloids which give out, on their decomposition, the forces expended by organized bodies. Thus these nitrogeneous and carbonaceous substances, being at once the materials for organic growth and the sources of organic force; it results that as much of them as is used up for the genesis of force, is taken away from the means of growth; and as much as is economized by diminishing the genesis of force, is available for growth. Given that limited quantity of nutritive matter which the pre-existing structure of an organism enables it to absorb; and it is a necessary corollary from the persistence of force, that the matter accumulated as growth, cannot exceed that surplus which remains undecomposed, after the production of the required amounts of sensible and insensible motion. This, which would be rigorously true under all conditions, if exactly the same substances were used in exactly the same proportions, for the production of force and for the formation of tissue, requires, however, to be taken with the qualification, that some of the force-evolving substances are not constituents of tissue; and that thus, there may be a genesis of force which is not at the expense of potential growth. But since organisms (or at least animal organisms, with which we are here chiefly concerned,) have a certain power of selective absorption, which, partially in an individual and more completely in a race, adapts the proportions of the substances absorbed to the needs of the system; then if a certain habitual expenditure of force, leads to a certain habitual absorption of force-evolving matters that are not available for growth; and if, were there less need for such matters, the ability to absorb matters available for growth would be increased to an equivalent extent; it follows that the antagonism described, does, in the long run, hold even without this qualification. Hence, growth is substantially equivalent to the absorbed nutriment, minus the nutriment used up in action.

This, however, is no answer to the question—why has individual growth a limit? The antagonism described, does not manifestly account for the fact, that in every domestic animal the increments of growth bear continually decreasing ratios to the mass, and finally come to an end. Nevertheless, it is demonstrable that the excess of absorbed over expended nutriment, must, other things equal, become less as the size of the animal becomes greater. In similarly-shaped bodies, the masses vary as the cubes of the dimensions; whereas the strengths vary as the squares of the dimensions. See here the solution of the problem. Supposing a creature which a year ago was one foot high, has now become two feet high, while it is unchanged in proportions and structure; what are the necessary concomitant changes that have taken place in it? It is eight times as heavy; that is to say, it has to resist eight times the strain which gravitation puts on its structure; and in producing, as well as in arresting, every one of its movements, it has to overcome eight times the inertia. Meanwhile, the muscles and bones have severally increased their contractile and resisting powers in proportion to the areas of their transverse sections; and hence are severally but four times as strong as they were. Thus, while the creature has doubled in height, and while its ability to overcome forces has quadrupled, the forces it has to overcome have grown eight times as great. Hence, to raise its body through a given space, its muscles have to be contracted with twice the intensity, at a double cost of matter expended. This necessity will be seen still more clearly if we leave out the motor apparatus, and consider only the forces required and the means of supplying them. For since, in similar bodies, the areas vary as the squares of the dimensions, and the masses vary as the cubes; it follows that the absorbing surface has become four times as great, while the weight to be moved by the matter absorbed has become eight times as great. If then, a year ago, the absorbing surface could take up twice as much nutriment as was needed for expenditure, thus leaving one-half for growth, it is now able only just to meet expenditure, and can provide nothing for growth. However great the excess of assimilation over waste, may be during the early life of an active organism, we see that because a series of numbers increasing as the cubes, overtakes a series increasing as the squares, even though starting from a much smaller number, there must be reached, if the organism lives long enough, a point at which the surplus assimilation is brought down to nothing—a point at which expenditure balances nutrition—a state of moving equilibrium. This, however, though the chief, is not the sole, varying relation between degrees of growth and amounts of expended force. There are two more; one of which conspires with the last, while the other conflicts with it. Consider in the first place, the cost at which nutriment is distributed through the body, and effete matters removed from it. Each increment of growth being added at the periphery of the organism, the force expended in the transfer of matter must increase in a rapid progression—a progression more rapid than that of the mass. But as the dynamic expense of distribution is small compared with the dynamic value of the materials distributed, this item in the calculation is unimportant. Now consider, in the second place, the changing proportion between production and loss of heat. In similar organisms, the quantities of heat generated by similar actions going on throughout their substance, must increase as the masses, or as the cubes of the dimensions. Meanwhile, the surfaces from which loss of heat by radiation takes place, increase only as the squares of the dimensions. Though the loss of heat does not therefore increase only as the squares of the dimensions, it certainly increases at a smaller rate than the cubes. And to the extent that augmentation of mass results in a greater retention of heat, it effects an economization of force. This advantage is not, however, so important as at first appears. Organic heat is a concomitant of organic action, and is so abundantly produced during action, that the loss of it is then of no consequence: indeed the loss is often not rapid enough to keep the supply from rising to an inconvenient excess. It is only in respect of that maintenance of heat which is needful during quiescence, that large organisms have an advantage over small ones in this relatively diminished loss. Thus these two subsidiary relations between degrees of growth and amounts of expended force, being in antagonism with each other, we may conclude that their differential result does not greatly modify the result of the chief relation previously set forth.

Any one who proceeds to test this deduction, will find some seeming incongruities between it and certain facts inductively established. Lest these should mislead him, it will be well to explain them. Throughout the vegetal kingdom, he may remark that there is no limit of growth except what death entails. Passing over a large proportion of plants which never exceed a comparatively small size, because they wholly or partially die down at the end of the year; and pointing to trees that annually send forth new shoots, even when their trunks are hollowed out by decay; he may ask—How does growth happen here to be unlimited? The answer is, that plants are only accumulators; they are in no appreciable degree expenders. As they do not undergo a waste which increases as the cubes of the dimensions, while assimilation increases as their squares; there is no reason why their growth should be arrested by the equilibration of assimilation and waste. Again, should he look among animals for an exact correspondence between the decreasing increments of growth as ascertained by observation and as determined by deduction, he will not find it. And there are sufficient reasons why the correspondence cannot be more than approximate. Besides the fact above noted, that there are other varying relations which complicate the chief one, he must bear in mind that the bodies compared are not truly similar: the proportions of trunk to limbs and trunk to head, vary considerably. The comparison is still more seriously vitiated by the inconstant ratio between the constituents of which the body is composed. In the flesh of adult mammalia, water forms from 68 to 71 per cent., organic substance from 24 to 28 per cent., and inorganic substance from 3 to 5 per cent.; whereas in the fœtal state, the water amounts to 87 per cent., and the solid organic constituents to only 11 per cent. Clearly this change from a state in which the force-evolving matter forms one tenth of the whole, to a state in which it forms two and a half tenths, must greatly interfere with the parallelism between the actual and the theoretical progression. Yet another difficulty may come under his notice. The crocodile is said to grow as long as it lives; and there appears reason to think that some predaceous fishes, such as the pike, do the same. That these animals of comparatively high organization, have no definite limits of growth, is, however, an exceptional fact due to the exceptional non-fulfilment of those conditions which entail limitation. What kind of life does a crocodile lead? It is a cold-blooded, or almost cold-blooded, creature; that is, it expends very little for the maintenance of heat. It is habitually inert: not chasing prey, but lying in wait for it; and undergoes considerable exertion only during its occasional brief contests with prey. Such other exertion as is, at intervals, needful for moving from place to place, is rendered small by the small difference between the animal's specific gravity and that of water. Thus the crocodile expends in muscular action, an amount of force that is insignificant compared with the force commonly expended by land-animals. Hence its habitual assimilation is diminished much less than usual by habitual waste; and beginning with an excessive disproportion between the two, it is quite possible for the one never quite to lose its advance over the other while life continues. On looking closer into such cases as this and that of the pike, which is similarly cold-blooded, similarly lies in wait, and is similarly able to obtain larger and larger kinds of prey as it increases in size; we discover a further reason for this absence of a definite limit. The mechanical causes necessitating a limit, are here only partially in action. For a creature living in a medium of nearly the same density as its body, has not constantly to overcome that gravitative force which is the chief resistance to be met by terrestrial animals: it has not to expend for this purpose, a muscular power that is large at the outset, and increases as the cubes of its dimensions. The only force increasing as the cubes of its dimensions, which it has thus to overcome, is the inertia of its parts. The exceptional continuance of growth observed in creatures so circumstanced, is therefore perfectly explicable.

§ 47. Obviously this antagonism between accumulation and expenditure, must be a leading cause of the contrasts in size between allied organisms that are in many respects similarly conditioned. The life followed by each kind of animal, is one involving a certain average amount of exertion for the obtainment of a given amount of nutriment—an exertion, part of which goes to the gathering or catching of food, part to the tearing and mastication of it, and part to the after-processes requisite for separating the nutritive atoms—an exertion which therefore varies according as the food is abundant or scarce, fixed or moving, according as it is mechanically easy or difficult to deal with when secured, and according as it is, or is not, readily soluble. Hence, while among animals of the same species having the same mode of life, there will be a tolerably constant ratio between accumulation and expenditure, and therefore a tolerably constant limit of growth; there is every reason to expect that different species, following different modes of life, will have unlike ratios between accumulation and expenditure, and therefore unlike limits of growth.

Though the facts as inductively established, show a general harmony with this deduction, we cannot usually trace this harmony in any specific way; since the conflicting and conspiring causes which affect growth are so numerous. The only contrast which seems fairly to the point, is the before-named one between the vertebrates which fly, and the most nearly-allied vertebrates which do not fly: the differences in degrees of organization and relations to food, being not such as seriously to affect the comparison. If it be admitted that birds habitually expend more force than mammals and reptiles, then it will follow *à priori*, that, other things being tolerably equal, they should have a lower limit of growth than mammals and reptiles; and this we know to be the fact *à posteriori*.

§ 48. One of the chief causes, if not the chief cause, of the differences between the sizes of organisms, has yet to be considered. We are introduced to it by pushing the above inquiry a little further. Small animals have been shown to possess an advantage over large ones, in the greater ratio which, other things equal, assimilation bears to expenditure; and we have seen that hence, small animals in becoming large ones, gradually lose that surplus of assimilative power which they had, and eventually cannot assimilate more than is required to balance waste. But how come these animals while young and small, to have surplus assimilative powers? Have all animals equal surplus of assimilative powers? And if not, how far do differences between the surpluses determine differences between the limits of growth? We shall find in the answers to these questions, the interpretation of many marked contrasts in growth that are not due to any of the causes above assigned. For example, an ox immensely exceeds a sheep in mass. Yet the two live from generation to generation in the same fields, eat the same grass and turnips, obtain these aliments with the same small expenditure of force, and differ scarcely at all in their degrees of organization. Whence arises, then, their striking unlikeness of bulk?

We noted when studying the phenomena of growth inductively, that organisms of the larger and higher types, commence their separate existences, as masses of organic matter having tolerable magnitudes. Speaking generally, we saw that throughout each organic sub-kingdom, the acquirement of great bulk occurs only where the incipient bulk and organization are considerable; and that they are the more considerable in proportion to the complexity of the life which the organism is to lead.

The deductive interpretation of this induction may best be commenced by an analogy. A street orange-vendor makes but a trifling profit on each transaction; and unless more than ordinarily fortunate, he is unable to realize during the day a larger amount than will meet his wants: leaving him to start on the morrow in the same condition as before. The trade of the huxter in ounces of tea and half-pounds of sugar, is one similarly entailing much labour for small returns. Beginning with a capital of a few pounds, it is impossible for him to have a shop large enough, or goods sufficiently abundant and various, to permit an extensive business: he must be content with the half-pence and pence which he makes by little sales to poor people; and if, avoiding bad debts, he is able by strict economy to accumulate anything, it can be but a trifle. A large retail trader is obliged to lay out much money in fitting up an adequate establishment; he must invest a still greater sum in stock; and he must have a further floating capital to meet the charges that fall due before his returns come in. Setting out, however, with means enough for these purposes, he is able to make numerous and comparatively large sales; and so to get greater and more numerous increments of profit. Similarly, to get returns in thousands, merchants and manufacturers must make their investments in tens of thousands. In brief, the rate at which a man's wealth accumulates, is measured by the surplus of income over expenditure; and this, save in exceptionably favourable cases, is determined by the capital with which he begins business. Now applying the analogy, we may trace in the transactions of an organism, the same three ultimate elements. There is the expenditure required for the obtainment and digestion of food; there is the gross return in the shape of nutriment assimilated, or fit for assimilation; and there is the difference between this gross return of nutriment and the nutriment that was used up in the labour of securing it—a difference which may be a profit or a loss. Clearly, however, a surplus implies that the force expended is less than the force latent in the assimilated food. Clearly, too, the increment of growth is limited to the amount of this surplus of income over expenditure; so that large growth implies both that the excess of nutrition over waste shall be relatively considerable, and that the waste and nutrition shall be on extensive scales.

And clearly, the ability of an organism to expend largely and assimilate largely, so as to make a large surplus, presupposes a large physiological capital, in the shape of organic matter more or less complete in its structural arrangements.

Throughout the vegetal kingdom, the illustrations of this truth are not conspicuous and regular: the obvious reason being, that since plants are accumulators and in so small a degree expenders, the premises of the above argument are but very partially fulfilled. The food of plants (excepting Fungi and certain parasites) being in a great measure the same for all, and bathing all so that it can be absorbed without effort, their vital processes result almost entirely in profit. Once fairly rooted in a fit place, a plant may thus from the outset add its entire returns to capital; and may soon be able to carry on its processes on a large scale, though it does not at first do so. When, however, plants are expenders, namely, during their germination and first stages of growth, their degrees of growth *are* determined by their amounts of vital capital. It is because the young tree commences life with a ready-formed embryo and store of food sufficient to last for some time, that it is enabled to strike root and lift its head above the surrounding herbage. Throughout the animal kingdom, however, the necessity of this relation is everywhere obvious. The small carnivore preying on small herbivores, can increase in size only by small increments: its organization unfitting it to digest larger creatures, even if it can kill them, it cannot profit by amounts of nutriment exceeding a narrow limit; and its possible increments of growth being small to set out with, and rapidly decreasing, must come to an end before any considerable size is attained. Manifestly the young lion, born of tolerable bulk, suckled until much bigger, and fed until half-grown, is enabled by the power and organization which he thus gets gratis, to catch and kill animals of size enough to give him the large supply of nutriment needed to meet his large expenditure, and yet leave a large surplus for growth. Thus then is explained the above-named contrast between the ox and the sheep. A calf and a lamb commence their physiological transactions on widely different scales; their first increments of growth are similarly contrasted in their amounts; and the two diminishing series of such increments, end at similarly-contrasted limits.

§ 49. Such are the several conditions by which the phenomena of growth are governed. Conspiring and conflicting in endless different ways and degrees, they in every case qualify more or less differently each other's effects. Hence it happens that we are obliged to state each generalization as true on the average, or to make the proviso—other things equal.

Understood, in this qualified form, our conclusions are these. First, that growth being an integration with the organism, of such environing matters as are of like nature with the matters composing the organism, its growth is dependent on the available supply of such matters: this is alike a truth established by experience, and an inference from the truth given in our forms of thought (*First Principles*, § 67). Second, that the available supply of assimilable matter being the same, and other conditions not dissimilar, the degree of growth varies according to the surplus of nutrition over expenditure—a generalization which is illustrated in some of the broader contrasts between different divisions of organisms, and is a direct corollary from the persistence of force. Third, that in the same organism, the surplus of nutrition over expenditure is a variable quantity; and that growth is unlimited or has a definite limit, according as the surplus does or does not progressively decrease. This proposition we found on the one hand exemplified by the unceasing growth of organisms that do not expend force; by the growth, slowly diminishing but never completely ceasing, of organisms that expend comparatively little force; and by the definitely limited growth of organisms that expend much force; and on the other hand, we found it to follow from a certain relative increase of expenditure that necessarily accompanies increase of bulk, and to be therefore an indirect corollary from the persistence of force. Fourth, that among organisms which are large expenders of force, the size ultimately attained is, other things equal, determined by the initial size: in proof of which conclusion we have abundant facts, as well as the *à priori* necessity that the sum-totals of analogous diminishing series, must depend upon the amounts of their initial terms. Fifth, that where the likeness of other circumstances permits a comparison, the possible extent of growth depends on the degree of organization: an inference testified to by the larger forms among the various divisions and sub-divisions of organisms; and inferable *à priori* from the conditions of existence.

# CHAPTER II.

## DEVELOPMENT.*

§ 50. CERTAIN general aspects of Development may be studied apart from any examination of internal structures. These fundamental contrasts between the modes of arrangement of parts, originating, as they do, the leading external distinctions among the various forms of organization, will be best dealt with at the outset. If all organisms have arisen by Evolution, it is of course not to be expected that such several modes of development can be absolutely demarcated: we may be sure of finding them united by transitional modes. But premising that a classification of modes can but approximately represent the facts, we shall find our general conceptions of Development aided by one.

*Development is primarily central.* All organic forms of which the entire history is known, set out with a symmetrical arrangement of parts round a centre. In organisms of the lowest grade, no other mode of arrangement is ever definitely established; and in the highest organisms, central development, though subordinate to another mode of development, continues to be habitually shown in the changes of

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* In ordinary speech, Development is often used as synonymous with Growth. It hence seems needful to say, that Development as here and hereafter used, means *increase of structure*, and not *increase of bulk*. It may be added, that the word Evolution, comprehending Growth as well as Development, is to be reserved for occasions when both are implied.

minute structure. Let us glance at these propositions in the concrete. Leaving out those Rhizopods which are wholly structureless, every plant and animal in its earliest stage, consists of a spherical sac, full of liquid containing organic matter, in which is suspended a nucleated cell, more or less distinct from the rest; and the first changes that occur in the germ thus constituted, are changes that take place round centres produced by division of the original centre. From this type of structure, the simplest organisms do not depart; or depart in no definite or conspicuous ways. Among plants, the *Uredo* and the several tribes of *Protococci* permanently maintain such a central distribution; while among animals, it is permanently maintained by creatures like the *Gregarina*, and in a different manner by the *Amœba*, *Actinophrys*, and their allies. In larger organisms, made up chiefly of units that are analogous in structure to these simplest organisms, the formation of units ever continues to take place round points or nuclei; though the arrangement of these units into groups and wholes may proceed after another method.

Central development may be distinguished into *unicentral* and *multicentral*; according as the product of the original germ, develops symmetrically round one centre, or develops without subordination to one centre—develops, that is, in subordination to many centres. Unicentral development, as displayed not in the formation of single cells but in the formation of aggregates, is not common. The animal kingdom shows it only in the small group named *Thalassicollæ*: inert, spherical masses of jelly, with scarcely any organization, which are found floating in southern seas. It is feebly represented in the vegetal kingdom by the *Volvox globator*. On the other hand, multicentral development, or development round insubordinate centres, is variously exemplified in both divisions of the organic world. It is exemplified in two distinct ways, according as the insubordination among the centres of development is partial or total.

We may most conveniently consider it under the heads hence arising.

Total insubordination among the centres of development, is shown where the units or cells, as fast as they are severally formed, part company and lead independent lives. This, in the vegetal kingdom, habitually occurs among the *Protophyta;* and in the animal kingdom, among the *Protozoa.* Partial insubordination is seen in those somewhat advanced organisms, that consist of units which, though they have not separated, have so little mutual dependence that the aggregate they form is irregular. Among plants, the Thallogens very generally exemplify this mode of development. Lichens, spreading with flat or corrugated edges in this or that direction, as the conditions determine, have no manifest co-ordination of parts. In the *Algæ,* the Nostocs similarly show us an unsymmetrical structure. Of *Fungi,* the sessile and creeping kinds display no further dependence of one part on another, than is implied by their cohesion. And even in such better-organized plants as the *Marchantia,* the general arrangement shows no reference to a directive centre. Among animals, many of the Sponges may be cited as being thus devoid of that co-ordination implied by symmetry: the Amœba-like units composing them, though they have some subordination to local centres, have no subordination to a general centre. To distinguish that kind of development in which the whole product of a germ coheres in one mass, from that kind of development in which it does not, Professor Huxley has introduced the words "*continuous*" and "*discontinuous;*" and these seem the best fitted for the purpose. Multicentral development, then, is divisible into continuous and discontinuous.

From central development we pass insensibly to that higher kind of development for which *axial* seems the most appropriate name. A tendency towards this is vaguely manifested almost everywhere. The great majority even of *Protophyta* and *Protozoa* have different longitudinal and transverse dimensions—have an obscure if not a distinct axial structure. The originally cellular units out of which higher organisms are mainly built up, usually pass into shapes that are subordinated to lines rather than to points. And in the higher organisms, considered as wholes, an arrangement of parts in relation to an axis is distinct and nearly universal. We see it in the superior orders of Thallogens; and in all the Acrogens, Endogens, and Exogens. With few exceptions the *Cœlenterata* clearly exhibit it; it is traceable, though less conspicuously, throughout the *Mollusca;* and the *Annulosa* and *Vertebrata* uniformly show it with perfect definiteness.

This kind of development, like the first kind, is of two orders. The whole germ-product may arrange itself round a single axis, or it may arrange itself round many axes; the structure may be *uniaxial* or *multiaxial.* Each division of the organic kingdom furnishes examples of both these orders. In such *Fungi* as exhibit axial development at all, we commonly see development round a single axis. Some of the *Algæ,* as the common tangle, show us this arrangement. And of the higher plants, many Endogens and small Exogens are uniaxial. Of animals, the advanced are without exception in this category. There is no known vertebrate in which the whole of the germ-product is not subordinated to a single axis. In the more fully-organized *Annulosa,* the like is almost universal; as it is also in the superior orders of *Mollusca.* Multiaxial development occurs in most of the plants we are familiar with—every branch of a shrub or tree being an independent axis. But while in the vegetal kingdom, multiaxial development prevails among the highest types; in the animal kingdom, it prevails only among the lowest types. It is extremely general, if not universal, among the *Cœlenterata;* it is characteristic of the *Molluscoida;* among Molluscs the compound Ascidians exhibit it; and it is seen, though under another form, in the inferior *Annulosa.*

Development that is axial, like development that is central, may be either continuous or discontinuous: the parts having different axes may continue united, or they may separate. Instances of each alternative are supplied by both plants and animals. Continuous, multiaxial development, is that which plants usually display; and need not be illustrated further than by reference to every garden. As cases of it in animals may be named, all the compound *Hydrozoa* and *Actinozoa;* and such molluscous forms as the *Botryllidæ.* Of multiaxial development that is discontinuous, a familiar instance among plants exists in the common strawberry. This sends out over the neighbouring surface, long slender shoots, bearing at their extremities buds that presently strike roots, and become new individuals; and these by and by lose their connexions with the original axis. Other plants there are that produce certain specialized buds called bulbils, which separating themselves and falling to the ground, grow into independent plants. Among animals the fresh-water polype very clearly shows this mode of development: the young polypes, budding out from its surface, severally arrange their parts around distinct axes, and eventually detaching themselves, lead separate lives, and produce other polypes after the same fashion. By some of the lower *Annulosa,* this multiplication of axes from an original axis, is carried on after a different manner: the string of segments spontaneously divides; and after further growth, division recurs in one or both of the halves. And in the *Aphides,* we have a still further modification of this process.

Grouping together its several modes as above delineated, we see that

$$\text{D\scriptsize EVELOPMENT \normalsize is}\left\{\begin{array}{l}\text{Central}\left\{\begin{array}{c}\text{Unicentral}\\ \text{or}\\ \text{Multicentral}\end{array}\right.\left\{\begin{array}{c}\text{Continuous}\\ \text{or}\\ \text{Discontinuous}\end{array}\right.\\ \quad\text{or}\\ \text{Axial}\left\{\begin{array}{c}\text{Uniaxial}\\ \text{or}\\ \text{Multiaxial}\end{array}\right.\left\{\begin{array}{c}\text{Continuous}\\ \text{or}\\ \text{Discontinuous}\end{array}\right.\end{array}\right.$$

Any one adequately acquainted with the facts, may readily raise objections to this arrangement. He may name forms which do not obviously come under any of these heads. He may point to plants that are for a time multicentral, but afterwards develop axially. And from lower types of animals, he may choose many in which the continuous and discontinuous modes are both displayed. But, as already hinted, an arrangement free from such anomalies must be impossible, if the various orders of organization have arisen by Evolution. The one above sketched out, is to be regarded as only a rough grouping of the facts, which helps us to a conception of them in their totality; and so regarded, it will be of service when we come to treat of Individuality and Reproduction.

§ 51. From these most general external aspects of organic development, let us now turn to its internal and more special aspects. When treating of Evolution as a universal process of things, a rude outline of the course of structural changes in organisms was given (*First Principles*, §§ 43, 55, 56). Here, however, it will be proper to describe these changes more fully.

The bud of any common plant in its earliest stage, consists of a small hemispherical or sub-conical projection. While it increases most rapidly at the apex, this presently develops on one side of its base, a smaller projection of like general shape with itself. Here is the rudiment of a leaf; which presently spreads more or less round the base of the central hemisphere or main axis. At the same time that the central hemisphere rises higher, this lateral prominence, also increasing, gives rise to subordinate prominences or lobes. These are the rudiments of stipules, where the leaves are stipulated. Meanwhile, towards the other side of the main axis, and somewhat higher up, another lateral prominence arising, marks the origin of a second leaf. By the time that the first leaf has produced another pair of lobes, and the second leaf has produced its primary pair, the central hemisphere, still increasing at its apex, exhibits the rudiment of a third leaf. Similarly throughout. While the germ of each succeeding leaf thus arises, the germs of the previous leaves, in the order of their priority, are changing their rude nodulated shapes into flattened-out expansions; which slowly put on those sharp outlines they show when unfolded. Thus from that extremely indefinite figure, a rounded lump, giving off from time to time lateral lumps, which severally becoming symmetrically lobed, gradually assume specific and involved forms, we pass little by little to that comparatively complex thing—a leaf-bearing shoot. Internally, a bud undergoes analogous changes. The layer of substance which forms the surface of the hemisphere, and in which these metamorphoses commence, consists of a transparent, irregularly-aggregated mass of cells and centres of growth, not formed into a tissue. Especially is this the case at the apex, where the vital activity is the greatest. Here the primitive cellular mass passes without any line of demarcation into the tissues that are developing from it. While, by continued cell-multiplication this layer increases, and doing so most rapidly at the apex thrusts outwards its lateral portions, these begin to exhibit differentiations. "Gradually," says Schleiden, "separate masses of cells, with a distinct and definite outline, appear in this chaos, and they cease to partake of the process of growth going on. At first the epidermis is separated, then the vascular bundles, later the parenchyma." Similarly with the lateral buds whence leaves arise. In the, at first, unorganized mass of cells constituting the rudimentary leaf, there are formed vascular bundles which eventually become the veins of the leaf; and gradually there appear also, though in ways that have not been specified, the parenchyma and the epithelium. Nor do we fail to find an essentially parallel set of changes, when we trace the histories of the individual cells. While the tissues they compose are separating, the cells are growing step by step more unlike. Some become flat, some polyhedral, some cylindrical, some prismatic, some spindle-shaped. These develop spiral fibres in their interiors; and those, net-works of fibres. Here a number of cells unite together to form a tube; and there they become solid by the internal deposition of woody or other matter. Through such changes, too numerous and involved to be here detailed, the originally uniform cells go on diverging and re-diverging, until there are produced various forms that seem to have very little in common.

The arm of a man makes its first appearance in as simple a way as does the shoot of a plant. According to Bischoff, it buds-out from the side of the embryo, as a little tongue-shaped projection, presenting no differences of parts; and it might serve for the rudiment of some one of the various other organs that also arise as buds. Continuing to lengthen, it presently becomes somewhat enlarged at its end; and is then described as a pedicle bearing a flattened, round-edged lump. This lump is the representative of the future hand; and the pedicle, of the future arm. By and by, at the edges of this flattened lump, there appear four clefts, dividing from each other the buds of the future fingers; and the hand as a whole grows a little more distinguishable from the arm. Up to this time, the pedicle has remained one continuous piece; but it now begins to show a bend at its centre, which indicates the division into arm and forearm. The distinctions thus rudely indicated, gradually increase: the fingers elongate and become jointed; and the proportions of all the parts, originally very unlike those of the complete limb, slowly approximate to them. During its bud-like stage, the rudimentary arm is nothing but a homogeneous mass of simple cells, without any arrangement. By the diverse changes they gradually undergo, these cells are transformed into bones, muscles, blood-vessels, and nerves. The extreme softness and delicacy of this primary cellular tissue, renders it difficult to trace the initial stages of these differentiations. In consequence of the colour of their contents, the blood-vessels are the first parts to become visible. Afterwards the cartilaginous parts, which are the bases of the future bones, become marked out by the denser aggregation of their constituent cells, and the production between these of a hyaline substance which unites them into a translucent mass. When first perceptible, the muscles are gelatinous, pale, yellowish, transparent, and indistinguishable from their tendons. The various other tissues of which the arm consists, beginning with very faintly-marked differences, become day by day more definite in their outlines and appearances. In like manner, the units composing these tissues, severally assume increasingly-specific characters. The fibres of muscle, at first made visible in the midst of their gelatinous matrix only by immersion in alcohol, grow more numerous and distinct; and by and by they begin to exhibit transverse stripes. The bone-cells put on by degrees their curious structure of branching canals. And so in their respective ways with the units of skin and the rest.

Thus in each of the organic sub-kingdoms, we see this change from an incoherent, indefinite homogeneity, to a coherent, definite heterogeneity, illustrated in a quadruple way. The originally-like units or cells, become unlike in various ways, and in ways more numerous and marked as the development goes on. The several tissues which these several classes of cells form by aggregation, grow little by little distinct from each other; and little by little put on those structural complexities, that arise from differentiations among their component units. In the shoot, as in the limb, the external form, originally very simple, and having much in common with countless simple forms, organic and inorganic, gradually acquires an increasing complexity, and an increasing unlikeness to other forms. And meanwhile, the remaining parts of the organism to which the shoot or limb belongs, having been severally assuming structures divergent from each other and from that of this particular shoot or limb, there has arisen a greater heterogeneity in the organism as a whole.

§ 52. One of the most remarkable inductions of embryology comes next in order. Von Baer found that in its earliest stage, every organism has the greatest number of characters in common with all other organisms in their earliest stages; that at a stage somewhat later, its structure is like the structures displayed at corresponding phases by a less extensive multitude of organisms; that at each subsequent stage, traits are acquired which successively distinguish the developing embryo from groups of embryos that it previously resembled—thus step by step diminishing the group of embryos which it still resembles; and that thus the class of similar forms, is finally narrowed to the species of which it is a member. This abstract proposition will perhaps not be fully realized by the general reader. It will be best to re-state it in a concrete shape. The germ out of which a human being is evolved, differs in no visible respect from the germ out of which every animal and plant is evolved. The first conspicuous structural change undergone by this human germ, is one characterizing the germs of animals only—differentiates them from the germs of plants. The next distinction established, is a distinction exhibited by all *Vertebrata;* but never exhibited by *Annulosa, Mollusca,* or *Cœlenterata.* Instead of continuing to resemble, as it now does, the rudiments of all fishes, reptiles, birds, and mammals; this rudiment of a man, assumes a structure that is seen only in the rudiments of mammals. Later, the embryo undergoes changes which exclude it from the group of implacental mammals; and prove that it belongs to the group of placental mammals. Later still, it grows unlike the embryos of those placental mammals distinguished as ungulate or hoofed; and continues to resemble only the unguiculate or clawed. By and by, it ceases to be like any fœtuses but those of the quadrumana; and eventually the fœtuses of only the higher quadrumana are simulated. Lastly, at birth, the infant, belonging to whichever human race it may do, is structurally very much like the infants of all other human races; and only afterwards acquires those various minor peculiarities of form that distinguish the variety of man to which it belongs.

The generalization here expressed and illustrated, must not be confounded with an erroneous semblance of it that has obtained considerable currency. An impression has been given by those who have popularized the statements of embryologists, that during its development, each higher organism passes through stages in which it resembles the adult forms of lower organisms—that the embryo of a man is at one time like a fish, and at another time like a reptile. This is not the fact. The fact established is, that up to a certain point, the embryos of a man and a fish continue similar, and that then differences begin to appear and increase—the one embryo approaching more and more towards the form of a fish; the other diverging from it more and more. And so with the resemblances to the more advanced types. Supposing the germs of all kinds of organisms to be simultaneously developing, we may say that all members of the vast multitude take their first steps in the same direction; that at the second step one-half of this vast multitude diverges from the other half, and thereafter follows a different course of development; that the immense assemblage contained in either of these divisions, very soon again shows a tendency to take two or more routes of development; that each of the two or more minor assemblages thus resulting, shows for a time but small divergences among its members, but presently again divides into groups which separate ever more widely as they progress; and so on, until each organism, when nearly complete, is accompanied in its further modifications only by organisms of the same species; and last of all, assumes the peculiarities which distinguish it as an individual—diverges to a slight extent to the organisms it is most like. The reader must also be cautioned against accepting this generalization as exact. The likenesses thus successively displayed are not precise but approximate. Only leading characteristics are the same: not all the details. It is as though in one of the diverging groups just described, each kind of organism, though having a general direction of development like that of the others it is for a time travelling with, shows from the first a tendency to leave the general route—a tendency which presently becomes strongly marked. Making all requisite qualifications, however, these resemblances remain conspicuous; and the fact that they follow each other in the way described, is a fact of great significance.

§ 53. This comparison between the course of development in any creature, and the course of development in all other creatures—this arrival at the conclusion that the course of development in each, at first the same as in all others, becomes stage by stage differentiated from the courses of all others, brings us within view of an allied conclusion. If we contemplate the successive stages passed through by any higher organism, and observe the relation between it and its environment at each of these stages; we shall see that this relation is modified in a way analogous to that in which the relation between the organism and its environment is modified, as we advance from the lowest to the highest grades. Along with the progressing differentiation of each organism from others, we find a progressing differentiation of it from its environment; like that progressing differentiation from the environment which we meet with in the ascending forms of life. Let us first glance at the way in which the ascending forms of life exhibit this progressing differentiation from the environment.

In the first place, it is illustrated in *structure*. Advance from the homogeneous to the heterogeneous, itself involves an increasing distinction from the inorganic world. In the lowest *Protozoa* we have a simplicity approaching to that of air, water, or earth; and the ascent to organisms of greater and greater complexity of structure, is an ascent to organisms that are in that respect more strongly contrasted with the structureless environment. In *form*, again, we see the same fact. An ordinary characteristic of inorganic matter is its indefiniteness of form; and this is also a characteristic of the lower organisms, as compared with the higher. Speaking generally, plants are less definite than animals, both in shape and size—admit of greater modifications from variations of position and nutrition. Among animals, the simplest Rhizopods are not only structureless but amorphous: the form is never specific, and is constantly changing. Of the organisms resulting from the aggregation of such creatures, we see that while some, as the *Foraminifera*, assume a certain definiteness of form, in their shells at least; others, as the Sponges, are very irregular. The Zoophytes and the *Polyzoa* are compound organisms, most of which have a mode of growth not more determinate than that of plants. But among the higher animals, we find not only that the mature shape of each species is very definite, but that the individuals of each species differ very little in size. A parallel increase of contrast is seen in *chemical composition.* With but few exceptions, and those only partial ones, the lowest animal and vegetal forms are inhabitants of the water; and water is almost their sole constituent. Desiccated *Protophyta* and *Protozoa* shrink into mere dust; and among the Acalephes, we find but a few grains of solid matter to a pound of water. The higher aquatic plants, in common with the higher aquatic animals, possessing as they do increased tenacity of substance, also contain a greater proportion of the organic elements; and so are chemically more unlike their medium. And when we pass to the superior classes of organisms—land-plants and land-animals—we find that, chemically considered, they have little in common either with the earth on which they stand or the air which surrounds them. In *specific gravity* too, we may note the like truth. The very simplest forms, in common with the spores and gemmules of higher ones, are as nearly as may be of the same specific gravity as the water in which they float; and though it cannot be said that among aquatic creatures, superior specific gravity is a standard of general superiority, yet we may fairly say that the superior orders of them, when divested of the appliances by which their specific gravity is regulated, differ more from water in their relative weight than do the lowest. In terrestrial organisms, the contrast becomes extremely marked. Trees and plants, in common with insects, reptiles, mammals, birds, are all of a specific gravity considerably less than that of the earth and immensely greater than that of the air. Yet further, we see the law similarly fulfilled in respect of *temperature*. Plants generate but extremely small quantities of heat, which are to be detected only by very delicate experiments; and practically they may be considered as having the same temperature as their environment. The temperature of aquatic animals is very little above that of the surrounding water: that of the invertebrata being mostly less than a degree above it, and that of fishes not exceeding it by more than two or three degrees; save in the case of some large red-blooded fishes, as the tunny, which exceed it in temperature by nearly ten degrees. Among insects, the range is from two to ten degrees above that of the air: the excess varying according to their activity. The heat of reptiles is from four to fifteen degrees more than the heat of their medium. While mammals and birds maintain a heat which continues almost unaffected by external variations, and is often greater than that of the air by seventy, eighty, ninety, and even a hundred degrees. Once more, in greater *self-mobility* a progressive differentiation is traceable. The especial characteristic by which we distinguish dead matter is its inertness: some form of independent motion is our most general test of life. Passing over the indefinite border-land between the animal and vegetal kingdoms, we may roughly class plants as organisms which, while they exhibit that species of motion implied in growth, are not only devoid of locomotive power, but with some unimportant exceptions are devoid of the power of moving their parts in relation to each other; and thus are less differentiated from the inorganic world than animals. Though in those microscopic *Protophyta* and *Protozoa* inhabiting the water—the spores of algæ, the gemmules of sponges, and the infusoria generally—we see locomotion produced by ciliary action; yet this locomotion, while rapid relatively to the size of the creatures, is absolutely slow. Of the *Cœlenterata*, a great part are either permanently rooted or habitually stationary; and so have scarcely any self-mobility but that implied in the relative movements of parts; while the rest, of which the common jelly-fish will serve as a sample, have mostly but little ability to move themselves through the water. Among the higher aquatic *Invertebrata*,—cuttle-fishes and lobsters, for instance,—there is a very considerable power of locomotion; and the aquatic *Vertebrata* are, considered as a class, much more active in their movements than the other inhabitants of the water. But it is only when we come to air-breathing creatures, that we find the vital characteristic of self-mobility manifested in the highest degree. Flying insects, mammals, birds, travel with a velocity far exceeding that attained by any of the lower classes of animals; and so are more strongly contrasted with their inert environment. Thus, on contemplating the various grades of organisms in their ascending order, we find them more and more distinguished from their inanimate media, in *structure*, in *form*, in *chemical composition*, in *specific gravity*, in *temperature*, in *self-mobility*. It is true that this generalization does not hold with complete regularity. Organisms which are in some respects the most strongly contrasted with the environing inorganic world, are in other respects less so than inferior organisms. As a class, mammals are higher than birds; and yet they are of lower temperature, and have smaller powers of locomotion. The stationary oyster is of higher organization than the free-swimming medusa; and the cold-blooded and less heterogeneous fish, is quicker in its movements than the warm-blooded and more heterogeneous sloth. But the admission that the several aspects under which this increasing contrast shows itself, bear variable ratios to each other, does not conflict with the general truth, that as we ascend in the hierarchy of organisms, we meet with not only an increasing differentiation of parts, but also an increasing differentiation from the surrounding medium in sundry other physical attributes. It would seem that this peculiarity has some necessary connexion with superior vital manifestations. One of those lowly gelatinous forms, so transparent and colourless as to be with difficulty distinguished from the water it floats in, is not more like its medium in chemical, mechanical, optical, thermal, and other properties, than it is in the passivity with which it submits to all the influences and actions brought to bear upon it; while the mammal does not more widely differ from inanimate things in these properties, than it does in the activity with which it meets surrounding changes by compensating changes in itself. And between these two extremes, we shall observe a constant ratio between these two kinds of contrast. Whence we may say, that in proportion as an organism is physically like its environment, does it remain a passive partaker of the changes going on in its environment; while in proportion as it is endowed with powers of counteracting such changes, it exhibits greater unlikeness to its environment.*

If now, from this same point of view, we consider the relation borne to its environment by any superior organism in its successive stages, we find an analogous series of contrasts. Of course in respect of degrees of *structure*, the parallelism is complete. The difference, at first small, between the comparatively structureless germ and the comparatively structureless inorganic world, becomes necessarily greater, step by step, as the differentiations of the germ become more numerous and definite. How of *form* the like holds, is equally manifest. The sphere, which is

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* This paragraph originally formed part of a review-article on "Transcendental Physiology," published in 1857

the point of departure common to all organisms, is the most generalized of figures; and one that is, under various circumstances, assumed by inorganic matter. While the incipient organism is spherical, it is not only like many particular inorganic masses; but it is like the rest, in the sense that it has the shape which would result, were all their irregularities averaged. But as it develops, it loses all likeness to inorganic objects in the environment; and eventually becomes distinct even from all organic objects in its environment. In *specific gravity*, the alteration, though not very marked, is still in the same direction. Development being habitually accompanied by a relative decrease in the quantity of water, and an increase in the quantity of constituents that are heavier than water, there results a small augmentation of relative weight. In power of maintaining a *temperature* above that of surrounding things, the differentiation from the environment that accompanies development, is marked. All ova are absolutely dependent for their heat on external sources. Like inorganic bodies, they gain or lose heat according as neighbouring bodies are colder or hotter. The mammalian young is, during its uterine life, dependent on the maternal heat; and at birth has but a partial power of making good the loss by radiation. But as it advances in development, it gains an ability to maintain a constant temperature above that of surrounding things: so becoming markedly unlike all surrounding things, save organisms of allied nature. Lastly, in *self-mobility* this increasing contrast is not less decided. Save in a few aberrant tribes, chiefly parasitic, we find the general fact to be, that the locomotive power, totally absent or very small at the outset, increases with the advance towards maturity. The more highly developed the organism becomes, the stronger grows the contrast between its activity and the inertness of the objects amid which it moves.

Thus we may say that the development of an individual organism, is at the same time a differentiation of its parts from each other, and a differentiation of the consolidated whole from the environment; and that in the last as in the first respect, there is a general analogy between the progression of an individual organism, and the progression from the lowest orders of organisms to the highest orders. It may be remarked that some kinship seems to exist between these generalizations and the doctrine of Schelling, that Life is the tendency to individuation. For evidently, in becoming more distinct from each other, and from their environment, organisms acquire more marked individualities. As far as I can gather from outlines of his philosophy, however, it appears that Schelling entertained this conception in a general and transcendental sense, rather than in a special and scientific one.

§ 54. The deductive interpretations of these general facts of development, in so far as they are at present possible, must be postponed until we arrive at the fourth and fifth divisions of this work; which will be chiefly occupied with them. There are, however, one or two general aspects of these inductions, which may be here most conveniently dealt with deductively.

The general law of development as displayed in organisms, is readily shown to be necessary, if the initial and terminal stages are such as we know them to be. Grant that each organism is at the outset homogeneous, and that when complete it is relatively heterogeneous; and of necessity it follows that development is a change from the homogeneous to the heterogeneous—a change during which there must be gone through all the infinitesimal gradations of heterogeneity that lie between these extremes. If, again, there is at first indefiniteness, and at last definiteness, the transition cannot but be from the one to the other of these, through all intermediate degrees of definiteness. Further, if the parts, originally incoherent or uncombined, eventually become relatively coherent or combined; there must be a continuous increase of coherence or combination. Hence the general truth that

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development is a change from incoherent, indefinite homogeneity, to coherent, definite heterogeneity, becomes a self-evident one, when observation has shown us the state in which organisms begin, and the state in which they end.

Just in the same way that the growth of an entire organism, is carried on by abstracting from the environment substances like those composing the organism; so the production of each organ within the organism, is carried on by abstracting from the substances contained in the organism, those required by this particular organ. Each organ at the expense of the organism as a whole, integrates with itself certain special kinds and proportions of the matters circulating around it; in the same way that the organism as a whole, integrates with itself certain special kinds and proportions of matters at the expense of the environment as a whole. So that the organs are qualitatively differentiated from each other, in a way analogous to that by which the entire organism is qualitatively differentiated from things around it. Evidently this selective assimilation illustrates the general truth, demonstrable *à priori*, that like units tend to segregate. It illustrates, moreover, the further aspect of this general truth, that the pre-existence of a mass of certain units, produces, probably by polar attraction, a tendency for diffused units of the same kind to aggregate with this mass, rather than elsewhere. It has been shown of particular salts, A and B, co-existing in a solution not sufficiently concentrated to crystallize, that if a crystal of the salt A be put into the solution, it will increase by uniting with itself the dissolved atoms of the salt A; and that similarly, though there otherwise takes place no deposition of the salt B, yet if a crystal of the salt B is placed in the solution, it will exercise a coercive force on the diffused atoms of this salt, and grow at their expense. No doubt much organic assimilation occurs in the same way. Particular parts of the organism are composed of special units, or have the function of secreting special units, which are ever present in them in large quantities. The fluids circulating through the body contain special units of this same order. And these diffused units are continually being deposited along with the groups of like units that already exist. How purely physical are the causes of this selective assimilation, is, indeed, conclusively shown by the fact, that abnormal constituents of the blood are segregrated in the same way. Cancer-cells having begun to be deposited at a particular place, continue to be deposited at that place. Tubercular matter, making its appearance at particular points, collects more and more round those points. And similarly in numerous pustular diseases. Where the component units of an organ, or some of them, do not exist as such in the circulating fluids, but are formed out of elements or compounds that exist separately in the circulating fluids; it is clear that the process of differential assimilation is of a more complex kind. Still, however, it seems not impossible that it is carried on in an analogous way. If there be an aggregate of compound atoms, each of which contains the constituents A, B, C; and if round this aggregate the constituents A and B and C are diffused in uncombined states; it may be suspected that the coercive polar force of these aggregated compound atoms A, B, C, may not only bring into union with themselves adjacent compound atoms A, B, C, but may cause the adjacent constituents A and B and C to unite into such compound atoms, and then aggregate with the mass. Should this be so, the process of differential assimilation, which plays so important a part in organic development, will not be difficult to understand. At present, however, chemical inquiry appears to have furnished no evidence either for or against such an hypothesis.

# CHAPTER III.

## FUNCTION.

§ 55. Does Structure originate Function, or does Function originate Structure? is a question about which there has been disagreement. Using the word Function in its widest signification, as the totality of all vital actions, the question amounts to this—does Life produce Organization, or does Organization produce Life?

To answer this question is not easy, since we habitually find the two so associated that neither seems possible without the other; and they appear uniformly to increase and decrease together. If it be said that the arrangement of organic substances in particular forms, cannot be the ultimate cause of vital changes, which must depend on the properties of such substances; it may be replied that, in the absence of structural arrangements, the forces evolved cannot be so directed and combined as to secure that correspondence between inner and outer actions which constitutes Life. Again, to the allegation that the vital activity of every germ whence an organism arises, is obviously antecedent to the development of its structures; there is the answer that such germ is not absolutely structureless, but consists of a mass of cells, containing a cell that differs from the rest, and initiates the developmental changes. There is, however, one fact implying that Function must be regarded as taking precedence of Structure. Of the lowest Rhizopods, which present no distinctions of parts, and nevertheless feed and grow and move about, Prof. Huxley has remarked that they exhibit Life without Organization. The perpetual changes of form which alone distinguish one of these creatures from an inanimate fragment, are no doubt totally irregular and undirected. Still they do, through an average of accidents, subserve the creatures' nutrition; and they do imply an expenditure of force that in some way depends on the consumption of nutriment. They do, therefore, though in the rudest way, display a vital adjustment of internal to external relations.

§ 56. Function falls into divisions of several kinds, according to our point of view. Let us take these divisions in the order of their simplicity.

Under Function in its widest sense, are included both the statical and the dynamical distributions of force which an organism opposes to the forces brought to bear on it. In a tree, the woody core of trunk and branches, and in an animal, the skeleton, internal or external, may be regarded as passively resisting the gravity and momentum which tend habitually or occasionally to derange the requisite relations between the organism and its environment; and since they resist these forces simply by their cohesion, their functions may be classed as *statical*. Conversely, the leaves and sap-vessels in a tree, and those organs which in an animal similarly carry on nutrition and circulation, as well as those which generate and direct muscular motion, must be considered as *dynamical* in their actions. From another point of view, Function is divisible into the *accumulation of force* (latent in food); the *expenditure of force* (latent in the tissues and certain matters absorbed by them); and the *transfer of force* (latent in the prepared nutriment or blood) from the parts which accumulate to the parts which expend. In plants we see little beyond the first of these: expenditure being inappreciable, and transfer required only to facilitate accumulation. In animals, the function of *accumulation* comprehends those processes by which the materials containing latent force are taken in, digested, and separated from other materials; the function of *transfer* comprehends those processes by which these materials, and such others as are needful to liberate the forces they contain, are conveyed throughout the organism; and the function of *expenditure* comprehends those processes by which the forces are liberated from these materials, and transformed into properly co-ordinated motions. Each of these three most general divisions, includes several more special divisions. The accumulation of force may be separated into *alimentation* and *aeration;* of which the first is again separable into the various acts gone through between prehension of food and the transformation of part of it into blood. By the transfer of force is to be understood what we call *circulation;* if the meaning of circulation be extended to embrace the duties of both the vascular system and the lymphatics. Under the head of expenditure of force, come *nervous actions* and *muscular actions:* though not absolutely co-extensive with expenditure, these are almost so. Lastly, there are the subsidiary functions which do not properly fall within any of these general functions, but subserve them by removing the obstacles to their performance: those, namely, of *excretion* and *exhalation,* whereby waste products are got rid of. Again, disregarding their purposes and considering them analytically, the general physiologist may consider functions in their widest sense as the correlatives of tissues—the actions of epidermic tissue, cartilaginous tissue, elastic tissue, connective tissue, osseous tissue, muscular tissue, nervous tissue, glandular tissue. Once more, physiology in its concrete interpretations, recognizes special functions as the ends of special organs—regards the teeth as having the office of mastication; the heart as an apparatus to propel blood; this gland as fitted to produce one requisite secretion and that to produce another; each muscle as the agent of a particular motion; each nerve as the vehicle of a special sensation or a special motor impulse.

It is clear that dealing with Biology only in its larger aspects, specialities of function do not concern us; except in so far as they serve to illustrate, or to qualify, its generalities.

§ 57. The first induction to be here set down, is a familiar and obvious one: the induction, namely, that complexity of function, is the correlative of complexity of structure. The leading aspects of this truth must be briefly noted.

Where there are no distinctions of structure, there are no distinctions of function. One of the Rhizopods above instanced as exhibiting life without organization, will serve as an illustration. From the outside of this creature, which has not even a limiting membrane, there are protruded numerous thread-like processes. Originating from any point of the surface, each of these may contract again and disappear; or it may touch some fragment of nutriment, which it draws with it, when contracting, into the general mass—thus serving as hand and mouth; or it may come in contact with its fellow-processes at a distance from the body, and become confluent with them; or it may attach itself to an adjacent fixed object, and help by its contraction to draw the body into a new position. In brief, this structureless speck of animated jelly, is at once all stomach, all skin, all mouth, all limb, and doubtless, too, all lung. In organisms having a fixed distribution of parts, there is a concomitant fixed distribution of actions. Among plants we see that when, instead of a uniform tissue like that of the *Algæ*, everywhere devoted to the same process of assimilation, there arise, as in the Exogens, root and stem and leaves, there arise correspondingly unlike processes. Still more conspicuously among animals, do there result varieties of function when the originally homogeneous mass is replaced by heterogeneous organs; since both singly and by their combinations, do modified parts generate modified changes. Up to the highest organic types, this dependence continues manifest; and it may be traced not only under this most general form, but also under the more special form, that in animals having one set of functions developed to more than usual heterogeneity, there is a correspondingly heterogeneous apparatus devoted to them. Thus among birds, which have more varied locomotive powers than mammals, the limbs are more widely differentiated; while mammals, which rise to more numerous and more involved adjustments of inner to outer relations than birds, have more complex nervous systems.

§ 58. It is a generalization almost equally obvious with the last, that functions, like structures, arise by progressive differentiations. Just as an organ is first an indefinite rudiment, having nothing but some most general characteristic in common with the form it is ultimately to take; so a function begins as a kind of action that is like the kind of action it will eventually become, only in a very vague way. And in functional development, as in structural development, the leading trait thus early manifested, is followed successively by traits of less and less importance. This holds equally throughout the ascending grades of organisms, and throughout the stages of each organism. Let us look at cases: confining our attention to animals, in which functional development is better displayed than in plants

The first differentiation established, separates the two fundamentally-opposed functions above named—the accumulation of force and the expenditure of force. Passing over the, (*Protozoa* among which, however, such tribes as present fixed distributions of parts show us substantially the same thing), and commencing with the lowest *Cœlenterata*, where definite tissues make their first appearance, we observe that the only marked functional distinction is between the endoderm, which absorbs nutriment, and the ectoderm, which, by its own contractions and those of the tentacles it bears, produces motion. That the functions of accumulation and expenditure are here very incompletely distinguished, may be admitted without affecting the position that this is the first specialization which begins to appear. These two most general and most radically-opposed functions, become, in the *Polyzoa*, much more clearly marked-off from each other; at the same time that each of them becomes partially divided into subordinate functions. The endoderm and ectoderm are no longer merely the inner and outer walls of the same simple sac into which the food is drawn; but the endoderm forms a true alimentary canal, separated from the ectoderm by a peri-visceral cavity, containing the nutritive matters absorbed from the food. That is to say, the function of accumulating force is exercised by a part distinctly divided from the part mainly occupied in expending force: the space between them, full of absorbed nutriment, effecting in a vague way that transfer of force which, at a higher stage of evolution, becomes a third leading function. Meanwhile, the endoderm no longer discharges the accumulative function in the same way throughout its whole extent; but its different portions, æsophagus, stomach and intestine, perform different portions of this function. And instead of a contractility uniformly diffused through the ectoderm, there have arisen in it, some parts which have the office of contracting (muscles), and some parts which have the office of making them contract (nerves and ganglia). As we pass upwards, the transfer of force, hitherto effected quite incidentally, comes to have a special organ. In the ascidian molluscs, circulation is produced by a muscular tube, open at both ends, which, by a wave of contraction passing along it, sends out at one end the nutrient fluid drawn in at the other; and which, having thus propelled the fluid for a time in one direction, reverses its movement and propels it in the opposite direction. By such means does this rudimentary heart generate alternating currents in the crude and dilute nutriment occupying the peri-visceral cavity. How the function of transferring force, thus vaguely indicated in these inferior forms, comes afterwards to be the definitely-separated office of a complicated apparatus made up of many parts, each of which has a particular portion of the general duty, need not be described. It is sufficiently manifest that this general function becomes more clearly marked-off from the others, at the same time that it becomes itself parted into subordinate functions.

In a developing embryo, the functions or more strictly the structures which are to perform them, arise in the same general order. A like primary distinction very early appears between the endoderm and the ectoderm—the part which has the office of accumulating force, and the part out of which grow those organs that are the great expenders of force. Between these two there presently becomes visible the rudiment of that vascular system, which has to fulfil the intermediate duty of transferring force. Of these three general functions, that of accumulating force is carried on from the outset: the endoderm, even while yet incompletely differentiated from the ectoderm, absorbs nutritive matters from the subjacent yelk. The transfer of force is also to some extent effected by the rudimentary vascular system, as soon as its central cavity and attached vessels are sketched out. But the expenditure of force (in the higher animals at least) is not appreciably displayed by the ectodermic structures that are afterwards to be mainly devoted to it: there is no sphere for the actions of these parts. Similarly with the chief subdivisions of these fundamental functions. If we look at those discharged by the ectoderm, potentially if not actually, we see that the distinction first established separates the office of transforming other force into mechanical motion, from the office of liberating the force to be so transformed—in the midst of the part out of which the muscular system is to be developed, there is marked-out the rudiment of the nervous system. This indication of structures which are to share between them the general duty of expending force, is soon followed by changes that foreshadow further specializations of this general duty. In the incipient nervous system, there begins to arise that contrast between the cerebral mass and the spinal cord, which, in the main, answers to the division of nervous actions into directive and executive; and at the same time, the appearance of vertebral laminæ foreshadows the separation of the osseous system, which has to resist the strains of muscular action, from the muscular system, which, in generating motion, entails these strains. Simultaneously there have been going on similar actual and potential specializations in the functions of accumulating force and transferring force. And throughout all subsequent phases, the method is substantially the same.

This progress from general, indefinite, and simple kinds of action, to special, definite, and complex kinds of action, has been aptly termed by Milne-Edwards, the "physiological division of labour." Perhaps no metaphor can more truly express the nature of this advance from vital activity in its lowest forms to vital activity in its highest forms. And probably the general reader cannot in any other way obtain so clear a conception of functional development in organisms, as he can by tracing out functional development in societies: noting how there first comes a distinction between the governing class and the governed class; how while in the governing class there slowly grow up such differences of duty as the civil, military, and ecclesiastical, there arise in the governed class, fundamentally industrial differences like those between agriculturists and artizans; and how there is a continual multiplication of such specialized occupations, and specialized shares of each occupation.

§ 59. Fully to understand this change from homogeneity to heterogeneity of function, which accompanies the change from homogeneity to heterogeneity of structure, it is needful to contemplate it under a converse aspect. Standing alone, the above exposition conveys both an inadequate and an erroneous idea. The divisions and subdivisions of function, becoming definite as they become multiplied, do not lead to a more and more complete independence of functions; as they would do were the process nothing beyond that just described; but by a simultaneous process they are rendered more mutually dependent. While in one respect they are separating from each other, they are in another respect combining with each other. At the same time that they are being differentiated, they are also being integrated. Some illustrations will make this plain.

In animals which display little beyond the primary differentiation of functions, the activity of that part which absorbs nutriment or accumulates force, is not immediately bound up with the activity of that part which, in producing motion, expends force. In the higher animals, however, the performance of the alimentary functions depends on the performance of various muscular and nervous functions. Mastication and swallowing are nervo-muscular acts; the rythmical contractions of the stomach and the allied vermicular motions of the intestines, result from the stimulation of certain muscular coats by the nerve-fibres distributed through them; the secretion of the several digestive fluids by their respective glands, is due to nervous excitation of them; and digestion, besides requiring these special aids, is not properly performed in the absence of a continuous discharge of energy from the great nervous centres. Again, the function of transferring nutriment or latent force, from part to part, though at first not closely connected with the other functions, eventually becomes so. The short contractile tube which propels backwards and forwards the crude dilute blood contained in the perivisceral cavity of an inferior mollusc, is neither structurally nor functionally much entangled with the creature's other organs. But on passing upwards through the higher molluscs, in which this simple tube is replaced by a system of branched tubes, that deliver their contents through their open ends into the tissues at distant parts; and on coming to those advanced types of animals which have closed arterial and venous systems, ramifying minutely in every corner of every organ; we find that the vascular apparatus, while it has become structurally interwoven with the whole body, has become unable to fulfil its office without the help of offices that are quite separated from its own. The heart is now a complex pump, worked by powerful muscles that are excited by a local nervous system; and the general nervous system also, takes a share in regulating the contractions both of the heart and of all the arteries. On the due discharge of the respiratory function, too, the function of circulation is directly dependent: if the aeration of the blood is impeded, the vascular activity is lowered; and arrest of the one very soon causes stoppage of the other. Similarly with the duties of the nervo-muscular system. Animals of low organization, in which the differentiation and integration of the vital actions have not been carried far, will move about for a considerable time after being eviscerated, or deprived of those appliances by which force is accumulated and transferred. But animals of high organization are instantly killed by the removal of these appliances, and even by the injury of minor parts of them: a dog's movements are suddenly brought to an end, by cutting one of the main canals along which the materials that evolve movements are conveyed. Thus while in well-developed creatures the distinction of functions is very marked, the combination of functions is very close. From instant to instant, the aeration of blood implies that certain respiratory muscles are being made to contract by certain nerves; and that the heart is duly propelling the blood to be aerated. From instant to instant digestion proceeds only on condition that there is a supply of aerated blood, and a due current of nervous energy through the digestive organs. That the heart may act, it must from instant to instant be excited by discharges from certain ganglia; and the discharges from these ganglia are made possible, only by the conveyance to them, from instant to instant, of the blood which the heart propels.

It is not easy to find an adequate expression for this double re-distribution of functions. It is not easy to realize a transformation through which the functions thus become in one sense separated and in another sense combined, or even interfused. Here, however, as before, an analogy drawn from social organization helps us. If we observe how the increasing division of labour in societies, is accompanied by a closer co-operation; and how the agencies of different social actions, while becoming in one respect more distinct, become in another respect more minutely ramified through each other; we shall understand better the increasing physiological co-operation that accompanies increasing physiological division of labour. Note, for example, that while local divisions and classes of the community have been growing unlike in their several occupations, the carrying on of their several occupations has been growing dependent on the due activity of that vast organization by which sustenance is collected and diffused. During the early stages of social development, every small group of people, and often every family, obtained separately its own necessaries; but now, for each necessary, and for each superfluity, there exists a combined body of wholesale and retail distributors, which brings its branched channels of supply within reach of all. While each citizen is pursuing a business that does not immediately aim at the satisfaction of his personal wants, his personal wants are satisfied by a general agency that brings from all places commodities for him and his fellow-citizens —an agency which could not cease its special duties for a few days, without bringing to an end his own special duties and those of most others. Consider, again, how each of these differentiated functions is everywhere pervaded by certain other differentiated functions. Merchants, manufacturers, wholesale distributors of their several species, together with lawyers, bankers, &c., all employ clerks. In clerks we have a specialized class dispersed through various other classes; and having its function fused with the different functions of these various other classes. Similarly commercial travellers, though having in one sense a separate occupation, have in another sense an occupation forming part of each of the many occupations which it aids. As it is here with the sociological division of labour, so is it with the physiological division of labour above described. Just as we see in an advanced community, that while the magisterial, the clerical, the medical, the legal, the manufacturing, and the commercial activities, have grown distinct, they have yet their agencies mingled together in every locality; so in a developed organism, we see that while the general functions of circulation, secretion, absorption, excretion, contraction, excitation, &c., have become differentiated, yet through the ramifications of the systems apportioned to them, they are closely combined with each other in every organ.

§ 60. The physiological division of labour, is usually not carried so far as wholly to destroy the primary physiological community of labour. As in societies the adaptation of special classes to special duties, does not entirely disable these classes from performing each others' duties on an emergency; so in organisms, tissues and structures that have become fitted to the particular offices they have ordinarily to discharge, often remain partially able to discharge other offices. It has been pointed out by Dr Carpenter, that " in cases where the different functions are highly specialized. the general structure retains, more or less, the primitive community of function which originally characterized it." A few instances will bring home this generalization

The roots and leaves of plants are widely differentiated in their functions: by the roots, water and mineral substances are absorbed; while the leaves take in, and decompose, carbonic acid. Nevertheless, leaves retain a considerable power of absorbing water; and in what are popularly called "air-plants," the absorption of water is wholly carried on by them and by the stems. Conversely, the underground parts can partially assume the functions of leaves: the exposed tuber of a potato develops chlorophyll on its surface, and in other cases, roots, properly so called, do the like. In trees, the trunks, which have in great measure ceased to produce buds, recommence producing them if the branches are cut off; and under such circumstances the roots, though not in the habit of developing leaf-bearing organs, send up numerous suckers. Much more various examples of vicarious function may be found among animals. Starting with the extreme case of the common hydra, which can live when the duties of skin and stomach have been interchanged by turning it inside out, we find in all grades, even up to the highest, that absorbent and excreting organs can partially supply each others' places. Among well-organized animals, the taking in of nutriment is effected exclusively by an internal membrane; but the external membrane is not wholly without the power to take in nutriment: when food cannot be swallowed, life may be prolonged by immersing the body in nutritive fluids. The excretion of carbonic acid and absorption of oxygen, are mainly performed by the lungs, in creatures which have lungs; but in such creatures there continues a certain amount of cutaneous respiration, and in soft-skinned batrachians like the frog, this cutaneous respiration is important. Again, when the kidneys are not discharging their duties, a notable quantity of urea is got rid of by perspiration. Other instances are supplied by the higher functions. In man, the limbs, which among lower vertebrates are almost wholly organs of locomotion, are specialized into organs of locomotion and organs of manipulation. Nevertheless, the human arms and legs do, when needful, fulfil, to some extent, each others' offices. Not only in childhood and old age are the arms used for purposes of support, but on occasions of emergency, as when mountaineering, they are so used by men in full vigour. And that legs are to a considerable degree capable of performing the duties of arms, is proved by the great amount of manipulatory skill reached by them when the arms are absent. Among the perceptions, too, there are examples of partial substitution. The deaf Dr Kitto described himself as having become excessively sensitive to vibrations propagated through the body; and as so having gained the power of perceiving, through his general sensations, those neighbouring concussions of which the ears ordinarily give notice. Blind people make hearing perform, in part, the office of vision. Instead of identifying the positions and sizes of neighbouring objects by the reflection of light from their surfaces, they do this in a rude way by the reflection of sound from their surfaces.

We see, as we might expect to see, that this power of performing more general functions, is great in proportion as the parts have been but little adapted to their special functions. In the hydra, where complete transposition of functions is possible, the histological differentiation that has been established, is extremely slight, or even inappreciable. Those parts of plants which show so considerable a power of discharging each others' offices, are not widely unlike in their minute structures. And the tissues that in animals are to some extent mutually vicarious, are tissues in which the original cellular composition is still conspicuous. But we do not find evidence that the muscular, nervous, or osseous tissues are able in any degree to perform those processes which the less differentiated tissues perform. Nor have we any proof that nerve can partially fulfil the duty of muscle, or muscle that of nerve. We must say, therefore, that the ability to resume the primordial community of function, varies inversely as the established specialization of function; and that it disappears when the specialization of function becomes great.

§ 61. Something approaching to *à priori* reasons may be given for the conclusions thus reached *à posteriori*. They must be accepted for as much as they seem worth.

It may be argued that on the hypothesis of Evolution, Life necessarily comes before organization. On this hypothesis, organic matter in a state of homogeneous aggregation, must precede organic matter in a state of heterogeneous aggregation. But since the passing from a structureless state to a structured state, is itself a vital process, it follows that vital activity must have existed while there was yet no structure: structure could not else arise. That function takes precedence of structure, seems also implied in the definition of Life. If Life consists of inner actions so adjusted as to balance outer actions—if the actions are the *substance* of Life, while the adjustment of them constitutes its *form*; then, may we not say that the actions to be formed must come before that which forms them—that the continuous change which is the basis of function, must come before the structure which brings function into shape? Or again, since throughout all phases of Life up to the highest, every advance is the effecting of some better adjustment of inner to outer actions; and since the accompanying new complexity of structure is simply a means of making possible this better adjustment; it follows that function is from beginning to end the determining cause of structure. Not only is this manifestly true where the modification of structure arises by reaction from modification of function; but it is also true where a modification of structure otherwise produced, apparently initiates a modification of function. For it is only when such so-called spontaneous modification of structure subserves some advantageous action, that it is permanently established: if it is a structural modification that happens to facilitate the vital activities, "natural selection" retains and increases it; but if not, it disappears.

The connexion which we noted between heterogeneity of structure and heterogeneity of function—a connexion made so familiar by experience as to appear scarcely worth specifying—is clearly a necessary one. It follows from the general truth that in proportion to the heterogeneity of any aggregate, is the heterogeneity it will produce in any incident force (*First Principles*, § 116). The force continually liberated in the organism by decomposition, is here the incident force; the functions are the variously modified forms produced in its divisions by the organs they pass through; and the more multiform the organs the more multiform must be the differentiations of the force passing through them.

It follows obviously from this, that if structure progresses from the homogeneous, indefinite, and incoherent, to the heterogeneous, definite, and coherent, so too must function. If the number of different parts in an aggregate must determine the number of differentiations produced in the forces passing through it—if the distinctness of these parts from each other, must involve distinctness in their reactions, and therefore distinctness between the divisions of the differentiated force; there cannot but be a complete parallelism between the development of structure and the development of function. If structure advances from the simple and general to the complex and special, function must do the same.

## CHAPTER IV.

### WASTE AND REPAIR.

§ 62. Throughout the vegetal kingdom, the processes of Waste and Repair are comparatively insignificant in their amounts. Though plants, and especially certain parts of them, do, in the absence of light or under particular conditions, give out carbonic acid; yet this carbonic acid, assuming it to indicate consumption of tissue, indicates but a small consumption. Of course if there is little waste, there can be but little repair—that is, little of the interstitial repair which restores the integrity of parts worn by functional activity. Nor, indeed, is there displayed by plants in any considerable degree, if at all, that other species of repair which consists in the restoration of lost or injured organs. Torn leaves and the shoots that are shortened by the pruner, do not reproduce their missing parts; and though when the branch of a tree is cut off close to the trunk, the place is in the course of years covered over, it is not by any reparative action in the wounded surface, but by the lateral growth of the adjacent bark. Hence, without saying that Waste and Repair do not go on at all in plants, we may fitly pass them over as of no importance.

There are but slight indications of waste in those lower orders of animals which, by their comparative inactivity, show themselves least removed from vegetal life. Actiniæ kept in an aquarium, do not appreciably diminish in bulk from prolonged abstinence. Even fish, though much more active than most other aquatic creatures, appear to undergo but little loss of substance when kept unfed during considerable periods. Reptiles, too, maintaining no great temperature, and passing their lives mostly in a state of torpor, suffer but little diminution of mass by waste. When, however, we turn to those higher orders of animals which are active and hot-blooded, we see that waste is rapid: producing when unchecked, a notable decrease in bulk and weight, ending very shortly in death. Besides finding that waste is inconsiderable in creatures that produce but little insensible and sensible motion, and that it becomes conspicuous in creatures that produce much insensible and sensible motion; we find that in the same creatures there is most waste when most motion is generated. This is clearly proved by hybernating animals. "Valentin found that the waking marmot excreted in the average 75 times more carbonic acid, and inhaled 41 times more oxygen than the same animal in the most complete state of hybernation. The stages between waking and most profound hybernation yielded intermediate figures. A waking hedgehog yielded about 20·5 times more carbonic acid, and consumed 18·4 times more oxygen than one in the state of hybernation." If we take these quantities of absorbed oxygen and excreted carbonic acid, as indicating something like the relative amounts of consumed organic substance, we see that there is a striking contrast between the waste accompanying the ordinary state of activity, and the waste accompanying complete quiescence and reduced temperature. This difference is still more definitely shown by the fact, that the mean daily loss from starvation in rabbits and guinea-pigs, bears to that from hybernation, the proportion of 18·3 : 1. Among men and domestic animals, the relation between degree of waste and amount of expended force, though one respecting which there is little doubt, is less distinctly demonstrable; since waste is not allowed to go on uninterfered with. We have however in the lingering lives of invalids who are able to take scarcely any nutriment, but are kept warm and still, an illustration of the extent to which waste diminishes as the expenditure of force declines.

Besides the connexion between the waste of the organism as a whole, and the production of sensible and insensible motion by the organism as a whole; there is a traceable connexion between the waste of special parts and the activities of such special parts. Experiments have shown that "the starving pigeon daily consumes in the average 40 times more muscular substance than the marmot in the state of torpor, and only 11 times more fat, 33 times more of the tissue of the alimentary canal, 18·3 times more liver, 15 times more lung, 5 times more skin." That is to say, in the hybernating animal the parts least consumed are the almost totally quiescent motor-organs, and the part most consumed is the hydro-carbonaceous deposit serving as a store of force; whereas in the pigeon, similarly unsupplied with food but awake and active, the greatest loss takes place in the motor-organs. The relation between special activity and special waste, is illustrated too in the daily experiences of all: not indeed in the measurable decrease of the active parts in bulk or weight, for this we have no means of ascertaining; but in the diminished ability of such parts to perform their functions. That legs exerted for many hours in walking, and arms long strained in rowing, lose their powers—that eyes become enfeebled by reading or writing without intermission—that concentrated attention unbroken by rest, so prostrates the brain as to incapacitate it for thinking; are familiar truths. And though we have no direct evidence to this effect, there is little danger in concluding that muscles exercised until they ache or become stiff, and nerves of sense rendered weary or obtuse by work, are organs so much wasted by action as to be partially incompetent.

Repair is everywhere and always making up for waste. Though the two processes vary in their relative rates, both are constantly going on. Though during the active, waking state of an animal, waste is in excess of repair, yet repair is in progress; and though during sleep, repair is in excess of waste, yet some waste is necessitated by the carrying on of certain never-ceasing functions. The organs of these never-ceasing functions furnish, indeed, the most conclusive proofs of the simultaneity of repair and waste. Day and night the heart never stops beating, but only varies in the rapidity and vigour of its beats; and hence the loss of substance which its contractions from moment to moment entail, must from moment to moment be made good. Day and night the lungs dilate and collapse; and the muscles which make them do this, must therefore be ever kept in a state of integrity by a repair which keeps pace with waste, or which alternately falls behind and gets in advance of it to a very slight extent.

On a survey of the facts, we see, as we might expect to see, that repair is most rapid when activity is most reduced. Assuming that the organs which absorb and circulate nutriment are in proper order, the restoration of the organism to a state of integrity, after the disintegration consequent on expenditure of force, is proportionate to the diminution in expenditure of force. Thus we all know that those who are in health, feel the greatest return of vigour after profound sleep—after complete cessation of motion. We know that a night during which the quiescence, bodily and mental, has been less decided, is usually not followed by that spontaneous overflow of energy that indicates a high state of efficiency throughout the organism. We know, again, that long-continued recumbency, even with wakefulness (providing the wakefulness is not the result of disorder), is followed by a certain renewal of strength; though a renewal less than that which would have followed the greater inactivity of slumber. We know, too, that when exhausted by labour, sitting brings a partial return of vigour. And we also know that after the violent exertion of running, a lapse into the less violent exertion of walking, results in a gradual disappearance of that prostration which the running produced. This series of illustrations conclusively proves that the rebuilding of the organism is ever making up for the pulling down of it caused by action; and that the effect of this rebuilding becomes manifest, in proportion as the pulling down is less rapid. From each digested meal, there is every few hours absorbed into the mass of prepared nutriment circulating through the body, a fresh supply of the needful organic compounds; and from the blood thus occasionally re-enriched, the organs through which it passes are ever taking up materials to replace the materials used up in the discharge of functions. During activity, the reintegration falls in arrear of the disintegration; until, as a consequence, there presently comes a general state of functional languor; ending, at length, in a quiescence which permits the reintegration to exceed the disintegration, and restore the parts to their state of integrity. Here, as wherever there are antagonistic actions, we see rhythmical divergences on opposite sides of the medium state—changes which equilibrate each other by their alternate excesses. (*First Principles*, §§ 96, 133.)

Illustrations are not wanting of special repair, that is similarly ever in progress, and similarly has intervals during which it falls below waste and rises above it. Every one knows that a muscle, or a set of muscles, continuously strained, as by holding out a weight at arm's length, soon loses its power; and that it recovers its power more or less fully after a short rest. The several organs of special sensation yield us like experiences: strong tastes, powerful odours, and loud sounds, temporarily unfit the nerves impressed by them, for appreciating faint tastes, odours, or sounds; but these incapacities are remedied by brief intervals of repose. Vision still better illustrates this simultaneity of waste and repair. Looking at the sun so affects the eye that, for a short time, it cannot perceive the ordinary contrasts of light and shade.

After gazing at a bright light of a particular colour, we see on turning the eyes to adjacent objects, an image of the complementary colour; showing that the retina has, for the moment, lost the power to feel small amounts of those rays which have strongly affected it. Such inabilities disappear in a few seconds or a few minutes, according to circumstances. And here, indeed, we are introduced to a conclusive proof that special repair is ever neutralizing special waste. For the rapidity with which the eyes recover their sensitiveness, varies with the reparative power of the individual. In youth, the visual apparatus is so quickly restored to its state of integrity, that many of these *photogenes*, as they are called, cannot be perceived. When sitting on the far side of a room, and gazing out of the window against a light sky, a person who is debilitated by disease or advancing years, perceives, on transferring the gaze to the adjacent wall, a momentary negative image of the window—the sash-bars appearing light and the squares dark; but a young and healthy person has no such experience. With a rich blood and vigorous circulation, the repair of the visual nerves after impressions of moderate intensity, is nearly instantaneous.

Function carried to excess, may produce waste so great, that repair cannot make up for it during the ordinary daily periods of rest; and there may result incapacities of the overtaxed organs, lasting for considerable periods. We know that eyes strained by long-continued minute work, lose their power for months or years: perhaps suffering an injury which they never wholly recover. Brains, too, are often so unduly worked that permanent relaxation fails to restore them to vigour. Even of the motor organs the like holds. The most frequent cause of what is called "wasting palsy," or atrophy of the muscles, is habitual excess of exertion: the proof being, that the disease occurs most frequently among those engaged in laborious handicrafts, and usually attacks first the muscles that have been most worked.

There has yet to be noticed another kind of repair;—that namely, by which injured or lost parts are restored. Among the *Hydrozoa* it is common for any portion of the body to reproduce the rest; even though the rest to be so reproduced is the greater part of the whole. In the more highly-organized *Actinozoa*, the half of an individual will grow into a complete individual. Some of the lower Annelids, as the *Nais*, may be cut into thirty or forty pieces, and each piece will eventually become a perfect animal. As we ascend to higher forms, we find this reparative power much diminished, though still considerable. The reproduction of a lost claw by a lobster or crab, is a familiar instance. Some of the inferior *Vertebrata* also, as lizards, can develop new limbs or new tails, in place of those that have been cut off; and can even do this several times over, though with decreasing completeness. The highest animals, however, thus repair themselves to but a very small extent. Mammals and birds do it only in the healing of wounds; and very often but imperfectly even in this. For in muscular and glandular organs, the tissues destroyed are not properly reproduced, but are replaced by tissue of an irregular kind, which serves to hold the parts together. So that the power of reproducing lost parts is greatest where the organization is lowest; and almost disappears where the organization is highest. And though we cannot say that between these extremes there is a constant inverse relation between reparative power and degree of organization; yet we may say that there is some approach to such a relation.

§ 63. There is a very obvious and complete harmony between the first of the above inductions, and the deduction that follows immediately from first principles. We have already seen (§ 23) "that whatever amount of power an organism expends in any shape, is the correlate and equivalent of a power that was taken into it from without." Motion, sensible or insensible, generated by an organism, is insensible motion which was absorbed in producing certain chemical compounds appropriated by the organism under the form of food. As much power as was required to raise the elements of these complex atoms to their state of unstable equilibrium, is given out in their falls to a state of stable equilibrium; and having fallen to a state of stable equilibrium, they can give out no further power, but have to be got rid of as inert and useless. It is an inevitable corollary "from the persistence of force, that each portion of mechanical or other energy which an organism exerts, implies the transformation of as much organic matter as contained this energy in a latent state;" and that this organic matter in yielding up its latent energy, loses its value for the purposes of life, and becomes waste matter needing to be excreted. The loss of these complex unstable substances must hence be proportionate to the quantity of expended force. Here then is the rationale of certain general facts lately indicated. Plants do not waste to any considerable degree, for the obvious reason that the sensible and insensible motions they generate are inconsiderable. Between the small waste, small activity, and low temperature of the inferior animals, the relation is similarly one admitting of *à priori* establishment. Conversely, the rapid waste of energetic, hot-blooded animals might be foreseen with equal certainty. And not less manifestly necessary is the variation in waste which, in the same organism, attends the variation in the heat and mechanical motion produced.

Between the activity of a special part and the waste of that part, a like relation may be deductively inferred; though it cannot be inferred that this relation is equally definite. Were the activity of every organ quite independent of the activities of other organs, we might expect to trace out this relation distinctly; but since one part of the force which any organ expends, is derived from materials brought to it by the blood from moment to moment in quantities varying with the demand, and since another part of the force which such organ expends, comes to it in the shape of nervous discharges from distant organs; it is clear that special waste and general waste are too much entangled to admit of a definite relation being established between special waste and special activity. We may fairly say, however, that this relation is quite as manifest as we can reasonably anticipate.

§ 64. Deductive interpretation of the phenomena of Repair, is by no means so easy. The tendency displayed by an animal organism, as well as by each of its organs, to return to a state of integrity by the assimilation of new matter, when it has undergone the waste consequent on activity, is a tendency which is not manifestly deducible from first principles; though it appears to be in harmony with them. If in the blood there existed ready-formed units exactly like in kind to those of which each organ consists, the sorting of these units, ending in the union of each kind with already existing groups of the same kind, would be merely a good example of Differentiation and Integration (*First Principles*, § 123). It would be analogous to the process by which, from a mixed solution of salts, there are deposited segregated masses of these salts, in the shape of different crystals. But as already said (§ 54), though the selective assimilation by which the repair of organs is effected, no doubt results in part from an action of this kind, which is consequent on the persistence of force (*First Principles*, § 129), the facts cannot be thus wholly accounted for; since organs are in part made up of units that do not exist as such in the circulating fluids. The process becomes comprehensible however, if it be shown that, as suggested in § 54, groups of compound units have a certain power of moulding adjacent fit materials into units of their own form. Let us see whether there is not reason to think such a power exists.

" The poison of small-pox or of scarlatina," remarks Mr Paget, " being once added to the blood, presently affects the composition of the whole: the disease pursues its course, and, if recovery ensue, the blood will seem to have returned to its previous condition: yet it is not as it was before; for now the same poison may be added to it with impunity." * * * "The change once effected, may be maintained through life. And herein seems to be a proof of the assimilative force in the blood; for there seems no other mode of explaining these cases than by admitting that the altered particles have the power of assimilating to themselves all those by which they are being replaced: in other words, all the blood that is formed after such a disease deviates from the natural composition, so far as to acquire the peculiarity engendered by the disease: it is formed according to the altered model." Now if the compound molecules of the blood, or of an organism considered in the aggregate, have the power of moulding into their own type, the matters which they absorb as nutriment; and if, as Mr Paget points out, they have the power when their type has been changed by disease, of moulding all materials afterwards received into the modified type; may we not reasonably suspect that the more or less specialized molecules of each organ, have, in like manner, the power of moulding the materials which the blood brings to them, into similarly specialized molecules? The one conclusion seems to be a corollary from the other. Such a power cannot be claimed for the component units of the blood, without being conceded to the component units of every tissue. Indeed the assertion of this power is little more than an assertion of the fact, that organs composed of specialized units *are* capable of resuming their structural integrity, after they have been wasted by function. For if they do this, they must do it by forming from the materials brought to them, certain specialized units like in kind to those of which they are composed; and to say that they do this, is to say that their component units have the power of moulding fit materials into other units of the same order.

The repair of a wasted tissue may therefore be considered as due to forces analogous to those by which a crystal reproduces its lost apex, when placed in a solution like that from which it was formed. In either case, a mass of units of a given kind, shows a power of integrating with itself diffused units of the same kind: the only difference being, that the organic mass of units arranges the diffused units into special compound forms, before integrating them with itself. In the case of the crystal, this reintegration is ascribed to polarity—a power of whose nature we know nothing. Whatever be its nature, however, it appears probable that the power by which organs repair themselves from the nutritive matters circulating through them, is of the same order.

§ 65. That other kind of repair which shows itself in the regeneration of lost members, is comprehensible only as an effect of actions like those just referred to. The ability of an organism to recomplete itself when one of its parts has been cut off, is of the same order as the ability of an injured crystal to recomplete itself. In either case, the newly-assimilated matter is so deposited as to restore the original outline. And if in the case of the crystal, we say that the whole aggregate exerts over its parts, a force which constrains the newly-integrated atoms to take a certain definite form; we must in the case of the organism, assume an analogous force. This is, in truth, not an hypothesis: it is nothing more than a generalized expression of the facts. If when the leg of a lizard has been amputated, there presently buds out the germ of a new one, which, passing through phases of development like those of the original leg, eventually assumes a like shape and structure; we assert nothing more than what we see, when we assert that the organism as a whole exercises such power over the newly-forming limb, as makes it a repetition of its predecessor. If a leg is reproduced where there was a leg, and a tail where there was a tail; we have no alternative but to conclude that the aggregate forces of the body, control the formative processes going on in each part. And on contemplating these facts in connexion with various kindred ones, there is suggested the hypothesis, that the form of each species of organism is determined by a peculiarity in the constitution of its units—that these have a special structure in which they tend to arrange themselves; just as have the simpler units of inorganic matter. Let us glance at the evidences which more especially thrust this conclusion upon us.

A fragment of a Begonia-leaf, imbedded in fit soil and kept at an appropriate temperature, will develop a young Begonia; and so small is the fragment which is thus capable of originating a complete plant, that something like a hundred plants might be produced from a single leaf. The friend to whom I owe this observation, tells me that various succulent plants have like powers of multiplication. Illustrating a similar power among animals, we have the often-cited experiments of Trembley on the common polype. Each of the four pieces into which one of these creatures was cut, grew into a perfect individual. In each of these again, bisection and tri-section effected a like result. And so with their segments, similarly produced, until as many as fifty polypes had resulted from the original one. Bodies when cut off regenerated heads; heads regenerated bodies; and when a polype had been divided into as many pieces as was practicable, nearly every piece survived and became a complete animal. What, now, is the implication? We cannot say that in each portion of a Begonia-leaf, and in every fragment of a Hydra's body, there exists a ready-formed model of the entire organism. Even were there warrant for the now abandoned doctrine, that the germ of every organism contains the perfect organism in miniature, it still could not be contended that each considerable part of the perfect organism resulting from such a germ, contains another such miniature. Indeed the one hypothesis obviously negatives the other. We have therefore no alternative but to say, that the living particles composing one of these fragments, have an innate tendency to arrange themselves into the shape of the organism to which they belong. We must infer that a plant or animal of any species, is made up of special units, in all of which there dwells the intrinsic aptitude to aggregate into the form of that species: just as in the atoms of a salt, there dwells the intrinsic aptitude to crystallize in a particular way. It seems difficult to conceive that this can be so; but we see that it *is* so. Groups of units taken from an organism (providing they are of a certain bulk and not much differentiated into special structures) *have* this power of re-arranging themselves; and we are thus compelled to recognize the tendency to assume the specific form, as inherent in all parts of the organism. Manifestly too, if we are thus to interpret the reproduction of an organism from one of its amorphous fragments, we must thus interpret the reproduction of any minor portion of an organism by the remainder. When in place of its lost claw, a lobster puts forth from the same spot a cellular mass, which, while increasing in bulk, assumes the form and structure of the original claw; we can have no hesitation in ascribing this result to a play of forces like that which moulds the materials contained in a piece of Begonia-leaf into the shape of a young Begonia. In the one case as in the other, the vitalized molecules composing the tissues, show their proclivity towards a particular arrangement; and whether such proclivity is exhibited in reproducing the entire form, or in completing it when rendered imperfect, matters not.

For this property there is no fit term. If we accept the word polarity, as a name for the force by which inorganic units are aggregated into a form peculiar to them; we may apply this word to the analogous force displayed by organic units. But, as above admitted, polarity, as ascribed to atoms, is but a name for something of which we are ignorant—a name for a hypothetical property which as much needs explanation as that which it is used to explain. Nevertheless, in default of another word, we must employ this: taking care, however, to restrict its meaning. If we simply substitute the term polarity, for the circuitous expression—the power which certain units have of arranging themselves into a special form, we may, without assuming anything more than is proved, use the term organic polarity or polarity of the organic units, to signify the proximate cause of the ability which organisms display of reproducing lost parts.

§ 66. As we shall have frequent occasion hereafter to refer to these units, which possess the property of arranging themselves into the special structures of the organisms to which they belong; it will be well here to ask what these units are, and by what name they may be most fitly called.

On the one hand, it cannot be in those proximate chemical compounds composing organic bodies, that this specific polarity dwells. It cannot be that the atoms of albumen, or fibrine, or gelatine, or the hypothetical protein-substance, possess this power of aggregating into specific shapes; for in such case, there would be nothing to account for the unlikenesses of different organisms. Millions of species of plants and animals, more or less contrasted in their structures, are all mainly built up of these complex atoms. But if the polarities of these atoms determined the forms of the organisms they composed, the occurrence of such endlessly varied forms would be inexplicable. Hence, what we may call the *chemical units*, are clearly not the possessors of this property.

On the other hand, this property cannot reside in what may be roughly distinguished as the *morphological units*. The germ of every organism is a microscopic cell. It is by multiplication of cells that all the early developmental changes are effected. The various tissues which successively arise in the unfolding organism, are primarily cellular; and in many of them the formation of cells continues to be, throughout life, the process by which repair is carried on. But though cells are so generally the ultimate visible components of organisms, that they may with some show of reason be called the morphological units; yet, as they are not universal, we cannot say that this tendency to aggregate into specified forms dwells in them. Finding that in many cases a fibrous tissue arises out of a structureless blastema, without cell-formation; and finding that there are creatures, such as Rhizopods, which are not cellular, but nevertheless exhibit vital activities, and perpetuate in their progeny certain specific distinctions; we are forbidden to ascribe to cells this peculiar power of arrangement. Nor, indeed, were cells universal, would such an hypothesis be acceptable; since the formation of a cell is, to some extent a manifestation of this same peculiar power.

If, then, this organic polarity can be possessed neither by the chemical units nor the morphological units, we must conceive it as possessed by certain intermediate units, which we may term *physiological.* There seems no alternative but to suppose, that the chemical units combine into units immensely more complex than themselves, complex as they are; and that in each organism, the physiological units produced by this further compounding of highly compound atoms, have a more or less distinctive character. We must conclude that in each case, some slight difference of composition in these units, leading to some slight difference in their mutual play of forces, produces a difference in the form which the aggregate of them assumes.

The facts contained in this chapter, form but a small part of the evidence which thrusts this assumption upon us. We shall hereafter find various reasons for inferring that such physiological units exist, and that to their specific properties, more or less unlike in each plant and animal, various organic phenomena are due.

## CHAPTER V.

### ADAPTATION.

§ 67. In plants, waste and repair being scarcely appreciable, there are not likely to arise appreciable changes in the proportions of already-formed parts. The only divergences from the average structure of a species, which we may expect particular conditions to produce, are those producible by the action of these conditions on parts in course of formation; and such divergences we do find. We know that a tree which, standing alone in an exposed position, has a short and thick stem, has a tall and slender stem when it grows in a wood; and that its branches then take a different inclination. We know that potato-sprouts which, on reaching the light, develop into foliage, will, in the absence of light, grow to a length of several feet without foliage. And every in-door plant furnishes proof, that shoots and leaves, by habitually turning themselves to the light, exhibit a certain adaptation—an adaptation due, as we must suppose, to the special effects of the special conditions on the still growing parts. In animals, however, besides analogous structural changes wrought during the period of growth, by subjection to circumstances unlike the ordinary circumstances; there are structural changes similarly wrought, after maturity has been reached. Organs that have arrived at their full size, possess a certain modifiability; so that while the organism as a whole, retains pretty nearly the same bulk, the proportions of its parts may be considerably varied. Their variations, here treated of under the title Adaptation, depend on specialities of individual action. We saw in the last chapter, that the actions of organisms entail re-actions on them; and that specialities of action entail specialities of re-action. Here it remains to be pointed out, that the special actions and re-actions do not end with temporary changes, but work permanent changes.

If, in an adult animal, the waste and repair in all parts were exactly balanced—if each organ daily gained by nutrition, exactly as much as it lost daily by the discharge of its function—if excess of function were followed only by such excess of nutrition as balanced the extra waste; it is clear that there would occur no change in the relative sizes of organs. But there is no such exact balance. If the excess of function, and consequent excess of waste, is moderate, it is not simply compensated by repair, but more than compensated —there is a certain increase of bulk. This is true to some degree of the organism as a whole, when the organism is framed for activity. A considerable waste giving considerable power of assimilation, is more favourable to accumulation of tissue, than is quiescence with its comparatively feeble assimilation: whence results a certain adaptation of the whole organism to its requirements. But it is more especially true of the parts of an organism in relation to each other. The illustrations fall into several groups. The growth of muscles exercised to an unusual degree, is a matter of common observation. In the often-cited blacksmith's arm, the dancer's legs, and the jockey's crural adductors, we have marked examples of a modifiability which almost every one has to some extent experienced. It is needless to multiply proofs. The occurrence of changes in the structure of the skin, where the skin is exposed to a stress of function, is also familiar. That thickening of the epidermis on a labourer's palm, results from continual pressure and friction, is certain: those who have not before exerted their hands, find that such an exercise as rowing, soon begins to produce a like thickening. This relation of cause and effect is still better shown by the marked indurations at the ends of a violinist's fingers. Even in mucous membrane, which ordinarily is not subject to mechanical forces of any intensity, similar modifications are possible: witness the callosity of the gums which arises in those who have lost their teeth, and have to masticate without teeth. The vascular system furnishes good instances of the increased growth that follows increased function. When, because of some permanent obstruction to the circulation, the heart has to exert a greater contractile force on the mass of blood which it propels at each pulsation into the arteries, and when there results the laboured action known as palpitation; there usually occurs dilatation, or hypertrophy, or a mixture of the two: the dilatation, which is a yielding of the heart's structure under the increased strain, implying a failure to meet the emergency; but the hypertrophy, which consists in a thickening of the heart's muscular walls, being an adaptation of it to the additional effort required. Again, when an aneurism in some considerable artery has been obliterated, either artificially or by a natural inflammatory process; and when this artery has consequently ceased to be a channel for the blood; some of the adjacent arteries which anastomose with it, become enlarged, so as to carry the needful quantity of blood to the parts supplied. Though we have no direct proof of analogous modifications in nervous structures; yet indirect proof is given by the greater efficiency that follows greater activity. This is manifested alike in the senses and the intellect. The palate may be cultivated into extreme sensitiveness, as in professional tea-tasters. An orchestral conductor gains by continual practice, an unusually great ability to discriminate differences of sound. And in the finger-reading of the blind, we have evidence that the sense of touch may be brought by exercise to a far higher capability than is ordinary. The increase of power which habitual exertion gives to mental faculties, needs no illustration: every person of education has personal experience of it. Even from the osseous structures, evidence may be drawn. The bones of men accustomed to great muscular action, are more massive and have more strongly marked processes for the attachment of muscles, than the bones of men who lead sedentary lives; and a like contrast holds between the bones of wild and tame animals of the same species. Adaptations of another order, in which there is a qualitative rather than a quantitative modification, arise after certain accidents to which the skeleton is liable. When the hip-joint has been dislocated, and long delay has made it impossible to restore the parts to their proper places, the head of the thigh-bone, imbedded in the surrounding muscles, becomes fixed in its new position by attachments of fibrous tissue, which afford support enough to permit a halting walk. But the most remarkable modification of this order occurs in ununited fractures. "False joints" are often formed—joints which rudely simulate the hinge structure or the ball-and-socket structure, according as the muscles tend to produce a motion of flexion and extension or a motion of rotation. In the one case, according to Rokitansky, the two ends of the broken bone become smooth and covered with periosteum and fibrous tissue, and are attached by ligaments that allow a certain backward and forward motion; and in the other case, the ends, similarly clothed with the appropriate membranes, become the one convex and the other concave, are inclosed in a capsule, and are even occasionally supplied with synovial fluid!

The general truth that extra function is followed by extra growth, must be supplemented by the equally general truth, that beyond a limit, usually soon reached, very little, if any, further modification can be produced. The experiences from which we draw the one induction thrust the other upon us. After a time, no training makes the pugilist or the athlete any stronger. The adult gymnast at last acquires the power to perform certain difficult feats; but certain more difficult feats, no additional practice enables him to perform. Years of discipline give the singer a particular loudness and range of voice, beyond which further discipline does not give greater loudness or wider range: on the contrary, increased vocal exercise, causing a waste in excess of repair, is often followed by decrease of power. In the perceptions we see similar limits. The culture which exalts the susceptibility of the ear to the intervals and harmonies of notes, will not turn a bad ear into a good one. Life-long effort fails to make this artist a correct draftsman, or that a fine colourist: each does better than he did at first, but each falls short of the power attained by some other artists. Nor is this truth less clearly illustrated among the more complex mental powers. Each man has a mathematical faculty, a poetical faculty, or an oratorical faculty, which special education improves to a certain extent. But unless he is unusually endowed in one of these directions, no amount of education will make him a first-rate mathematician, a first-rate poet, or a first-rate orator. Thus the general fact appears to be, that while in each individual, certain changes in the proportions of parts, may be caused by variations of function, the congenital structure of each individual puts a limit to the modifiability of every part. Nor is this true of individuals only: it holds, in a sense, of species. Leaving open the question whether, in indefinite time, indefinite modification may not be produced; experience proves that within assigned times, the changes wrought in races of organisms by changes of conditions fall within narrow limits. We see, for instance, that though by discipline, aided by selective breeding, one variety of horse has had its locomotive power increased considerably beyond the locomotive powers of other varieties; yet that further increase takes place, if at all, at an inappreciable rate. The different kinds of dogs, too, in which different forms and capacities have been established, do not show aptitudes for diverging in the same directions at considerable rates. In domestic animals generally, certain accessions of intelligence have been produced by culture; but accessions beyond these are inconspicuous. It seems that in each species of organism, there is a margin for functional oscillations on all sides of a mean state, and a consequent margin of structural variations; that it is possible rapidly to push functional and structural changes towards the extreme of this margin in any direction, both in an individual and in a race; but that to push these changes further in any direction, and so to alter the organism as to bring its mean state up to the extreme of the margin in that direction, is a comparatively slow process.*

We have also to note that the limited increase of size produced in any organ by a limited increase of its function, is not maintained unless the increase of function is permanent. A mature man or other animal, led by circumstances into exerting particular members in unusual degrees, and acquiring extra size and power in these members, begins to lose such extra size and power on ceasing to exert these members; and eventually lapses more or less nearly into the original state. Legs strengthened by a pedestrian tour, become weak again after a prolonged return to sedentary life. The acquired ability to perform feats of skill, disappears in course of time, if the performance of them is given up. For comparative failure in executing a piece of music, in playing a game at chess, or in anything requiring special culture, the being out of practice is a reason of which every one recognizes the validity. It is observable, too, that the rapidity and completeness with which an artificial power is lost, is proportionate to the shortness of the cultivation which evoked it. One who has for many years persevered in habits which exercise special muscles or special faculties of mind, retains the extra

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* Here, as in sundry places throughout this chapter, the necessities of the argument have obliged me to forestall myself, by assuming the conclusion reached in a subsequent chapter, that modifications of structure produced by modifications of function, are transmitted to offspring.

capacity produced, to a very considerable degree, even after a long period of desistance; but one who has persevered in such habits for but a short time, has, at the end of a like period, scarcely any of the facility he had gained. Here, too, as before, successions of organisms present an analogous fact. A species in which domestication, continued through many generations, has organized certain peculiarities; and which afterwards, escaping domestic discipline, returns to something like its original habits; soon loses, in great measure, such peculiarities. Though it is not true, as alleged, that it resumes completely the structure it had before domestication; yet it approximates to that structure. The Dingo, or wild dog of Australia, is one of the instances given of this; and the wild horse of South America is another. Mankind, too, supplies us with instances. In the Australian bush, and in the backwoods of America, the Anglo-Saxon race, in which civilization has developed the higher feelings to a considerable degree, rapidly lapses into comparative barbarism: adopting the moral code, and sometimes the habits, of savages.

§ 68. It is important to reach, if possible, some rationale of these general truths—especially of the last two. A right understanding of these laws of organic modification, underlies a right understanding of the great question of species. While, as before hinted (§ 40), the action of structure on function, is one of the factors in that process of differentiation by which unlike forms of plants and animals are produced, the re-action of function on structure, is another factor. Hence, it is well worth while inquiring how far these inductions are deductively interpretable.

The first of them is the most difficult to deal with. Why an organ exerted somewhat beyond its wont, should presently grow, and thus meet increase of demand by increase of supply, is not obvious. We know, indeed, (*First Principles*, §§ 96, 133,) that of necessity, the rhythmical changes produced by antagonist organic actions, cannot any of them be carried to an excess in one direction, without there being produced an equivalent excess in the opposite direction. It is a corollary from the persistence of force, that any deviation effected by a disturbing cause, acting on some member of a moving equilibrium, must (unless it altogether destroys the moving equilibrium) be eventually followed by a compensating deviation. Hence, that excess of repair should succeed excess of waste, is to be expected. But how happens the mean state of the organ to be changed? If daily extra waste naturally brings about daily extra repair, only to an equivalent extent, the mean state of the organ should remain constant. How then comes the organ to augment in size and power?

Such answer to this question as we may hope to find, must be looked for in the effects wrought on the organism as a whole, by increased function in one of its parts. For since the discharge of its function by any part, is possible only on condition that those various other functions on which its own is immediately dependent, are also discharged; it follows that excess in its function presupposes some excess in their functions. Additional work given to a muscle, implies additional work given to the branch arteries which bring it blood, and additional work, smaller in proportion, to the arteries from which these branch arteries come. Similarly, the smaller and larger veins which take away the blood, as well as the absorbents which carry off effete products, must have more to do. And yet further, on the nervous centres which excite the muscle, a certain extra duty must fall. But excess of waste will entail excess of repair, in these parts as well as in the muscle. The several appliances by which the nutrition and excitation of an organ are carried on, must also be influenced by this rhythm of action and re-action; and therefore, after losing more than usual by the destructive process, they must gain more than usual by the constructive process. But temporarily-increased efficiency in these appliances by which blood and nervous force are brought to an organ, will cause extra assimilation in the organ, beyond that required to balance its extra expenditure. Regarding the functions as constituting a moving equilibrium, we may say, that divergence of any function in the direction of increase, causes the functions with which it is bound up to diverge in the same direction; that these again cause the functions which they are bound up with, also to diverge in the same direction; and that these divergences of the connected functions, allow the specially-affected function to be carried further in this direction than it could otherwise be —further than the perturbing force could carry it if it had a fixed basis.

It must be admitted that this is but a vague explanation. Among actions so involved as these, we can scarcely expect to do more than dimly discern a harmony with first principles. That the facts are to be interpreted in some such way, may, however, be inferred from the circumstance that an extra supply of blood continues for some time to be sent to an organ that has been unusually exercised; and that when unusual exercise is long continued, a permanent increase of vascularity results.

§ 69. Answers to the questions—Why do these adaptive modifications in an individual animal, soon reach a limit? and why, in the descendants of such animal, similarly conditioned, is this limit very slowly extended?—are to be found in the same direction as was the answer to the last question. And here the connexion of cause and consequence is much more manifest.

Since the function of any organ is dependent on the functions of the organs which supply it with materials and forces; and since the functions of these subsidiary organs are dependent on the functions of organs which supply them with materials and forces; it follows that before any great extra power of discharging its function, can be gained by a specially-exercised organ, a considerable extra power must be gained by a series of immediately-subservient organs, and some extra power by a secondary series of remotely-subservient organs. Thus there are required numerous and wide-spread modifications. Before the artery which feeds a hard-worked muscle, can permanently furnish a large additional quantity of blood, it must increase in diameter and contractile power; and that its increase of diameter and contractile power may be of use, the main artery from which it diverges, must also be so far modified as to bring this additional quantity of blood to the branch artery. Similarly with the veins; similarly with the absorbents; similarly with the nerves. And when we ask what these subsidiary changes imply, we are forced to conclude that there must be an analogous group of more numerous changes, ramifying throughout the system. The growth of the arteries primarily and secondarily implicated, cannot go to any extent, without growth in the minor blood-vessels on which their nutrition depends; while their greater contractile power involves enlargement of the nerves which excite them, and some modification of that part of the spinal cord whence these nerves proceed. Thus, without tracing the like remote alterations implied by extra growth of the veins, absorbents, and other agencies, it is manifest that a large amount of rebuilding must be done throughout the organism, before any organ of importance can be permanently increased in size and power to a great extent. Hence, though such extra growth in any part as does not necessitate considerable changes throughout the rest of the organism, may rapidly take place; a further growth in this part, requiring a remodelling of numerous parts remotely and slightly affected, must take place but slowly.

We have before found our conceptions of vital processes made clearer by studying analogous social processes. In societies there is a mutual dependence of functions, essentially like that which exists in organisms; and there is also an essentially like re-action of functions on structures. From the laws of adaptive modification in societies, we may therefore hope to get a clue to the laws of adaptive modification in organisms. Let us suppose, then, that a society has arrived at a state of equilibrium like that of a mature animal—a state not like our own, in which growth and structural development are rapidly going on; but a state of settled balance among the functional powers of the various classes and industrial bodies, and a consequent fixity in the relative sizes of such classes and bodies. Further, let us suppose that in a society thus balanced, there occurs something which throws an unusual demand on some one industry—say an unusual demand for ships (which we will assume to be built of iron) in consequence of a competing mercantile nation having been prostrated by famine or pestilence. The immediate result of this additional demand for iron ships, is the employment of more workmen, and the purchase of more iron, by the ship-builders; and when, presently, the demand continuing, the builders find their premises and machinery insufficient, they enlarge them. If the extra requirement persists, the high interest and high wages bring such extra capital and labour into the business, as are needed for new ship-building establishments. But such extra capital and labour do not come quickly; since, in a balanced community, not increasing in population and wealth, labour and capital have to be drawn from other industries, where they are already yielding the ordinary returns. Let us now go a step further. Suppose that this iron-ship-building industry, having enlarged as much as the available capital and labour permit, is still unequal to the demand; what limits its immediate further growth? The lack of ron. By the hypothesis, the iron-producing industry, like all the other industries throughout the community, yields only as much iron as is habitually required for all the purposes to which iron is applied: ship-building being only one. If, then, extra iron is required for ship-building, the first effect is to withdraw part of the iron habitually consumed for other purposes, and to raise the price of iron. Presently, the iron-makers feel this change, and their stocks dwindle. As, however, the quantity of iron required for ship-building, forms but a small part of the total quantity required for all purposes; the extra demand on the iron-makers, can be nothing like so great in proportion as is the extra demand on the ship-builders. Whence it follows, that there will be much less tendency to an immediate enlargement of the iron-producing industry—the extra quantity will for some time be obtained by working extra hours. Nevertheless, if, as fast as more iron can be thus supplied, the ship-building industry goes on growing—if, consequently, the iron-makers experience a permanently-increased demand, and out of their greater profits get higher interest on capital, as well as pay higher wages; there will eventually be an abstraction of capital and labour from other industries, to enlarge the iron-producing industry: new blast-furnaces, new rolling-mills, new cottages for workmen, will be erected. But obviously, the inertia of capital and labour to be overcome, before the iron-producing industry can grow by a decrease of some other industries, will prevent its growth from taking place until long after the increased ship-building industry has demanded it; and meanwhile, the growth of the ship-building industry must be limited by the deficiency of iron. A remoter restraint of the same nature, meets us if we go a step further—a restraint which can be overcome, only in a still longer time. For the manufacture of iron depends on the supply of coal. The production of coal being previously in equilibrium with the consumption; and the consumption of coal for the manufacture of iron, being but a small part of the total consumption; it follows that a considerable extension of the iron manufacture, when it at length takes place, will cause but a comparatively small additional demand on the coal-owners and coal-miners—a demand which will not, for a long period, suffice to cause enlargement of the coal-trade, by drawing capital and labour from other investments and occupations. And until the permanent extra demand for coal, has become great enough to draw from other investments and occupations, sufficient capital and labour to sink new mines, the increasing production of iron must be restricted by the scarcity of coal; and the multiplication of ship-yards and ship-builders, must be checked by the want of iron. Thus, in a community which has reached a state of moving equilibrium, though any one industry directly affected by an additional demand, may rapidly undergo a small extra growth; yet a growth beyond this, requiring, as it does, the building-up of subservient industries, less directly and strongly affected, as well as the partial *un*building of other industries, can take place only with comparative slowness. And a still further growth, requiring structural modifications of industries still more distantly affected, must take place still more slowly.

Returning from this analogy, we realize more clearly the truth, that any considerable member of an animal organism, cannot be greatly enlarged without some general re-organization. Besides a building-up of the primary, secondary, and tertiary groups of subservient parts, there must be an *un*building of sundry non-subservient parts;—or at any rate, there must be permanently established, a lower nutrition of such non-subservient parts. For it must be remembered that in a mature animal, or one which has reached a balance between assimilation and expenditure, there cannot be an increase in the nutrition of some organs, without a decrease in the nutrition of others; and an organic establishment of the increase, implies an organic establishment of the decrease—implies more or less change in the processes and structures throughout the entire system. And here, indeed, is disclosed one reason why growing animals undergo adaptations so much more readily than adult ones. For while there is surplus nutrition, it is possible for specially-exercised parts to be specially enlarged, without any positive deduction from other parts. There is required only that negative deduction, shown in the diminished growth of other parts.

§ 70. Pursuing the argument further, we reach an explanation of the third general truth; namely, that organisms, and species of organisms, which, under new conditions, have undergone adaptive modifications, soon return to something like their original structures, when restored to their original conditions. Seeing, as we have done, how excess of action and excess of nutrition in any part of an organism, must affect action and nutrition in subservient parts, and these again in other parts, until the re-action has divided and subdivided itself throughout the organism, affecting in decreasing degrees the more and more numerous parts more and more remotely implicated; we see that the consequent changes in the parts remotely implicated, constituting the great mass of the organism, must be extremely slow. Hence, if the need for the adaptive modification ceases, before the great mass of the organism has been much altered in its structure by these ramified but minute re-actions; we shall have a condition in which the specially-modified part, is not in equilibrium with the rest. All the remotely-affected organs, as yet but little changed, will, in the absence of the perturbing cause, resume very nearly their previous actions. The parts that depend on them, will consequently by and by do the same. Until at length, by a reversal of the adaptive process, the organ at first affected will be brought back almost to its original state. Reconsidering the above-drawn analogy between an organism and society, will enable us better to realize this necessity. If, in the case supposed, the extra demand for iron ships, after causing the erection of some additional ship-yards and the drawing of iron from other manufactures, were to cease; the old dimensions of the ship-building trade would be quickly returned to: discharged workmen would seek fresh occupations, and the new yards would be devoted to other uses. But if the increased need for ships lasted long enough, and became great enough, to cause a flow of capital and labour from other industries into the iron-manufacture, a falling off in the demand for ships, would much less rapidly entail a dwindling of the ship-building industry. For iron being now produced in greater quantity, a diminished consumption of it for ships, would cause a fall in its price, and a consequent fall in the cost of ships: thus enabling the ship-builders to meet the competition which we may suppose led to a decrease in the orders they received. And since, when new blast-furnaces and rolling-mills, &c., had been built with capital drawn from other industries, its transference back into other industries, would involve great loss; the owners, rather than transfer it, would accept unusually low interest; and an excess of iron would continue to be produced; resulting in an undue cheapness of ships, and a maintenance of the ship-building industry at a size beyond the need. Eventually, however, if the number of ships required still diminished, the production of iron in excess would become very unremunerative: some of the blast-furnaces would be blown out; and as much of the capital and labour as remained available, would be re-distributed among other occupations. Without repeating the steps of the argument, it will be clear that were the enlargement of the ship-building industry great enough, and did it last long enough, to cause an increase in the number of coal-mines; the ship-building industry would be still better able to maintain itself under adverse circumstances; but that it would, though at a more distant period, end by sinking down to the needful dimensions. Thus our conclusions are:—First, that if the extra activity and growth of a particular industry, has lasted long enough only to remodel the proximately-affected industries; it will dwindle away again after a moderate period, if the need for it disappears. Second, that an enormous period must be required before the re-actions produced by an enlarged industry, can cause a re-construction of the whole society, and before the countless re-distributions of capital and labour, can again reach a state of equilibrium. And third, that only when such a new state of equilibrium is eventually reached, can the adaptive modification become a permanent one. How, in animal organisms, the like argument will hold, needs not be pointed out. The reader will readily follow the parallel.

That organic types should be comparatively stable, might be anticipated on the hypothesis of Evolution. If we assume, as we must according to this hypothesis, that the structure of any organism is a product of the almost infinite series of actions and re-actions to which all ancestral organisms have been exposed; we shall see that any unusual actions and re-actions brought to bear on an individual, can have but an infinitesimal effect in permanently changing the structure of the organism as a whole. The new set of forces, compounded with all the antecedent sets of forces, can but inappreciably modify that moving equilibrium of functions which all these antecedent sets of forces have established. Though there may result a considerable perturbation of certain functions—a considerable divergence from their ordinary rhythms; yet the general centre of equilibrium cannot be sensibly changed. On the removal of the perturbing cause, the previous balance will be quickly restored: the effect of the new forces being almost obliterated by the enormous aggregate of forces which the previous balance expresses.

§ 71. As thus understood, the phenomena of adaptation fall into harmony with first principles. The inference that organic types are fixed, because the deviations from them which can be produced within assignable periods, are relatively small; and because, when a force producing deviation ceases, there is a return to something like the original state; proves to be an invalid inference. Without assuming fixity of species, we find good reasons for anticipating that kind and degree of stability which is observed. We find grounds for concluding, *à priori,* that an adaptive change of structure, will soon reach a point beyond which further adaptation will be slow; for concluding that when the modifying cause has been but a short time in action, the modification generated, will be evanescent; for concluding that a modifying cause acting even for many generations, will do but little towards permanently altering the organic equilibrium of a race; and for concluding that on the cessations of such cause, its effects will become unapparent in the course of a few generations.

# CHAPTER VI.

## INDIVIDUALITY.

§ 72. What is an individual? is a question which many readers will think it easy to answer. Yet it is a question that has led to much controversy among Zoologists and Botanists; and no quite satisfactory reply to it seems possible. As applied to a man, or to any one of the higher animals, which are all sharply-defined and independent, the word individual has a clear meaning; though even here, when we turn from average cases to exceptional cases—as a calf with two heads and two pairs of fore-limbs—we find ourselves in doubt whether to predicate one individuality or two. But when we extend our range of observation to the organic world at large, we find that difficulties allied to this exceptional one, meet us everywhere under every variety of form.

Each uniaxial plant may perhaps fairly be regarded as a distinct individual; though there are botanists who do not make even this admission. What, however, are we to say of a multiaxial plant? It is, indeed, usual to speak of a tree with its many branches and shoots, as singular; but strong reasons may be urged for considering it as plural. Every one of its axes has a more or less independent life, and when cut off and planted, may grow into the likeness of its parent; or by grafting and budding, parts of this tree may be developed upon another tree, and there manifest their specific peculiarities. Shall we regard all the growing axes thus resulting from slips and grafts and buds, as parts of one individual, or as distinct individuals? If a strawberry-plant sends out runners carrying buds at their ends, which strike root and grow into independent plants, that separate from the original one by decay of the runners, must we not say that they possess separate individualities; and yet if we do this, are we not at a loss to say when their separate individualities were established, unless we admit that each bud was from the beginning an individual? Commenting on such perplexities, Schleiden says—"Much has been written and disputed concerning the conception of the individual, without, however, elucidating the subject, principally owing to the misconception that still exists as to the origin of the conception. Now the individual is no conception, but the mere subjective comprehension of an actual object, presented to us under some given specific conception, and on this latter it alone depends whether the object is or is not an individual. Under the specific conception of the solar system, ours is an individual: in relation to the specific conception of a planetary body, it is an aggregate of many individuals." * * * "I think, however, that looking at the indubitable facts already mentioned, and the relations treated of in the course of these considerations, it will appear most advantageous and most useful, in a scientific point of view, to consider the vegetable cell as the general type of the plant (simple plant of the first order). Under this conception, *Protococcus* and other plants consisting of only one cell, and the spore and pollen-granule, will appear as individuals. Such individuals may, however, again, with a partial renunciation of their individual independence, combine under definite laws into definite forms (somewhat as the individual animals do in the globe of the *Volvox globator**). These again appear empirically as individual beings, under a conception of a species

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* It is now generally agreed that the *Volvox globator* is a plant.

(simple plants of the second order) derived from the form of the normal connexion of the elementary individuals. But we cannot stop here, since nature herself combines these individuals, under a definite form, into larger associations, whence we draw the third conception of the plant, from a connexion, as it were, of the second power (compound plants —plants of the third order). The simple plant proceeding from the combination of the elementary individuals is then termed a bud (*gemma*), in the composition of plants of the third order."

The animal kingdom presents still greater difficulties. When, from sundry points on the body of a common polype, there bud-out young polypes, which, after acquiring mouths and tentacles and closing up the communications between their stomachs and the stomach of the parent, finally separate from the parent; we may with propriety regard them as distinct individuals. But when, in the allied compound *Hydrozoa*, we find that these young polypes continue permanently connected with the parent; and when, by this continuous budding-out, there is presently produced a tree-like aggregation, having a common alimentary canal into which the digestive cavity of each polype opens; it is no longer so clear that these little sacs furnished with mouths and tentacles, are severally to be regarded as distinct individuals. We cannot deny a certain individuality to the polypedom. And on discovering that some of the buds, instead of unfolding in the same manner as the rest, are transformed into capsules in which eggs are developed—on discovering that certain of the incipient polypes thus become wholly dependent on the aggregate for their nutrition, and discharge functions which have nothing to do with their own maintenance, we have still clearer proof that the individualities of the members are partially merged in the individuality of the group. Other organisms belonging to the same order, display still more decidedly this transition from simple individualities to a complex individuality. In the *Diphyes* there is a special modification of one or more members of the polypedom into a swimming apparatus, which, by its rhythmical contractions, propels itself through the water, drawing the polypedom after it. And in the more differentiated *Physalia*, various organs result from the metamorphosis of parts that are the homologues of individual polypes. In this last instance, the individuality of the aggregate is so predominant, that the individualities of the members are practically lost. This combination of individualities in such way as to produce a composite individual, meets us in other forms among the ascidian molluscs. While in some of these, as in the *Clavelina*, the animals associated are but little subordinated to the community they form; in others, as in the *Botryllidæ*, they are so fused into a rounded mass, as to present the appearance of a single animal with several mouths and stomachs.

On the hypothesis of Evolution, perplexities of this nature are just such as we might anticipate. If Life in general, commenced with minute and simple forms, like those out of which all individual organisms, however complex, now originate; and if the transitions from these primordial units to organisms made up of groups of such units, and to higher organisms made up of groups of such groups, took place by degrees; it is clear that individualities of the first and simplest order, would merge gradually in those of a larger and more complex order, and these again in others of an order having still greater bulk and organization; and that hence it would be impossible to say where the lower individualities ceased, and the higher individualities commenced.

§ 73. To meet these difficulties, it has been proposed that the whole product of a single fertilized germ, shall be regarded as a single individual: whether such whole product be organized into one mass, or whether it be organized into many masses, that are partially or completely separate. It is urged that whether the development of the fertilized germ be continuous or discontinuous (§ 50) is a matter of secondary importance; that the totality of living tissue to which the fertilized germ gives rise in any one case, is the equivalent of the totality to which it gives rise in any other case; and that we must recognize this equivalence, whether such totality of living tissue takes a concrete or a discrete arrangement. In pursuance of this view, a zoological individual is constituted either by any such single animal as a mammal or bird, which may properly claim the title of a *zoon*, or by any such group of animals as the numerous *Medusæ* that have been developed from the same egg, which are to be severally distinguished as *zooids*.

Admitting it to be very desirable that there should be words for expressing these relations and this equivalence, it may still be objected, that to apply the word individual to a number of separate living bodies, is inconvenient: conflicting so much, as it does, with the ordinary conception which this word suggests. It seems a questionable use of language to say that the countless masses of *Anacharis Alsinastrum*, which, within these few years, have grown up in our rivers, canals, and ponds, are all parts of one individual; and yet as this plant does not seed in England, these countless masses, having arisen by discontinuous development, must be so regarded, if we accept the above definition.

It may be contended, too, that while it does violence to our established way of thinking, this mode of interpreting the facts is not without its difficulties—smaller, perhaps, than those it escapes, but still considerable. Something seems to be gained by restricting the application of the title individual, to organisms which, being in all respects fully developed, possess the power of producing their kind after the ordinary sexual method; and denying this title to those incomplete organisms which have not this power. But the definition does not really establish this distinction for us. On the one hand, we have cases in which, as in the working bee, the whole of the germ-product is aggregated into a single organism; and yet, though an individual according to the definition, this organism has no power of reproducing its kind. On the other hand, we have cases like that of the perfect *Aphides*, where the organism is but an infinitesimal part of the germ-product; and yet has that completeness required for sexual reproduction. Moreover, if we adopt the proposed view, we find ourselves committed to the anomalous position, that among many orders of animals, there are no concrete individuals at all. If the individual is constituted by the whole germ-product, whether continuously or discontinuously developed, then, not only must individuality be denied to each of the imperfect *Aphides*, but also to each of the perfect males and females; since no one of them is more than a minute fraction of the total germ-product. And yet further, it might be urged with some show of reason, that if the conception of individuality involves the conception of completeness; then, an organism which possesses an independent power of reproducing itself, being more complete than an organism in which this power is dependent on the aid of another organism, is more individual.

§ 74. There is, indeed, as already implied, no definition of individuality that is unobjectionable. All we can do is to make the best practicable compromise.

As applied either to an animate or an inanimate object, the word individual ordinarily connotes union among the parts of the object, and separateness from other objects. This fundamental element in the conception of individuality, we cannot with propriety ignore in the biological application of the word. That which we call an individual plant or animal, must, therefore, be some concrete whole, and not a discrete whole. If, however, we say that each concrete living whole is to be regarded as an individual, we are still met by the question—What constitutes a concrete living whole? A young organism arising by internal or external gemmation from a parent organism, passes gradually from a state in which it is an indistinguishable part of the parent organism, to a state in which it is a separate organism of like structure with the parent. At what stage does it become an individual? And if its individuality be conceded only when it completely separates from the parent, must we deny individuality to all organisms thus produced, which permanently retain their connexions with their parents? Or again, what must we say of the *Hectocotylus*, which is an arm of the Cuttle-fish that undergoes a special development, and then detaching itself, lives independently for a considerable period? And what must we say of that larval *Echinus*, which is left to move about awhile after being robbed of its viscera by the young *Echinus* developed within it?

To answer such questions, we must revert to the definition of Life. The distinction between individual in its biological sense, and individual in its more general sense, must consist in the manifestation of Life, properly so called. Life we have seen to be, "the definite combination of heterogeneous changes, both simultaneous and successive, in correspondence with external co-existences and sequences." Hence, a biological individual is any concrete whole having a structure which enables it, when placed in appropriate conditions, to continuously adjust its internal relations to external relations, so as to maintain the equilibrium of its functions. In pursuance of this conception, we must consider as individuals, all those wholly or partially independent organized masses, which arise by multicentral and multiaxial development that is either continuous or discontinuous (§ 50). We must accord the title to each separate aphis, each polype of a polypedom, each bud or shoot of a flowering plant, whether it detaches itself as a bulbil or remains attached as a branch.

By thus interpreting the facts, we do not, indeed, avoid all anomalies. While, among flowering plants, the power of independent growth and development, is usually possessed only by shoots or axes; yet, in some cases, as in that of the Begonia-leaf awhile since mentioned, the appendage of an axis, or even a small fragment of such appendage, is capable of initiating and carrying on the functions of life; and in other cases, as shown by M. Naudin in the *Drosera intermedia*, young plants are occasionally developed from the surfaces of leaves, while still connected with the parent plant. Nor among forms like the compound *Hydrozoa*, does the definition enable us to decide where the line is to be drawn between the individuality of the group and the individualities of the members—merging into each other, as these do, in different degrees. But, as before said, such difficulties must necessarily present themselves, if organic forms have arisen by insensible gradations. We must be content with a course which commits us to the smallest number of incongruities; and this course is, to consider as an individual, any centre or axis that is capable of independently carrying on that continuous adjustment of inner to outer relations which constitutes Life.

# CHAPTER VII.

## GENESIS.

§ 75. Having concluded what constitutes an individual, we are in a position to deal with the multiplication of individuals. For this, the title Genesis is here chosen, as being the most comprehensive title—the least specialized in its meaning. By some biologists, Generation has been used to signify one method of multiplication, and Reproduction to signify another method; and each of these words has been thus rendered in some degree unfit to signify multiplication in general.

Here the reader is indirectly introduced to the fact, that the production of new organisms is carried on in fundamentally unlike ways. Up to quite recent times, it was believed, even by naturalists, that all the various processes of multiplication observable in different kinds of organisms, have one essential character in common: it was supposed that in every species, the successive generations are alike. It has now been proved, however, that in plants, and in numerous animals, the successive generations are not alike; that from one generation there proceeds another whose members differ more or less in structure from their parents; that these produce others like themselves, or like their parents, or like neither; but that eventually, the original form re-appears. Instead of there being, as in the cases most familiar to us, a constant recurrence of the same form, there is a cyclical recurrence of the same form. These two distinct processes of multiplication, may be aptly termed *homogenesis* and *heterogenesis*.* Under these heads let us consider them more closely.

The kind of genesis, once supposed to be universal, in which the successive generations are alike, is always sexual genesis; or, as it has been otherwise called—*gamogenesis.* In every species of organism which multiplies by homogenesis, each generation consists of males and females; and from the fertilized germs they produce, the next generation of similar males and females arises. This method of propagation is further distinguished by the peculiarity, that each fertilized germ gives rise to but one individual—the product of development is always organized round one axis, and not round several axes. Between the different kinds of homogenesis, the most marked contrast, and the only one which need here detain us, is that between the oviparous and the viviparous. The oviparous kind is that in which the fertilized germ is detached from the parent, before it has undergone any considerable development. The viviparous kind is that in which development is considerably advanced, or almost completed, before final detachment takes place. This distinction is, however, not a sharply-defined one: there are transitions between the oviparous and the viviparous processes. In ovo-viviparous genesis, there is an internal incubation; and though the young are in this case finally detached from the parent in the shape of eggs, they do not leave the parent's body until after they have assumed something like the parental form. Looking around, we find that homogenesis is universal among the *Vertebrata:* there is no known vertebrate animal but what arises from a fertilized germ, and unites into its single individuality the whole products of this fertilized germ. In

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* Unfortunately the word *heterogenesis*, has been already used as a synonyme for "spontaneous generation." Save by those few who believe in "spontaneous generation," however, little objection will be felt to using the word in a sense that seems much more appropriate.

the mammals or highest *Vertebrata*, this homogenesis is in every case viviparous; in birds it is uniformly oviparous; and in reptiles and fishes, it is always essentially oviparous, though there are cases, of the kind above referred to, in which viviparity is simulated. Passing to the *Invertebrata*, we find oviparous homogenesis universal among the *Arachnida* (except the Scorpions, which are ovo-viviparous); universal among the higher *Crustacea*, but not among the lower; extremely general, though not universal, among Insects; and universal among the higher *Mollusca*, though not among the lower. Along with extreme inferiority among animals, we find homogenesis to be the exception rather than the rule; and in the vegetal kingdom, there appear to be no cases, save those of a few aberrant parasites like the *Rafflesiaceæ*, in which the centre or axis which arises from a fertilized germ, becomes the immediate producer of fertilized germs.

Where propagation is carried on by heterogenesis, or is characterized by unlikeness of the successive generations, there is always asexual genesis with occasionally-recurring sexual genesis; in other words—*agamogenesis* interrupted more or less frequently by *gamogenesis*. If we set out with a generation of perfect males and females; then, from their ova or seeds, there arise individuals that are neither males nor females, but that produce the next generation from buds. By this method of multiplication, many individuals originate from a single fertilized germ: the product of development is organized round more than one centre or axis. The simplest form of heterogenesis is that seen in uniaxial plants. If, as we find ourselves obliged to do, we regard each separate shoot or axis of growth, as a distinct individual; then, in uniaxial plants, the successive individuals are not represented by the series A, A, A, A, &c., like those resulting from homogenesis; but they are represented by the series A, B, A, B, A, B, &c. For in plants which were before classed as uniaxial (§ 50), and which may be conveniently so distinguished from other plants, the axis which shoots up from the seed, and substantially constitutes the plant, does not itself flower and bear seed; but gives lateral origin to flowering, or seed-bearing, axes. Though in uniaxial plants, the fructifying apparatus *appears* to be at the end of the primary, vertical axis; yet dissection shows that, morphologically considered, each fructifying axis is usually an offspring from the primary axis. There arises from the seed, a sexless individual, from which spring by gemmation, individuals having reproductive organs; and from these there result fertilized germs or seeds, that give rise to sexless individuals. That is to say, gamogenesis and agamogenesis alternate: the peculiarity being, that the sexual individuals arise from the sexless ones by continuous development. The *Salpæ* show us an allied form of heterogenesis in the animal kingdom. Individuals developed from fertilized ova, instead of themselves producing fertilized ova, produce, by gemmation, strings of individuals; from which fertilized ova again originate. In multiaxial plants, we have a succession of generations represented by the series A, B, B, B, &c., A, B, B, B, &c. Supposing A to be a flowering axis, or sexual individual; then, from any fertilized germ it casts off, there grows up a sexless individual, B; from this there bud-out other sexless individuals, B; and so on for generations more or less numerous; until at length, from some of these sexless individuals, there bud-out seed-bearing individuals of the original form A. Branched herbs, shrubs, and trees, exhibit this form of heterogenesis: the successive generations of sexless individuals thus produced, being in most cases continuously developed, or aggregated into a compound individual; but being in some cases discontinuously developed. Among animals, a kind of heterogenesis represented by the same succession of letters, occurs in such compound polypes as the *Sertularia;* and in those of the *Hydrozoa* which assume alternately the polypoid form, and the form of the *Medusa:* the chief differences presented by these groups, arising from the fact that the successive generations of sexless individuals produced by budding, are in some cases continuously developed, and in others discontinuously developed; and from the fact that, in some cases, the sexual individuals give off their fertilized germs while still growing on the parent-polypedom, but in other cases, not until after leaving the parent-polypedom and undergoing further development. Where, as in all the foregoing kinds of agamogenesis, the new individuals bud-out, not from any specialized reproductive organs, but from unspecialized parts of the parent; the process has been named, by Prof. Owen, *metagenesis.* In most instances, the individuals thus produced, grow from the outsides of the parents—the metagenesis is external. But there is also a kind of metagenesis which we may distinguish as internal. Certain *entozoa* of the genus *Distoma*, exhibit it. From the egg of a *Distoma*, there results a rudely-formed creature known to naturalists as the "King's-yellow worm." Gradually as this increases in size, the greater part of its inner substance is transformed into young animals called *Cercariæ* (which are the larvæ of *Distomata*); until at length, it becomes little more than a living sac, full of living offspring. In the *Distoma pacifica*, the brood of young animals thus arising by internal gemmation, are not *Cercariæ*, but are of the same form as their parent: themselves becoming the producers of *Cercariæ* after the same manner, at a subsequent period. So that sometimes the succession of forms is represented by the series A, B, A, B, &c.; and sometimes by the series A, B, B, A, B, B, &c. Both cases, however, exemplify internal metagenesis, in contrast with the several kinds of external metagenesis described above. That agamogenesis which is carried on in a reproductive organ—either a true ovarium or the homologue of one—has been called, by Prof. Owen, *parthenogenesis.* In his work published under this title, he embraced those cases in which the buds arising in the pseud-ovarium, are not ova in the full sense of the word; but rather, as they have since been called by Prof. Huxley, pseud-ova. Von Siebold and other naturalists, have hence applied the term parthenogenesis to a narrower class of cases. Perhaps it would be best to distinguish this process, which is intermediate between metagenesis and parthenogenesis, by the term *pseudo-parthenogenesis*. It is the process familiarly exemplified in the *Aphides*. Here, from the fertilized eggs laid by perfect females, there grow up imperfect females, in the pseud-ovaria of which there are developed pseud-ova; and these, rapidly assuming the organization of other imperfect females, are born viviparously. From this second generation of imperfect females, there by and by arises, in the same manner, a third generation, of the same kind; and so on for many generations: the series being thus symbolized by the letters A, B, B, B, B, B, &c., A. Respecting this kind of heterogenesis, it should be added, that in animals, as in plants, the number of generations of sexless individuals produced before the re-appearance of sexual ones, is indefinite; both in the sense that in the same species it may go on to a greater or less extent according to circumstances, and in the sense that among the generations of individuals proceeding from the same fertilized germ, a recurrence of sexual individuals takes place earlier in some of the diverging lines of multiplication than in others. In trees we see that on some branches, flower-bearing axes arise while other branches are still producing only leaf-bearing axes; and in the successive generations of *Aphides*, a parallel truth has been observed. Lastly has to be set down, that form of heterogenesis in which, along with gamogenesis, there occurs a form of agamogenesis exactly like it, save in the absence of fecundation. This is called true parthenogenesis—reproduction carried on by virgin mothers, which are in all respects like other mothers. In the silk-worm-moths this parthenogenesis is exceptional, rather than ordinary: usually the eggs of these insects are fertilized; but if they are not, they are still laid, and some of them produce larvæ. In certain *Lepidoptera*, however, of the groups *Psychidæ* and

*Tineidæ*, parthenogenesis appears to be a normal process—indeed, so far as is known, the only process; for of some species the males have never been found.

A general conception of the relations among the different modes of Genesis, thus briefly described, will be best given by the following tabular statement.

**Genesis** is
- Homogenesis, which is Gamogenesis
    - Oviparous
    - or
    - Ovo-viviparous
    - or
    - Viviparous
- or
- Heterogenesis, which is
    - Gamogenesis alternating with Agamogenesis
        - Parthenogenesis
        - or
        - Pseudo-parthenogenesis
        - or
        - Metagenesis
            - Internal
            - or
            - External

This, like all other classifications of such phenomena, presents anomalies. It may be justly objected, that the processes here grouped under the head agamogenesis, are the same as those before grouped under the head of discontinuous development (§ 50): thus making development and genesis partially coincident. Doubtless it seems awkward that what are from one point of view considered as structural changes, are from another point of view considered as modes of multiplication.*

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* Prof. Huxley avoids this difficulty by making every kind of Genesis a mode of development. His classification, which suggested the one given above, is as follows:—

**Development**
- **Continuous**
    - **Growth**
    - **Metamorphosis**
- **Discontinuous**
    - **Agamogenesis**
        - **Metagenesis**
        - **Parthenogenesis**
    - **Gamogenesis**

There is, however, nothing for us but a choice of imperfections. We cannot by any logical dichotomies, accurately express relations which, in Nature, graduate into each other insensibly. Neither the above, nor any other scheme, can do more than give an approximate idea of the truth.

§ 76. Genesis under every form, is a process of negative or positive disintegration; and is thus essentially opposed to that process of integration, which is one element of individual evolution. Negative disintegration occurs in those cases where, as among the compound *Hydrozoa*, there is a continuous development of new individuals by budding from the bodies of older individuals; and where the older individuals are thus prevented from growing to a greater size, or reaching a higher degree of integration. Positive disintegration occurs in those cases of agamogenesis where the formation of new individuals is discontinuous, and in all cases of gamogenesis. The degrees of disintegration are various. At the one extreme, the parent organism is completely broken up, or dissolved into new individuals; and at the other extreme, the new individual forms but a small deduction from the parent organism. *Protozoa* and *Protophyta*, show us that form of disintegration called spontaneous fission: two or four individuals being produced by the splitting-up of the original one. The *Volvox* and the *Hydrodictyon*, are plants which, having developed broods of young plants within themselves, give them exit by bursting; and among animals, the one lately referred to, which arises from the *Distoma* egg, entirely loses its individuality in the individualities of the numerous *Distoma*-larvæ with which it becomes filled. Speaking generally, the degree of disintegration becomes less marked, as we approach the higher organic forms. Plants of advanced types throw off from themselves, whether by gamogenesis or agamogenesis, parts that are relatively small; and among the higher animals, there is no case in which the parent individuality is habitually lost, in the production of new individualities. To the last, however, there is of necessity a greater or less disintegration. The seeds and pollen-grains of a flowering plant, are disintegrated portions of tissue; as are also the ova and spermatozoa of animals. And whether the fertilized germs carry away from their parents small or large quantities of nutriment, these quantities of nutriment in all cases involve further negative or positive disintegrations of the parents.

New individuals that result from agamogenesis, usually do not separate from the parent-individuals, until they have undergone considerable development, if not complete development. The agamogenetic offspring of those lowest organisms which develop centrally, do not, of course, pass beyond central structure; but the agamogenetic offspring of organisms that develop axially, commonly assume an axial structure before they become independent. The vegetal kingdom shows us this in the advanced organization of detached bulbils, and of buds that root themselves before separating. Of animals, the *Hydrozoa*, the *Trematoda*, the *Salpæ*, and the *Aphides*, present us with different kinds of agamogenesis, in all of which the new individuals are organized to a considerable extent before being cast off. This rule is not without exceptions, however. The winter-eggs of the *Plumatella*, developed in an unspecialized part of the body, present us with a case of metagenesis, in which centres of development, instead of axes, are detached; and in the above-described parthenogenesis of moths and bees, such centres are detached from an ovarium.

When produced by gamogenesis, the new individuals become independent of the parents while in the shape of centres of development, rather than axes of development; and this even where the reverse is apparently the case. The fertilized germs of those inferior plants which are central, or multicentral, in their development, are of course thrown off as centres. In the higher plants, of the two elements that go to the formation of the fertilized germ, the pollen-cell is absolutely separated from the parent-plant under the shape of a centre; and the embryo-cell, though not absolutely separated from the parent, is still no longer subordinate to the organizing forces of the parent. So that when, the embryo-cell having been fertilized by matter from the pollen-tube, the development commences, it proceeds without parental control: the new individual, though remaining physically united with the old individual, becomes structurally and functionally separate while still only a centre of development; and takes on its axial form by processes of its own—the old individual doing no more than supply materials. Throughout the animal kingdom, the new individuals produced by gamogenesis, are obviously separated in the shape of centres of development wherever the reproduction is oviparous: the only conspicuous variation being in the quantity of nutritive matter bequeathed by the parent to the new centre of development, at the time of its separation. And though, where the reproduction is viviparous, the process appears to be different, and in one sense is so; yet, intrinsically, it is the same. For in these cases, the new individual really detaches itself from the parent while still only a centre of development; but instead of being finally cast off in this state, it is re-attached, and supplied with nutriment until it assumes a more or less complete axial structure.

§ 77. Under all its various forms, the essential act in gamogenesis, is the union of two centres or cells, produced by different parent organisms: the sperm-cell being the male product, and the germ-cell the female. There are very many modes and modifications of modes in which these cells are produced; very many modes and modifications of modes by which they are brought into contact; and very many modes and modifications of modes by which the resulting fertilized germs have secured to them the fit conditions for their development. But passing over these many divergent and re-divergent kinds of sexual multiplication, which it would take too much space here to specify, the one universal peculiarity which it concerns us to remark, is, this coalescence of a detached portion of one organism, with a more or less detached portion of another.

Such protophytes as the *Palmellæ* and the *Desmidieæ*, which are sometimes distinguished as unicellular plants, show us a coalescence, not of detached portions of two organisms, but of two entire organisms: in the *Palmellæ*, conjugation is a complete fusion of the individuals; and in the *Desmidieæ*, the entire contents of the individuals unite to form the germ-mass. Where, as among the *Confervæ*, we have aggregated cells whose individualities are scarcely at all subordinate to that of the aggregate, the gamogenetic act is effected by the union of the contained granules of two adjacent cells. In *Spirogyra*, it is not adjacent cells in the same thread which thus combine; but cells of one thread with those of another. As we ascend to plants of high organization, we find that the two reproductive elements become quite distinct in their characters; and further, that they arise in different organs set apart for their production: the arrangements being such, that the sperm-cells of one plant combine with the germ-cells of another.

There is reason to think that, among the lowest *Protozoa*, a fusion of two individualities, analogous to that which occurs in the conjugation of certain *Algæ*, is the process from which results the germ of a new series of individuals. But in animals formed by the aggregation of units that are homologous with *Protozoa*, the sperm-cells and germ-cells are differentiated. And even in these humble forms, where there is no differentiation of sexes, we have good evidence that, as in all higher forms, the union is not between sperm-cells and germ-cells that have arisen in the same individual; but between those that have arisen in different individuals.

The marvellous phenomena initiated by the meeting of sperm-cell and germ-cell, naturally suggest the conception of some quite special and peculiar properties possessed by these cells. It seems obvious that this mysterious power which they display, of originating a new and complex organism, distinguishes them in the broadest way from portions of organic substance in general. Nevertheless, the more we study the evidence, the more is this assumption shaken—the more are we led towards the conclusion, that these cells have not been made by some unusual elaboration, fundamentally different from all other cells. The first fact which points to this modified conclusion, is the fact recently dwelt upon (§ 63), that in many plants and inferior animals, a small fragment of tissue that is but little differentiated, is capable of developing into the form of the organism from which it was taken. Conclusive proof obliged us to admit, that the component units of organisms, have inherent powers of arranging themselves into the forms of the organisms to which they belong. And if to these component units, which we distinguished as physiological, such powers must be conceded—if, under fit conditions, and when not much specialized, they manifest such powers in a way as marked as that in which the contents of sperm-cells and germ-cells manifest them; then, it becomes clear that the properties of sperm-cells and germ-cells are not so peculiar as we are apt to assume. Again, the organs for preparing sperm-cells and germ-cells, have none of the speciality of structure which might be looked for, did sperm-cells and germ-cells need endowing with properties essentially unlike those of all other organic agents. On the contrary, these reproductive centres proceed from tissues that are characterized by their low organization. In plants, for example, it is not appendages that have acquired considerable structure, which produce the fructifying particles: these arise at the extremities of the axes, where the degree of structure is the least. The embryo-cells are formed in the undifferentiated part of the cambium-layer; the pollen-grains are formed at the little-differentiated extremities of the stamens; and both are homologous with simple epithelium-cells. Among many inferior animals devoid of special reproductive organs, such as the *Hydra*, the ova and spermatozoa originate in the layer of indifferent tissue that lies between the endoderm and the ectoderm; that is, they consist of portions of the least specialized substance. And in the higher animals, these same generative agents appear to be merely modified epithelium-cells—cells not remarkable for their complexity of structure, but rather for their simplicity. If, by way of demurrer to this view, it is asked why other epithelium-cells do not exhibit like properties; there are two replies. The first is, that other epithelium-cells are usually so far changed to fit them to their special functions, that they are unfitted for assuming the reproductive function. The second reply is, that in some cases, where the epithelium-cells are but very little specialized, they *do* exhibit the like properties: not, indeed, by uniting with other epithelium-cells to produce new germs, but by producing new germs without such union. I learn from Dr Hooker, that the *Begonia phyllomaniaca* habitually develops young plants from the scales of its stem and leaves—nay, that many young plants are developed by a single scale. The epithelium-cells composing one of these scales, swell, here and there, into large globular cells; form chlorophyll in their interiors; shoot out rudimentary axes; and then, by spontaneous constrictions, cut themselves off; drop to the ground; and grow into Begonias. It appears, too, that in a succulent English plant, the *Malaxis paludosa*, a like process occurs: the self-detached cells being, in this case, produced by the surfaces of the leaves. Thus, there is no warrant for the assumption that sperm-cells and germ-cells possess powers fundamentally unlike those of other cells. The inference to which the facts point, is, that they differ from the rest, mainly in not having undergone modifications such as those by which the rest are adapted to particular functions. They are cells that have departed but little from the original and most general type. Or, in the words suggested by a friend, it is not that they are peculiarly specialized, but rather that they are unspecialized: such specializations as some of them exhibit in the shape of locomotive appliances, &c., being interpretable not as intrinsic, but as extrinsic, modifications, that have reference to nothing beyond certain mechanical requirements. Sundry facts tend likewise to show, that there does not exist the profound distinction which we are apt to assume, between the male and female reproductive elements. In the common polype, sperm-cells and germ-cells are developed in the same layer of indifferent tissue; and in *Tethya*, one of the sponges, Prof. Huxley has observed that they occur mingled together in the general parenchyma. The pollen-grains and embryo-cells of plants, arise in adjacent parts of the cambium-layer; and from a description of a monstrosity in the Passion-flower, recently given by Mr Salter to the Linnæan Society, it appears, both that ovules may, in their general structure, graduate into anthers, and that they may produce pollen in their interiors. All which evidence is in perfect harmony with the foregoing conclusion; since, if sperm-cells and germ-cells have natures not essentially unlike those of unspecialized cells in general, their natures cannot be essentially unlike each other.

The next general fact to be noted, is, that these cells whose union constitutes the essential act of gamogenesis, are cells in which the developmental changes have come to a close—cells which, however favourably circumstanced in respect of nutrition, are incapable of further evolution. Though they are not, as many cells are, unfitted for growth and metamorphosis by being highly specialized; yet they have lost the power of growth and metamorphosis. They have severally reached a state of equilibrium. And while the internal balance of forces prevents a continuance of constructive changes, it is readily overthrown by external destructive forces. For it uniformly happens that sperm-cells and germ-cells which are not brought in contact, disappear. In a plant, the embryo-cell, if not fertilized, is absorbed or dissipated, while the ovule aborts; and the unimpregnated ovum eventually decomposes.

Such being the characters of these cells, and such being their fates if kept apart, we have now to observe what happens when they are united. For a long time, the immediate sequence of their contact was not ascertained. This is at length, however, decided. It has been shown that in plants, the extremity of the elongated pollen-cell applies itself to the surface of the embryo-sac, but does not enter the embryo-sac. In animals, however, the process is different. Careful observers agree, that the spermatozoon passes through the limiting membrane of the ovum. The result in both cases is presumed to be a mixture of the contents of the two cells. The evidence goes to show that in plants, matter passes by osmose from the pollen-cell into the embryo-cell; and that in animals, the substance contained in the spermatozoon becomes mingled with the substance contained in the ovum, either by simple diffusion or by cell-multiplication. But the important fact which it chiefly concerns us to notice, is, that on the union of these reproductive elements, there begins, either at once or on the return of favourable conditions, a new series of developmental changes. The state of equilibrium at which each of them had arrived, is destroyed by their mutual influence; and the constructive changes which had come to a close, recommence: a process of cell-multiplication is set up; and the resulting cells presently begin to aggregate into the rudiment of a new organism.

Thus, passing over the variable concomitants of gamogenesis, and confining our attention to what is constant in it, we see:—that there is habitually, if not universally, a fusion of two portions of organic substance, which are either themselves distinct individuals, or are thrown off by distinct individuals; that these portions of organic substance, which are severally distinguished by their low degree of specialization, have arrived at states of structural quiescence or equilibrium; that if they are not united, this equilibrium ends in dissolution; but that by the mixture of them, this equilibrium is destroyed, and a new evolution initiated.

§92

§ 78. What are the conditions under which Genesis takes place? How does it happen that some organisms multiply by homogenesis, and others by heterogenesis? Why is it that where agamogenesis prevails, it is usually from time to time interrupted by gamogenesis? These are questions of extreme interest; but questions to which decisive answers cannot yet be given. In the existing state of Biology, we must be content if we can learn the direction in which answers lie. A survey of the facts, discloses certain correlations which, if not universal, are too general to be without significance.

Where the multiplication of individuals is carried on by heterogenesis, we find, in numerous cases, that agamogenesis continues as long as the forces which result in growth, are greatly in excess of the antagonistic forces. While conversely, we find that the recurrence of gamogenesis, takes place when the conditions are no longer so favourable to growth. In like manner, where there is homogenetic multiplication, new individuals are usually not formed while the preceding individuals are still rapidly growing—that is, while the forces producing growth exceed the opposing forces to a great extent; but the formation of new individuals begins when nutrition is nearly equalled by expenditure. To specify all the facts that seem to warrant these inductions, would take more space than can be here spared. A few of them must suffice.

The relation between fructification and innutrition, among plants, was long ago asserted by a German biologist—by Wolff, I am told. When, some years ago, I met with the assertion, I was not acquainted with the evidence on which it rested. Since that time, however, I have, when occasion favoured, examined into the facts for myself. The result has been a conviction, strengthened by every further inquiry, that such a relation exists. Uniaxial plants begin to produce their lateral, flowering axes, only after the main axis has developed the great mass of its leaves, and is showing its diminished nutrition by smaller leaves, or shorter internodes, or both. In multiaxial plants, two, three, or more generations of leaf-bearing axes, or sexless individuals, are produced before any seed-bearing individuals show themselves. When, after this first stage of rapid growth and agamogenetic multiplication, some gamogenetic individuals arise, they do so where the nutrition is least;—not on the main axis, or on the secondary axes, or even on the tertiary axes; but on axes that are the most removed from the channels which supply nutriment. Again, a flowering axis is commonly less bulky than the others: either much shorter, or, if long, much thinner. And further, it is an axis of which the terminal internodes are undeveloped: the foliar organs, which instead of becoming leaves become sepals, and petals, and stamens, follow each other in close succession, instead of being separated by portions of the still-growing axis. Another group of evidences meets us, when we observe the variations of fruit-bearing that accompany variations of nutrition, in the plant regarded as a whole. Besides finding, as above, that gamogenesis commences only when the luxuriance of early growth has been somewhat checked, by the extension of the remoter parts of the plant to some distance from the roots; we find that gamogenesis is induced at an earlier stage than usual, by checking the nutrition. Trees are made to fruit while still quite small, by cutting their roots, or putting them in pots; and luxuriant branches which have had the flow of sap into them diminished, by what gardeners call "ringing," begin to produce flower-shoots instead of leaf-shoots. Moreover, it is to be remarked that trees which, by flowering early in the year, seem to show a direct relation between gamogenesis and increasing nutrition, really do the reverse; for in such trees, the flower-buds are formed in the autumn—that structure which determines these buds into sexual individuals, is given when the nutrition is declining. Conversely, very high nutrition in plants, prevents, or arrests, gamogenesis. It is notorious that unusual richness of soil, or too large a quantity of manure, results in a continuous production of leaf-bearing, or sexless, shoots. Besides being prevented from producing sexual individuals, by excessive nutrition, plants are, by excessive nutrition, made to change the sexual individuals they were about to produce, into sexless ones. This arrest of gamogenesis may be seen in various stages. The familiar instance of flowers made barren by the transformation of their stamens into petals, shows us the lowest degree of this reversed metamorphosis. Where the petals and stamens are partially changed into green leaves, the return from the gamogenetic structure towards the agamogenetic structure, is more marked; and it is still more marked when, as occasionally happens in luxuriantly-growing plants, new flowering axes, and even leaf-bearing axes, grow out of the centres of flowers.* The anatomical

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* Among various examples of this which I have observed, some of the most remarkable were among Foxgloves, growing in great numbers and of large size, in a wood between Whatstandwell Bridge and Crich, in Derbyshire. In one case, the lowest flower on the stem, contained, in place of a pistil, a shoot or spike of flower-buds, similar in structure to the embryo-buds of the main spike. I counted seventeen buds on it; of which the first had three stamens, but was otherwise normal; the second had three; the third, four; the fourth, four; &c. Another plant, having more varied monstrosities, evinced excess of nutrition with equal clearness. The following are the notes I took of its structure:—1st, or lowest flower on the stem, very large; calyx containing eight divisions, one partly transformed into a corolla, and another transformed into a small bud with bract (this bud consisted of a five-cleft calyx, four sessile anthers, a pistil, and a rudimentary corolla); the corolla of the main flower, which was complete, contained six stamens, three of them bearing anthers, two others being flattened and coloured, and one rudimentary; there was no pistil, but, *in place of it*, a large bud, consisting of a three-cleft calyx, of which two divisions were tinted at the ends, an imperfect corolla, marked internally with the usual purple spots and hairs, three anthers sessile on this mal-formed corolla, a pistil, a seed-vessel with ovules, and, growing to it, another bud of which the structure was indistinct. 2nd flower, large; calyx of seven divisions, one being transformed into a bud

structure of the sexual axis, affords corroborative evidence: giving very much the impression, as it does, of an aborted sexless axis. Besides lacking those internodes which the leaf-bearing axis commonly possesses, the flowering axis differs by the absence of rudimentary lateral axes. In a leaf-bearing axis, the axil of every leaf usually contains a small bud, which may or may not develop into a lateral axis; but though the petals of a flower are homologous with leaves, they do not bear homologous buds at their bases. Ordinarily, too, the foliar appendages of sexual axes, are much smaller than those of sexless ones—the stamens and pistils especially, which are the last formed, being extremely dwarfed; and there is even reason for thinking that the absence of chlorophyll from the parts of fructification, is a fact of like meaning. Moreover, the formation of the seed-vessel appears to be a direct consequence of arrested nutrition. If a gloved-finger be taken to represent a growing shoot, (the finger standing for the core of the shoot, and the glove for the cambium-layer, in which the process of growth takes place); and if it be supposed that there is a diminished supply of material for growth; then, it seems a fair inference, that growth will first cease at the apex of the cambium-layer, represented by the end of the glove-finger; and supposing growth to continue in those parts of the cambium-layer that are nearer to the supply of nutriment, their further longitudinal extension will lead to the formation of a cavity at the extremity of the shoot, like that which results in a glove-finger when the finger is partially withdrawn and the glove sticks to its end. Whence it seems,

with bract, but much smaller than the other; corolla large but cleft along the top; six stamens with anthers, pistil, and seed-vessel. 3rd flower, large; six-cleft calyx, cleft corolla, with six stamens, pistil, and seed-vessel, with a second pistil half unfolded at its apex. 4th flower, large; divided along the top, six stamens. 5th flower, large; corolla divided into three parts, six stamens. 6th flower, large; corolla cleft, calyx six-cleft, the rest of the flower normal. 7th, and all succeeding flowers, normal.

both that this introversion of the cambium-layer may be considered as due to failing nutrition, and that the ovules growing from its introverted surface (which would have been its outer surface but for the defective nutrition) are extremely aborted homologues of external appendages—either leaves or lateral axes: the essential organs of fructification thus arising where the defective nutrition has reached its extreme.* To all which let us not forget to add, that the sperm-cells and germ-cells are formed at the very ends of the organs of fructification.

Those kinds of animals which multiply by heterogenesis, present us with a parallel relation between the recurrence of gamogenesis and the recurrence of conditions unfavourable to growth—at least, this is shown where experiments have thrown light on the connexion of cause and effect; namely, among the *Aphides*. These creatures, hatched from eggs in the spring, multiply by agamogenesis throughout the summer. When the weather becomes cold, and plants no longer afford abundant sap, perfect males and females are produced; and from gamogenesis there result fertilized ova. But now observe that beyond this evidence, we have much more conclusive evidence. For it has been shown, both that the rapidity of the agamogenesis is proportionate to the warmth and nutrition, and that if the temperature and

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* It appears that botanists do not agree respecting the homologies of the ovules: some thinking that they are rudimentary foliar organs, and others that they are rudimentary axial organs. Possibly the dispute will prove a bootless one; since there seems evidence that ovules may be transformed into either one or the other. Mr Salter's paper, lately referred to, shows that they may graduate into stamens, which are foliar organs; and the case of the Foxglove, which I have described above, shows that they may develop into flower-buds, which are axial organs. I would venture to suggest, that the conflicting evidence can be reconciled, only by regarding ovules as the homologues of lateral appendages; and considering a lateral appendage as composed of a leaf, plus a rudimentary axis, either of which may abort. This is the view which seems countenanced by development; since, in its first stage, a lateral bud, whence a lateral appendage arises, shows no division into rudimentary leaf and rudimentary axis; and it is to the lateral bud in this first stage, that the seed-bud or ovule is homologous.

supply of food be artificially maintained, the agamogenesis continues through the winter. Nay more—it not only, under these conditions, continues through one winter, but it has been known to continue for four successive years: some forty or fifty sexless generations being thus produced. And those who have investigated the matter, see no reason to doubt the indefinite continuance of this agamogenetic multiplication, so long as the external requirements are duly met. Evidence of another kind, which points very distinctly to the same conclusion, is furnished by the heterogenesis of the *Daphnia*—a small crustacean commonly known as the Water-flea, which inhabits ponds and ditches. From the nature of its habitat, this little creature is exposed to very variable conditions. Besides being frozen up in winter, the small bodies of water in which it lives, are often unduly heated by the summer sun, or dried up by continued drought. The circumstances favourable to the *Daphnia's* life and growth, being thus liable to interruptions which, in our climate, have a regular irregularity of recurrence; we may, in conformity with the hypothesis, expect to find both that the gamogenesis recurs along with evidence of declining nutrition, and that its recurrence is very variable. This we do find. From Mr Lubbock's paper on the *Daphnia* in the "Philosophical Transactions" for 1857, and from further information which he has been good enough to furnish me, the following general facts are deducible:—First, that in each ovarium, along with the rudiments of agamic eggs, or eggs which, if developed, produce young by true parthenogenesis, there usually, if not always, exists the rudiment of an ephippial egg; which, from sundry evidences, is inferred to be a sexual or gamic egg. Second, that according to circumstances, either agamogenesis or gamogenesis takes place; but that if the agamic eggs develop, the rudimentary gamic egg disappears, or becomes absorbed; and conversely, if the gamic egg develops, the agamic eggs disappear, or are absorbed by it. Third, that the brood of agamic eggs contained in each ovarium, amounts, under favourable circumstances, to as many as eight or nine; while of the gamic eggs, only one at a time is produced in each ovarium, and occasionally one of the ovaria produces none: whence it follows, that as the gamic egg is not more than twice the bulk of the agamic egg, the quantity of matter contained in an agamic brood, is four times, and occasionally even eight times, as great as that contained in a gamic brood. Thus the quantity of nutriment expended in gamogenesis during a given period (making allowance for that which goes to the formation of the ephippium), is far less than that expended in agamogenesis during a like period. Seeing, then, this constant preparation for either gamic or agamic genesis, in a creature liable to such irregular variations of nutrition; and seeing that the agamogenesis implies by its amount, a large excess of nutrition, while the gamogenesis implies by its amount, a small excess of nutrition; we can scarcely doubt that the one or the other mode of multiplication occurs, according as the external conditions are or are not favourable to nutrition.

Passing now to animals which multiply by homogenesis—animals in which the whole product of a fertilized germ aggregates round a single centre or axis, instead of round many centres or axes; we see, as before, that so long as the conditions allow rapid increase in the mass of this germ-product, the formation of new individuals by gamogenesis does not take place. Speaking generally, we find that only when growth is declining in relative rapidity, do perfect sperm-cells and germ-cells begin to appear; and that the fullest activity of the reproductive function, arises as growth ceases—speaking generally, we must say, because, though this relation is tolerably definite in the highest orders of animals which multiply by gamogenesis, it is less definite in the lower orders. This admission does not militate against the hypothesis, as it seems to do; for the indefiniteness of the relation occurs where the limit of growth is comparatively indefinite. We saw (§ 46) that among active, hot-blooded creatures, such as mammals and birds, the inevitable balancing of assimilation by expenditure, establishes, for each species, an almost uniform adult size; and among creatures of these kinds, (birds especially, in which this restrictive effect of expenditure is most conspicuous), the connexion between cessation of growth and commencement of reproduction, is distinct. But we also saw (§ 46) that where, as in the Crocodile and the Pike, the conditions and habits of life are such, that expenditure does not overtake assimilation as the size increases, there is no precise limit of growth; and in creatures thus circumstanced, we may naturally look for a comparatively indeterminate relation between declining growth and commencing reproduction.* There is, indeed, among fishes, at least one case which appears very anomalous. The male parr, or young of the male salmon, a fish of four or five inches in length, is said to produce milt. Having, at this early stage of its growth, not one hundredth of the weight of a full-grown salmon, how does its production of milt consist with the alleged general law? The answer must be in a great measure hypothetical. If the salmon is (as it appears in its young state) a species of fresh-water trout, that has contracted the habit of annually migrating to the sea, where it finds a food on which it thrives—if the original size of this species was not much greater than that of the parr (which is nearly as large as some varieties of lake-trout and river-trout)—and if the limit of growth in the trout tribe is very indefinite, as we know it to be; then we may reasonably infer, that the parr has nearly the adult form and size of this species of trout, before it acquired its migratory habit; and that this production of milt, is,

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* I owe to Mr Lubbock an important confirmation of this view. After stating his belief, that between Crustaceans and Insects, there exists a physiological relation analogous to that which exists between water-vertebrata and land-vertebrata; he pointed out to me, that while among Insects, there is a definite limit of growth, and an accompanying definite commencement of reproduction, among Crustaceans, where growth has no definite limit, there is no definite relation between the commencement of reproduction and the decrease or arrest of growth.

in such case, a concomitant of the incipient decline of growth naturally arising in the species, when living under the conditions of its remote ancestors. If this be admitted, the immense subsequent growth of the parr into the salmon, must be regarded as due to a suddenly-increased facility in obtaining food—a facility which removes to a great distance the limit at which assimilation is balanced by expenditure; and which has the effect, analogous to that produced in plants, of arresting the incipient reproductive process, and causing a resumption of growth. A confirmation of this view may be drawn from the fact, that when the parr, after its first migration to the sea, returns to fresh water, having increased in a few months from a couple of ounces to five or six pounds, it no longer shows any fitness for propagation: the grilse, or immature salmon, does not produce milt or spawn. But without citing further illustrations, or attempting to meet further difficulties, it has, I think, been made sufficiently clear, that some such connexion as that alleged, exists. Traversed, as is this relation between commencement of sexual reproduction and declining rate of growth, by various other relations, it is quite as manifest as we can expect it to be.

The general law to which both homogenesis and heterogenesis conform, thus appears to be, that the products of a fertilized germ go on accumulating by simple growth, so long as the forces whence growth results are greatly in excess of the antagonist forces; but that when diminution of the one set of forces, or increase of the other, causes a considerable decline in this excess, and an approach towards equilibrium, fertilized germs are again produced. Whether the germ-product be organized round one axis, or round the many axes that arise by agamogenesis—whether the development be continuous or discontinuous; matters not. Whether, as in concrete organisms like the higher animals, this approach to equilibrium results from that disproportionate increase of expenditure entailed by increase of size; or whether, as in partially and wholly discrete organisms, like most plants and many inferior animals, this approach to equilibrium results from absolute or relative decline of nutrition; matters not. In any case, the recurrence of gamogenesis is associated with a more or less marked decrease in the excess of tissue-producing power. We cannot say, indeed, that a decrease in this excess always results in gamogenesis; for we have evidence to the contrary, in the fact that some organisms multiply for an indefinite period by agamogenesis only. Thus, the weeping willow, which has been propagated throughout Europe, does not seed in Europe; and yet, as the weeping willow, by its large size and the multiplication of generation upon generation of lateral axes, presents the same causes of local innutrition as other trees, we cannot ascribe the absence of sexual axes to the continued predominance of nutrition. Among animals, too, the anomalous case of the *Tineidæ*, a group of moths in which parthenogenetic multiplication goes on for generation after generation, shows us that gamogenesis does not necessarily result from an approximate balance of assimilation by expenditure. What we must say, is, that an approach towards equilibrium between the forces which cause growth and the forces which oppose growth, is the chief condition to the recurrence of gamogenesis; but that there are other unknown conditions, in the absence of which this approach to equilibrium is not followed by gamogenesis.

See § 92

§ 79. The above induction is an approximate answer to the question—*When* does gamogenesis recur? but not to the question which was propounded—*Why* does gamogenesis recur?—*Why* cannot multiplication be carried on in all cases, as it is in many cases, by agamogenesis? As already said, biologic science is not yet advanced enough to reply. Meanwhile, the evidence above brought together, suggests a certain hypothetical answer, which it may be well to set down.

Seeing as we do, on the one hand, that gamogenesis recurs only in individuals that are approaching towards a state of organic equilibrium; and seeing, on the other hand, as we do, that the sperm-cells and germ-cells thrown off by such individuals, are cells in which developmental changes have ended in quiescence, but in which, after their union, there arises a process of active cell-formation; we may suspect that the approach towards a state of general equilibrium in such gamogenetic individuals, is accompanied by an approach towards molecular equilibrium in them; and that the need for this union of sperm-cell and germ-cell, is the need for overthrowing this equilibrium, and re-establishing active molecular change in the detached germ—a result which is probably effected by mixing the slightly different physiological units of slightly different individuals. The several arguments that may be brought in support of this view, cannot be satisfactorily set forth until after the topics of Heredity and Variation have been dealt with. Leaving it for the present, I propose hereafter to reconsider this question, in connexion with sundry others that are raised by the phenomena of Genesis.

Before ending the chapter, however, it may be well to note the relations between these different modes of multiplication, and the conditions of existence under which they are respectively habitual. While the explanation of the teleologist is untrue, it is often an obverse to the truth; for though, on the hypothesis of Evolution, it is clear that things are not arranged thus or thus for the securing of special ends, it is also clear, that arrangements which *do* secure these special ends, tend continually to establish themselves—are established by their fulfilment of these ends. Besides insuring a structural fitness between each kind of organism and its circumstances, the working of "natural selection" also insures a fitness between the mode and rate of multiplication of each kind of organism and its circumstances. We may, therefore, without any teleological implication, consider the fitness of homogenesis and heterogenesis to the needs of the different classes of organisms which exhibit them.

One of the facts to be observed, is, that heterogenesis prevails among organisms of which the food, though abundant compared with their expenditure, is dispersed in such a way that it cannot be appropriated in a wholesale manner. *Protophyta*, subsisting on diffused gases and decaying organic matter in a state of minute subdivision; and *Protozoa*, to which food comes in the shape of extremely small floating particles; are enabled by their rapid agamogenetic multiplication, to obtain materials for growth, better than they would do did they not thus continually divide and disperse in pursuit of it. The higher plants, having for nutriment the carbonic acid of the air and certain mineral components of the soil, show us modes of multiplication adapted to the fullest utilization of these substances. A herb, with but little power of forming the woody-fibre requisite to make a stem that can support wide-spreading branches, after producing a few sexless axes, produces sexual ones; and maintains its race better by the consequent early dispersion of seeds, than by a further production of sexless axes. But a tree, able to lift its successive generations of sexless axes high into the air, where each axis gets carbonic acid and light almost as freely as if it grew by itself, may with advantage go on budding-out sexless axes year after year; since it thereby increases its subsequent power of budding-out sexual axes. Meanwhile, it may advantageously transform into seed-bearers, those axes which, in consequence of their less direct access to materials absorbed by the roots, are failing in their nutrition; for in doing this, it is throwing-off from a point at which sustenance is deficient, a migrating group of germs that may find sustenance elsewhere. The heterogenesis displayed by animals of the Cœlenterate type, has evidently a like utility. A polype, feeding on minute annelids and crustaceans, which, flitting through the water, come in contact with its tentacles;

and limited to that quantity of prey which chance brings within its grasp; buds out young polypes which, either as a colony or as dispersed individuals, spread their tentacles through a larger space of water than the parent alone can; and by producing them, the parent better insures the continuance of its species, than it would do if it went on slowly growing until its nutrition was nearly balanced by its waste, and then multiplied by gamogenesis. Similarly with the *Aphis*. Living on sap sucked through its proboscis from tender shoots and leaves, and able thus to take in but a very small quantity in a given time, this creature's race is more likely to be preserved by a rapid asexual propagation of small individuals, which disperse themselves over a wide but nowhere rich area of nutrition, than it would be did the individual growth continue so as to produce large individuals multiplying sexually. While at the same time we see, that when autumnal cold and diminishing supply of sap, put a check to growth, the recurrence of gamogenesis, and production of fertilized ova that remain dormant through the winter, is more favourable to the preservation of the race, than would be a further continuance of agamogenesis. On the other hand, it is obvious that among the higher animals, living on food which, though dispersed, is more or less aggregated into large masses, this alternation of gamic and agamic reproduction ceases to be useful. The development of the germ-product into a single organism of considerable bulk, is in many cases a condition without which these large masses of nutriment could not be appropriated; and here the formation of many individuals instead of one, would be fatal. But we still see the beneficial results of the general law—the postponement of gamogenesis until the rate of growth begins to decline. For so long as the rate of growth continues rapid, it is a proof that the organism gets food with great facility—that expenditure is not such as seriously to check accumulation; and that the size reached is as yet not disadvantageous—or rather, indeed, that it is advantageous. But when the rate of growth is much decreased by the comparatively rapid increase of expenditure—when the excess of assimilative power is diminishing in such a way as to indicate its approaching disappearance; it becomes needful for the maintenance of the species, that this excess shall be turned to the production of new individuals; since, did growth continue until this excess disappeared through the complete balancing of assimilation and expenditure, the production of new individuals would be either impossible or fatal to the parent. And it is clear that "natural selection" will continually tend to determine the period at which gamogenesis commences, in such a way as most favours the maintenance of the race.

Here, too, may fitly be pointed out the fact, that, by "natural selection," there will in every case be produced, the most advantageous proportion of males and females. If the conditions of life are such as to render a greater or less inequality of the sexes beneficial to the species, in respect either of the number of the offspring, or the character of the offspring; then, those varieties of the species which, from any cause, approach more than other varieties towards this beneficial degree of inequality, will be apt to supplant other varieties. And conversely, where equality in the number of males and females is beneficial, the equilibrium will be maintained by the dying out of such varieties as produce offspring among which the sexes are not balanced.

# CHAPTER VIII.

## HEREDITY.

§ 80. Already, in the last two chapters, the law of hereditary transmission has been tacitly assumed; as, indeed, it unavoidably is in all such discussions. Understood in its entirety, the law is, that each plant or animal produces others of like kind with itself: the likeness of kind consisting, not so much in the repetition of individual traits, as in the assumption of the same general structure. This truth has been rendered so familiar by daily illustration, as almost to have lost its significance. That wheat produces wheat—that existing oxen have descended from ancestral oxen—that every unfolding organism eventually takes the form of the class, order, genus, and species from which it sprang; is a fact which, by force of repetition, has acquired in our minds almost the aspect of a necessity. It is in this, however, that Heredity is principally displayed: the phenomena commonly referred to it, being quite subordinate manifestations. And, as thus understood, Heredity is universal. The various instances of heterogenesis lately contemplated, seem, indeed, to be at variance with this assertion. But they are not really so. Though the recurrence of like forms, is, in these instances, not direct but cyclical, still, the like forms do recur; and when taken together, the group of forms produced during one of the cycles, is as much like the groups produced in preceding cycles, as the single individual arising by homogenesis, is like ancestral individuals.

While, however, the general truth that organisms of a given type uniformly descend from organisms of the same type, is so well established by infinite illustrations, as to have assumed the character of an axiom; it is not universally admitted that non-typical peculiarities are inherited. While the botanist would be so incredulous if told that a plant of one class had produced a plant of another class, or that from seeds belonging to one order individuals belonging to another order had grown, that he would deem it needless to examine the evidence; and while the zoologist would treat with contempt the assertion, that from the egg of a fish a reptile had arisen, or that an implacental mammal had borne a placental mammal, or that an unguiculate quadruped had sprung from an ungulate quadruped, or even that from individuals of one species offspring of an allied species had proceeded; yet there are botanists and zoologists who do not consider it certain, that the minor specialities of organization are transmitted from one generation to another. Some naturalists seem to entertain a vague belief, that the law of Heredity applies only to main characters of structure, and not to details; or, at any rate, that though it applies to such details as constitute differences of species, it does not apply to smaller details. The circumstance that the tendency to repetition, is in a slight degree qualified by the tendency to variation (which, as we shall hereafter see, is but an indirect result of the tendency to repetition), leads some to doubt whether Heredity is unlimited. A careful weighing of the evidence, however, and a due allowance for the influences by which the minuter manifestations of Heredity are obscured will remove the grounds for this scepticism.

First in order of importance, comes the fact, that not only are there uniformly transmitted from an organism to its offspring, those traits of structure which distinguish the class, order, genus, and species; but also those which distinguish the variety. We have numerous cases, among both plants and animals, where, by natural or artificial conditions, there have been produced divergent modifications of the same species; and abundant proof exists that the members of any one sub-species, habitually transmit their distinctive peculiarities to their descendants. Agriculturists and gardeners can furnish unquestionable illustrations. Several varieties of wheat are known; of which each reproduces itself. Since its introduction into England, there have been formed from the potato, a number of sub-species: some of them differing greatly in their forms, sizes, qualities, and periods of ripening. Of peas, also, the like may be said. And the case of the cabbage-tribe, is often cited as showing the permanent establishment of races that have diverged widely from a common stock. Among fruits and flowers, the multiplication of kinds, and the continuance of each kind with certainty by agamogenesis, and to some extent by gamogenesis, might be exemplified without end. From all sides evidence may be gathered showing a like persistence of varieties in each species of animal. We have our distinct breeds of sheep, our distinct breeds of cattle, our distinct breeds of horses: each breed maintaining its characteristics. The several sorts of dogs, which, if we accept the physiological test, we must consider as all of one species, show us in a marked manner the hereditary transmission of small differences—each sort, when kept pure, reproducing itself not only in size, form, colour, and quality of hair, but also in disposition and speciality of intelligence. Rabbits, too, have their permanently-established races. And in the Isle of Man, we have a tail-less kind of cat. Even in the absence of other evidence, that which ethnology furnishes would suffice. Grant them to be derived from one stock, and the varieties of man yield proof upon proof that non-specific traits of structure are bequeathed from generation to generation. Or grant only that there is evidence of their derivation from several stocks, and we still have, between races descended from a common stock, distinctions which prove the inheritance of minor peculiarities. Besides seeing that negroes continue to produce negroes, copper-coloured men to produce men of a copper colour, and the fair-skinned races to perpetuate their fair skins—besides seeing that the broad-faced and flat-nosed Calmuck begets children with broad faces and flat noses, while the Jew bequeaths to his offspring the features which have so long characterized Jews; we see that those small unlikenesses which distinguish more nearly-allied varieties of men, are maintained from generation to generation. In Germany, the ordinary shape of skull is appreciably different from that common in Britain: near akin though the Germans are to the British. The average Italian face continues to be unlike the faces of northern nations. The French character is now, as it was centuries ago, contrasted in sundry respects with the characters of neighbouring peoples. Nay, even between races so closely allied as the Scotch Celts, the Welch Celts, and the Irish Celts, appreciable differences of form and nature have become established.

That sub-species and sub-sub-species, thus exemplify that same general law of inheritance which shows itself in the perpetuation of ordinal, generic, and specific peculiarities; is strong reason for the belief that this general law is unlimited in its application. In addition to the warrant which this belief derives from evidence of this kind, it has also the support of still more special evidence. Numerous illustrations of Heredity are yielded by experiment, and by direct observation of successive generations. They are divisible into two classes. In the one class come cases where congenital peculiarities, not traceable to any obvious causes, are bequeathed to descendants. In the other class come cases where the peculiarities thus bequeathed are not congenital, but have resulted from changes of functions during the lives of the individuals bequeathing them. We will consider first the cases that come in the first class.

§ 81. Note at the outset the character of the chief testimony. Excluding those inductions that have been so fully verified as to rank with exact science, there are no inductions so trustworthy as those which have undergone the mercantile test. When we have thousands of men whose profit or loss depends on the truth of the inferences they draw from simple and perpetually-repeated observations; and when we find that the inference arrived at, and handed down from generation to generation of these deeply-interested observers, has become an unshakable conviction; we may accept it without hesitation. In breeders of animals we have such a class, led by such experiences, and entertaining such a conviction—the conviction that minor peculiarities of organization are inherited as well as major peculiarities. Hence the immense prices given for successful racers, bulls of superior forms, sheep that have certain desired peculiarities. Hence the careful record of pedigrees of high-bred horses and sporting dogs. Hence the care taken to avoid intermixture with inferior stocks. Citing the highest authorities respecting the effects of breeding from animals having certain superiorities, with the view of propagating those superiorities, Mr Darwin writes:—"Youatt, who was probably better acquainted with the works of agriculturists than almost any other individual, and who was himself a very good judge of an animal, speaks of the principle of selection as 'that which enables the agriculturist not only to modify the character of his flock, but to change it altogether. It is the magician's wand, by means of which he may summon into life whatever form and mould he pleases.'" Lord Somerville, speaking of what breeders have done for sheep, says:—"It would seem that they had chalked upon a wall a form perfect in itself and then given it existence." That most skilful breeder, Sir John Sebright, used to say, with respect to pigeons, that "he would produce any given feather in three years, but it would take him six years to obtain head and beak." In all which statements the tacit assertion is, that individual traits are bequeathed from generation to generation; and that when they are not brought into conflict with opposite traits, they may be so perpetuated and increased as to become permanent distinctions.

Of special instances, there are many besides that of the often-cited Otter-breed of sheep, descended from a single short-legged lamb, and that of the six-fingered Gratio Kelleia, who transmitted his peculiarity in different degrees, to several of his children and to some of his grandchildren. In a paper contributed to the *Edinburgh New Philosophical Journal* for July 1863, Dr Struthers gives several cases of hereditary digital variations. Esther P—, who had six fingers on one hand, bequeathed this malformation, along some lines of her descendants, for two, three, and four generations. A— S— inherited an extra digit on each hand and each foot from his father; and C— G—, who also had six fingers and six toes, had an aunt and a grandmother similarly formed. A collection of evidence has been made by Mr Sedgwick, and published by him in the *Medico-Chirurgical Review* for April and for July 1863, in two articles on "The Influence of Sex in limiting Hereditary Transmission." From these articles are selected the following cases and authorities:—Augustin Duforet, a pastry-cook of Douai, who had but two instead of three phalanges to all his fingers and toes, inherited this malformation from his grandfather and father, and had it in common with an uncle and numerous cousins. An account has been given by Dr Lepine, of a man with only three fingers on each hand and four toes on each foot, and whose grandfather and son exhibited the like anomaly. Béchet describes Victoire Barré as a woman who, like her father and sister, had but one developed finger on each hand, and but two toes on each foot, and whose monstrosity re-appeared in two daughters. And there is a case where the absence of two distal phalanges on the hands was traced for two generations. The various recorded instances in which there has been transmission from one generation to another, of webbed-fingers, of webbed-toes, of hare-lip, of congenital luxation of the thigh, of absent patellæ, of club-foot, &c., would occupy more space than can here be spared. Defects in the organs of sense are also not unfrequently inherited. Four sisters, their mother, and grandmother, are described by Duval as similarly affected by cataract. Prosper Lucas details an example of hereditary amaurosis affecting the females of a family for three generations. Duval, Graffe, Dufon, and others testify to like cases coming under their observation.* Deafness, too, is occasionally transmitted from parent to child. There are deaf-mutes whose imperfections have been derived from ancestors; and malformations of the external ears have also been perpetuated in offspring. Of transmitted peculiarities of the skin and its appendages, many illustrations have been noted. One is that of a family remarkable for enormous black eyebrows; another that of a family in which every member had a lock of hair of a lighter colour than the rest on the top of the head; and there are also instances of congenital baldness being hereditary. Entire absence of teeth, absence of particular teeth, and anomalous arrangements of teeth, are recorded as traits that have descended to children. And we have evidence that soundness and unsoundness of teeth are transmissible.

The inheritance of such diseases as gout, consumption, and insanity, is universally admitted. Among the less-common diseases of which the descent from one generation to another has been observed, are, ichthyosis, leprosy, pityriasis, sebaceous tumours, plica polonica, dipsomania, somnambulism, catalepsy, epilepsy, asthma, apoplexy, elephantiasis. General nervousness displayed by parents, almost always re-appears in their children. Even a bias towards suicide appears to be sometimes hereditary.

§ 82. To prove the transmission of those structural peculiarities that have resulted from functional peculiarities, is,

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* While this chapter is passing through the press, I learn from Mr White Cooper, that not only are near sight, long sight, dull sight, and squinting, hereditary; but that a peculiarity of vision confined to one eye, is frequently transmitted—re-appearing in the same eye in offspring.

for several reasons, comparatively difficult. Changes produced in the sizes of parts by changes in their amounts of action, are mostly unobtrusive. A muscle that has increased in bulk, is so obscured by natural or artificial clothing, that unless the alteration is extreme it passes without remark. Such nervous developments as are possible in the course of a single life, cannot be seen externally. Visceral modifications of a normal kind, are observable but obscurely, or not at all. And if the changes of structure worked in individuals by changes in their habits, are thus difficult to trace; still more difficult to trace must be the transmission of them—further hidden, as this is, by the influence of other individuals that are often otherwise modified by other habits. Moreover, such specialities of structure as are due to specialities of function, are usually entangled with specialities of structure that are, or may be, due to selection, natural or artificial. In the majority of cases, it is impossible to say that a structural peculiarity which seems to have arisen in offspring from a functional peculiarity in the parent, is wholly independent of some congenital peculiarity of structure in the parent, which induced this functional peculiarity. We are restricted to cases with which natural or artificial selection can have had nothing to do; and such cases are difficult to find. Some, however, may here be noted.

A species of plant that has been transferred from one soil or climate to another, frequently undergoes what botanists call "a change of habit"—a change which, without affecting its specific characters, is yet conspicuous. In its new locality, the species is distinguished by leaves that are much larger, or much smaller, or differently shaped, or more fleshy; or instead of being, as before, comparatively smooth, it becomes hairy; or its stem becomes woody instead of being herbaceous; or its branches, no longer growing upwards, assume a drooping character. Now these "changes of habit" are clearly determined by functional changes. Occurring, as they do, in many individuals that have undergone the same transportation, they cannot be classed as "spontaneous variations." They are modifications of structure, consequent on modifications of function, that have been produced by modifications in the actions of external forces. And as these modifications re-appear in succeeding generations, we have, in them, examples of functionally-established variations that are hereditarily transmitted. Further evidence is supplied by what are called "sports" in plants. These are of two kinds—the gamogenetic and the agamogenetic. The gamogenetic may be ascribed wholly to "spontaneous variations;" or if they are partly due to the inheritance of structural changes that are produced by functional changes, this cannot be proved. But where the individuals displaying the variations arise by agamogenesis, the reverse is the case: spontaneous variation is out of the question; and the only possible interpretation is deviation of structure caused by deviation of function. A new axis which buds out from a parent-axis, assumes an unlike character—gives off lobed leaves in place of single leaves, or has an otherwise different mode of growth. This change of structure implies change in the developmental actions which produced the new bud—change, that is, in the actions going on in the parent shoot—functional change. And since the modified structure thus impressed on the new shoot by modified function, is transmitted by it to all the shoots it bears; we are obliged to regard the case as one of acquired modification that has become hereditary.

Evidence of analogous changes in animals, is difficult to disentangle. Only among domesticated animals, have we any opportunity of tracing the effects of altered habits; and here, in nearly all cases, artificial selection has obscured the results. Still, there are some facts which seem to the point. Mr Darwin, while ascribing almost wholly to "natural selection" the production of those modifications which eventuate in differences of species, nevertheless admits the effects of use and disuse. He says—"I find in the domestic duck that the bones of the wing weigh less and the bones of the leg more, in proportion to the whole skeleton, than do the same bones in the wild duck; and I presume that this change may be safely attributed to the domestic duck flying much less, and walking more, than its wild parent. The great and inherited development of the udders in cows and goats in countries where they are habitually milked, in comparison with the state of these organs in other countries, is another instance of the effect of use. Not a single domestic animal can be named which has not in some country drooping ears; and the view suggested by some authors, that the drooping is due to the disuse of the muscles of the ear, from the animals not being much alarmed by danger, seems probable." Again—"The eyes of moles and of some burrowing rodents are rudimentary in size, and in some cases are quite covered up by skin and fur. This state of the eyes is probably due to gradual reduction from disuse, but aided perhaps by natural selection." * * * "It is well known that several animals, belonging to the most different classes, which inhabit the caves of Styria and of Kentucky, are blind. In some of the crabs the footstalk of the eye remains, though the eye is gone; the stand for the telescope is there, though the telescope with its glasses has been lost. As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute their loss wholly to disuse." The direct inheritance of an acquired peculiarity is sometimes observable. Mr Lewes gives a case. He "had a puppy taken from its mother at six weeks old, who, although never taught, 'to beg' (an accomplishment his mother had been taught), spontaneously took to begging for everything he wanted when about seven or eight months old: he would beg for food, beg to be let out of the room, and one day was found opposite a rabbit hutch begging for rabbits." Instances are on record, too, of sporting dogs which spontaneously adopted in the field, certain modes of behaviour which their parents had learnt.

But the best examples of inherited modifications produced by modifications of function, occur in the human race. To no other cause can be ascribed the rapid metamorphoses undergone by the British races when placed in new conditions. It is notorious that, in the United States, the descendants of the immigrant Irish lose their Celtic aspect, and become Americanized. This cannot be ascribed to intermarriage with Americans; since the feeling with which Irish are regarded by Americans, prevents any considerable amount of intermarriage. Equally marked is the case of the immigrant Germans, who, though they keep themselves very much apart, rapidly assume the prevailing type. To say that "spontaneous variation" increased by natural selection, can have produced this effect, is going too far. Races so numerous, cannot have been supplanted in the course of two or three generations by varieties springing from them. Hence there is no escape from the conclusion, that physical and social conditions have here wrought modifications of function and structure, which offspring have inherited and increased. Similarly with special cases. In the *Cyclopædia of Practical Medicine*, Vol. II. p. 419, Dr Brown states that he "has in many instances observed in the case of individuals whose complexion and general appearance has been modified by residence in hot climates, that children born to them subsequently to such residence, have resembled them rather in their acquired than primary mien."

Some special modifications of organs caused by special changes in their functions, may also be noted. That large hands are inherited by men and women whose ancestors led laborious lives ; and that men and women whose descent, for many generations, has been from those unused to manual labour, commonly have small hands ; are established opinions. It seems very unlikely that in the absence of any such connexion, the size of the hand should thus have come to be generally regarded as some index of extraction. That there exists a like relation between habitual use of the feet and largeness of the feet, we have strong evidence in the customs of the Chinese. The torturing practice of artificially arresting the growth of the feet, could never have become established among the ladies of China, had they not found abundant proof that a small foot was significant of superior rank—that is of a luxurious life—that is of a life without bodily labour. There is some evidence, too, that modifications of the eyes, caused by particular uses of the eyes, are inherited. Short sight appears to be uncommon in rural populations; but it is frequent among classes of people who use their eyes much for reading and writing; and in these classes, short sight is often congenital. Still more marked is this relation in Germany. There, the educated classes are notoriously studious; and judging from the numbers of young Germans who wear spectacles, there is reason to think that congenital myopia is very frequent among them.

Some of the best illustrations of functional heredity, are furnished by the mental characteristics of human races. Certain powers which mankind have gained in the course of civilization, cannot, I think, be accounted for, without admitting the inheritance of acquired modifications. The musical faculty is one of these. To say that "natural selection" has developed it, by preserving the most musically endowed, seems an inadequate explanation. Even now that the development and prevalence of the faculty have made music an occupation by which the most musical can get sustenance and bring up families; it is very questionable whether, taking the musical life as a whole, it has any advantage over others in the struggle for existence and multiplication. Still more if we look back to those early stages through which the faculty must have passed, before definite perception of melody was arrived at, we fail to see how those possessing the rudimental faculty in a somewhat greater degree than the rest, would thereby be enabled the better to maintain themselves and their children. If so, there is no explanation but that the habitual association of certain cadences of human speech with certain emotions, has slowly established in the race an organized and inherited connexion between such cadences and such emotions; that the combination of such cadences, more or less idealized, which constitutes melody, has all along had a meaning in the average mind, only because of the meaning which cadences had acquired in the average mind; and that by the continual hearing and practice of melody, there has been gained and transmitted an increasing musical sensibility. Confirmation of this view may be drawn from individual cases. Grant that among a people endowed with musical faculty to a certain degree, spontaneous variation will occasionally produce men possessing it in a higher degree; it cannot be granted that spontaneous variation accounts for the frequent production, by such highly-endowed men, of men still more highly endowed. On the average, the offspring of marriage with others not similarly endowed, will be less distinguished rather than more distinguished. The most that can be expected is, that this unusual amount of faculty shall re-appear in the next generation undiminished. How then shall we explain cases like those of Bach, Mozart, and Beethoven, who were all sons of men having unusual musical powers, but who greatly excelled their fathers in their musical powers? What shall we say to the facts, that Haydn was the son of the organist, that Hummel was born to a music master, and that Weber's father was a distinguished violinist? The occurrence of so many cases in one nation, within a short period of time, cannot rationally be ascribed to the coincidence of "spontaneous variations." It can be ascribed to nothing but inherited developments of structure, caused by augmentations of function.

But the clearest proof that structural alterations caused by alterations of function, are inherited, occurs when the alterations are morbid. "Certain modes of living engender gout;" and gout is transmissible. It is well known that in persons previously healthy, consumption may be produced by unfavourable conditions of life—by bad and insufficient food; by foul, damp, unventilated habitations; and even by long-continued anxiety. It is still more notorious that the consumptive diathesis is conveyed from parent to child. Unless, then, a distinction be assumed between constitutional consumption and consumption induced by unwholesome conditions—unless it be asserted that consumption of unknown origin is transmissible, while functionally-produced consumption is not; it must be admitted that those changes of structure from which the consumptive diathesis results, may be caused in parents by changes of function, and may be inherited by their children. Most striking of all, however, is the fact lately brought to light, that functional disorders artificially established, may be conveyed to offspring. Some few years since M. Brown-Sequard, in the course of inquiries into the nature and causes of epilepsy, hit on a method by which epilepsy could be originated. Guinea-pigs were the creatures on which, chiefly, he experimented; and eventually, he discovered the remarkable fact, that the young of these epileptic guinea-pigs were epileptic: the functionally-established epilepsy in the parents, became constitutional epilepsy in the offspring. Here we have an instance which, standing even alone, decides the question. We have a special form of nervous action, not caused by any natural variation of structure that had arisen spontaneously in the organism, but one caused by a certain incidence of external forces. We have this special form of nervous action becoming confirmed by repetition: the fits are more and more easily induced—there is established the epileptic *habit*. That is to say, the connected nervous actions constituting a fit, produce in the nervous system such changes of structure, that subsequent connected nervous actions of like kind, follow one another with increased readiness. And that this epileptic habit is inherited, proves conclusively that these structural modifications worked by functional modifications, are impressed on the whole organism in such way as to affect the reproductive centres, and cause them to unfold into organisms that exhibit like modifications.

Evidence nearly allied to this, and scarcely less significant, is furnished by that transmission of general nervousness, noticed in the last section. Nervousness is especially common among classes of people who tax their brains much. Among these classes, we daily see this constitutional modification *produced* by excess of function, in men whose progenitors were not nervous; and the children of such men habitually inherit more or less of the modification.

§ 83. Two modified manifestations of Heredity remain to be noticed. The one is the re-appearance in offspring, of traits not borne by the parents, but borne by the grandparents or by remoter ancestors. The other is the limitation of Heredity by sex—the restriction of certain transmitted peculiarities to offspring of the same sex as the parent possessing these peculiarities.

Atavism, which is the name given to the recurrence of ancestral traits, is proved by many and varied facts. In the picture-galleries of old families, and on the monumental brasses in the adjacent churches, are often seen types of feature that are still, from time to time, repeated in members of these families. It is matter of common remark that some constitutional diseases, such as gout and insanity, after missing a generation, will show themselves in the next. Dr Struthers, in his above-quoted paper on "Variation in the Number of Fingers and Toes, and of the Phalanges, in Man," gives cases of malformations that were common to grandparent and grandchild, but of which the parent had no trace. M. Girou (as quoted by Mr Sedgwick) says—"One is often surprised to see lambs black, or spotted with black, born of ewes and rams with white wool, but if one takes the trouble to go back to the origin of this phenomenon, it is found in the ancestors." Instances still more remarkable, in which the remoteness of the ancestors copied is very great, are given by Mr Darwin. He points out that in crosses between varieties of the pigeon, there will sometimes re-appear the plumage of the original rock-pigeon, from which these varieties descended; and he instances the faint zebra-like markings occasionally traceable in horses, as having probably a like meaning.

The limitation of Heredity by sex, cannot yet be regarded as established. While in many cases it seems clearly manifested; it is in other cases manifested to a very small degree, if at all. In Mr Sedgwick's essays, already named, will be found evidence implying that there exists some such tendency to limitation, which does or does not show itself distinctly, according to the nature of the organic modification to be conveyed. But more facts must be collected before any positive conclusion can be reached.

§ 84. A positive explanation of Heredity is not to be expected in the present state of Biology. We can look for nothing beyond a simplification of the problem; and a reduction of it to the same category with certain other problems which also admit of hypothetical solution only. If an hypothesis which certain other wide-spread phenomena have already thrust upon us, can be shown to render the phenomena of Heredity more intelligible than they at present seem, we shall have reason to entertain it. The applicability of any method of interpretation to two different but allied classes of facts, is evidence of its truth.

The power which organisms display of reproducing lost parts, we saw to be inexplicable except on the assumption that the units of which any organism is built have an innate tendency to arrange themselves into the shape of that organism (§ 65). We inferred that these units must be the possessors of special polarities, resulting from their special structures; and that by the mutual play of their polarities they are compelled to take the form of the species to which they belong. And the instance of the *Begonia phyllomaniaca* left us no escape from the admission that the ability thus to arrange themselves, is latent in the units contained in every undifferentiated cell. Quite in harmony with this conclusion, are certain implications since noticed, respecting the characters of sperm-cells and germ-cells. We saw sundry reasons for rejecting the supposition that these are highly-specialized cells and for accepting the opposite supposition, that they are cells differing from others rather in being unspecialized. And here the assumption to which we seem driven by the *ensemble* of the evidence, is, that sperm-cells and germ-cells are essentially nothing more than vehicles, in which are contained small groups of the physiological units in a fit state for obeying their proclivity towards the structural arrangement of the species they belong to.

Thus the phenomena of Heredity are seen to assimilate with other phenomena; and the assumption which these other phenomena thrust on us, appears to be equally thrust on us by the phenomena of Heredity. We must conclude that the likeness of any organism to either parent, is conveyed by the special tendencies of the physiological units derived from that parent. In the fertilized germ we have two groups of physiological units, slightly different in their structures. These slightly-different units, severally multiply at the expense of the nutriment supplied to the unfolding germ—each kind moulding this nutriment into units of its own type. Throughout the process of evolution, the two kinds of units, mainly agreeing in their polarities and in the form which they tend to build themselves into, but having minor differences, work in unison to produce an organism of the species from which they were derived, but work in antagonism to produce copies of their respective parent-organisms. And hence ultimately results, an organism in which traits of the one are mixed with traits of the other.

If the likeness of offspring to parents is thus determined, it becomes manifest, *à priori*, that besides the transmission of generic and specific peculiarities, there will be a transmission of those individual peculiarities which, arising without assignable causes, are classed as "spontaneous." For if the assumption of a special arrangement of parts by an organism, is due to the proclivity of its physiological units towards that arrangement; then the assumption of an arrangement of parts slightly different from that of the species, implies physiological units slightly unlike those of the species; and these slightly-unlike physiological units, communicated through the medium of sperm-cell or germ-cell, will tend, in the offspring, to build themselves into a structure similarly diverging from the average of the species.

It is not equally manifest, *à priori*, however, that on this hypothesis, alterations of structure caused by alterations of function, must be transmitted to offspring. It is not obvious that change in the form of a part, caused by changed action, involves such change in the physiological units throughout the organism, that these, when groups of them are thrown off in the shape of reproductive centres, will unfold into organisms that have this part similarly changed in form. Indeed, when treating of Adaptation (§ 69), we saw that an organ modified by increase or decrease of function, can but slowly so re-act on the system at large, as to bring about those correlative changes required to produce a new equilibrium; and yet only when such new equilibrium has been established, can we expect it to be *fully* expressed in the modified physiological units of which the organism is built—only then can we count on a complete transfer of the modification to descendants. Nevertheless, that changes of structure caused by changes of action, must also be transmitted, however obscurely, from one generation to another, appears to be a deduction from first principles—or if not a specific deduction, still, a general implication. For if an organism A, has, by any peculiar habit or condition of life, been modified into the form A′, it follows inevitably, that all the functions of A′, reproductive function included, must be in some degree different from the functions of A. An organism being a combination of rhythmically-acting parts in moving equilibrium, it is impossible to alter the action and structure of any one part, without causing alterations of action and structure in all the rest; just as no member of the Solar System could be modified in motion or mass, without producing re-arrangements throughout the whole Solar System. And if the organism A, when changed to A′, must be changed in all its functions; then the offspring of A′ cannot be the same as they would have been had it retained the form A. It involves a denial of the persistence of force to say that A may be changed into A′, and may yet beget offspring exactly like those it would have begotten had it not been so changed. That the change in the offspring must, other things equal, be in the same direction as the change in the parent, we may dimly see is implied by the fact, that the change propagated throughout the parental system is a change towards a new state of equilibrium—a change tending to bring the actions of all organs, reproductive included, into harmony with these new actions. Or, bringing the question to its ultimate and simplest form, we may say that as, on the one hand, physiological units will, because of their special polarities, build themselves into an organism of a special structure; so, on the other hand, if the structure of this organism is modified by modified function, it will impress some corresponding modification on the structures and polarities of its units. The units and the aggregate must act and re-act on each other. The forces exercised by each unit on the aggregate and by the aggregate on each unit, must ever tend towards a balance. If nothing prevents, the units will mould the aggregate into a form in equilibrium with their pre-existing polarities. If, contrariwise, the aggregate is made by incident actions to take a new form, its forces must tend to re-mould the units into harmony with this new form. And to say that the physiological units are in any degree so re-moulded as to bring their polar forces towards equilibrium with the forces of the modified aggregate, is to say that when separated in the shape of reproductive centres, these units will tend to build themselves up into an aggregate modified in the same direction.

# CHAPTER IX.

## VARIATION.

§ 85. EQUALLY conspicuous with the truth that every organism bears a general likeness to its parents, is the truth that no organism is exactly like either parent. Though similar to both in generic and specific traits, and usually, too, in those traits which distinguish the variety, it diverges in numerous traits of minor importance. No two plants are indistinguishable; and no two animals are without differences. Variation is co-extensive with Heredity.

The degrees of variation have a wide range. There are deviations so small as to be not easily detected; and there are deviations great enough to be called monstrosities. In plants, we may pass from cases of slight alteration in the shape or texture of a leaf, to cases where, instead of a flower with its calyx above the seed-vessel, there is produced a flower with its calyx below the seed-vessel; and while in one animal, there arises a scarcely noticeable unlikeness in the length or colour of the hair, in another, an organ is absent, or a supernumerary organ appears. Though small variations are by far the most general, yet variations of considerable magnitude are not uncommon; and even those variations constituted by additions or suppressions of parts, are not so rare as to be excluded from the list of causes by which organic forms are changed. Cattle without horns are frequent. Of sheep there are horned breeds and breeds that have lost their horns. At one time, there existed in Scotland a race of pigs with solid feet instead of cleft feet. In pigeons, according to Mr Darwin, "the number of the caudal and sacral vertebræ vary; as does the number of the ribs, together with their relative breadth and the presence of processes."

That variations both small and large which arise without any specific assignable cause, tend to become hereditary, was shown in the last chapter. Indeed the evidence which proves Heredity in its smaller manifestations, is the same evidence which proves Variation; since it is only when there occur variations, that the inheritance of anything beyond the structural peculiarities of the species, can be proved. It remains here, however, to be observed, that the transmission of variations is itself variable; and that it varies both in the direction of decrease and in the direction of increase. An individual trait of one parent, may be so counteracted by the influence of the other parent, that it may not appear in the offspring; or not being so counteracted, the offspring may possess it, perhaps in an equal degree or perhaps in a less degree; or the offspring may exhibit the trait in even a still higher degree. Of the illustrations of this, one must suffice. I quote it from the essay by Dr Struthers, referred to in the last chapter.

"The great-great-grandmother, Esther P—— (who married A—— L——), had a sixth little finger on one hand. Of their eighteen children (twelve daughters and six sons), only one (Charles) is known to have had digital variety. We have the history of the descendants of three of the sons, Andrew, Charles, and James.

"(1.) Andrew L—— had two sons, Thomas and Andrew; and Thomas had two sons all without digital variety. Here we have three successive generations without the variety possessed by the great-grandmother showing itself.

"(2.) James L——, who was normal, had two sons and seven daughters, also normal. One of the daughters became Mrs J—— (one of the informants), and had three daughters and five sons, all normal except one of the sons, James J——, now æt. 17, who had six fingers on each hand. * * *

"In this branch of the descendants of Esther, we see it passing over two generations and reappearing in one member of the third generation, and now on both hands.

"(3.) Charles L——, the only child of Esther who had digital variety, had six fingers on each hand. He had three sons, James, Thomas, and John, all of whom were born with six fingers on each hand, while John has also a sixth toe on one foot. He had also five other sons and four daughters, all of whom were normal.

"(*a.*) Of the normal children of this, the third generation, the five sons had twelve sons and twelve daughters, and the four daughters have had four sons and four daughters, being the fourth generation, all of whom were normal. A fifth generation in this sub-group consists as yet of only two boys and two girls, who are also normal.

"In this sub-branch, we see the variety of the first generation present in the second, passing over the third and fourth, and also the fifth as far as it has yet gone.

"(*b.*) James had three sons and two daughters, who are normal.

"(*c.*) Thomas had four sons and five daughters, who are normal; and has two grandsons, also normal.

"In this sub-branch of the descent, we see the variety of the first generation, showing itself in the second and third, and passing over the fourth, and (as far as it yet exists) the fifth generation.

"(*d.*) John L —— (one of the informants) had six fingers, the additional finger being attached on the outer side, as in the case of his brothers James and Thomas. All of them had the additional digits removed. John has also a sixth toe on one foot, situated on the outer side. The fifth and sixth toes have a common proximal phalanx, and a common integument invests the middle and distal phalanges, each having a separate nail.

"John L—— has a son who is normal, and a daughter, Jane, who was born with six fingers on each hand and six toes on each foot. The sixth fingers were removed. The sixth toes are not wrapped with the fifth as in her father's case, but are distinct from them. The son has a son and daughter, who, like himself, are normal.

"In this, the most interesting sub-branch of the descent, we see digital increase, which appeared in the first generation on one limb, appearing in the second on two limbs, the hands; in the third on three limbs, the hands and one foot; in the fourth on all the four limbs. There is as yet no fifth generation in uninterrupted transmission of the variety. The variety does not yet occur in any number of the fifth generation of Esther's descendants, which consists, as yet, only of three boys and one girl, whose parents were normal, and of two boys and two girls, whose grandparents were normal. It is not known whether in the case of the great-great-grandmother, Esther P——, the variety was original or inherited."*

§ 86. Where there is great uniformity among the members of a species, the divergences of offspring from the average type, are usually small; but where, among the members of a species, considerable unlikenesses have once been established, unlikenesses among the offspring are frequent and great. Wild plants growing in their natural habitats, are uniform over large areas, and maintain from generation to generation like structures; but when cultivation has caused appreciable differences among the members of any species of plant, extensive and numerous deviations are apt to arise. Similarly, between wild and domesticated

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* This remarkable case appears to militate against the conclusion, drawn some few pages back, that the increase of a peculiarity by coincidence of "spontaneous variations" in successive generations, is very improbable; and that the special superiorities of musical composers cannot have thus arisen. The reply is, that the extreme frequency of the occurrence among so narrow a class as that of musical composers, forbids the interpretation 'hus suggested.

animals of the same species, we see the contrast, that though the homogeneous wild race maintains its type with great persistence, the comparatively heterogeneous domestic race frequently produces individuals more unlike the average type than the parents are.

Though unlikeness among progenitors is one antecedent of variation, it is by no means the sole antecedent. Were it so, the young ones successively born to the same parents would be alike. If any peculiarity in a new organism were a direct resultant of the structural differences between the two organisms which produced it; then all subsequent new organisms produced by these two, would show the same peculiarity. But we know that the successive offspring have different peculiarities: no two of them are ever exactly alike.

One cause of such structural variation in progeny, is functional variation in parents. Proof of this is given by the fact that, among the progeny of the same parents, there is more difference between those begotten under different constitutional states, than between those begotten under the same constitutional state. It is notorious that twins are more nearly alike than children borne in succession. The functional conditions of the parents being the same for twins, but not the same for their brothers and sisters (all other antecedents being constant); we have no choice but to admit that variations in the functional conditions of the parents, are the antecedents of those greater unlikenesses which their brothers and sisters exhibit.

Some other antecedent remains, however. The parents being the same, and their constitutional states the same, variation, more or less marked, still manifests itself. Plants grown from seeds out of one pod, and animals produced at one birth, are not alike; and sometimes differ considerably. In a litter of pigs or of kittens, we rarely see uniformity of markings; and occasionally, there are important structural contrasts. I have myself recently been shown a litter of Newfoundland puppies, some of which had four digits to their feet, while in others, there was present on each hind-foot, what is called the "dew-claw"—a rudimentary fifth digit.

Thus, induction points to three causes of variation, all in action together. We have heterogeneity among progenitors, which, did it act uniformly and alone in generating, by composition of forces, new deviations, would impress such new deviations to the same extent on all offspring of the same parents; which it does not. We have functional variation in the parents, which, acting either alone or in combination with the preceding cause, would entail like variations on all young ones simultaneously produced; which it does not. And there is consequently some third cause of variation, yet to be found, which acts along with the structural and functional variations of ancestors and parents.

§ 87. Already, in the last section, there has been implied some relation between variation and the action of external conditions. The above-cited contrast, between the uniformity of wild species and the multiformity of the same species when cultivated or domesticated, thrusts this truth upon us. Respecting the variations of plants, Mr Darwin remarks that "'sports' are extremely rare under nature, but far from rare under cultivation." Others who have studied the matter assert, that if a species of plant which, up to a certain time, has maintained great uniformity, once has its constitution thoroughly disturbed, it will go on varying indefinitely. Though, in consequence of the remoteness of the periods at which they were domesticated, there is a lack of positive proof that our extremely variable domestic animals have become variable under the changed conditions implied by domestication, having been previously constant; yet competent judges do not doubt that this has been the case.

Now the constitutional disturbance which precedes variation, can be nothing else than an overthrowing of the preestablished equilibrium of functions. Transferring a plant from forest lands to a ploughed field or a manured garden, is altering the balance of forces to which it has been hitherto subject; by supplying it with different proportions of the assimilable matters it requires, and taking away some of the positive impediments to its growth which competing wild plants before offered. An animal taken from woods or plains, where it lived on wild food of its own procuring, and placed under restraint, while artificially supplied with food not quite like what it had before, is an animal subject to new outer actions, to which its inner actions must be re-adjusted. From the general law of equilibration we found it to follow, that "the maintenance of such a moving equilibrium" as an organism displays, "requires the habitual genesis of internal forces corresponding in number, directions, and amounts, to the external incident forces — as many inner functions, single or combined, as there are single or combined outer actions to be met" (*First Principles*, § 133); and more recently (§ 27), we have seen that Life itself is "the definite combination of heterogeneous changes, both simultaneous and successive, in correspondence with external co-existences and sequences." Necessarily, therefore, an organism exposed to a permanent change in the arrangement of outer forces, must undergo a permanent change in the arrangement of inner forces. The old equilibrium must be destroyed; and a new equilibrium must be established. There must be functional perturbations, ending in a re-adjusted balance of functions.

If, then, change of conditions is the only known cause by which the original homogeneity of a species is destroyed; and if change of conditions can affect an organism only by altering its functions; it follows that alteration of functions is the only known internal cause to which the commencement of variation can be ascribed. That such minor functional changes as parents undergo from year to year, are influential on the offspring, we have seen to be proved by the greater unlikeness that exists between children born to the same parents at different times, than exists between twins. And here we seem forced to conclude, that the larger functional variations produced by greater external changes, are the initiators of those structural variations which, when once commenced in a species, lead by their combinations and antagonisms to multiform results. Whether they are or are not the direct initiators, they must still be the indirect initiators.

§ 88. That they are not in all cases, or even in most cases, the direct initiators, is clear. Were they so, those unlikenesses which exist between plants that grow from seeds out of the same seed-vessel, or between animals belonging to the same litter, would be inexplicable. Here, all the antecedents, structural and functional, appear to be alike for each of the new organisms. Any deviations caused by structural contrasts or functional disturbances in the parents, must be equally shared in by all simultaneously-produced offspring. Hence, an explanation of the variations arising under such conditions, has still to be sought.

These are the variations termed "spontaneous." Not that those who apply to them this word or some equivalent, mean to imply that they are uncaused. Mr Darwin expressly guards himself against such an interpretation. He says:—"I have hitherto sometimes spoken as if the variations—so common and multiform in organic beings under domestication, and in a lesser degree in those in a state of nature—had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation." Not only, however, do I hold, in common with Mr Darwin, that there must be some cause for these apparently-spontaneous variations; but it seems to me that a definite cause is assignable. I think it may be shown that unlikenesses must necessarily arise between the new individuals simultaneously produced by the same parents. Instead of the occurrence of such variations being inexplicable, we shall presently see that the absence of them would be inexplicable.

In any series of dependent changes, a small initial difference often works a marked difference in the results. The mode in which a particular breaker bursts on the beach, may determine whether the seed of some foreign plant which it bears, is or is not stranded—may cause the presence or absence of this plant from the Flora of the land; and may so affect, for millions of years, in countless ways, the living creatures throughout the land. A single touch, by introducing into the body some morbid matter, may set up an immensely-involved set of functional disturbances and structural alterations. The whole tenor of a life may be changed by a word of advice; or a glance may determine an action which alters thoughts, feelings, and deeds throughout a long series of years. In those still more involved combinations of changes which societies exhibit, this truth is still more conspicuous. A hair's-breadth difference in the direction of some soldier's musket at the battle of Arcola, by killing Napoleon, might have changed events throughout Europe: though the social organization in each European country, would have been now very much what it is, yet in countless details it would have been different.

Illustrations like these, with which pages might be filled, prepare us for the conclusion, that organisms produced by the same parents at the same time, must be more or less differentiated both by insensible initial differences, and by slight differences in the conditions to which they are subject during their evolution. We need not, however, rest with assuming such initial differences: the necessity of them is demonstrable. The individual germ-cells which, in succession or simultaneously, are separated from the same parent, can never be exactly alike; nor can the sperm-cells which fertilize them. When treating of the instability of the homogeneous (*First Principles*, § 109), we saw that no two parts of any aggregate, can be similarly conditioned with respect to incident forces; and that being subject to forces that are more or less unlike, they must become more or less unlike. Hence, no two ova in an ovarum or ovules in a seed-vessel—no two spermatozoa or pollen-cells, can be identical. Whether or not there arise other contrasts, there are certain to arise quantitative contrasts; since the process of nutrition cannot be absolutely alike for all. The reproductive centres must begin to differentiate from the very outset. Such being the necessities of the case, what will happen on any successive or simultaneous fertilizations? There will inevitably result more or less unlikeness between the combined parental influences in every instance. Quantitative differences among the sperm-cells and among the germ-cells, will insure this. Grant that the number of physiological units contained in any one reproductive cell, can rarely if ever be exactly equal to the number contained in any other, ripened at the same time or at a different time; and it follows that among the fertilized germs produced by the same parents, the physiological units derived from each parent will bear a different numerical ratio to each other in every case. If now the parents are constitutionally alike, that is, alike in the polarities of their physiological units, the variation in the ratio between the physiological units they severally bequeath to the fertilized germs, cannot cause unlikenesses among the offspring. But if otherwise, no two of the offspring can be alike. In every case, the small initial difference in the proportions of the slightly-unlike units, will lead, during evolution, to a continual multiplication of differences: the insensible divergence at the outset, will generate sensible divergences at the conclusion. Possibly some may hence infer, that though, in such case, the offspring must differ somewhat from each other and from both parents; yet that in every one of them there must result a homogeneous mixture of the traits of the two parents. A little consideration shows that the reverse is inferable. If, throughout the process of development, the physiological units derived from each parent, preserved the same ratio to each other in all parts of the growing organism, each organ would show as much as every other, the influence of either parent. But we know, *à priori*, that no such uniform distribution is possible. It has been shown (*First Principles*, § 123), that in any mixed aggregate of units, segregation must inevitably go on. Incident forces will tend ever to cause separation of the two orders of units from each other—will integrate groups of the one order in one place, and groups of the other order in another place. Hence there must arise, not a homogeneous mean between the two parents; but a mixture of organs, some of which mainly follow the one parent and some the other. And this is the kind of mixture which observation shows us.

Still it may be fairly objected, that however the attributes of the two parents are variously mixed in their several offspring, they must in all the offspring fall between the extremes displayed in the parents. In no characteristic could one of the young exceed both parents, were there no cause of "spontaneous variation" but the one alleged. Evidently, then, there is a cause yet unfound.

§ 89. Thus far we have contemplated the process under its simplest aspect. While we have assumed the two parents to be somewhat unlike, we have assumed that each parent has a homogeneous constitution—is built up of physiological units that are exactly alike. But in no case can such a homogeneity exist. Each parent had parents that were more or less contrasted—each parent inherited at least two orders of physiological units, not quite identical. Here then we have a further cause of variation. The sperm-cells or germ-cells which any organism produces, will differ from each other not quantitatively only, but qualitatively. Of the slightly-unlike physiological units bequeathed to an organism, its reproductive cells cannot habitually contain the same proportions; and we may expect the proportions to vary not slightly but greatly. Just as, during the evolution of an organism, the physiological units derived from the two parents tend to segregate, and produce likeness to the male parent in this feature and to the female parent in that; so, during the formation of reproductive cells by such organism, there will arise in one cell a predominance of the physiological units derived from one parent, and in another cell a predominance of the physiological units derived from the other parent. The instability of the homogeneous forbids us to assume an even distribution of the two orders of units in all the reproductive cells. And inequalities once arising among them, must tend ever to become more marked; since, wherever units of a given order have begun to segregate, the process of differentiation and integration tends to segregate them more and more. Thus, then, every fertilized germ, besides containing different *amounts* of the two parental influences, will contain different *kinds* of influences—this having received a marked impress from one maternal or paternal ancestor, and that from another.

Here, then, we have a clue to the multiplied variations, and sometimes extreme variations, that arise in races which have once begun to vary. Amid countless different combinations of units derived from parents, and through them from ancestors, immediate and remote—amid the various conflicts in their slightly-different polarities, opposing and conspiring with each other in all ways and degrees; there will from time to time arise special proportions causing special deviations. From the general law of probabilities it is inferable, that while these involved influences, derived from many progenitors, must, on the average of cases, obscure and partially neutralize one another; there must occasionally result such combinations of them as will produce considerable divergences from average structures; and at rare intervals, such combinations as will produce very marked divergences. There is thus a correspondence between the inferable results, and the results as habitually witnessed.

§ 90. Still there remains a difficulty. It may be said that admitting functional change to be the initiator of variation —granting that the physiological units of an organism, modified by long subjection to new conditions, will tend to become modified in such way as to cause change of structure in offspring; yet there will still be no cause of the supposed heterogeneity among the physiological units of different individuals. There seems validity in the objection, that as all the members of a species whose circumstances have been altered, will be affected in the same manner, the results, when they begin to show themselves in descendants, will show themselves in the same manner: not multiform variations will arise, but deviations all in one direction.

The reply is simple. The members of a species thus circumstanced, will *not* be similarly affected. In the absence of absolute uniformity among them, the functional changes caused in them will be more or less dissimilar. Just as men of slightly-unlike dispositions behave in quite opposite ways under the same circumstances; or just as men of slightly-unlike constitutions get diverse disorders from the same cause, and are diversely acted on by the same medicine; so, the insensibly-differentiated members of a species whose conditions have been changed, may at once begin to undergo various kinds of functional changes. As we have already seen, small initial contrasts may lead to large terminal contrasts. The intenser cold of the climate into which a species has migrated, may cause in one individual increased consumption of food, to balance the greater loss of heat; while in another individual, the new requirement may be met by a thicker growth of fur. Or, when meeting with the new foods which the new region furnishes, mere accident may determine one member of the species to begin with one kind and another member with another kind; and hence may arise established habits in these respective members and their descendants. Now when the functional divergences thus set up in sundry families of a species, have lasted long enough to affect their constitutions profoundly, and to modify somewhat the physiological units thrown off in their reproductive cells, the divergences produced by these in offspring, will be of diverse kinds. And the original homogeneity of constitution having been thus destroyed, variation may go on with increasing facility. There will result a heterogeneous mixture of modifications of structure, caused by modifications of function; and of still more numerous correlated modifications, indirectly so caused. By natural selection of the most divergent forms, the unlikenesses of parents will grow more marked, and the limits of variation wider. Until at length the divergences of constitutions and modes of life, become great enough to lead to segregation of the varieties.

§ 91. That variations must occur, and that they must ever tend, both directly and indirectly, towards adaptive modifications, are conclusions deducible from first principles; apart from any detailed interpretations like the above. That the state of homogeneity is an unstable state, we have found to be a universal truth. Each species must pass from the uniform into the more or less multiform, unless the incidence of external forces is exactly the same for all its members; which it never can be. Through the process of differentiation and integration, which of necessity brings together, or keeps together, like individuals, and separates unlike ones from them, there must nevertheless be maintained a tolerably uniform species; so long as there continues a tolerably uniform set of conditions in which it may exist. But if the conditions change, either absolutely by some disturbance of the habitat, or relatively by spread of the species into other habitats, then the divergent individuals that result, must be segregated by the divergent sets of conditions into distinct varieties (*First Principles*, § 126). When, instead of contemplating a species in the aggregate, we confine our attention to a single member and its descendants, we see it to be a corollary from the general law of equilibration, that the moving equilibrium constituted by the vital actions in each member of this family, must remain constant so long as the external actions to which they correspond remain constant; and that if the external actions are changed, the disturbed balance of internal changes, if not overthrown, cannot cease undergoing modification until the internal changes are again in equilibrium with the external actions: corresponding structural alterations having arisen.

Or passing from these derivative laws to the ultimate law, we see that Variation is necessitated by the persistence of force. The members of a species inhabiting any area, cannot be subject to like aggregates of forces over the whole of that area. And if, in different parts of the area, different kinds or amounts or combinations of forces act on them, they cannot but become different in themselves and in their progeny. To say otherwise, is to say that differences in the forces will not produce differences in the effects; which is to deny the persistence of force.

Whence it is also manifest, that there can be no variation of structure, but what is directly or indirectly consequent on variation of function. On the one hand, organisms in complete equilibrium with their conditions, cannot be changed except by change in their conditions; since, to assert otherwise, is to assert that there can be an effect without a cause; which is to deny the persistence of force. On the other hand, any change of conditions can affect an organism only by changing the actions going on in it—only by altering its functions. The alterations of functions being necessarily towards a re-establishment of the equilibrium, (for if not, the equilibrium must be destroyed and the life cease, either in the individual or in descendants,) it follows that the structural alterations directly caused, are adaptations; and that the correlated structural alterations indirectly caused, are the concomitants of adaptations. Hence, though, by the intercourse of organisms that have been functionally and structurally modified in different directions, there may result organisms that deviate in compound ways which appear unrelated to external conditions, the deviations of such organisms must still be regarded as indirect results of functional adaptations. We must say that in all cases, adaptive change of function is the primary and ever-acting cause of that change of structure which constitutes variation; and that the variation which appears to be "spontaneous," is derivative and secondary.

# CHAPTER X.

## GENESIS, HEREDITY, AND VARIATION.

§ 92. A QUESTION raised, and hypothetically answered, in §§ 78 and 79, was there postponed until we had dealt with the topics of Heredity and Variation. Let us now resume the consideration of this question, in connexion with sundry others which the facts suggest.

After contemplating the several methods by which the multiplication of organisms is carried on — after ranging them under the two heads of Homogenesis, in which the successive generations are similarly produced, and Heterogenesis, in which they are dissimilarly produced—after observing that Homogenesis is always sexual genesis, while Heterogenesis is asexual genesis with occasionally-recurring sexual genesis; we came to the questions—why is it that some organisms multiply in the one way, and some in the other? and why is it that where agamogenesis prevails, it is usually, from time to time, interrupted by gamogenesis? In seeking an answer to this question, we inquired whether there are, common to both Homogenesis and Heterogenesis, any conditions under which alone sperm-cells and germ-cells arise and are united, for the production of new organisms; and we reached the conclusion that, in all cases, they arise only when there is an approach to equilibrium between the forces which produce growth and the forces which oppose growth. This answer to the question—*when* does gamogenesis recur?

still left unanswered the question—*why* does gamogenesis recur? And to this the reply suggested was, that the approach towards general equilibrium in organisms, "is accompanied by an approach towards molecular equilibrium in them; and that the need for this union of sperm-cell and germ-cell, is the need for overthrowing this equilibrium, and re-establishing active molecular change in the detached germ—a result which is probably effected by mixing the slightly-different physiological units of slightly-different individuals." This is the hypothesis which we have now to consider. Let us first look at the evidences which certain inorganic phenomena furnish.

The molecules of any aggregate which have not a balanced arrangement, inevitably tend towards a balanced arrangement. As before mentioned (*First Principles*, § 103) amorphous wrought iron, when subject to continuous jar, begins to arrange itself into crystals—its atoms assume a condition of polar equilibrium. The particles of unannealed glass, which are so unstably arranged that slight disturbing forces make them separate into small groups, take advantage of that greater freedom of movement given by a raised temperature, to adjust themselves into a state of relative rest. During any such re-arrangement, the aggregate exercises a coercive force over its units. Just as in a growing crystal, the atoms successively assimilated from the solution, are made by the already-crystallized atoms to take a certain form, and even to re-complete that form when it is broken; so in any mass of unstably-arranged atoms that passes into a stable arrangement, each atom conforms to the forces exercised on it by all the other atoms. This is a corollary from the general law of equilibration. We saw (*First Principles*, § 130) that every change is towards equilibrium; and that change can never cease until equilibrium is reached. Organisms, above all other aggregates, conspicuously display this progressive equilibration; because their units are of such kinds, and so conditioned, as to admit of easy re-arrangement. Those extremely active changes which go on during the early stages of evolution, imply an immense excess of the molecular forces over those antagonist forces which the aggregate exercises on the molecules. While this excess continues, it is expended in growth, development, and function—expenditure for any of these purposes, being proof that part of the force embodied in molecular tensions, remains unbalanced. Eventually, however, this excess diminishes. Either, as in organisms which do not expend much force, decrease of assimilation leads to its decline; or, as in organisms which expend much force, it is counterbalanced by the rapidly-increasing re-actions of the aggregate (§ 46). The cessation of growth, when followed, as in some organisms, by death, implies the arrival at an equilibrium between the molecular forces, and those forces which the aggregate opposes to them. When, as in other organisms, growth ends in the establishment of a moving equilibrium, there is implied such a decreased preponderance of the molecular forces, as leaves no surplus beyond that which is used up in functions. The declining functional activity, characteristic of advancing life, expresses a further decline in this surplus. And when all vital movements come to an end, the implication is, that the actions of the units on the aggregate and the re-actions of the aggregate on the units, are completely balanced. Hence, while a state of rapid growth indicates such a play of forces among the units of an aggregate, as will produce active re-distribution; the diminution and arrest of growth, shows that the units have fallen into such relative positions that re-distribution is no longer so facile. When, therefore, we see that gamogenesis recurs only when growth is decreasing, or has come to an end, we must say that it recurs only when the organic units are approximating to equilibrium—only when their mutual restraints prevent them from readily changing their arrangements in obedience to incident forces.

That units of like forms can be built up into a more stable aggregate than units of slightly unlike forms, is tolerably manifest, *à priori*. And we have facts which prove that mixing allied but somewhat different units, *does* lead to comparative instability. Most metallic alloys exemplify this truth. Common solder, which is a mixture of lead and tin, melts at a much lower temperature than either lead or tin. The compound of lead, tin, and bismuth, called "fusible metal," becomes fluid at the temperature of boiling water; while the temperatures at which lead, tin, and bismuth become fluid, are, respectively, 612°, 442°, and 497°, F. Still more remarkable is the illustration furnished by potassium and sodium. These metals are very near akin in all respects—in their specific gravities, their atomic weights, their chemical affinities, and the properties of their compounds. That is to say, all the evidences unite to show that their units, though not identical, have a close resemblance. What now happens when they are mixed? Potassium alone melts at 136°, sodium alone melts at 190°, but the alloy of potassium and sodium, is liquid at the ordinary temperature of the air. Observe the meaning of these facts, expressed in general terms. The maintenance of a solid form by any group of units, implies among them an arrangement so stable, that it cannot be overthrown by the incident forces. Whereas the assumption of a liquid form, implies that the incident forces suffice to destroy the arrangement of the units. In the one case, the thermal undulations fail to dislocate the parts; while in the other case, the parts are so dislocated by the thermal undulations, that they fall into total disorder—a disorder admitting of easy re-arrangement into any other order. For the liquid state is a state in which the units become so far free from mutual restraints, that incident forces can change their relative positions very readily. Thus we have reason to conclude, that an aggregate of units which, though in the main similar to each other, have minor differences, must be more unstable than an aggregate of homogeneous units: the one will yield to disturbing forces which the other successfully resists.

Now though the colloidal atoms of which organisms are mainly built, are themselves highly composite; and though the physiological units compounded out of these colloidal atoms, must have structures far more involved; yet it must happen with such units, as with simple units, that those which have exactly like forms, will admit of arrangement into a more stable aggregate than those which have slightly-unlike forms. Among units of this order, as among units of a simpler order, imperfect similarity must entail imperfect polar balance, and consequent diminished ability to withstand disturbing forces. Hence, given two organisms which, by diminished nutrition or increased expenditure, are being arrested in their growths—given in each an approaching equilibrium between the forces of the units and the forces of the aggregate—given, that is, such a comparatively-balanced state among the units, that re-arrangement of them by incident forces is no longer so easy; and it will follow that by uniting a group of units from the one organism with a group of slightly-different units from the other, the tendency towards equilibrium will be diminished, and the mixed units will be rendered more modifiable in their arrangements by the forces acting on them: they will be so far freed as to become again capable of that re-distribution which constitutes evolution. This view of the matter is in harmony with the results of observation on the initial stages of development. Some pages back, it was asserted that sperm-cell and germ-cell severally arrive, before their union, at a condition of equilibrium. Though approximately true, this is not literally true. I learn from Dr W. H. Ransom, who has investigated the question with great care, that the unfertilized ovum continues, for a time, to undergo changes similar to those which the fertilized ovum undergoes; but that these changes, becoming languid and incomplete, are finally arrested by decomposition. Here we find what might be expected. In the first place, an organism which develops germ-cells, is not in a state of molecular equilibrium, but in a state of approach to such equilibrium. Hence, a group of physiological units cast off from it, will not be wholly without a tendency to undergo the structural re-arrangements which we call development; but will have this tendency unduly restrained by partially-balanced polarities. In the second place, undue restraint of the physiological units, while it renders them as wholes less-easily altered in their relative positions by incident forces, thereby also renders them more liable to be individually decomposed by incident forces: the same thermal undulations which, if the physiological units are comparatively free, will aid their re-arrangement by giving them still greater freedom, will, if they are comparatively fixed, begin to change the arrangements of their components—will decompose them. In the third place, their decomposition will be prevented as well as their re-distribution facilitated, by such disturbance of their polarities as we have seen must result from mixing with them the slightly-unlike units of another organism.

And now let us test this hypothesis, by seeing what power it gives us of interpreting established inductions.

§ 93. The majority of plants being hermaphrodites, it has, until quite recently, been supposed that the ovules of each flower are fertilized by pollen from the anthers of the same flower. Mr Darwin, however, has shown that the arrangements are generally such as to prevent this: either the ovules and the pollen are not ripe simultaneously, or obstacles prevent access of the one to the other. At the same time, he has shown that there exist arrangements, often of a remarkable kind, which facilitate the transfer of pollen by insects from the stamens of one flower to the pistil of another. Similarly, it has been found that among the lower animals, hermaphrodism does not usually involve the production of fertile germs, by the union of sperm-cells and germ-cells developed in the same individual; but that the reproductive centres of one individual are united with those of another, to produce fertile germs. Either, as in the *Pyrosoma*, the *Perophora*, and in many higher molluscs, the ova and spermatozoa are matured at different times; or, as in annelids, they are prevented by their relative positions from coming in contact.

Remembering the fact that among the higher classes of organisms, fertilization is always effected by combining the sperm-cell of one individual with the germ-cell of another; and joining with it the fact that among hermaphrodite organisms, the germ-cells developed in any individual, are usually not fertilized by sperm-cells developed in the same individual; we see reason for thinking that the essential thing in fertilization, is the union of specially-fitted portions of *different* organisms. If fertilization depended on the peculiar properties of sperm-cell and germ-cell, as such; then, in hermaphrodite organisms, it would be a matter of indifference whether the united sperm-cells and germ-cells were those of the same individual, or those of different individuals. But the circumstance that there exist in such organisms, elaborate appliances for mutual fertilization, shows that unlikeness of derivation in the united reproductive centres, is the desideratum. Now this is just what the foregoing hypothesis implies. If, as was concluded, fertilization has for its object the disturbance of that approximate equilibrium existing among the physiological units separated from an adult organism; and if, as we saw reason to think, this object is effected by mixture with the slightly-different physiological units of another organism; then, we at the same time see reason to think, that this object will not be effected by mixture with physiological units belonging to the same organism. Thus, the hypothesis leads us to expect such provisions as we find exist.

§ 94. But here a difficulty presents itself. These propositions seem to involve the conclusion, that self-fertilization is impossible. It apparently follows from them, that a group of physiological units from one part of an organism, ought to have no power of altering the state of approaching balance in a group from another part of it. Yet self-fertilization does occur. Though the ovules of one plant, are generally fertilized by pollen from another plant of the same kind; yet they may be, some of them, fertilized by the pollen of the same plant. And though, among hermaphrodite animals, self-fertilization is usually negatived by structural or functional arrangements; yet in certain *Entozoa*, there appear to be special provisions by which the sperm-cells and germ-cells of the same individual may be united, when not previously united with those of another individual. Certainly, at first sight, these facts do not consist with the above supposition. Nevertheless, there is a satisfactory solution of them.

In the last chapter, when considering the variations that may result in offspring from the combination of unlike parental constitutions, it was pointed out that in an unfolding organism, composed of slightly-different physiological units derived from slightly-different parents, there cannot be maintained an even distribution of the two orders of units. We saw that the instability of the homogeneous, negatives the uniform blending of them; and that, by the process of differentiation and integration, they must be more or less separated; so that in one part of the body the influence of one parent will predominate, and in another part of the body the influence of the other parent: an inference which harmonizes with daily observation. And we also saw, that the sperm-cells or germ-cells produced by such an organism, must, in virtue of these same laws, be more or less unlike one another. It was shown that through segregation, some of the sperm-cells or germ-cells will get an excess of the physiological units derived from one side, and some of them an excess of those derived from the other side: a cause which accounts for the unlikenesses among offspring simultaneously produced. Now from this segregation of the different orders of physiological units, inherited from different parents and lines of ancestry, there arises the possibility of self-fertilization in hermaphrodite organisms. If the physiological units contained in the sperm-cells and germ-cells of the same flower, are not quite homogeneous—if in some of the ovules the physiological units derived from the one parent greatly predominate, and in some of the ovules those derived from the other parent; and if the like is true of the pollen-cells; then, some of the ovules may be nearly as much contrasted with some of the pollen-cells, in the characters of their contained units, as were the ovules and pollen-cells of the parents from which the plant proceeded. Between part of the sperm-cells and part of the germ-cells, the community of nature will be such that fertilization will not result from their union; but between some of them, the differences of constitution will be such that their union will produce the requisite molecular instability. The facts, so far as they are known, seem in harmony with this deduction. Self-fertilization in flowers, when it takes place, is not so efficient as mutual fertilization. Though some of the ovules produce seeds, yet more of them than usual are abortive. From which, indeed, results the establishment of varieties that have structures favourable to mutual fertilization; since, being more prolific, these have, other things equal, greater chances in the "struggle for existence."

Further evidence is at hand in support of this interpretation. There is reason to believe that self-fertilization, which at the best is comparatively inefficient, loses all efficiency in course of time. After giving an account of the provisions for an occasional, or a frequent, or a constant crossing between flowers; and after quoting Prof. Huxley to the effect that among hermaphrodite animals, there is no case in which "the occasional influence of a distinct individual can be shown to be physically impossible;" Mr Darwin writes—"from these several considerations and from the many special facts which I have collected, but which I am not here able to give, I am strongly inclined to suspect that, both in the vegetable and animal kingdoms, an occasional intercross with a distinct individual is a law of nature. * * * in none, as I suspect, can self-fertilization go on for perpetuity." This conclusion, based wholly on observed facts, is just the conclusion to which the foregoing argument points. That necessary action and the re-action between the parts of an organism and the organism as a whole—that power of the aggregate to re-mould the units, which is the correlative of the power of the units to build up into such an aggregate; implies that any differences existing between the units inherited by an organism, must gradually diminish. Being subject in common to the total forces of the organism, they will in common be modified towards congruity with these forces; and therefore towards likeness with each other. If, then, in a self-fertilizing organism and its self-fertilizing descendants, such contrasts as originally existed among the physiological units, are progressively obliterated — if, consequently, there can no longer be a segregation of different physiological units in different sperm-cells and germ-cells; self-fertilization will become impossible: step by step the fertility will diminish, and the series will finally die out.

And now observe, in confirmation of this view, that self-fertilization is limited to organisms in which an approximate equilibrium among the organic forces, is not long maintained. While growth is actively going on, and the physiological units are subject to a continually-changing distribution of forces, no decided assimilation of the units can be expected: like forces acting on the unlike units, will tend to segregate them, so long as continuance of evolution permits further segregation; and only when further segregation cannot go on, will the like forces tend to assimilate the units. Hence, where there is no prolonged maintenance of an approximate organic balance, self-fertilization may be possible for some generations; but it will be impossible in organisms distinguished by a sustained moving equilibrium.

§ 95. The interpretation which it affords of sundry phenomena familiar to breeders of animals, adds probability to the hypothesis. Mr Darwin has collected a large " body of facts, showing, in accordance with the almost universal belief of breeders, that with animals and plants a cross between different varieties, or between individuals of the same variety but of another strain, gives vigour and fertility to the offspring; and on the other hand, that *close* interbreeding diminishes vigour and fertility,"—a conclusion harmonizing with the current belief respecting family-intermarriages in the human race. Have we not here a solution of these facts? Relations must, on the average of cases, be individuals whose physiological units are more nearly alike than usual. Animals of different varieties must be those whose physiological units are more unlike than usual. In the one case, the unlikeness of the units may frequently be insufficient to produce fertilization; or, if sufficient to produce fertilization, not sufficient to produce that active molecular change required for vigorous development. In the other case, both fertilization and vigorous development will be made probable.

Nor are we without a cause for the irregular manifestation of these general tendencies. The mixed physiological units composing any organism, being, as we have seen, more or less segregated in the reproductive centres it throws off; there may arise various results, according to the degrees of difference among the units, and the degrees in which the units are segregated. Of two cousins who have married, the common grandparents may have had either similar or dissimilar constitutions; and if their constitutions were dissimilar, the probability that their married grandchildren will have offspring will be greater than if their constitutions were similar. Or the brothers and sisters from whom these cousins descended, instead of severally inheriting the constitutions of their parents in tolerably equal degrees, may have severally inherited them in very different degrees: in which last case, intermarriages among the grandchildren will be less likely to prove infertile. Or the brothers and sisters from whom these cousins descended, may severally have married persons very like, or very unlike, themselves; and from this cause there may have resulted, either an undue likeness, or a due unlikeness, between the married cousins. These several causes, conspiring and conflicting in endless ways and degrees, will work multiform effects. Moreover, differences of segregation will make the reproductive centres produced by the same nearly-related organisms, vary considerably in their amounts of unlikeness; and therefore, supposing their amounts of unlikeness great enough to cause fertilization, this fertilization will be effective in various degrees. Hence it may happen that among offspring of nearly-related parents, there may be some in which the want of vigour is not marked, and others in which there is decided want of vigour. So that we are alike shown why in-and-in breeding tends to diminish both fertility and vigour; and why the effect cannot be a uniform effect, but only an average effect.

§ 96. While, if the foregoing arguments are valid, gamogenesis has for its main end, the initiation of a new development by the overthrow of that approximate equilibrium arrived at among the molecules of the parent-organisms; a further end appears to be subserved by it. Those inferior organisms which habitually multiply by agamogenesis, have conditions of life that are simple and uniform; while those organisms that have highly-complex and variable conditions of life, habitually multiply by gamogenesis. Now if a species has complex and variable conditions of life, its members must be severally exposed to sets of conditions that are slightly different: the aggregates of incident forces cannot be alike for all the scattered individuals. Hence, as functional deviation must ever be inducing structural deviation, each individual throughout the area occupied, tends to become fitted for the particular habits which its particular conditions necessitate; and in so far, *un*fitted for the average habits proper to the species. But these undue specializations are continually checked by gamogenesis. As Mr Darwin remarks "intercrossing plays a very important part in nature in keeping the individuals of the same species, or of the variety, true and uniform in character:" the idiosyncratic divergences obliterate each other. Gamogenesis, then, is a means of turning to positive advantage, the individual differentiations which, in its absence, would result in positive disadvantage. Were it not that individuals are ever being made unlike each other by their unlike conditions, there would not arise among them those contrasts of molecular constitution, which we have seen to be needful for producing the fertilized germs of new individuals. And were not these individual differentiations ever being mutually cancelled, they would end in a fatal narrowness of adaptation.

This truth will be most clearly seen if we reduce it to its purely abstract form, thus:—Suppose a quite homogeneous species, placed in quite homogeneous conditions; and suppose the constitutions of all its members in complete concord with their absolutely-uniform and constant conditions; what must happen? The species, individually and collectively, is in a state of perfect moving equilibrium. All disturbing forces have been eliminated. There remains no force which can, in any way, change the state of this moving equilibrium; either in the species as a whole or in its members. But we have seen (*First Principles*, § 133) that a moving equilibrium is but a transition towards complete equilibration, or death. The absence of differential or un-equilibrated forces among the members of a species, is the absence of all forces that can cause changes in the conditions of its members—is the absence of all forces which can initiate new organisms. To say, as above, that complete molecular homogeneity existing among the members of a species, must render impossible that mutual molecular disturbance which constitutes fertilization, is but another way of saying, that the actions and re-actions of each organism, being in perfect balance with the actions and re-actions of the environment upon it, there remains in each organism, no force by which it differs from any other —no force which any other does not meet with an exactly equal force—no force which can set up a new evolution among the units of any other.

And so we reach the remarkable conclusion, that the life of a species, like the life of an individual, is maintained by the unequal and ever-varying actions of incident forces on its different parts. An individual homogeneous throughout, and having its substance everywhere continuously subject to like actions, could undergo none of those changes which life consists of; and similarly, an absolutely-uniform species, having all its members exposed to identical influences, would be deprived of that initiator of change which maintains its existence as a species. Just as, in each organism, incident forces constantly produce divergences from the mean state in various directions, which are constantly balanced by opposite divergences indirectly produced by other incident forces; and just as the combination of rhythmical functions thus maintained, constitutes the life of the organism; so, in a species, there is, through gamogenesis, a perpetual neutralization of those contrary deviations from the mean state, which are caused in its different parts by different sets of incident forces; and it is similarly by the rhythmical production and compensation of these contrary deviations, that the species continues to live. The moving equilibrium in a species, like the moving equilibrium in an individual, would rapidly end in complete equilibration, or death, were not its continually-dissipated forces continually re-supplied from without. Besides owing to the external world, those energies which, from moment to moment, keep up the lives of its individual members; every species owes to certain more indirect actions of the external world, those energies which enable it to perpetuate itself in successive generations.

§ 97. What evidence still remains, may be conveniently woven up along with a recapitulation of the argument pursued through the last three chapters. Let us contemplate the facts in their synthetic order.

That compounding and re-compounding through which we pass from the simplest inorganic substances to the most complex organic substances, has several concomitants. Each successive stage of composition, presents us with atoms that are severally larger or more integrated, that are severally more heterogeneous, that are severally more unstable, and that are more numerous in their kinds (*First Principles*, § 111). And when we come to the substances of which living bodies are formed, we find ourselves among multiplied, divergent groups and sub-groups of compounds, the units of which are large, heterogeneous, and unstable, in high degrees. There is no reason to assume that this process ends with the formation of those complex colloids which characterize organic matter. A more probable assumption is, that out of the complex colloidal atoms, there are evolved, by a still further integration, atoms that are still more heterogeneous, and of kinds that are still more multitudinous. What must be their properties? Already the colloidal atoms are extremely unstable—capable of being variously modified in their characters by very slight incident forces; and already the complexity of their polarities prevents them from readily falling into those positions of polar equilibrium which result in crystallization. Now the organic atoms composed of these colloidal atoms, must be similarly characterized in far higher degrees. Far more numerous must be the minute changes that can be wrought in them by minute external forces; far more free must they remain for a long time to obey forces tending to re-distribute them; and far greater must be the number of their kinds.

Setting out with these physiological units, the existence of which various organic phenomena compel us to recognize, and the production of which the general law of Evolution thus leads us to anticipate; we get an insight into the phenomena of Genesis, Heredity, and Variation. If each organism is built of certain of these highly-plastic units peculiar to its species—units which slowly work towards an equilibrium of their complex polarities, in producing an aggregate of the specific structure, and which are at the same time slowly modifiable by the re-actions of this aggregate—we see why the multiplication of organisms proceeds in the several ways, and with the various results, which naturalists have observed.

Heredity, as shown not only in the repetition of the specific structure, but in the repetition of ancestral deviations from it, becomes a matter of course; and it falls into unison with the fact that, in various simple organisms, lost parts can be replaced, and that, in still simpler organisms, a fragment can develop into a whole.

While an aggregate of physiological units continues to grow, by the assimilation of matter which it moulds into other units of like type; and while it continues to undergo changes of structure; no equilibrium can be arrived at between the whole and its parts. Under these conditions, then, an un-differentiated portion of the aggregate—a group of physiological units not bound up into a specialized tissue—will be able to arrange itself into the structure peculiar to the species; and will so arrange itself, if freed from controlling forces, and placed in fit conditions of nutrition and temperature. Hence the continuance of agamogenesis in little-differentiated organisms, so long as assimilation continues to be greatly in excess of expenditure.

But let growth be checked and development approach its completion—let the units of the aggregate be severally exposed to an almost constant distribution of forces; and they must begin to equilibrate themselves. Arranged as they will gradually be, into comparatively stable attitudes in relation to each other, their mobility will diminish; and groups of them, partially or wholly detached, will no longer readily re-arrange themselves into the specific form. Agamogenesis will be no longer possible; or, if possible, will be no longer easy.

When we remember that the force which keeps the Earth in its orbit, is the gravitation of each particle in the Earth towards every one of the group of particles existing 91,000,000 of miles off; we cannot reasonably doubt, that each unit in an organism, acts, by its polar forces, on all the other units, and is re-acted on by them. When, too, we learn that glass has its molecular constitution changed by light, and that substances so rigid and stable as metals, have their atoms re-arranged by forces radiated in the dark from adjacent objects; we are obliged to conclude that the excessively-unstable units of which organisms are built, must be sensitive in a transcendant degree, to all the forces pervading the organisms composed of them—must be tending ever to re-adjust, not only their relative positions, but their molecular structures, into equilibrium with these forces. Hence, if aggregates of the same species are differently conditioned, and re-act differently on their component units, their component units will be rendered somewhat different; and they will become the more different the more widely the re-actions of the aggregates upon them differ, and the greater the number of generations through which these different re-actions of the aggregates upon them are continued.

If, then, unlikenesses of function among individuals of the same species, produce unlikenesses between the physiological units of one individual and those of another; it becomes comprehensible that when groups of units derived from two individuals are united, the group formed will be more unstable than either of the groups was before their union: the mixed units will be less able to resist those re-distributing forces which cause evolution; and may so have restored to them, the capacity for development which they had lost.

This view harmonizes with the conclusion which we saw reason to draw, that fertilization does not depend on any intrinsic peculiarities of sperm-cells and germ-cells; but depends on their derivation from different individuals. It explains the fact that nearly-related individuals are less likely to have offspring than others; and that their offspring, when they have them, are frequently feeble. And it gives us a key to the converse fact, that the crossing of varieties results in unusual fertility and vigour.

Bearing in mind that the slightly-different orders of physiological units which an organism inherits from its parents, are subject to the same set of forces; and that when the organism is fully developed, this set of forces, becoming constant, tends slowly to re-mould the two orders of units into the same form; we see how it happens that self-fertilization becomes impossible in the higher organisms, while it remains possible in the lower organisms. In long-lived creatures that have tolerably-definite limits of growth, this assimilation of the somewhat-unlike physiological units, is liable to go on to an appreciable extent; whereas in organisms which do not continuously subject their component units to constant forces, there will be much less of this assimilation. And where the assimilation is not considerable, the segregation of mixed units, may cause the sperm-cells and germ-cells developed in the same individual, to be sufficiently different to produce, by their union, fertile germs; and several generations of self-fertilizing descendants may succeed one another, before the two orders of units have had their unlikenesses so far diminished, that they will no longer do this. The same principles explain for us the variable results of union between nearly-related organisms. According to the contrasts among the physiological units they inherit from parents and ancestors; according to the unlike proportions of the contrasted units which they severally inherit; and according to the degrees of segregation of such units in different sperm-cells and germ-cells; it may happen that two kindred individuals will produce the ordinary number of offspring, or will produce none; or will at one time be fertile and at another not; or will at one time have offspring of tolerable strength, and at another time feeble offspring.

To the like causes are also ascribable the phenomena of Variation. These are unobtrusive while the tolerably-uniform conditions of a species maintain tolerable uniformity among the physiological units of its members; but they become obtrusive when differences of conditions, entailing considerable functional differences, have entailed decided differences among the physiological units; and when the different physiological units, differently mingled in every individual, come to be variously segregated and variously combined.

Did space permit, it might be shown that this hypothesis is a key to many further facts—to the fact that mixed races are comparatively plastic under new conditions; to the fact that pure races show predominant influences when crossed with mixed races; to the fact that while mixed breeds are often of larger growth, pure breeds are the more hardy—have functions less-easily thrown out of balance. But without further argument, it will, I think, be admitted, that the power of this hypothesis to explain so many phenomena, and to bring under a common bond phenomena that seem so little allied, is strong evidence of its truth. And such evidence gains greatly in strength on observing that this hypothesis brings the facts of Genesis, Heredity, and Variation into harmony with first principles. When we see that these plastic physiological units, which we find ourselves obliged to assume, are just such more integrated, more heterogeneous, more unstable, and more multiform atoms, as would result from continuance of the steps through which organic matter is reached—when we see that the differentiations of them assumed to occur in differently-conditioned aggregates, and the equilibrations of them assumed to occur in aggregates which maintain constant conditions, are but corollaries from those universal principles implied by the persistence of force—when we see that the maintenance of life in the successive generations of a species, becomes a consequence of the continual incidence of new forces on the species, to replace the forces that are ever being rhythmically equilibrated in the propagation of the species—and when we thus see that these apparently-exceptional phenomena displayed in the multiplication of organic beings, fall into their places as results of the general laws of Evolution; we have weighty reasons for entertaining the hypothesis which affords us this interpretation.

# CHAPTER XI.

## CLASSIFICATION.

§ 98. THAT orderly arrangement of objects called Classification, has two purposes; which, though not absolutely distinct, are distinct in great part. It may be employed to facilitate identification; or it may be employed to organize our knowledge. If a librarian places his books in the alphabetical succession of the author's names, he places them in such way that any particular book may easily be found; but not in such way that books of a given nature stand together. When, conversely, he makes a distribution of books according to their subjects, he neglects various superficial similarities and distinctions, and groups them according to certain primary and secondary and tertiary attributes, which severally imply many other attributes—groups them so that any one volume being inspected, the general characters of all the neighbouring volumes may be inferred. He puts together in one great division, all works on History; in another all Biographical works; in another all works that treat of Science; in another Voyages and Travels; and so on. Each of his great groups he separates into sub-groups; as when he puts different kinds of pure Literature, under the heads of Fiction, Poetry, and the Drama. In some cases he makes sub-sub-groups; as when, having divided his Scientific treatises into abstract and concrete, putting in the one Logic and Mathematics, and in the other Physics, Astronomy, Geology, Chemistry, Physiology, &c.; he goes on to sub-divide his books on Physics, into those which treat of Mechanical Motion, those which treat of Heat, those which treat of Light, of Electricity, of Magnetism.

Between these two modes of classification, note the essential distinctions. Arrangement according to any single conspicuous attribute is comparatively easy, and is the first that suggests itself: a child may place books in the order of their sizes, or according to the styles of their bindings. But arrangement according to combinations of attributes, which, though fundamental, are not conspicuous, requires analysis; and does not suggest itself till analysis has made some progress. Even when aided by the information which the author gives on his title page, it requires considerable knowledge to classify rightly an essay on Polarization; and in the absence of a title page, it requires much more knowledge. Again, classification by a single attribute, which the objects possess in different degrees, may be more or less serial, or linear. Books may be put in the order of their dates, in single file; or if they are grouped as works in one volume, works in two volumes, works in three volumes, &c., the groups may be placed in an ascending succession. But groups severally formed of things distinguished by some common attribute which implies many other attributes, do not admit of serial arrangement. You cannot rationally say, either that Historical Works should come before Scientific Works, or Scientific Works before Historical Works; nor of the sub-divisions of creative Literature, into Fiction, Poetry, and the Drama, can you give a good reason why any one should take precedence of the others.

Hence this grouping of the like and separation of the unlike, which constitutes Classification, can reach its complete form only by slow steps. We saw (*First Principles,* § 36) that, other things equal, the relations among phenomena are recognized in the order of their conspicuousness; and that, other things equal, they are recognized in the order of their simplicity. The first classifications are sure, therefore, to be groupings of objects that resemble each other in external or easily-perceived attributes, and attributes that are not of complex characters. Those likenesses among things which are due to their possession in common of simple obvious properties, may or may not coexist with further likenesses among them. When geometrical figures are classed as curvilinear and rectilinear, or when the rectilinear are divided into trilateral, quadrilateral, &c., the distinctions made, connote various other distinctions, with which they are necessarily bound up; but if liquids be classed according to their visible characters—if water, alcohol, sulphuret of carbon, &c., be grouped as colourless and transparent, we have things placed together which are unlike in their essential natures. Thus, where the objects classed have numerous attributes, the probabilities are, that the early classifications, based on simple and manifest attributes, unite under the same head many objects that have no resemblances in the majority of their attributes. As the knowledge of objects increases, it becomes possible to make groups of which the members have more numerous properties in common; and to ascertain what property, or combination of properties, is most characteristic of each group. And the classification eventually arrived at, is one in which the segregation has been carried so far, that the objects integrated in each group have more attributes in common with one another, than they have in common with any excluded objects; one in which the groups of such groups are integrated on the same principle; and one in which the degrees of differentiation and integration are proportioned to the degrees of intrinsic unlikeness and likeness. And the ultimate classification, while it serves most completely to identify the things, serves also to express the greatest amount of knowledge concerning the things—enables us to predicate the greatest number of facts concerning each thing; and by so doing proves that it expresses the most precise correspondence between our conceptions and the realities.

§ 99. Biological classifications illustrate well these phases, through which classifications in general necessarily pass. In early attempts to arrange organic beings in some systematic manner, we see at first, a guidance by conspicuous and simple characters, and a tendency towards arrangement in linear order. In successively later attempts, we see more regard paid to combinations of characters which are essential but often inconspicuous; and a gradual abandonment of a linear arrangement for an arrangement in divergent groups and re-divergent sub-groups.

In the popular mind, plants are still classed under the heads of Trees, Shrubs, and Herbs; and this serial classing according to the single attribute of magnitude, swayed the earliest observers. They would have thought it absurd to call a bamboo, thirty feet high, a kind of grass; and would have been incredulous if told that the Hart's-tongue should be placed in the same great division with the Tree-ferns. The zoological classifications that were current before Natural History became a science, had divisions similarly superficial and simple. Beasts, Birds, Fishes, and Creeping-things, are names of groups marked off from one another by conspicuous differences of appearance and modes of life—creatures that walk and run, creatures that fly, creatures that live in the water, creatures that crawl. And these groups were thought of in the order of their importance.

The first arrangements made by naturalists were based either on single characters, or on very simple combinations of characters. Describing plant-classifications, Lindley says: — "Rivinus invented, in 1690, a system depending upon the formation of the corolla; Kamel, in 1693, upon the fruit alone; Magnol, in 1720, on the calyx and corolla; and finally, Linnæus, in 1731, on variations in the stamens and pistil." In this last system, which has been for so long current as a means of identification, simple external attributes are still depended on; and an arrangement, in great measure serial, is based on the degrees in which these attributes are possessed. In 1703, some thirty years before the time of Linnæus, our countryman Ray had sketched the outlines of a more advanced system. He said that—

Plants are either
    Flowerless, or
    Flowering; and these are
        Dicotyledones, or
        Monocotyledones.

Among the minor groups which he placed under these general heads, "were Fungi, Mosses, Ferns, Composites, Cichoraceæ Umbellifers, Papilionaceous plants, Conifers, Labiates, &c., under other names, but with limits not very different from those now assigned to them." Being much in advance of his age, Ray's ideas remained dormant until the time of Jussieu; by whom they were developed into what has become known as the Natural System. Passing through various modifications in the hands of successive botanists, the Natural System has now taken the following form; which I copy (adding the alliances to the classes) from Prof. Lindley's *Vegetable Kingdom.**

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* From this table I have omitted the class *Rhizogens*, which other botanists do not agree with Lindley in regarding as a separate class. The plants respecting which there has arisen this difference of opinion, are certain flowering plants, which grow parasitically on the roots of trees. The reasons assigned by Endlicher and Lindley, for erecting them into a separate group of Phænogams, are, that in place of true leaves they have only cellular scales; that the stem is an amorphous fungous mass, imperfectly supplied with spiral vessels; and that they are without chlorophyll. Mr Griffith and Dr Hooker, however, have given preponderating reasons why they should be restored to the class Exogens. It seems here worth remarking, that certain zoological facts suggest an explanation of these anomalous botanical facts; and confirm the conclusion reached by Dr Hooker and Mr Griffith. It very commonly happens that animal-parasites are aberrant forms of the types to which they belong; and, by analogy, we may not unreasonably expect to find among parasitic plants, the most aberrant forms of vegetal types. More than this is true. The kind of aberration which we see in the one case, we see in the other; and in both cases, the meaning of the aberration is manifest. In such *Epizoa* as the *Lerneæ*, the Crustacean type is disguised by the almost entire loss of the limbs and organs of sense, by the simplification of the digestive apparatus, and by the great development of the reproductive system :

*Asexual, or Flowerless Plants.*

| | | |
|---|---|---|
| Stems and leaves undistinguishable | I. THALLOGENS | Algales<br>Fungales<br>Lichenales |
| Stems and leaves distinguishable | II. ACROGENS | Muscales<br>Lycopodales<br>Filicales |

*Sexual, or Flowering Plants.*

| | | | |
|---|---|---|---|
| Wood of stem youngest in centre; cotyledon single. | | | |
| Leaves parallel-veined, permanent; wood confused | III. ENDOGENS | | Glumales<br>Arales<br>Palmales<br>Hydrales<br>Narcissales<br>Amomales<br>Orchidales<br>Xyridales<br>Juncales<br>Liliales<br>Alismales |
| Leaves net-veined, deciduous; wood, when perennial, arranged in a circle with a central pith | IV. DICTYOGENS. | | |
| Wood of stem youngest at circumference, always concentric; cotyledons two or more. | | | |
| Seeds quite naked | V. GYMNOGENS. | | |
| Seeds enclosed in seed-vessels | VI. EXOGENS | Diclinous | Amentales<br>Urticales<br>Euphorbiales<br>&c. &c. |
| | | Hypogynous | Violales<br>Cistales<br>Malvales<br>&c. &c. |
| | | Perigynous | Ficoidales<br>Daphnales<br>Rosales<br>&c. &c. |
| | | Epigynous | Campanales<br>Myrtales<br>Cactales<br>&c. &c. |

Here, linear arrangement has disappeared: there is a breaking up into groups and sub-groups and sub-sub-groups, which do not admit of being placed in serial order, but only in divergent and re-divergent order. Were there space to exhibit the way in which the Alliances are subdivided into Orders, and these into Genera, and these into Species; the

the parts no longer needed, abort, and those parts develop which favour the preservation of the race. Similarly in the *Rhizogens*, the abortive development of the leaves. the absence of chlorophyll, and the imperfect supply of spiral vessels, are changes towards a structure fit for a plant which lives on the juices absorbed from another plant; while the rapid and great development of the fructifying organs, are correlative changes advantageous to a plant, the seeds of which have but small chances of rooting themselves. And just the same reason that exists for the production of immensely numerous but extremely small eggs by *Entozoa*, exists for the production by *Rhizogens*, of seeds that are great in number and almost spore-like in size.

same principle of co-ordination would be still further manifested. On studying the definitions of these primary, secondary, and tertiary classes, it will be found that the largest are marked off from each other by some attribute which connotes sundry other attributes; that each of the smaller classes comprehended in one of these largest classes, is marked off in a similar way from the smaller classes bound up with it; and that so, each successively smaller class, has an increased number of co-existing attributes.

§ 100. Zoological classification has had a parallel history. The first attempt which we need notice, to arrange animals in such a way as to display their affinities, is that of Linnæus. He grouped them thus:*—

CL. 1. MAMMALIA. *Ord.* Primates, Bruta, Feræ, Glires, Pecora, Belluæ, Cete.

CL. 2. AVES. *Ord.* Accipitres, Picæ, Anseres, Grallæ, Gallinæ, Passeres.

CL. 3. AMPHIBIA. *Ord.* Reptiles, Serpentes, Nantes.

CL. 4. PISCES. *Ord.* Apodes, Jugulares, Thoracici, Abdominales.

CL. 5. INSECTA. *Ord.* Coleoptera, Hemiptera, Lepidoptera, Neuroptera, Diptera, Aptera.

CL. 6. VERMES. *Ord.* Intestina, Mollusca, Testacea, Lithophyta, Zoophyta.

This arrangement of classes, is obviously based on apparent gradations of rank; and the placing of the orders similarly betrays an endeavour to make successions, beginning with the most superior forms and ending with the most inferior forms. While the general and vague idea of perfection, determines the leading character of the classification, its detailed groupings are determined by the most conspicuous external attributes. Not only Linnæus, but his opponents, who proposed other systems, were "under the impression that animals were to be arranged together into classes, orders, genera, and species, according to their more or less close external resemblance." This conception survived till the time of Cuvier. "Naturalists,"

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* This classification, and the three which follow it, I quote (abridging some of them) from Prof. Agassiz's "Essay on Classification."

says Agassiz, "were bent upon establishing one continual uniform series to embrace all animals, between the links of which it was supposed there were no unequal intervals. The watchword of their school was: *Natura non facit saltum.* They called their system *la chaine des êtres.*"

The classification of Cuvier, based on internal organization instead of external appearance, was a great advance. He asserted that there are four principal forms, or four general plans, on which animals are constructed; and in pursuance of this assertion, he drew out the following scheme.

First Branch. ANIMALIA VERTEBRATA.
  - CL. 1. MAMMALIA.
  - CL. 2. BIRDS.
  - CL. 3. REPTILIA.
  - CL. 4. FISHES.

Second Branch. ANIMALIA MOLLUSCA.
  - CL. 1. CEPHALAPODA.
  - CL. 2. PTEROPODA.
  - CL. 3. GASTEROPODA.
  - CL. 4. ACEPHALA.
  - CL. 5. BRACHIOPODA.
  - CL. 6. CIRRHOPODA.

Third Branch. ANIMALIA ARTICULATA.
  - CL. 1. ANNELIDES.
  - CL. 2. CRUSTACEA.
  - CL. 3. ARACHNIDES.
  - CL. 4. INSECTS.

Fourth Branch. ANIMALIA RADIATA.
  - CL. 1. ECHINODERMS.
  - CL. 2. INTESTINAL WORMS.
  - CL. 3. ACALEPHÆ.
  - CL. 4. POLYPI.
  - CL. 5. INFUSORIA.

But though Cuvier emancipated himself from the conception of a serial progression throughout the Animal-Kingdom; sundry of his contemporaries and successors remained fettered by the old error. Less regardful of the differently-co-ordinated sets of attributes displayed by the different sub-kingdoms; and swayed by the belief in a progressive development, which was erroneously supposed to imply the possibility of arranging animals in a linear series; they persisted in thrusting organic forms into a quite unnatural order. The following classification of Lamarck illustrates this.

INVERTEBRATA.

| | |
|---|---|
| I. Apathetic Animals.<br>Cl. 1. Infusoria.<br>Cl. 2. Polypi.<br>Cl. 3. Radiaria.<br>Cl. 4. Tunicata.<br>Cl. 5. Vermes. | Do not feel, and move only by their excited irritability. No brain, not elongated medullary mass; no senses; forms varied; rarely articulations. |
| II. Sensitive Animals.<br>Cl. 6. Insects.<br>Cl. 7. Arachnids.<br>Cl. 8. Crustacea.<br>Cl. 9. Annelids.<br>Cl. 10. Cirripeds.<br>Cl. 11. Conchifera.<br>Cl. 12. Mollusks. | Feel, but obtain from their sensations only perceptions of objects, a sort of simple ideas, which they are unable to combine to obtain complex ones. No vertebral column; a brain and mostly an elongated medullary mass; some distinct senses; muscles attached under the skin; form symmetrical, the parts being in pairs. |

VERTEBRATA.

| | |
|---|---|
| III. Intelligent Animals.<br>Cl. 13. Fishes.<br>Cl. 14. Reptiles.<br>Cl. 15. Birds.<br>Cl. 16. Mammalia. | Feel; acquire preservable ideas; perform with them operations by which they obtain others; are intelligent in different degrees. A vertebral column; a brain and a spinal marrow; distinct senses; the muscles attached to the internal skeleton; form symmetrical, the parts being in pairs. |

Passing over sundry classifications in which the serial arrangement dictated by the notion of ascending complexity, is variously modified by the recognition of conspicuous anatomical facts, we come to the classifications which recognize another order of facts—those of development. The embryological inquiries of Von Baer, led him to arrange animals as follows:—

I. Peripheric Type. (RADIATA.) *Evolutio radiata.* The development proceeds from a centre, producing identical parts in a radiating order.
II. Massive Type. (MOLLUSCA.) *Evolutio contorta.* The development produces identical parts curved around a conical or other space.
III. Longitudinal Type. (ARTICULATA.) *Evolutio gemina.* The development produces identical parts arising on both sides of an axis, and closing up along a line opposite the axis.
IV. Doubly Symmetrical type. (VERTEBRATA.) *Evolutio bigemina.* The development produces identical parts arising on both sides of an axis, growing upwards and downwards, and shutting up along two lines, so that the inner layer of the germ is inclosed below, and the upper layer above. The embryos of these animals have a dorsal cord, dorsal plates, and ventral plates, a nervous tube and branchial fissures.

Recognizing these fundamental differences in the modes of evolution, as answering to fundamental divisions in the animal kingdom, Von Baer shows (among the *Vertebrata* at least) how the minor differences that arise at successively later stages of evolution, correspond with the minor divisions.

Like the modern classification of plants, the classification of animals that has now been arrived at, is one in which the linear order is completely broken up. In his lectures at the Royal Institution, in 1857, Prof. Huxley expressed the relations existing among the several great groups of the animal kingdom, by placing these groups at the ends of four or five radii, diverging from a centre. The diagram I cannot obtain; but in the published reports of his lectures at the School of Mines the groups were arranged thus:—

VERTEBRATA

(*Abranchiata*)
Mammalia
Aves
Reptilia
(*Branchiata*)
Amphibia
Pisces

MOLLUSCA

Cephalopoda Heteropoda
Gasteropoda-dioecia
Pulmonata Gasteropoda-
Pteropoda monœcia
Lamellibranchiata

ANNULOSA

*Articulata*
Insecta Arachnida
Myriapoda Crustacea

*Annuloida*
Annellata Scoleidæ
Echinodermata Trematoda
Rotifera Tœniadæ
Turbellaria
Nematoidea

CŒLENTERATA

Hydrozoa Actinozoa.

PROTOZOA

Infusoria Spongiadæ Gregarinidæ
*Noctilucidæ* Foraminifera *Thallassicollidæ*

What remnant there may seem to be of linear succession in some of these sub-groups, is merely an accident of typographical convenience. Each of them is to be regarded simply as a cluster. Were Prof. Huxley now to revise this scheme, he would probably separate more completely some of the great sub-groups, in conformity with the views expressed in his Hunterian Lectures delivered at the College of Surgeons in 1863. And if he were further to develop the arrangement, by dispersing the sub-groups and sub-sub-groups on the same principle, there would result an arrangement perhaps not very much unlike that shown in the annexed diagram.

In this diagram, the dots represent orders, the names of which it is impracticable to insert. If it be supposed that when magnified, each of these dots resolves itself into a cluster of clusters, representing genera and species, an approximate idea will be formed of the relations among the successively-subordinate groups constituting the animal kingdom. Besides the subordination of groups and their general distribution, some other facts are indicated. By the distances of the great divisions from the general centre, are rudely symbolized their respective degrees of divergence from the form of simple, undifferentiated organic matter; which we may regard as their common source. Within each group, the remoteness from the local centre represents, in a rough way, the degree of departure from the general plan of the group. And the distribution of the sub-groups within each group, is in most cases such, that those which come nearest to neighbouring groups, are those which show the nearest resemblances to them—in their analogies though not in their homologies. No diagram, however, can give a correct conception. Even supposing the above diagram expressed the relations of animals to one another as truly as they can be expressed on a plane surface, (which of course it does not,) it would still be inadequate. Such relations cannot be represented in space of two dimensions; but only in space of three dimensions.

§ 101. While the classifications of botanists and zoologists have become more and more natural in their arrangements, there has grown up a certain artificiality in their abstract nomenclature. When aggregating the smallest groups into larger groups, and these into groups still larger, naturalists adopted certain general terms expressive of the successively more comprehensive divisions; and the habitual use of these terms, needful for purposes of convenience, has led to the tacit assumption that they answer to actualities in Nature. It has been taken for granted that species, genera, orders, and classes, are assemblages of definite values—that every genus is the equivalent of every other genus, in respect of its degree of distinctness; and that orders are separated by lines of demarcation that are as broad in one place as another. Though this conviction is not a formulated one, yet the disputes continually arising among naturalists on the questions, whether such and such organisms are specifically or generically distinct, and whether this or that peculiarity is or is not of ordinal importance, imply that the conviction is entertained even where it is not avowed. Yet that differences of opinion like these continually arise, and remain unsettled, except when they end in the establishment of sub-species, sub-genera, sub-orders, and sub-classes, sufficiently shows that no such conviction is justifiable. And this is equally shown by the impossibility of obtaining any definition of the degree of difference, which warrants each further elevation in the hierarchy of classes.

It is, indeed, a wholly gratuitous assumption that organisms admit of being placed in groups of equivalent values; and that these may be united into larger groups that are also of equivalent values; and so on. There is no *à priori* reason for expecting this; and there is no *à posteriori* evidence implying it, save that which begs the question—that which asserts one distinction to be generic and another to be ordinal, because it is assumed that such distinctions must be either generic or ordinal. The endeavour to thrust plants and animals into these definite partitions, is of the same nature as the endeavour to thrust them into a linear series. Not that it does violence to the facts in anything like the same degree; but still, it does violence to the facts. Doubtless the making of divisions and sub-divisions, is extremely useful; or rather, it is absolutely necessary. Doubtless, too, in reducing the facts to something like order, they must be partially distorted. So long as the distorted form is not mistaken for the actual form, no harm results. But it is needful for us to remember, that while our successively subordinate groups have a certain general correspondence with the realities, they inevitably give to the realities a regularity which does not exist.

§ 102. A general truth of much significance is exhibited in these classifications. On observing the natures of the attributes which are common to the members of any group of the first, second, third, or fourth rank, we see that groups of the widest generality are based on characteristics of the greatest importance, physiologically considered ; and that the characteristics of the successively-subordinate groups, are characteristics of successively-subordinate importance. The structural peculiarity in which all members of one sub-kingdom differ from all members of another sub-kingdom, is a peculiarity that affects the vital actions more profoundly, than does the structural peculiarity which distinguishes all members of one class from all members of another class. Let us look at a few cases.

We saw (§ 56), that the broadest division among the functions is the division into "the *accumulation of force* (latent in food); the *expenditure of force* (latent in the tissues and certain matters absorbed by them); and the *transfer of force* (latent in the prepared nutriment or blood) from the parts which accumulate to the parts which expend." Now the lowest animals, united under the general name *Protozoa*, are those in which there is either no separation of the parts performing these functions or very indistinct separation: in the *Rhizopoda*, all parts are alike accumulators of force, expenders of force, and transferrers of force; and though in the most differentiated members of the group, the *Infusoria*, there are something like specializations corresponding to these functions, yet there are no distinct tissues appropriated to them. The animals known as *Cœlenterata* are characterized in common by the possession of a part which accumulates force more or less marked off from the part which does not accumulate force, but only expends it; and the *Hydrozoa* and *Actinozoa*, which are sub-divisions of the *Cœlenterata*, are contrasted in this, that in the one these parts are very indefinitely distinguished, but in the other definitely separated, as well as more complicated. Besides a completer differentiation of the organs respectively devoted to the accumulation of force and the expenditure of force, the animals classed as *Molluscoida*, possess rude appliances for the transfer of force: the peri-visceral sac, or closed cavity between the intestine and the walls of the body, serves as a reservoir of absorbed nutriment, from which the surrounding tissues take up the materials they need. The more highly-organized animals, belonging to whichever sub-kingdom, all of them possess definitely-constructed channels for the transfer of force; and in all of them, the function of expenditure is divided between a directive apparatus and an executive apparatus—a nervous system and a muscular system. But these higher sub-kingdoms are clearly separated from each other by differences in the relative positions of their component sets of organs. Prof. Huxley defines the type of the *Vertebrata*, as one in which the ganglionic nervous system lies on the dorsal side of the alimentary canal, while the central vascular system lies on its ventral side; and one which is yet further characterized by the possession of a second, and more conspicuous, nervous system, placed on the dorsal side of the vertebral axis—an extra endowment which is perhaps the most essentially distinctive. The types of the *Annulosa* and *Mollusca*, are together marked off from the vertebrate type, by the singleness of the nervous system, and by its occupation of the ventral side of the body: the habitual attitudes of annulose and molluscous creatures, is such that the neural centres are below the alimentary canal and the hæmal centres above. And while by these traits the annulose and molluscous types are separated from the vertebrate, they are separated from each other by this, that in the one the body is "composed of successive segments, usually provided with limbs," but the other, the body is not segmented, "and no true articulated limbs are ever developed."

The sub-kingdoms being thus distinguished from one another, by the presence or absence of parts devoted to fundamental functions, or else by differences in the distributions of such parts; we find, on descending to the classes, that these are distinguished from each other, either by modifications in the structures of fundamental parts, or by the presence or absence of subsidiary parts, or by both. Fishes and *Amphibia* are unlike higher vertebrates in possessing branchiæ; either throughout life or early in life. And every higher vertebrate, besides having lungs, is characterized by having, during development, an amnion and an allantois. Mammals, again, are marked off from Birds and Reptiles by the presence of mammæ, as well as by the form of the occipital condyles. Among Mammals, the next division is based on the presence or absence of a placenta. And divisions of the *Placentalia* are mainly determined by the characters of the organs of external action.

Thus, without multiplying illustrations and without descending to genera and species, we see that, speaking generally, the successively smaller groups, are distinguished from one another by traits of successively less importance, physiologically considered. The attributes possessed in common by the largest assemblages of organisms, are few in number but all-essential in kind—affect fundamentally the most vital actions. Each secondary assemblage, included in one of the primary assemblages, is characterized by further common attributes that influence the functions less profoundly. And so on with each lower grade of assemblage.

§ 103. What interpretation is to be put on these truths of classification? We find that organic forms admit of an arrangement everywhere expressive of the fact, that along with certain attributes, certain other attributes, which are not directly connected with them, always exist. How are we to account for this fact? And how are we to account for the fact that the attributes possessed in common by the largest assemblages of forms, are the most vitally-important attributes?

No one can believe that combinations of this kind may have arisen fortuitously. Or if any one believes this, it is easy to prove to him that the law of probabilities negatives the assumption. Even supposing fortuitous combinations of attributes might result in organisms that would work, we should still be without a clue to this special mode of combination. The chances would be infinity to one against organisms which possessed in common certain fundamental attributes, having also in common numerous non-essential attributes.

No one, again, can allege that such combinations are necessary, in the sense that all other combinations are impracticable. There is not, in the nature of things, any reason why creatures covered with feathers should always have beaks: jaws holding teeth would, in many cases, have served them equally well or better. The most general characteristic of an entire sub-kingdom, equal in extent to the *Vertebrata,* might have been the possession of nictitating membranes; while the internal organizations throughout this sub-kingdom, might have been on many different plans.

If, on the other hand, this peculiar subordination of attributes which organic forms display, be ascribed to design, other difficulties suggest themselves. To suppose that a certain plan of organization was fixed on by a Creator, for each vast and varied group, the members of which were to lead many different modes of life; and that he bound himself to adhere rigidly to this plan, even in the most aberrant forms of the group, where some other plan would have been more appropriate; is to ascribe a very strange motive. When we discover that the possession of seven cervical vertebræ is a general characteristic of mammals, whether the neck be immensely long, as in the giraffe, or quite rudimentary, as in the whale; shall we say that though, for the whale's neck, one vertebra would have been equally good, and though, for the giraffe's neck, a dozen would probably have been better than seven, yet seven was the number adhered to in both cases, because seven was fixed upon for the mammalian type?

And then, when it turns out that this possession of seven cervical vertebræ is not an absolutely-universal characteristic of mammals, shall we conclude that while, in a host of cases, there is a needless adherence to a plan for the sake of consistency, there is yet, in some cases, an inconsistent abandonment of the plan? I think we may properly refuse to draw any such conclusion.

What, then, is the meaning of these peculiar relations of organic forms? The answer to this question must be postponed. Having here contemplated the problem as presented in these wide inductions which naturalists have reached; and having seen what proposed solutions of it are inadmissible; we shall see, in the next division of this work, what is the only possible solution.

# CHAPTER XII.

## DISTRIBUTION.

§ 104. THERE is a distribution of organisms in Space, and there is a distribution of organisms in Time. Looking first at their distribution in Space, we observe in it two different classes of facts. On the one hand, the plants and animals of each species, manifestly have their habitats limited by external conditions: they are necessarily restricted to spaces in which their vital actions can be performed. On the other hand, the existence of certain conditions does not determine the presence of organisms that are the fittest for them: there are many spaces perfectly adapted for life of a high order, in which only life of a much lower order is found. While, in this inevitable restriction of organisms to environments with which their natures correspond, we find a *negative* cause of distribution; there remains to be found that *positive* cause of distribution, whence results the presence of organisms in some of the places appropriate to them, and their absence from other places that are equally appropriate and more appropriate. Let us consider the phenomena under these categories.

§ 105. Facts which illustrate the limiting influence of surrounding conditions, are abundant, and familiar to all readers. It will be needful, however, here to cite a few typical ones of each order.

The confinement of different kinds of plants and different kinds of animals, to the media for which they are severally adapted, is the broadest fact of distribution. We have extensive groups of plants that are respectively sub-aerial and sub-aqueous; and of the sub-aqueous, some are exclusively marine, while others exist only in rivers and lakes. Among animals, we similarly find some classes confined to the air and others to the water; and of the water-breathers, some are restricted to salt water and others to fresh water. Less familiar is the fact, that within each of these strongly contrasted media, there are further wide-spread limitations. In the sea, certain organisms exist only between certain depths, while other organisms exist only between other depths—the limpet within the littoral zone, and the *Globigerina* at the bottom of the Atlantic; and on the land, there are Floras and Faunas peculiar to low regions, and others peculiar to high regions. Next we have the well-known geographical limitations, made by climate. There are temperatures that restrict each kind of organism between certain isothermal lines; and hygrometric states that prevent the spread of each kind of organism beyond areas having a certain humidity or a certain dryness. Besides such general limitations, we find much more special limitations. Some minute vegetal forms occur only in snow. Hot springs have their peculiar *Infusoria*. The habitats of certain Fungi are mines or other dark places. And there are creatures unknown beyond the water contained in particular caves. After these limits to distribution imposed by physical conditions, come limits of a different class, imposed by the presence or absence of other organisms. Obviously, graminivorous animals are confined within tracts which produce plants fit for them to feed on. Large carnivores cannot exist out of regions where there are creatures numerous enough and large enough to serve for prey. The requirements of the sloth, limit it to certain forest-covered spaces; and there can be no insectivorous bats, where there are no night-flying insects. To these dependences of the relatively-superior organisms on the relatively-inferior organisms which they consume, must be added certain reciprocal dependences of the inferior on the superior. Mr Darwin's inquiries have shown how generally the fertilization of plants is due to the agency of insects; and how certain plants, being fertilizable only by insects of a certain structure, are limited to regions inhabited by insects of this structure. Conversely, the spread of organisms is often bounded by the presence of particular organisms beyond the bounds—either competing organisms or organisms directly inimical. A plant that is fit for some territory adjacent to its own, fails to overrun it, because the territory is pre-occupied by some plant that is its superior, either in fertility or power of resisting destructive agencies; or else because there lives in the territory some mammal which browses on its foliage, or bird which devours nearly all its seeds. Similarly, an area in which animals of a particular species might thrive, is not colonized by them, because they are not fleet enough to escape some beast of prey inhabiting this area; or because the area is infested by some insect which destroys them, as the tsetse destroys the cattle in parts of Africa. Yet another more special series of limitations, accompanies parasitism. There are parasitic plants that flourish only on trees of some few kinds; and others that have certain animals for their habitats—as the fungus which is fatal to the silk-worm, or that which so strangely grows out of a New Zealand caterpillar. Of animal-parasitism we have various kinds: severally involving their specialities of distribution. We have that kind in which one creature uses another for purposes of locomotion; as the *Chelonobia* uses the turtle, and as a certain *Actinia* uses the shell inhabited by a hermit-crab. We have that kind in which one creature habitually accompanies another to share its prey; like the annelid which takes up its abode in the shell occupied by a hermit-crab, and snatches from the hermit-crab, the morsels of food it is eating. We have again the commoner parasitism of the *Epizoa*—animals which attach themselves to the surfaces of other animals, and feed on their juices or on their secretions. And once more, we have the equally common parasitism of the *Entozoa*—creatures which live within other creatures. Besides being restricted in its distribution to the bodies of the organisms it infests, each species of parasite has usually still narrower limitations: in some cases the infested organisms furnish fit habitats for the parasites only in certain regions; and in other cases, only when in certain constitutional states. There are various more indirect modes in which the distributions of organisms affect each other. Plants of particular kinds are eaten by animals, only in the absence of kinds that are preferred to them; and the prosperity of such plants, hence partly depends on the presence of the preferred plants. Mr Bates has pointed out that some South American butterflies, thrive in regions where insectivorous birds would else destroy them, because they closely resemble butterflies of another genus which are disliked by those birds. And Mr Darwin gives cases of dependence still more remote and involved.

Such are the chief negative causes of distribution—the inorganic and organic agencies, that set bounds to the spaces which organisms of each species inhabit Fully to understand their actions, we must contemplate them as working not separately, but in concert. We have to regard the physical influences, varying from year to year, as now producing an extension or restriction of the habitat in this direction, and now in that; and as producing secondary extensions and restrictions, by their effects on other kinds of organisms. We have to regard the distribution of each organism, not only as affected by causes which favour multiplication of prey or of enemies within its own area; but also by causes which produce such results in neighbouring areas. We have to conceive the forces by which the limit is maintained, as including all meteorologic influences, united with the influences, direct or more or less remote, of nearly all co-existing organisms.

One general truth, indicated by sundry of the above illustrations, calls for special notice—the truth that organisms are ever intruding on each other's spheres of existence. Of the various modes in which this is shown, the commonest is the invasion of territory. That tendency which we see in the human races, to overrun and occupy each other's lands, as well as the lands inhabited by inferior creatures, is a tendency exhibited by all classes of organisms in all varieties of ways. Among them, as among mankind, there are permanent conquests, temporary occupations, and occasional raids. Annual migrations are instances of this process in its most familiar form. Every spring an inroad is made into the area which our own fly-catchers occupy, by the swallows of the South; and every winter the fieldfares of the North, come to share the hips and haws of our hedges with native birds—a partial possession of their territory, which entails on our native birds, some mortality. Besides these regularly-recurring raids, there are irregular ones: as of locusts into countries not usually visited by them; or of strange birds which in small flocks from time to time visit areas adjacent to their own. Every now and then, an incursion ends in permanent settlement—perhaps in conquest over indigenous species. Within these few years, an American water-weed has taken possession of our ponds and rivers, and to some extent supplanted native water-weeds. Of animals, may be named a small kind of red ant, having habits allied to those of tropical ants, which has of late overrun many houses in London. The case of the rat, which must have taken to infesting ships within these few centuries, is a good illustration of the readiness of animals to occupy new places that are available. And the way in which vessels visiting India, are cleared of the European cockroach by the kindred *Blatta orientalis*, shows us how these successful invasions last only until there come more powerful invaders. Organisms encroach on one another's spheres of existence, in further ways than by trespassing on one another's areas: they adopt one another's modes of life. There are cases in which this usurpation of habits is slight and temporary; and there are cases where it is marked and permanent. Grey crows frequently join gulls and curlews in picking up food between tide-marks; and gulls and curlews may be occasionally seen many miles inland, feeding in ploughed fields and on moors. Mr Darwin has watched a fly-catcher catching fish. He says that the greater titmouse sometimes adopts the practices of the shrike, and sometimes of the nuthatch; and that some South American woodpeckers are frugivorous, while others chase insects on the wing. Of habitual intrusions on the occupations of other creatures, one case is furnished by the sea-eagle; which, besides hunting the surface of the land for prey, like the rest of the hawk-tribe, often swoops down upon fish. And Mr Darwin names a species of petrel that has taken to diving, and has a considerable, modified organization. These last cases introduce us to a still more remarkable class of facts of kindred meaning. This intrusion of organisms on one another's modes of life, goes to the extent of intruding on one another's media. The great mass of flowering plants are terrestrial; and are required to be so by their process of fructification. But there are some which live in the water, and protrude only their flowers above the surface. Nay, there is a still more striking instance: on the sea-shore may be found an alga a hundred yards inland, and a phænogam rooted in salt-water. Among animals, these interchanges of media are numerous. Nearly all coleopterous insects are terrestrial; but the water-beetle, which like the rest of its order is an air-breather, has aquatic habits. Water appears to be an especially unfit medium for a fly; and yet Mr Lubbock has lately discovered more than one species of fly living beneath the surface of the water, and coming up only occasionally for air. Birds, as a class, are especially fitted for an aerial existence;

but certain tribes of them have taken to an aquatic existence—swimming on the surface of the water and making continual incursions beneath its surface; and there are some genera that have wholly lost the power of flight. Among mammals, too, which have limbs and lungs implying an organization for terrestrial life, may be named kinds that live more or less in the water, and are more or less adapted to it. We have water-rats and otters, which unite the two kinds of life, and show but little modification; hippopotami passing the greater part of their time in the water, and somewhat more fitted to it; seals living almost exclusively in the sea, and having the mammalian form greatly obscured; whales wholly confined to the sea, and having so little the aspect of mammals as to be mistaken for fish. Conversely, sundry inhabitants of the water make more or less prolonged excursions on the land. Eels migrate at night from one pool to another. There are fish with specially-modified gills, and fin-rays serving as stilts, which, when the rivers they inhabit are partially dried-up, travel in search of better quarters. And while some kinds of crabs do not make land-excursions beyond high-water mark, other kinds pursue lives almost wholly terrestrial.

Joining together these two classes of facts, we must regard the bounds to each species' sphere of existence, as determined by the balancing of two antagonist sets of forces. The tendency which every species has to intrude on other areas, other modes of life, and other media, is restrained by the direct and indirect resistance of conditions, organic and inorganic. And these expansive and repressive energies, varying continually in their respective intensities, rhythmically equilibrate each other—maintain a limit that perpetually oscillates from side to side of a certain mean.

§ 106. As implied at the outset, the character of a region, when unfavourable to any species, sufficiently accounts for the absence of this species; and thus its absence is not incongruous with the hypothesis, that each species was originally placed in the regions most favourable to it. But the absence of a species from regions that *are* favourable to it, cannot be thus accounted for. Were plants and animals localized wholly with reference to the fitness of their constitutions to surrounding conditions, we might expect Floras to be similar and Faunas to be similar, where the conditions are similar; and we might expect dissimilarities among Floras and among Faunas, proportionate to the dissimilarities of their conditions. But we do not find such anticipations verified.

Mr Darwin says that "in the Southern hemisphere, if we compare large tracts of land in Australia, South Africa, and western South America, between latitudes 25° and 35°, we shall find parts extremely similar in all their conditions, yet it would not be possible to point out three faunas and floras more utterly dissimilar. Or again we may compare the productions of South America south of lat. 35° with those north of 25°, which consequently inhabit a considerably different climate, and they will be found incomparably more closely related to each other, than they are to the productions of Australia or Africa under nearly the same climate." Still more striking are the contrasts which Mr Darwin points out, between closely-adjacent areas that are totally cut-off from each other. "No two marine faunas are more distinct, with hardly a fish, shell, or crab in common, than those of the eastern and western shores of South and Central America; yet these great faunas are separated only by the narrow, but impassable, isthmus of Panama." On opposite sides of high mountain-chains, also, there are marked differences in the organic forms—differences not so marked as where the barriers are absolutely impassable; but much more marked than are necessitated by unlikenesses of physical conditions.

Not less suggestive is the converse fact, that wide geographical areas which offer decided geologic and meteorologic contrasts, are peopled by nearly-allied groups of organisms, if there are no barriers to migration. "The naturalist in travelling, for instance, from north to south never fails to be struck by the manner in which successive groups of beings, specifically distinct, yet clearly related, replace each other. He hears from closely allied, yet distinct kinds of birds, notes nearly similar, and sees their nests similarly constructed, but not quite alike, with eggs coloured in nearly the same manner. The plains near the Straits of Magellan are inhabited by one species of Rhea (American Ostrich), and north-ward the plains of La Plata by another species of the same genus; and not by a true ostrich or emeu, like those found in Africa and Australia under the same latitude. On these same plains of La Plata, we see the agouti and bizcacha, animals having nearly the same habits as our hares and rabbits and belonging to the same order of Rodents, but they plainly display an American type of structure. We ascend the lofty peaks of the Cordillera and we find an alpine species of bizcacha; we look to the waters, and we do not find the beaver or musk-rat, but the coypu and capybara, rodents of the American type. Innumerable other instances could be given. If we look to the islands off the American shore, however much they may differ in geological structure, the inhabitants, though they may be all peculiar species, are essentially American."

What is the generalization that expresses these two groups of facts? On the one hand, we have similarly-conditioned, and sometimes nearly-adjacent, areas, occupied by quite different Faunas. On the other hand, we have areas remote from each other in latitude, and contrasted in soil as well as climate, which are occupied by closely-allied Faunas. Clearly then, as like organisms are not universally, or even generally, found in like habitats; nor very unlike organisms, in very unlike habitats; there is no manifest pre-determined adaptation of the organisms to the habitats. The organisms do not occur in such and such places, solely because they are either specially fit for these places, or more fit for them than all other organisms.

The induction under which these facts come, and which unites them with various other facts, is a totally-different one. When we see that the similar areas peopled by dissimilar forms, are those between which there are impassable barriers; while the dissimilar areas peopled by similar forms, are those between which there are no such barriers; we are at once reminded of the general truth exemplified in the last section:—the truth that each species of organism, tends ever to expand its sphere of existence—to intrude on other areas, other modes of life, other media; and through these perpetually-recurring attempts to thrust itself into every accessible habitat, spreads until it reaches limits that are for the time insurmountable.

§ 107. We pass now to the distribution of organic forms in Time. Geological inquiry has established the truth, that during a Past of immeasurable duration, plants and animals have existed on the Earth. In all countries their buried remains are found in greater or less abundance. From comparatively small areas, multitudinous different forms have been exhumed. Every exploration of new areas, and every closer inspection of areas already explored, brings more such forms to light. And beyond question, an exhaustive examination of all exposed strata, and of all strata now covered by the sea, would disclose forms immensely out-numbering all those at present known. Further, it is now becoming manifest to geologists, that even had we before us every kind of fossil which exists, we should still have nothing like a complete index to the past inhabitants of our globe. It has been long known that many sedimentary deposits have been so altered by the heat of adjacent molten matter, as greatly to obscure the organic remains contained in them. The extensive formations once called "transition," and now re-named "metamorphic," are acknowledged to be formations of sedimentary origin, from which all traces of such fossil as they probably included, have been obliterated by igneous action. And the conclusion forcing itself into acceptance, is, that igneous rock has everywhere resulted from the complete melting-up of beds of detritus, originally deposited by water. How long the reactions of the Earth's molten nucleus on its cooled crust, have been thus destroying the records of Life which this cooled crust entombed, it is impossible to say; but there are strong reasons for believing that the records which remain, bear but a small ratio to the records which have been destroyed. Thus we have but extremely-imperfect data for any conclusions respecting the distribution of organic forms in Time. Some few generalizations, however, may be regarded as established.

One is, that the plants and animals now existing, mostly differ from the plants and animals which have existed. Though there are species common to our present Fauna and to past Faunas; yet the *facies* of our present Fauna differs, more or less, from the *facies* of each past Fauna. On carrying out the comparison, we find that past Faunas differ from each other; and that the differences between them are proportionate to their degrees of remoteness from each other in Time, as measured by their relative positions in the sedimentary series. So that if we take the assemblage of organic forms living now, and compare it with the successive assemblages of organic forms that have lived in successive geologic epochs, we find that the farther we go back into the past, the greater does the unlikeness become: the number of species and genera common to the compared assemblages, becomes smaller and smaller; and the assemblages differ more and more in their general characters. Though a species of brachiopod now extant, is almost identical with a species found in Silurian strata, and though between the Silurian Fauna and our own, there are sundry common genera of molluscs; it is still undeniable that there is a proportion between lapse of time and divergence of organic forms.

This divergence is comparatively slow and continuous, where there is continuity in the geological formations; but is sudden and comparatively wide, wherever there occurs a great break in the succession of strata. The contrasts which thus arise gradually or all at once, in formations that are continuous or discontinuous, are of two kinds. Faunas of different eras, are distinguished partly by the absence from one of types that are present in the other; and partly by the unlikenesses between the types that are common to both. Such distinctions between Faunas as are due to the appearance or disappearance of types, are of secondary significance: they possibly, or probably, do not imply anything more than migrations or extinctions. The most significant distinctions are those between successive groups of organisms of the same type. And among such, as above said, the differences that arise are, speaking generally, small and continuous where a series of conformable strata gives proof of continued existence of the type in the locality; while they are comparatively large and abrupt, where there is evidence that between the deposit of the adjacent formations, a long period elapsed.

Another general fact, referred to by Mr. Darwin as one which palæontology has made tolerably certain, is that forms and groups of forms which have once disappeared from the Earth, do not reappear. Some few species and a good many genera, have continued throughout the whole period geologically recorded. But omitting these as exceptional, it may be said that each species after arising, spreading for an era, and continuing abundant for an era, eventually declines and becomes extinct; and that similarly, each genus during a longer period increases in the number of its species, and during a longer period dwindles and at last dies out. Having made its exit, neither species nor genus ever re-enters. And the like is true, even of those larger groups called orders. Four types of reptiles that were once abundant, have not been found in modern formations, and do not at present exist. Though nothing less than an exhaustive examination of all strata, can prove conclusively that a special or general form of organization when once lost is never reproduced; yet so many facts point to this inference, that its truth can scarcely be doubted.

To form a conception of the total amount and general direction of the change that has arisen in organic forms during the geologic time measured by our sedimentary series, is at present impossible—the data are insufficient. The immense contrast between the few and low forms of the earliest-known Fauna, and the many and high forms of our existing Fauna, has been commonly supposed to prove, not only great change but great progress. Nevertheless, this appearance of progress may be, and probably is, mainly illusive. Wider knowledge and increased power of interpretation, have made it manifest that remains of comparatively well-organized creatures, really existed in strata long supposed to be devoid of them; and that where they are actually absent, the nature of the strata often supplies a sufficient explanation of their absence, without assuming that they did not exist when these strata were formed. It has now become a tenable hypothesis, that the successively-higher types fossilized in our successively-later deposits, indicate nothing more than successive migrations from pre-existing continents, to continents that were step by step emerging from the ocean—migrations which necessarily began with the inferior orders of organisms, and included the successively-superior orders as the new lands became more accessible to them, and better fitted for them.*

While the evidence usually supposed to prove progression, is thus untrustworthy, there is trustworthy evidence that there has been, in many cases, little or no progression. Though the types which have existed from palæozoic and mesozoic times down to the present day, are almost universally changed; yet a comparison of ancient and modern members of these types, shows that the total amount of change is not relatively great, and that it is not manifestly towards a higher organization. Though nearly all the living forms which have prototypes in early formations, differ from these prototypes specifically, and in most cases generically; yet ordinal peculiarities are, in very numerous cases, maintained from the earli-

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* For explanations, see "Illogical Geology." *Essays: Second Series.*

est times geologically recorded, down to our own time; and we have no visible evidence of superiority in the existing genera of these orders. In his lecture "On the Persistent Types of Animal Life," Prof. Huxley enumerates many cases. On the authority of Dr. Hooker, he stated "that there are Carboniferous plants which appear to be generically identical with some now living; that the cone of the Oolitic *Araucaria* is hardily distinguishable from that of an existing species; that a true *Pinus* appears in the Purbecks and a *Juglans* in the chalk." Among animals he named palæozoic and mesozoic corals which are very like certain extant corals; genera of Silurian molluscs that answer to existing genera; insects and arachnids in the coal formations, that are not more than generically different from some of our own insects and arachnids. He instanced "the Devonian and Carboniferous *Pleuracanthus*, which differs no more from existing sharks than these do from one another;" early mesozoic reptiles "identical in the essential characters of their organization with those now living;" and Triassic mammals which did not differ "nearly so much from some of those which now live, as these differ from one another." Continuing the argument in his "Anniversary Address to the Geological Society" in 1862, Prof. Huxley gave many cases in which the changes that have taken place, are not changes towards a more specialized or higher organization—asking "in what sense are the Liassic Chelonia inferior to those which now exist? How are the Cretaceous Ichthyosauria, Plesiosauria, or Pterosauria less embryonic or more differentiated species than those of the Lias?" While, however, contending that in most instances "positive evidence fails to demonstrate any sort of progressive modification towards a less embryonic or less generalized type in a great many groups of animals of long-continued geological existence;" Prof. Huxley added, that there are other groups "co-existing with them, under the same conditions, in which more or less distinct indications of such a process seem to be traceable." And in illustration of this, he named that better development of the vertebræ which characterizes some of the more modern fishes and reptiles, when compared with ancient fishes and reptiles of the same orders; and the "regularity and evenness of the dentition of the *Anoplotherium* as contrasting with that of existing Artiodactyles."

The facts thus summed up, do not show that higher forms have not arisen on the Earth in the course of geologic time, any more than the facts commonly cited prove that higher forms have arisen; nor are they regarded by Prof. Huxley as showing this. Were the types which have survived from palæozoic and mesozoic periods down to our own day, the only types; and did the modifications, rarely of more than generic value, which these types have undergone, give no better evidences of increased complexity than are actually given by them; then it would be inferable that there has been no appreciable advance among organic forms. But there now exist, and have existed during the more recent geologic epochs, various types which are not known to have existed in earlier epochs — some of them widely unlike these persistent types, and some of them nearly allied to these persistent types. As yet, we know nothing respecting the origins of these new types. But it is quite possible that causes like those which have produced generic differences in the persistent types, may, in some or many cases, have produced modifications great enough to constitute ordinal differences—may have resulted in the formation of types that are now classed as separate. If structural contrasts not exceeding certain moderate limits, are held to mark only generic distinctions; and if organisms displaying larger structural contrasts are considered ordinally or typically distinct; it is clear that the persistence of a given type through a long geologic period without apparently undergoing deviations of more than generic value, by no means disproves the occurrence of far greater deviations; since the forms resulting from such far greater deviations, being regarded as typically distinct forms, will not be taken as evidence of great change in the original type. That which Prof. Huxley's argument proves, and that only which he considers it to prove, is that organisms have no innate tendencies to assume higher forms, and that "any admissible hypothesis of progressive modification, must be compatible with persistence without progression through indefinite periods."

One very significant fact must be added, concerning the relation between distribution in Time and distribution in Space. I quote it from Mr Darwin:—"Mr Clift many years ago showed that the fossil mammals from the Australian caves were closely allied to the living marsupals of that continent. In South America, a similar relationship is manifest, even to an uneducated eye, in the gigantic pieces of armour like those of the armadillo, found in several parts of La Plata; and Professor Owen has shown in the most striking manner that most of the fossil mammals, buried there in such numbers, are related to the South American types. This relationship is even more clearly seen in the wonderful collection of fossil bones made by MM. Lund and Clausen in the caves of Brazil. I was so much impressed with these facts that I strongly insisted, in 1839 and 1845, on this 'law of the succession of types,'—on 'this wonderful relationship in the same continent between the dead and the living.' Professor Owen has subsequently extended the same generalization to the mammals of the Old World. We see the same law in this author's restorations of the extinct and gigantic birds of New Zealand. We see it also in the birds of the caves of Brazil. Mr Woodward has shown that the same law holds good, with sea-shells, but from the wide distribution of most genera of molluscs, it is not well displayed by them. Other cases could be added, as the relation between the extinct and living land-shells of Madeira; and between the extinct and living brackish-water shells of the Aralo-Caspian Sea.'"

The general results then, are these. Our knowledge of distribution in Time, being derived wholly from the evidence afforded by fossils, is limited to that geologic time of which some records remain: cannot extend to those pre-geologic times the records of which have been obliterated. From these remaining records, which probably form but a small fraction of the whole, the general facts deducible are:—That such organic types as have lived through successive epochs, have almost universally undergone modifications of specific and generic values—modifications which have commonly been great in proportion as the period has been long. That besides the types that have persisted from ancient eras down to our own era, other types have from time to time made their appearance in the ascending series of our strata—types of which some are lower and some higher than the types previously recorded; but whence these new types came, and whether any of them arose by divergence from the previously-recorded types, the evidence does not yet enable us to say. That in the course of long geologic epochs, nearly all species, most genera, and a few orders, become extinct; and that a species, genus, or order, which has once disappeared from the Earth, never reappears. And, lastly, that the Fauna now occupying each separate area of the Earth's surface, is very nearly allied to the Fauna which existed on that area during recent geologic times.

§ 108. Omitting sundry minor generalizations, the exposition of which would involve too much detail, what is to be said of these major generalizations?

The distribution in Space cannot be said to imply that organisms have been designed for their particular habitats, and placed in them; since, besides the habitat in which an organism is found there are commonly other habitats, as well or better for it, from which it is absent—habitats to which it is so much better fitted than organisms now occupying them, that it extrudes these organisms when allowed the opportunity. Neither can we suppose that one end has been to establish varieties of Floras and Faunas; since, if so, why are the Floras and Faunas but little divergent in widely-sundered areas between which migration is possible, while they are markedly divergent in adjacent areas between which migration is impossible?

Passing to distributions in Time, there arise the questions —why during nearly the whole of that vast period geologically recorded, have there existed none of those highest organic forms which have now overrun the Earth?—how is it that we find no traces of a creature endowed with large capacities for knowledge and happiness? The answer that the Earth was not, in remote times, a fit habitation for such a creature, besides being unwarranted by the evidence, suggests the equally awkward question—why during untold millions of years did the Earth remain fit only for inferior creatures? What, again, is the meaning of this extinction of types? To conclude that the saurian type was replaced by other types at the beginning of the tertiary period, because this type was not adapted to the conditions which then arose, is to conclude that this type could not be modified into fitness for the conditions; and this conclusion is quite at variance with the hypothesis that creative skill is shown in the multiform adaptations of one type to many ends.

What interpretations may rationally be put on these and other general facts of distribution in Space and Time, we shall see in the next division of this work; to which let us now pass.

# PART III.

## THE EVOLUTION OF LIFE.

# CHAPTER I.

## PRELIMINARY.

§ 109. In the foregoing Part, we have contemplated the most important of the generalizations to which biologists have been led by observation of organisms. These Inductions of Biology have also been severally glanced at on their deductive sides; for the purpose of noting the harmony that exists between them, and those primordial truths set forth in *First Principles.* Having thus studied the leading phenomena of life separately, we are prepared for studying them in their *ensemble,* with the view of arriving at the most general interpretation of them.

There is an *ensemble* of vital phenomena presented by each organism in the course of its growth, development, and decay; and there is an *ensemble* of vital phenomena presented by the organic world as a whole. Neither of these can be properly dealt with apart from the other. But the last of them may be separately treated more conveniently than the first. What interpretation we put on the facts of structure and function in each living body, depends entirely on our conception of the mode in which living bodies in general have originated. To form some conclusion respecting this mode—a provisional if not a permanent conclusion—must therefore be our first step.

We have to choose between two hypotheses—the hypothesis of Special Creation and the hypothesis of Evolution.

Either the multitudinous kinds of organisms that now exist, and the still more multitudinous kinds that have existed during past geologic eras, have been from time to time separately made; or they have arisen by insensible steps, through actions such as we see habitually going on. Both hypotheses imply a Cause. The last, certainly as much as the first, recognizes this Cause as inscrutable. The point at issue is, how this inscrutable Cause has worked in the production of living forms. This point, if it is to be decided at all, is to be decided only by examination of evidence. Let us inquire which of these antagonist hypotheses is most congruous with established facts.

# CHAPTER II.

## GENERAL ASPECTS OF THE SPECIAL-CREATION-HYPOTHESIS.*

§ 110. EARLY ideas are not usually true ideas. Undeveloped intellect, be it that of an individual or that of the race, forms conclusions which require to be revised and re-revised, before they reach a tolerable correspondence with realities. Were it otherwise, there would be no discovery, no increase of intelligence. What we call the progress of knowledge, is the bringing of Thoughts into harmony with Things; and it implies that the first Thoughts are either wholly out of harmony with Things, or in very incomplete harmony with them.

If illustrations be needed, the history of every science furnishes them. The primitive notions of mankind as to the structure of the heavens, were wrong; and the notions which replaced them were successively less wrong. The original belief respecting the form of the Earth was wrong; and this wrong belief survived through the first civilizations. The earliest ideas that have come down to us concerning the natures of the elements were wrong; and only in quite recent times has the composition of matter in its various forms been better understood. The interpretations of mechanical facts, of meteorological facts, of physiological facts,

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* Several of the arguments used in this chapter and in that which follows it, formed parts of an essay on "the Development Hypothesis," originally published in 1852.

were at first wrong. In all these cases men set out with beliefs which, if not absolutely false, contained but small amounts of truth disguised by immense amounts of error.

Hence the hypothesis that living beings resulted from special creations, being a primitive hypothesis, is probably an untrue hypothesis. If the interpretations of Nature given by aboriginal men, were erroneous in other directions, they were most likely erroneous in this direction. It would be strange if, while these aboriginal men failed to reach the truth in so many cases where it is comparatively conspicuous, they yet reached the truth in a case where it is comparatively hidden.

§ 111. Besides the improbability given to the belief in special creations, by its association with mistaken early beliefs in general; a further improbability is given to it by its association with a special class of mistaken beliefs. It belongs to a family of beliefs which have one after another been destroyed by advancing knowledge; and is, indeed, almost the only member of the family that survives among educated people.

We all know that the savage thinks of each striking phenomenon, or group of phenomena, as caused by some separate personal agent; that out of this fetishistic conception there grows up a polytheistic conception, in which these minor personalities are variously generalized into deities presiding over different divisions of nature; and that these are eventually further generalized. This progressive consolidation of causal agencies, may be traced in the creeds of all races; and is far from complete in the creeds of the most advanced races. The unlettered rustics who till our fields, do not let the consciousness of a supreme power wholly absorb the aboriginal conceptions of good and evil spirits, and charms or secret potencies dwelling in particular objects. The earliest mode of thinking changes, only as fast as the constant relations among phenomena are established. Scarcely less familiar is the truth, that while accumulating knowledge makes these conceptions of personal causal agents gradually more vague, as it merges them into general causes, it also destroys the habit of thinking of them as working after the methods of personal agents. We do not now, like Kepler, assume guiding spirits to keep the planets in their orbits. It is no longer the universal belief that the sea was once for all mechanically parted from the dry land; or that the mountains were placed where we see them by a sudden creative act. All but a narrow class have ceased to suppose sunshine and storm to be sent in some arbitrary succession. The majority of educated people have given up thinking of epidemics as punishments inflicted by an angry deity. Nor do even the common people regard a madman as one possessed by a demon. That is to say, we everywhere see fading away the anthropomorphic conception of the Unknown Cause. In one case after another, is abandoned that interpretation which ascribes phenomena to a will analogous to the human will, working by methods analogous to human methods.

If, then, of this once-numerous family of beliefs, the immense majority have become extinct, we may not unreasonably expect that the few remaining members of the family will become extinct. One of these is the belief we are here considering—the belief that each species of organism was specially created. Many who in all else have abandoned the aboriginal theory of things, still hold this remnant of the aboriginal theory. Ask any tolerably-informed man whether he accepts the cosmogony of the Indians, or the Greeks, or the Hebrews, and he will regard the question as next to an insult. Yet one element common to these cosmogonies he very likely retains: not bearing in mind its origin. For whence did he get the doctrine of special creations? Catechise him, and he is forced to confess that it was put into his mind in childhood, as one portion of a story which, as a whole, he has long since rejected. Why this fragment is likely to be right while all the rest is wrong, he is unable to say. May we not then expect, that the relinquishment of all other parts of this story, will bye and bye be followed by the relinquishment of this remaining part of it?

§ 112. The belief which we find thus questionable, both as being a primitive belief and as being a belief belonging to an almost-extinct family, is a belief that is not countenanced by a single fact. No one ever saw a special creation; no one ever found proof of an indirect kind, that a special creation had taken place. It is significant, as Dr Hooker remarks, that naturalists who suppose new species to be miraculously originated, habitually suppose the origination to occur in some region remote from human observation. Wherever the order of organic nature is exposed to the view of zoologists and botanists, it expels this conception; and the conception survives only in connexion with imagined places, where the order of organic phenomena is unknown.

Besides being absolutely without evidence to give it external support, this hypothesis of special creations cannot support itself internally—cannot be framed into a coherent thought. It is one of those illegitimate symbolic conceptions, so continually mistaken for legitimate symbolic conceptions (*First Principles*, § 9), because they remain untested. Immediately an attempt is made to elaborate the idea into anything like a definite shape, it proves to be a pseud-idea, admitting of no definite shape. Is it supposed that a new organism, when specially created, is created out of nothing? If so, there is a supposed creation of matter; and the creation of matter is inconceivable—implies the establishment of a relation in thought between nothing and something—a relation of which one term is absent—an impossible relation. Is it supposed that the matter of which the new organism consists, is not created for the occasion, but is taken out of its pre-existing forms and arranged into a new form? If so, we are met by the question—how is the re-arrangement

effected? Of the myriad atoms going to the composition of the new organism, all of them previously dispersed through the neighbouring air and earth, does each, suddenly disengaging itself from its combinations, rush to meet the rest, unite with them into the appropriate chemical compounds, and then fall with certain others into its appointed place in the aggregate of complex tissues and organs? Surely thus to assume a myriad supernatural impulses, differing in their directions and amounts, given to as many different atoms, is a multiplication of mysteries rather than the solution of a mystery. For every one of these impulses, not being the result of a force locally existing in some other form, implies the creation of force; and the creation of force is just as inconceivable as the creation of matter. And thus is it with all attempted ways of representing the process. The old Hebrew idea that God takes clay and moulds a new creature, as a potter might mould a vessel, is probably too grossly anthropomorphic to be accepted by any modern defender of the special-creation doctrine. But having abandoned this crude belief, what belief is he prepared to substitute? If a new organism is not thus produced, then in what way is a new organism produced? or rather—in what way can a new organism be conceived to be produced? We will not ask for the ascertained mode, but will be content with a mode that can be consistently imagined. No such mode, however,
pah! is assignable. Those who entertain the proposition that each kind of organism results from a divine interposition, do so because they refrain from translating words into thoughts. The case is one of those where men do not really believe, but rather *believe they believe.* For belief, properly so called, implies a mental representation of the thing believed; and no such mental representation is here possible. to me who has not read [illegible]

§ 113. If we imagine mankind to be contemplated by some creature as short-lived as an ephemeron, but possessing intelligence like our own—if we imagine such a being studying men and women, during his few hours of life, and speculating as to the mode in which they came into existence; it is manifest that, reasoning in the usual way, he would suppose each man and woman to have been separately created. No appreciable changes of structure occurring in any of them during the few hours over which his observations extended, this being would probably infer that no changes of structure were taking place, or had taken place; and that from the outset, each man and woman had possessed all the characters then visible—had been orginally formed with them. This would naturally be the first impression. The application is obvious. A human life is ephemeral compared with the life of a species; and even the period over which the records of human experience extend, is ephemeral compared with the life of a species. There is thus a parallel contrast between the immensely-long series of changes that have occurred during the life of a species, and that small portion of the series open to our view. And there is no reason to suppose that the first conclusion drawn by mankind from this small part of the series visible to them, is any nearer the truth, than would be the conclusion of the supposed ephemeral being respecting men and women.

This analogy, suggesting as it does how the hypothesis of special creations is merely a formula for our ignorance, raises the question—what reason have we to assume special creations of species but not of individuals; unless it be that in the case of individuals we directly know the process to be otherwise, but in the case of species do not directly know it to be otherwise? Have we any ground for concluding that species were specially created, except the ground that we have no immediate knowledge of their origin? And does our ignorance of the manner in which they arose, warrant us in asserting that they arose by special creation?

Another question is suggested by this analogy. Those who, in the absence of immediate evidence of the way in which species arose, assert that they arose not in any way analogous to that in which individuals arise, but in a totally distinct way, think that by this supposition they honour the Unknown Cause of things; and they oppose any antagonist doctrine as amounting to an exclusion of divine power from the world. But if divine power is demonstrated by the separate creation of each species, would it not have been still better demonstrated by the separate creation of each individual? Why should there exist this process of natural genesis? Why should not omnipotence have been proved by the supernatural production of plants and animals everywhere throughout the world from hour to hour? Is it replied that the Creator was able to make individuals arise from one another in a natural succession, but not to make species thus arise? This is to assign a limit to power instead of magnifying it. Is it replied that the occasional miraculous origination of a species was practicable, but that the perpetual miraculous origination of countless individuals was impracticable? This also is a derogation. Either it was possible or not possible to create species and individuals after the same general method. To say that it was not possible is suicidal in those who use this argument; and if it was possible, it is required to say what end is served by the special creation of species that would not have been better served by the special creation of individuals. Again, what is to be thought of the fact that the great majority of these supposed special creations took place before mankind existed? Those who think that divine power is demonstrated by special creations, have to answer the question—to whom demonstrated? Tacitly or avowedly, they regard the demonstrations as being for the benefit of mankind. But if so, to what purpose were the millions of these demonstrations which took place on the Earth when there were no intelligent beings to contemplate them? Did the Unknowable thus demonstrate his power to himself? Few will have the hardihood to say that any such demonstration was needful. There is no choice but to regard them, either as superfluous exercises of power, which is a derogatory supposition, or as exercises of power that were necessary because species could not be otherwise produced, which is also a derogatory supposition.

§ 114. Those who espouse the hypothesis of special creations, entangle themselves in other theological difficulties. This assumption that each kind of organism was specially designed, carries with it the implication that the designer intended everything that results from the design. There is no escape from the admission, that if organisms were severally constructed with a view to their respective ends; then the character of the constructor is indicated both by the ends themselves, and the perfection or imperfection with which the organisms are fitted to them. Observe the consequences.

Without dwelling on the question put in a recent chapter, why during untold millions of years there existed on the Earth no beings endowed with capacities for wide thought and high feeling, we may content ourselves with asking why, at present, the Earth is largely peopled by creatures which inflict on each other, and on themselves, so much suffering? Omitting the human race, whose defects and miseries the current theology professes to account for, and limiting ourselves to the lower creation, what must we think of the countless different pain-inflicting appliances and instincts with which animals are endowed? Not only now, and not only ever since men have lived, has the Earth been a scene of warfare among all sentient creatures; but palæontology shows us that, from the earliest eras geologically recorded, there has been going on this universal carnage. Fossil structures, in common with the structures of existing animals, show us elaborate weapons for destroying other animals. We have unmistakable proof that throughout all past time, there has been a perpetual preying of the superior on the inferior—a ceaseless devouring of the weak by the strong. How is this to be explained? How happens it that animals were so designed as to render this bloodshed necessary? How happens it that in almost every species, the number of individuals annually born is such that the majority die of starvation or by violence before arriving at maturity? Whoever contends that each kind of animal was specially designed, must assert either that there was a deliberate intention on the part of the Creator to produce these results, or that there was an inability to prevent them. Which alternative does he prefer? To cast an imputation on the divine character, or assert a limitation of the divine power? It is useless for him to plead that the destruction of the less powerful by the more powerful, is a means of preventing the miseries of decrepitude and incapacity, and therefore works beneficently. For even were the chief mortality among the aged instead of among the young, there would still arise the unanswerable question—why were not animals constructed in such ways as to avoid these evils? why were not their rates of multiplication, their degrees of intelligence, and their propensities, so adjusted that these sufferings might be escaped? And if decline of vigour was a necessary accompaniment of age, why was it not provided that the organic actions should end in sudden death, whenever they fell below the level required for pleasurable existence? Will any one who contends that organisms were specially designed, assert that they could not have been designed so as to prevent suffering? And if he admits that they could have been made so as to prevent suffering, will he assert that the Creator preferred so making them as to inflict suffering?

Even as thus presented, the difficulty is sufficiently great; but it appears immensely greater when we examine the facts more closely. So long as we contemplate only the preying of the superior on the inferior, some good appears to be extracted from the evil—a certain amount of life of a higher order, is supported by sacrificing a great deal of life of a lower order. So long, too, as we leave out all mortality but that which, by carrying off the least perfect members of each species, leaves the most perfect members to continue the species; we see some compensating benefit reached through the suffering inflicted. But what shall we say on finding innumerable cases in which the suffering inflicted brings no compensating benefit? What shall we say when we see the inferior destroying the superior? What shall we say on discovering elaborate appliances for securing the prosperity of organisms incapable of feeling, at the expense of misery to organisms capable of happiness?

Of the animal kingdom as a whole, more than half the species are parasites. "The number of these parasites," says Prof. Owen, "may be conceived when it is stated that almost every known animal has its peculiar species, and generally more than one, sometimes as many as, or even more kinds than, infest the human body." Passing over the evils thus inflicted on animals of inferior dignity, let us limit ourselves to the case of man. The *Bothriocephalus latus* and the *Tænia solium*, are two kinds of tape-worm, which flourish in the human intestines; producing great constitutional disturbances, sometimes ending in insanity; and from the germs of the *Tænia*, when carried into other parts of the body, arise certain partially-developed forms known as *Cysticerci*, *Echinococci*, and *Cœnuri*, which cause disorganization more or less extensive in the brain, the lungs, the liver, the heart, the eye, &c., often ending fatally after long-continued suffering. Five other parasites, belonging to a different class, are found in the viscera of man — the *Trichocephalus*, the *Oxyuris*, the *Strongylus* (two species), the *Ancylostomum*, and the *Ascaris;* which, beyond that defect of nutrition which they necessarily cause, sometimes induce certain irritations that lead to complete demoralization. Of another class of *entozoa*, belonging to the subdivision *Trematoda*, there are five kinds found in different organs of the human body—the liver and gall ducts, the portal vein, the intestine, the bladder, the eye. Then we have the *Trichina spiralis,* which passes through one phase of its existence imbedded in the muscles and through another phase of its existence in the intestine; and which, by the induced disease *Trichiniasis,* has lately committed such ravages in Germany, as to cause a panic. And to these we must add the Guinea-worm, which in some part of Africa and India, makes men miserable by burrowing in their legs. From this list of *entozoa,* which is by no means complete, let us pass to the *epizoa.* There are two kinds of *Acari,* one of them inhabiting the follicles of the skin, and the other producing the itch. There are other creatures that bury themselves beneath the skin, and lay their eggs there; and there are three species of lice which infest the surface of the body. Nor is this all: besides animal parasites, there are sundry vegetal parasites, which grow and multiply at our cost. The *Sarcina ventriculi* inhabits the stomach, and produces gastric disturbance. The *Leptothrix buccalis* is extremely general in the mouth, and may have something to do with the decay of teeth. And besides these, there are microscopic fungi which produce ringworm, porrigo, pityriasis, thrush, &c. Thus the human body is the habitat of parasites, internal and external, animal and vegetal, numbering, if all were set down, some two or three dozen species; sundry of which are peculiar to man, and many of which produce in man great suffering and not unfrequently death. What interpretation is to be put on these facts by those who espouse the hypothesis of special creations? According to this hypothesis, all these parasites were designed with a view to their respective modes of life. They were endowed with constitutions fitting them to live by absorbing the juices of the human body; they were furnished with appliances, often of a formidable kind, enabling them to root themselves in and upon the human body; and they were made prolific in an almost incredible degree, that their germs might have a sufficient number of chances of finding their way into the human body. In short, elaborate contrivances were combined to insure the continuance of their respective races; and to make it impossible for the successive generations of men to avoid being preyed upon by them. What shall we say to this arrangement? Shall we say that man, "the head and crown of things," was provided as a habitat for these parasites? Or shall we say that these degraded creatures, incapable of thought or enjoyment, were created that they might cause unhappiness to man? One or other of these alternatives must be chosen by those who contend that every kind of organism was separately devised by the Creator. Which do they prefer? With the conception of two antagonistic powers, which severally work good and evil in the world, the facts are congruous enough. But with the conception of a supreme beneficence, this gratuitous infliction of misery on man, in common with all other terrestrial creatures capable of feeling, is absolutely incompatible.

§ 115. See then the results of our examination. The belief in special creations of organisms, is a belief that arose among men during the era of profoundest darkness; and it belongs to a family of beliefs which have nearly all died out as enlightenment has increased. It is without a solitary established fact on which to stand; and when the attempt is made to put it into definite shape in the mind, it turns out to be only a pseud-idea. This mere verbal hypothesis, which men idly accept as a real or thinkable hypothesis, is of the same nature as would be one, based on a day's observation of human life, that each man and woman was specially created—an hypothesis not suggested by evidence, but by lack of evidence—an hypothesis which formulates absolute ignorance into a semblance of positive knowledge. Further, we see that this hypothesis, wholly without support, essentially inconceivable, and thus failing to satisfy men's intellectual need of an interpretation, fails also to satisfy their moral sentiment. It is quite inconsistent with those conceptions of the divine nature which they profess to entertain. If infinite power was to be demonstrated, then, either by the special creation of every individual, or by the production of species after a method akin to that in which individuals are produced, it would be better demonstrated than by the use of the two methods which the hypothesis assumes to be necessary. And if infinite goodness was to be demonstrated, then, not only do the provisions of organic structure, if they are especially devised, fail to demonstrate it; but there is an enormous mass of them which imply malevolence rather than benevolence.

Thus, however regarded, the hypothesis of special creations turns out to be worthless — worthless by its derivation; worthless in its intrinsic incoherence; worthless as absolutely without evidence; worthless as not supplying an intellectual need; worthless as not satisfying a moral want. We must therefore consider it as counting for nothing, in opposition to any other hypothesis respecting the origin of organic beings.

# CHAPTER III.

## GENERAL ASPECTS OF THE EVOLUTION-HYPOTHESIS.

§ 116. JUST as the supposition that races of organisms have been specially created, is discredited by its origin; so, conversely, the supposition that races of organisms have been evolved, is credited by its origin. Instead of being a conception suggested and accepted when mankind were profoundly ignorant, it is a conception born in times of comparative enlightenment. Moreover, the belief that all organic forms have arisen in conformity with uniform laws, instead of through breaches of uniform laws, is a belief that has come into existence in the most-instructed class, living in these better-instructed times. Not among those who have paid no attention to the order of Nature, has this idea made its appearance; but among those whose pursuits have familiarized them with the order of Nature. Thus the derivation of this modern hypothesis is as favourable as that of the ancient hypothesis is unfavourable.

§ 117. A kindred antithesis exists between the two families of beliefs, to which the beliefs we are comparing severally belong. While the one family has been dying out, the other family has been multiplying. Just as fast as men have ceased to regard different classes of phenomena as caused by special personal agents, acting irregularly; so fast have they come to regard these different classes of phenomena as caused by a general agency acting uniformly—the two changes being correlative. And as, on the one hand, the hypothesis that each species resulted from a supernatural act, having lost nearly all its kindred hypotheses, may be expected soon to become extinct; so, on the other hand, the hypothesis that each species resulted from the action of natural causes, being one of an ever-increasing family of hypotheses, may be expected to survive and become established.

Still greater will the probability of its survival and establishment appear, when we observe that it is one of a particular genus of hypotheses that has been rapidly extending. The interpretation of phenomena as resulting from Evolution, has been independently showing itself in various fields of inquiry, quite remote from one another. The supposition that the Solar System has been gradually evolved out of diffused matter, is a supposition wholly astronomical in its origin and application. Geologists, without being led thereto by astronomical considerations, have been step by step advancing towards the conviction, that the Earth has reached its present varied structure through a process of Evolution. The inquiries of biologists have proved the falsity of the once general belief, that the germ of each organism is a minute repetition of the mature organism, differing from it only in bulk; and they have shown, contrariwise, that every organism, arising out of apparently-uniform matter, advances to its ultimate multiformity through insensible changes. Among philosophical politicians, there has been spreading the perception that the progress of society is an evolution: the truth that "constitutions are not made but grow," is a part of the more general truth that societies are not made but grow. It is now universally admitted by philologists, that languages, instead of being artificially or supernaturally formed, have been developed. And the histories of religion, of philosophy, of science, of the fine arts, and of the industrial arts, show that these have passed through stages as unobtrusive as those through which the mind of a child passes on its way to maturity. If, then, the recognition of evolution as the law of many diverse orders of phenomena, has been spreading; may we not say that there thence arises the probability that evolution will presently be recognized as the law of the phenomena we are considering? Each further advance of knowledge, confirms the belief in the unity of Nature; and the discovery that evolution has gone on, or is going on, in so many departments of Nature, becomes a reason for believing that there is no department of Nature in which it does not go on.

§ 118. The hypotheses of Special Creation and Evolution, are no less contrasted in respect of their legitimacy as hypotheses. While, as we have seen, the one belongs to that order of symbolic conceptions which are proved to be illusive by the impossibility of realizing them in thought; the other is one of those symbolic conceptions which are more or less completely realizable in thought. The production of all organic forms by the slow accumulation of modifications upon modifications, and by the slow divergences resulting from the continual addition of differences to differences, is mentally representable in outline, if not in detail. Various orders of our experiences enable us to conceive the process. Let us look at one of the simplest.

There is no apparent similarity between a straight line and a circle. The one is a curve; the other is defined as without curvature. The one encloses a space; the other will not enclose a space though produced for ever. The one is finite; the other may be infinite. Yet, opposite as the two are in all their properties, they may be connected together by a series of lines no one of which differs from the adjacent ones in any appreciable degree. Thus, if a cone be cut by a plane at right angles to its axis, we get a circle. If, instead of being perfectly at right angles, the plane subtends with the axis an angle of 89° 59′, we have an ellipse which no human eye, even when aided by an accurate pair of compasses, can distinguish from a circle. Decreasing the angle minute by minute, the ellipse becomes first perceptibly eccentric, then manifestly so, and by and by acquires so immensely elongated a form, as to bear no recognizable resemblance to a circle. By continuing this process, the ellipse changes insensibly into a parabola. On still further diminishing the angle, the parabola becomes an hyperbola. And finally, if the cone be made gradually more obtuse, the hyperbola passes into a straight line, as the angle of the cone approaches 180°. Now here we have five different species of line—circle, ellipse, parabola, hyperbola, and straight line—each having its peculiar properties and its separate equation, and the first and last of which are quite opposite in nature, connected together as members of one series, all producible by a single process of insensible modification.

But the experiences which most clearly illustrate to us the process of general evolution, are our experiences of special evolution, repeated in every plant and animal. Each organism exhibits, within a short space of time, a series of changes which, when supposed to occupy a period indefinitely great, and to go on in various ways instead of one way, give us a tolerably clear conception of organic evolution in general. In an individual development, we have compressed into a comparatively infinitesimal space, a series of metamorphoses equally vast with those which the hypothesis of evolution assumes to have taken place during those immeasurable epochs that the Earth's crust tells us of. A tree differs from a seed immeasurably in every respect—in bulk, in structure, in colour, in form, in specific gravity, in chemical composition: differs so greatly that no visible resemblance of any kind can be pointed out between them. Yet is the one changed in the course of a few years into the other: changed so gradually, that at no moment can it be said—Now the seed ceases to be, and the tree exists. What can be more widely contrasted than a newly-born child and the small, semi-transparent, gelatinous spherule constituting the human ovum? The infant is so complex in structure that a cyclopædia is needed to describe its constituent parts. The germinal vesicle is so simple that it may be defined in a line. Nevertheless, a few months suffice to develope the one out of the other; and that, too, by a series of modifications so small, that were the embryo examined at successive minutes, even a microscope would with difficulty disclose any sensible changes. Aided by such facts, the conception of general evolution may be rendered as definite a conception as any of our complex conceptions can be rendered. If instead of the successive minutes of a child's fœtal life, we take successive generations of creatures—if we regard the successive generations as differing from each other no more than the fœtus did in successive minutes; our imaginations must indeed be feeble if we fail to realize in thought, the evolution of the most complex organism out of the simplest. If a single cell, under appropriate conditions, becomes a man in the space of a few years; there can surely be no difficulty in understanding how, under appropriate conditions, a cell may, in the course of untold millions of years, give origin to the human race.

It is true that many minds are so unfurnished with those experiences of Nature out of which this conception is built, that they find difficulty in forming it. Habitually looking at things rather in their statical than in their dynamical aspects, they never realize the fact that, by small increments of modification, any amount of modification may in time be generated. That surprise which they feel on finding one whom they last saw as a boy, grown into a man, becomes incredulity when the degree of change is greater. To such, the hypothesis that by any series of changes a protozoon should ever give origin to a mammal, seems grotesque—as grotesque as did Galileo's assertion of the Earth's movement seem to the Aristotleans; or as grotesque as the assertion of the Earth's sphericity seems now to the New Zealanders. But those who accept a literally-unthinkable proposition as quite satisfactory, may not unnaturally be expected to make a converse mistake.

§ 119. The hypothesis of evolution is contrasted with the hypothesis of special creations, in a further respect. It is not simply legitimate instead of illegitimate, because representable in thought instead of unrepresentable; but it has the support of some evidence, instead of being absolutely unsupported by evidence. Though the facts at present assignable in *direct* proof that by progressive modifications, races of organisms that are apparently distinct may result from antecedent races, are not sufficient; yet there are numerous facts of the order required. It has been shown beyond all question that unlikenesses of structure gradually arise among descendants from the same stock. We find that there *is* going on a modifying process of the kind alleged as the source of specific differences: a process which, though slow in its action, does, in time, if the circumstances demand it, produce conspicuous changes—a process which, to all appearance, would produce in the millions of years, and under the great varieties of conditions which geological records imply, any amount of change.

In the chapters on "Heredity" and "Variation," contained in the preceding Part, many such facts were given; and plenty more might be added. Although comparatively little attention has been paid to the matter until recent times, the evidence already collected shows that there take place in successive generations, alterations of structure quite as marked as those which, in successive short intervals, arise in a developing embryo—nay, often much more marked; since, besides differences due to changes in the relative sizes of parts, there sometimes arise differences due to additions and suppressions of parts. The structural modification proved to have taken place since organisms have been observed, is not less than the hypothesis demands—bears as great a ratio to this brief period, as the total amount of structural change seen in the evolution of a complex organism out of a simple germ, bears to that vast period during which living forms have existed on the Earth.

We have, indeed, much the same kind and quantity of direct evidence that all organic beings have gradually arisen through the actions of natural causes, which we have that all the structural complexities of the Earth's crust have arisen through the actions of natural causes. It may, I think, be fairly said, that between the known modifications undergone by organisms, and the totality of modifications displayed in their structures, there is no greater disproportion than between the geological changes which have been witnessed, and the totality of geological changes supposed to be similarly caused. Here and there are pointed out sedimentary deposits now slowly taking place. At this place, it is proved that a shore has been encroached on by the sea to a considerable extent within recorded times; and at another place, an estuary is known to have become shallower within the space of some generations. In one region a general upheaval is going on at the rate of a few feet in a century; while in another region occasional earthquakes are shown to cause slight variations of level. Appreciable amounts of denudation by water are visible in some localities; and in other localities glaciers are detected in the act of grinding down the rocky surfaces over which they glide. But the changes thus instanced, are infinitesimal compared with the aggregate of changes to which the Earth's crust testifies, even in its still extant systems of strata. If, then, from the small changes now being wrought on the Earth's crust by natural agencies, we may legitimately conclude that by such natural agencies acting through vast epochs, all the structural complexities of the Earth's crust have been produced; may we not from the small known modifications produced in races of organisms by natural agencies, similarly infer that from natural agencies have slowly arisen all those structural complexities which we see in them?

The hypothesis of Evolution then, has direct support from facts which, though small in amount, are of the kind required; and the proportion which these facts bear to the conclusion drawn, seems as great as is the proportion between facts and conclusion which, in another case, produces acceptance of the conclusion.

§ 120. Let us put ourselves for a moment in the position of those who, from their experiences of human modes of action, draw inferences respecting the mode of action of that ultimate power manifested to us through phenomena. We shall find the supposition that each kind of organism was separately designed and put together, to be much less consistent with their professed conception of this ultimate power, than is the supposition that all kinds of organisms have resulted from one unbroken process. Irregularity of method is a mark of weakness. Uniformity of method is a mark of strength. Continual interposition to alter a pre-arranged set of actions, implies defective arrangement in those actions. The maintenance of those actions, and the working out by them of the highest results, implies completeness of arrangement. If human workmen, whose machines as at first constructed require perpetual adjustment, show their increasing skill by making their machines self-adjusting; then, those who figure to themselves the production of the world and its inhabitants by a "Great Artificer," must admit that the achievement of this end by a persistent process, adapted to all contingencies, implies greater skill than its achievement by the process of meeting the contingencies as they severally arise.

So, too, it is with the contrast under its moral aspect. We saw that to the hypothesis of special creations, a difficulty is presented by the absence of high forms of life during those immeasurable epochs of the Earth's existence which geology records. But to the hypothesis of evolution, this absence is no such obstacle. Suppose evolution, and this question is necessarily excluded. Suppose special creations, and this question, unavoidably raised, can have no satisfactory answer. Still more marked is this contrast between the two hypotheses, in presence of that vast amount of suffering entailed on all orders of sentient beings, by their imperfect adaptations to their conditions of life; and the further vast amount of suffering entailed on them by enemies and by parasites. We saw that if organisms were severally designed for their respective places in Nature, the inevitable conclusion is, that these thousands of kinds of inferior organisms which prey upon superior organisms, were intended to inflict all the pain and mortality which results. But the hypothesis of evolution involves us in no such dilemma. Slowly, but surely, evolution brings about an increasing amount of happiness: all evils being but incidental. By its essential nature, the process must everywhere produce greater fitness to the conditions of existence; be they what they may. Applying alike to the lowest and the highest forms of organization, there is in all cases a progressive adaptation; and a survival of the most adapted. If, in the uniform working out of the process, there are evolved organisms of low types, which prey on those of higher types, the evils inflicted form but a deduction from the average benefits. The universal and necessary tendency towards supremacy and multiplication of the best, applying to the organic creation as a whole as well as to each species, is ever diminishing the damage done—tends ever to maintain those most superior organisms which, in one way or other, escape the invasions of the inferior, and so tends to produce a type less liable to the invasions of the inferior. Thus the evils accompanying evolution are ever being self-eliminated. Though there may arise the question — Why could they not have been avoided? there does not arise the question—Why were they deliberately inflicted? Whatever may be thought of them, it is clear that they do not imply gratuitous malevolence.

§ 121. In all respects, then, the hypothesis of evolution contrasts favourably with the hypothesis of special creation. It has arisen in comparatively-instructed times, and in the most cultivated class. It is one of those beliefs in the uniform concurrence of phenomena, which are gradually supplanting beliefs in their irregular and arbitrary concurrence; and it belongs to a genus of these beliefs which has of late been rapidly spreading. It is a definitely-conceivable hypothesis: being simply an extension to the organic world at large, of a conception built from our experiences of individual organisms; just as the hypothesis of universal gravitation, was an extension of the conception which our experiences of terrestrial gravitation had produced. This definitely-conceivable hypothesis, besides the support of numerous analogies, has the support of direct evidence: we have positive proof that there is going on a process of the kind alleged; and though the results of this process, as actually witnessed, are minute in comparison with the totality of results ascribed to it, yet they bear to such totality, a ratio as great as that by which an analogous hypothesis is justified. Lastly, that sentiment which the doctrine of special creations is thought necessary to satisfy, is much better satisfied by the doctrine of evolution; since this doctrine raises no contradictory implications respecting the Unknown Cause, such as are raised by the antagonist doctrine.

And now, having observed how, under its most general aspects, the hypothesis of evolution commends itself to us, by its derivation, by its coherence, by its analogies, by its direct evidence, by its implications; let us go on to consider the several orders of facts which yield indirect support to it. We will begin by noting the harmonies that exist between it, and sundry of the inductions set forth in Part II.

# CHAPTER IV.

## THE ARGUMENTS FROM CLASSIFICATION.

§ 122. In § 103, we saw that the relations which exist among the species, genera, orders, and classes of organisms, are not interpretable as results of any such causes as have been usually assigned. We will here consider whether they are interpretable as the results of evolution. Let us first contemplate some familiar facts.

The Norwegians, Swedes, Danes, Germans, Dutch, and Anglo-Saxons, form together a group of Scandinavian races, that are but slightly divergent in their characters. Welsh, Irish, and Highlanders, though they have differences, have not differences such as to hide a decided community of nature: they are classed together as Celts. Between the Scandinavian race as a whole and the Celtic race as a whole, there is a recognized distinction greater than that between the sub-divisions which make up one or the other. And the several peoples inhabiting Southern Europe are more nearly allied to one another, than the aggregate they form is allied to the aggregates of Northern peoples. If, again, we compare these European varieties of man taken as a group, with that group of Eastern varieties which had a common origin with it, we see a stronger contrast than between the European varieties themselves. And once more, ethnologists find differences of still higher importance, between the Aryan stock as a whole and the Mongolian stock as a whole, or the Negro stock as a whole. Though these contrasts are partially obscured by intermixtures; yet they are not so obscured as to hide the truths that the most-nearly-allied varieties of man, are those which diverged from one another at a comparatively-recent period; that each group of nearly-allied varieties, is more strongly contrasted with other such groups that had a common origin with it at a remoter period; and so on, until we come to the largest groups, which are the most strongly contrasted, and of whose divergence no trace is extant.

The relations existing among the classes and sub-classes of languages, have been briefly referred to by Mr Darwin, in illustration of his argument. We know that languages have arisen by evolution. Let us then see what grouping of them evolution has produced. On comparing the dialects of adjacent counties in England, we find that their differences are so small as scarcely to distinguish them. Between the dialects of the Northern counties taken together, and those of the Southern counties taken together, the contrast is stronger. These clusters of dialects, together with those of Scotland and Ireland, are nevertheless so similar, that we regard them as one language. The several languages of Scandinavian Europe, including English, are much more unlike one another, than are the several dialects which each of them includes; in correspondence with the fact that they diverged from one another at earlier periods than did their respective dialects. The Scandinavian languages have nevertheless a certain community of character, which distinguishes them as a group from the languages of Southern Europe; between which there are general and special affinities that similarly unite them into a group formed of sub-groups containing sub-sub-groups. And this wider divergence between the order of languages spoken in Northern Europe, and the order of languages spoken in Southern Europe, answers to the longer time that has elapsed since their differentiation commenced. Further, these two orders of modern European languages, as well as Latin and Greek and certain extinct and spoken languages of the East, are shown to have traits in common, which, notwithstanding the wide gaps between them, unite them together as one great class of Aryan languages; radically distinguished from the classes of languages spoken by the other great divisions of the human race.

§ 123. Now this kind of subordination of groups, which we see arises in the course of continuous descent, multiplication, and divergence, is just the kind of subordination of groups which plants and animals exhibit: it is just this kind of subordination which has thrust itself on the attention of naturalists, in spite of pre-conceptions.

The original idea was that of arrangement in linear order. We saw that even after a considerable acquaintance with the structures of organisms had been acquired, naturalists continued their efforts to reconcile the facts with the notion of a uni-serial succession. The accumulation of evidence necessitated the breaking up of the imagined chain into groups and sub-groups. Gradually there arose the conviction that these groups do not admit of being placed in a line. And the conception finally arrived at, is, that of certain great sub-kingdoms, very widely divergent, each made up of classes much less widely divergent, severally containing orders still less divergent; and so on with genera and species. The diagram on page 303, shows the general relations of these divisions in their degrees of subordination.

Hence this "grand fact in natural history of the subordination of group under group, which from its familiarity does not always sufficiently strike us," is perfectly in harmony with the hypothesis of evolution. The extreme significance of this kind of relation among organic forms, is dwelt on by Mr Darwin; who shows how an ordinary genealogical tree represents, on a small scale, a system of grouping analogous to that which exists among organisms in general, and which is explained on the supposition of a genealogical tree by which all organisms are affiliated. If, wherever we can trace direct descent, multiplication, and divergence, this formation of groups within groups takes place; there results a strong presumption that the groups within groups which constitute the animal and vegetal kingdoms, have arisen by direct descent, multiplication, and divergence—that is, by evolution.

§ 124. Strong confirmation of this inference is furnished by the fact, that the more marked differences which divide groups, are, in both cases, distinguished from the less marked differences which divide sub-groups, by this, that they are not simply greater in *degree*, but they are more radical in *kind*. Objects, as the stars, may present themselves in small clusters, which are again more or less aggregated into clusters of clusters, in such manner that the individuals of each simple cluster, are much closer together than are the simple clusters composing a compound cluster: in which case, the kinship that unites groups of groups differs from the kinship that unites groups, not in *nature*, but only in *amount*. But this is not the case either with the groups and sub-groups which we know have resulted from evolution, or with those which we here infer have resulted from evolution. Among these, we find the highest or most general classes, are separated from one another by fundamental differences that have no common measure with the differences that separate small classes. Observe the parallelism.

We saw that each sub-kingdom of animals is marked off from the other sub-kingdoms, by a total unlikeness in its plan of organization: that is, the members of any sub-kingdom are bound together, not by some superficial attribute which they all have, but by some attribute determining the general nature of their organizations. While, contrariwise, the members of the smallest groups are united together, and separated from the members of other small groups, by modifications which do not affect the essential relations of parts. That this is just the kind of arrangement which results from evolution, the case of languages will show.

If we compare the dialects spoken in different parts of England, we find scarcely any differences but those of pronunciation: the structures of the sentences are almost uniform. Between English and the allied modern languages, there are decided divergences of structure: there are some unlikenesses of idiom; some unlikenesses in the ways of modifying the meanings of verbs; and considerable unlikenesses in the uses of genders. But these unlikenesses are not sufficient to hide a general community of organization. A greater contrast of structure exists between these modern languages of Western Europe, and the classic languages. That differentiation into abstract and concrete elements, which is shown by the substitution of auxiliary words for inflections, has produced a higher specialization distinguishing these languages as a group from the older languages. Nevertheless, both the ancient and modern languages of Europe, together with some Eastern languages derived from the same original, have, under all their differences of organization, a fundamental community of organization; inasmuch as all of them exhibit the formation of words by such a coalescence and integration of roots as destroys the independent meanings of the roots. These Aryan languages, and others which have the *amalgamate* character, are united by it into a class distinguished from the *aptotic* and *agglutinate* languages; in which the roots are either not united at all, or so incompletely united that one of them still retains its independent meaning. And philologists find that these fundamental differences which severally determine the grammatical forms, or modes of combining ideas, are really characteristic of the primary divisions among languages.

That is to say, among languages, where we know that evolution has been going on, the greatest groups are marked off from one another by the strongest structural contrasts; and as the like holds among groups of organisms, there results a further reason for inferring that these have been evolved.

§ 125. There is yet another parallelism of like meaning. We saw (§ 101) that the successively-subordinate classes, orders, genera, and species, into which zoologists and botanists segregate animals and plants, have not, in reality, those definite values conventionally given to them. There are well-marked species, and species so imperfectly defined that certain systematists regard them as varieties. Between genera, strong contrasts exist in many cases; and in other cases, contrasts so much less decided as to leave it doubtful whether they constitute generic distinctions. So, too, is it with orders and classes: in some of which there have been introduced intermediate sub-divisions, having no equivalents in others. Even of the sub-kingdoms the same truth holds. The contrast between the *Molluscoida* and the *Mollusca*, is far less than that between the *Mollusca* and the *Annulosa;* and there are naturalists who think that the *Vertebrata* are so much more widely separated from the other sub-kingdoms, than these are from one another, that the *Vertebrata* should have a classificatory value equal to that of all the other sub-kingdoms taken together.

Now just this same indefiniteness of value, or incompleteness of equivalence, is observable in those simple and compound and re-compound groups, which we see arising by evolution. In every case, the endeavour to arrange the divergent products of evolution, is met by a difficulty like that which would meet the endeavour to classify the branches of a tree, into branches of the first, second, third, fourth, &c., orders—the difficulty, namely, that branches of intermediate degrees of composition exist. The illustration furnished by languages will serve us once more. Some dialects of English are but little contrasted; others are strongly contrasted. The alliances of the several Scandinavian tongues with one another are different in degree. Dutch is much less distinct from German than Swedish is; while between the Danish and Swedish there is so close a kinship, that they might almost be regarded as widely-divergent dialects. Similarly on comparing the larger divisions, we see that the various languages of the Aryan stock, have deviated from the original to very unlike distances. The general conclusion is manifest. While the kinds of human speech fall into groups, and sub-groups, and sub-sub-groups; yet the groups are not equal to one another in value, nor have the sub-groups equal values, nor the sub-sub-groups.

If, then, the classification of organisms results in several orders of assemblages, such that assemblages of the same order are but indefinitely equivalent; and if, where evolution is known to have taken place, there have arisen assemblages between which the equivalence is similarly indefinite; there is additional reason for inferring that organisms are products of evolution.

§ 126. A fact of much significance remains. If groups of organic forms have arisen by divergence and re-divergence; and if, while the groups have been developing from simple groups into compound groups, each group and sub-group has been giving origin to more complex forms of its own type; then it is inferable that there once existed greater structural likenesses between the members of allied groups, than exist now. Hence, if we take the simplest members of any group to be those which have undergone the least change; we may expect to find a greater likeness between them and the simplest members of an allied group, than we find between the more complex members of the two groups. This, speaking generally, proves to be so.

Between the sub-kingdoms, the gaps are extremely wide; but such distant kinships as may be discerned, bear out anticipation. Speaking of that extremely-degraded vertebrate animal the *Amphioxus*, which has several molluscous traits in its organization, Dr Carpenter remarks, that it "furnishes an apt illustration of another important fact, that it is by the *lowest* rather than by the highest forms of two natural groups, that they are brought into closest relation." What are the faint traces of community between the *Annulosa* and the *Mollusca?* They are the thread-cells which some of their inferior groups have in common with the *Cœlenterata.* More decided approximations exist between the lower members of classes. In tracing down the *Crustacea* and the *Arachnida* from their more complex to their simpler forms, zoologists meet with difficulties: respecting some of these simpler forms, it becomes a question which class they belong to. The *Lepidosiren,* about which there have been disputes whether it is a fish or an amphibian, is inferior in the organization of its skeleton, to the great majority of both fishes and amphibia. Widely as they differ from them, the lower mammals have some characters in common with birds, which the higher mammals do not possess.

Now since this kind of relationship of groups is not accounted for by any other hypothesis, while the hypothesis of evolution gives us a clue to it; we must include it among the evidences of this hypothesis, which the facts of classification furnish.

§ 127. What shall we say of these several leading truths when taken together? That naturalists have been gradually compelled to arrange organisms in groups within groups; and that this is the arrangement which we see arises by descent, alike in individual families and among races of men, is a striking circumstance. That while the smallest groups are the most nearly related, there exist beween the great sub-kingdoms, structural contrasts of the profoundest kind; cannot but impress us as remarkable, when we see that where it is known to take place, evolution actually produces these feebly-distinguished small groups, and these strongly-distinguished great groups. The impression made by these two parallelisms, which add meaning to each other, is deepened by the third parallelism, which enforces the meaning of both —the parallelism, namely, that as, between the species, genera, orders, classes, &c., which naturalists have formed, there are transitional gradations; so between the groups, sub-groups, and sub-sub-groups, which we know to have been evolved, groups of intermediate values exist. And these three correspondences between the known results of evolution, and the results here ascribed to evolution, have further weight given to them by the circumstance, that the kinship of groups through their lowest members, is just the kinship which the hypothesis of evolution implies.

Even in the absence of these specific agreements, the broad fact of unity amid multiformity, which organisms so strikingly display, is strongly suggestive of evolution. Freeing ourselves from pre-conceptions, we shall see good reason to think with Mr Darwin, "that propinquity of descent—the only known cause of the similarity of organic beings—is the bond, hidden as it is by various degrees of modification, which is partly revealed to us by our classifications." When we consider that this only known cause of similarity, joined with the only known cause of divergence, which we have in the influence of conditions, gives us a key to these likenesses obscured by unlikenesses, to which no consistent interpretation can otherwise be given, even if purely hypothetical causes be admitted; we shall see that were there none of those very remarkable harmonies above pointed out, the truths of classification would still yield strong support to our conclusion.

## CHAPTER V.

### THE ARGUMENTS FROM EMBRYOLOGY.

§ 128. THERE was briefly set forth in § 52, a remarkable induction established by Von Baer; who "found that in its earliest stage, every organism has the greatest number of characters in common with all other organisms in their earliest stages; that at a stage somewhat later, its structure is like the structures displayed at corresponding phases by a less extensive multitude of organisms; that at each subsequent stage, traits are acquired which successively distinguish the developing embryo from groups of embryos that it previously resembled—thus step by step diminishing the class of embryos which it still resembles; and that thus the class of similar forms is finally narrowed to the species of which it is a member." Though this generalization is to be taken with qualifications, yet, as an average truth, it may be regarded as beyond question; and as an average truth, it has a profound significance.

For if we follow out in thought the implications of this truth—if we conceive the germs of all kinds of organisms simultaneously developing; if after taking their first step together, we imagine at the second step, one half of the vast multitude diverging from the other half; if, at the next step, we mentally watch each of these great assemblages beginning to take two or more routes of development; if we represent to ourselves this bifurcation simultaneously going on, stage after stage, in all the branches; we shall see that there must result an aggregate analogous, in its arrangement of parts, to a tree. If this vast genealogical tree be contemplated as a whole, made up of trunk, great branches, secondary branches, and so on, as far as the terminal twigs; it will be perceived that all the various kinds of organisms represented by these terminal twigs, forming the periphery of the tree, will stand related to each other in small groups, which are united into groups of groups, and so on. The embryological tree, expressing the developmental relations of organisms, will be similar to the tree which symbolizes their classificatory relations. That subordination of classes, orders, genera, and species, to which naturalists have been gradually led, is just that subordination which results from the divergence and re-divergence of embryos, as they all unfold. On the hypothesis of evolution, this parallelism has a meaning—indicates that primordial kinship of all organisms, and that progressive differentiation of them, which the hypothesis alleges. But on any other hypothesis the parallelism is meaningless: or rather, it raises a difficulty; since it implies either an effect without a cause, or a design without a purpose.

§ 129. It was said above, that this great embryological law is to be taken with certain qualifications. The resemblances which hold together great groups of embryos in their early stages, and which hold together smaller and smaller groups in their later and later stages, are not special or exact, but general or approximate; and in some cases, the conformity to this general law is very imperfect. These irregularities, however, instead of being at variance with the hypothesis of evolution, afford further support to it.

Observe, first, that the only two other possible suppositions respecting developmental changes, are negatived, the one by this general law and the other by the minor nonconformities to it. If it be said that the conditions of the case necessitated the derivation of all organisms from simple germs, and therefore necessitated a morphological unity in their primitive states; there arises the obvious answer, that the morphological unity thus implied, is not the only morphological unity to be accounted for. Were this the only unity, the various kinds of organisms, setting out from a common primordial form, should all begin from the first to diverge individually, as so many radii from a centre; which they do not. If, otherwise, it be said that organisms were framed upon certain types, and that those of the same type continue developing together in the same direction, until it is time for them to begin putting on their specialities of structure; then, the answer is, that when they do finally diverge, they ought severally to develop in direct lines towards their final forms. No reason can be assigned why, having once parted company, some should progress towards their final forms by irregular or circuitous routes. On the hypothesis of design, such deviations are inexplicable.

The hypothesis of evolution, however, while it pre-supposes those general relations among embryos which are found to exist, also affords explanations of these minor nonconformities. If, as any rational theory of evolution pre-supposes, the progressive differentiations of organic forms from one another during past times, have resulted, as they are resulting still, from the direct and indirect effects of external conditions—if organisms have become different, either by immediate adaptations to unlike habits of life, or by the mediate adaptations resulting from preservation of the individuals most fitted for such habits of life, or by both; and if the embryonic changes are related to the changes that were undergone by ancestral races; then these irregularities must be expected. For the successive changes in modes of life pursued by successive ancestral races, can have had no regularity of sequence. In some cases they must have been more numerous than in others; in some cases they must have been greater in degree than in others; in some cases they must have been to lower modes, in some cases to higher modes, and in some cases to modes neither higher nor lower. Of two connate races which diverged in the remote past, the one may have had descendants that have remained tolerably constant in their habits, while the other may have had descendants that have passed through widely-aberrant modes of life; and yet some of these last may have eventually taken to modes of life like those of the divergent races derived from the same stock. And if the metamorphoses of embryos, indicate, in a general way, the changes of structure undergone by ancestors; then, the later embryologic changes of such two allied races, will be somewhat different, though they may end in very similar forms. An illustration will make this clear. Mr Darwin says:—"Petrels are the most aërial and oceanic of birds, but in the quiet sounds of Tierra del Fuego, the *Puffinuria berardi*, in its general habits, in its astonishing power of diving, its manner of swimming, and of flying when unwillingly it takes flight, would be mistaken by any one for an auk or grebe; nevertheless, it is essentially a petrel, but with many parts of its organization profoundly modified." Now if we suppose these grebe-like habits to be continued through a long epoch, the petrel-form to be still more obscured, and the approximation to the grebe-form still closer; it is manifest that while the chicks of the grebe and the *Puffinuria* will, during their early stages of development, display that likeness involved by their common derivation from some early type of bird, the chick of the *Puffinuria* will eventually begin to show deviations, representative of the ancestral petrel-structure, and will afterwards begin to lose these distinctions, and assume the grebe-structure.

Hence, remembering the perpetual intrusions of organisms on one another's modes of life, often widely different; and remembering that these intrusions have been going on from the beginning; we shall be prepared to find that the general law of embryologic parallelism, is qualified by irregularities that are mostly small, in many cases considerable, and occasionally great. The hypothesis of evolution accounts for these: it does more—it implies the necessity of them.

§ 130. The substitutions of organs and the suppressions of organs, are among those secondary embryological phenomena which harmonize with the belief in evolution but cannot be reconciled with any other belief. There are cases where, during its earlier stages of development, an embryo possesses organs that afterwards dwindle away, as there arise other organs to discharge the same functions. And there are cases where organs make their appearance, grow to certain points, have no functions to discharge, and disappear by absorption.

We have a remarkable instance of this substitution in the successive temporary appliances for aërating the blood, which the mammalian embryo exhibits. During the first phase of its development, the mammalian embryo circulates its blood through a system of vessels distributed over what is called the *area vasculosa*—a system of vessels homologous with one which, among fishes, serves for aërating the blood until the permanent respiratory organs come into play. After a time, there buds out from the mammalian embryo, a vascular membrane called the allantois, homologous with one which, in birds and reptiles, replaces the first as a breathing apparatus. But while in the higher oviparous vertebrates, the allantois serves the purpose of a lung during the rest of embryonic life, it does not do so in the mammalian embryo. In implacental mammals, it aborts, having no function to discharge; and in the higher mammals, it becomes "placentiferous, and serves as the means of intercommunication between the parent and the offspring"—becomes an organ of nutrition more than of respiration. Now since the first system of external blood-vessels, not being in contact with a directly-oxygenated medium, cannot be very serviceable to the mammalian embryo as a lung; and since the second system of external blood-vessels is, to the implacental embryo, of no greater avail than the first; and since the communication between the embryo and the placenta among placental mammals, might as well or better have been made directly, instead of by metamorphosis of the allantois; these substitutions appear unaccountable as results of design. But they are quite congruous with the supposition, that the mammalian type arose out of lower vertebrate types. For in such case, the mammalian embryo, passing through states representing, more or less distinctly, those which its remote ancestors had in common with the lower *Vertebrata*, develops these subsidiary organs in like ways with the lower *Vertebrata*.

Even more striking than the substitutions of organs are the suppressions of organs. Mr Darwin names some cases as "extremely curious; for instance, the presence of teeth in fœtal whales, which when grown up have not a tooth in their heads; * * * It has even been stated on good authority that rudiments of teeth can be detected in the beaks of certain embryonic birds." Not even temporary functions can be assigned for these organs that are first built up and then pulled down again. They are absolutely useless—their formation is absolutely superfluous. Irreconcilable with any teleological theory, they do not even harmonize with the theory of fixed types which are maintained by the development of all the typical parts, even where not wanted; seeing that the disappearance of these incipient organs during fœtal life, spoils the typical resemblance. But while to all other hypotheses these facts are stumbling-blocks, they yield strong support to the hypothesis of evolution.

Allied to these cases, are the cases of what has been called retrograde development. Many parasitic creatures and creatures which, after leading active lives for a time, eventually become fixed, lose, in their adult states, the limbs and senses which they had when young. It may be alleged, however, that these creatures could not secure the habitats needful for them, without possessing during their larval stages, eyes and swimming appendages which eventually become useless; that though, by losing these, their organization retrogresses in one direction, it progresses in another direction; and that, therefore, they do not exhibit the needless development of a higher type on the way to a lower type. Nevertheless there are instances of a descent in organization, following an apparently-superfluous ascent. Mr Darwin says that in some genera of cirripedes, "the larvæ become developed either into hermaphrodites having the ordinary structure, or into what I have called complemental males, and in the latter, the development has assuredly been retrograde; for the male is a mere sack, which lives for a short time, and is destitute of mouth, stomach, or other organ of importance, excepting for reproduction."

§ 131. Comparative embryology shows us that besides substitutions of organs, there are what may be called substituted modes of development. The same kind of structure is not always produced in the same way; and some allied groups of organisms have modes of evolution which appear to be radically contrasted. The two modes are broadly distinguishable as the *direct* and the *indirect*. They may severally characterize the general course of evolution as a whole, and the course of evolution in particular organs.

Thus in the immense majority of articulate animals, metamorphoses, more or less marked and more or less numerous, are passed through on the way to maturity. The familiar transformations of insects show us how circuitous is the route by which the embryo-form arrives at the adult form, among some divisions of the *Articulata*. But there are other divisions, as the lower *Arachnida*, in which the unfolding of the egg into the adult takes place in the simplest manner: the substance grows towards its appointed shape by the shortest route. The *Mollusca* furnish contrasts which, though less marked, are essentially of the same nature. Among some Gasteropods, according to Vogt, the germ-mass, after undergoing its earliest changes in the same way as germ-masses in general, begins to transform itself bodily into the finished structure: in one part, the component cells coalesce to form the heart, in another part to form the liver, and so on. But in other classes of molluscs, as the Cephalopods, the embryo is moulded out of the blastoderm, or superficial layer of the germ-mass; and the various organs, mostly arising out of this blastoderm by a process of budding, reach their ultimate shapes through successive modifications, while they grow at the expense of the nutriment absorbed from the rest of the germ-mass. And this indirect development is universal among the *Vertebrata.*

Now on contemplating in their *ensemble,* the facts thus briefly indicated, we may trace among these irregularities something like a general rule. The indirect development characterizes the most-highly-organized forms. In the sub-kingdom *Vertebrata,* which, considered as a whole, stands far above the rest in complexity, the development is uniformly indirect. It is indirect in the great mass of the *Articulata.* It is indirect in the highest *Mollusca.* Conversely, it is direct in a large proportion of the lower types. The eggs of *Protozoa,* of *Cœlenterata,* of inferior *Annuloida,* originate the respective structures proper to them, by transformations that are almost immediate; each of the cycle of forms passed through, is assumed, when the proper time comes, in the simplest way; and where they multiply by budding, the substance of the bud passes by as short a process as may be, into the finished form. Where among the simpler types of animals, the evolution is indirect, its indirectness generally appears to be related to some transitional mode of life, which the larva passes through on its way to maturity; and where we find direct evolution among the more complex types, it is in their most degraded members: instance the *Acari* among the *Articulata*.*

We have before found that the facts of social organization, furnish us with hints towards interpreting the phenomena exhibited in individual organisms. Let us see whether analogies hence derived, do not help us here. A factory, or other producing establishment, or a town made up of such establishments, is an agency for elaborating some commodity consumed by society at large; and may be regarded as analogous to a gland or viscus in an individual organism. If, now, we inquire what is the primitive mode in which one of these producing establishments grows up, we find it to be this. A single worker, who himself sells the produce of his labour, is the germ. His business increasing, he employs helpers—his sons or others; and having done this, he becomes a vendor not only of his own handiwork, but of that of others. A further increase of his business compels him to multiply his assistants, and his sale grows so rapid that he is obliged to confine himself to the process of selling; that is, he ceases to be a producer, and becomes simply a channel through which the produce of others is conveyed to the public. Should his prosperity rise yet higher, he finds that he is unable to manage even the sale of his commodities, and has to employ others, probably of his own family, to aid him in selling; that is, to him as a main channel are now added subordinate channels; and so on continuously. Moreover,

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* It may be urged that the mode of development is obviously related to the *size* of the mass which is to be transformed into the embryo. Doubtless it is true that direct transformation is characteristic of small ova, and indirect transformation of large ova; and some such connexion may be necessary. Very possibly that polarity of the physiological units, which determines the specific structure, will not act throughout a large mass in such way as to transform it bodily into the specific structure; though it will thus act throughout a small mass. But that the bulk of the ovum is not the *sole* cause of this difference of method, is proved by the fact that in some cases where the development is comparatively direct, as in *Acteon*, the ovum is very much larger than in cases where it is comparatively indirect, as in minute insects.

when there grow up in one place, as a Manchester or a Birmingham, many establishments of like kind, this process is carried still further. There arise factors and agents, who are the channels through which are transmitted the produce of many mills; and we believe that primarily, these factors were manufacturers who undertook to dispose of the produce of smaller houses as well as their own, and ultimately became salesmen only. Now this, which is the original mode in which social agencies of all kinds are evolved, does not continue to be the mode. There is a tendency everywhere manifested to substitute a direct process for this indirect process. Manufacturing establishments are no longer commonly developed through the series of modifications above described; but mostly arise by the immediate transformation of a number of persons into master, clerks, foremen, workers, &c. Instead of business-partnerships being formed, as they originally were, by some slow unobtrusive union between traders and their sons or assistants; we now have joint-stock-companies resulting by sudden metamorphoses of groups of citizens. The like is true with larger and more complex social agencies. A new town in the United States arises not at all after the old method of gradual accumulations round a nucleus, and successive small modifications of structure accompanying increase of size; but it grows up over a large area, according to a pre-determined plan; and there are developed at the outset, those various civil, ecclesiastical, and industrial centres, which the incipient city will require. Even in the formation of colonies we may similarly see, that the whole type of social organization proper to the race from which the colony comes, begins at once to show itself. There is not a gradual passing through all those developmental phases passed through by the mother-society; but there is a comparatively direct transformation of the assemblage of colonists, into a social organism allied in structure to the social organism of which it was an offset.

Let us now return to the development of individual organisms; carrying back this idea with us. On the hypothesis of evolution, all organs must have been originally formed after the indirect method, by the accumulation of modifications upon modifications; and if the development of the embryo repeats the development of ancestral races, organs must be thus formed in the embryo. To a considerable extent they are thus formed. There is a striking parallelism between the mode in which, as above described, manufacturing agencies are originally evolved, and the mode in which secreting organs are evolved. Out of the group of bile-cells forming the germ of the liver, some centrally-placed ones, lying next to the intestine, are transformed into ducts through which the secretion of the peripheral bile-cells is poured into the intestine; and as the peripheral bile-cells multiply, there similarly arise secondary ducts emptying themselves into the main ones; tertiary ones into these; and so on. But while in this and in other organs, the development remains in a great degree indirect; there are organs, as the heart, in which it is comparatively direct. The heart of the vertebrate embryo does not arise from a bud; but it is first traceable as an aggregated mass of cells, becoming distinct from the cells amid which it is imbedded: its transformation into a contractile chamber, is effected by the consolidation of its outer cells while its inner cells liquify. And the comparatively direct development thus displayed in some organs of the higher embryos, is, as we have seen, characteristic of the entire development in many lower embryos.

On the hypothesis of evolution, the direct mode of development in animals, must have been substituted for the indirect mode; as we see that it is substituted in societies. How comes it to have been substituted? By studying the cause of the substitution in the social organism, we may perhaps get some insight into its cause in the individual organism. The direct mode of forming social agencies replaces the indirect mode, when these social agencies have either been so long established, or have become so prevalent, or both, as to modify the people's habits and ideas. Groups of citizens unite into corporate bodies which quickly organize, because the habit of forming such combinations has so far modified the thoughts and feelings of citizens, that it becomes natural to them thus to arrange themselves. So, too, is it with the men who form a colony. The rapid assumption by them of a social structure, as similar as circumstances permit to the structure of the mother-society, is manifestly due to the fact, that the organization of the mother-society has moulded the emotions and beliefs of its members into conformity with itself; so that when some of its members are transferred to a colony, they arrange themselves directly into a structure of like type with that of the mother-society: they do not repeat all the stages through which the mother-society passed, because their natures have been too far modified to allow of their doing this. That action and reaction between a social organism and its units, which we here see accounts for changes in modes of social development, must be paralleled by the action and reaction between an individual organism and its units. Various classes of phenomena compelled us to conclude, that each kind of organism is composed of physiological units, having certain peculiarites which force them to arrange themselves into the form of the species to which they are peculiar. And in the chapters on Genesis, Heredity, and Variation, we saw reason to believe, that while the polarities of the physiological units determine the structure of the organism as a whole; the organism as a whole, if its structure is changed by incident forces, reacts on the physiological units, and modifies them towards conformity with its new structure. Now this action and reaction between an organic aggregate and its units, tending ever to bring the two into absolute harmony, must be continually making the developmental processes more direct;

and will show its effects in all kinds of ways and degrees, according to the ancestral history of each species. Supposing it were possible for a race of organisms to have continued propagating itself through an indefinitely-long period without any change of conditions, necessitating change of structure; there would be reached so complete a congruity between the organic aggregate and its physiological units, that the units would arrange themselves directly into a structure like that of the adult organism: the germ would put on the proper characters of the species, with little or no transposition of substance. But in the absence of any such constancy of conditions and structure, what may we expect? We may expect that where the conditions and structure have been most constant, the mode of development will be the most direct; and that it will be the most indirect, where there have been the greatest and most numerous changes in the habits and structures of ancestral races of organisms. And we may also expect that developmental changes corresponding to early ancestral forms, will undergo an obliteration that is great in proportion to the fixity of organization that has been since maintained. The facts appear in harmony with this conclusion. We see a comparatively-direct development in those inferior types of animals, which show us, by their inferiority, that they have not, since the commencement of organic life, passed through many sets of changes. And where we find direct development among higher types of animals, it characterizes the simpler rather than the more complex members of the types.

Between different parts in the same embryo, there are unlikenesses in the method of formation, which seem to have kindred meanings. The heart, of which the development is in great measure direct, is an organ that appears comparatively early among the ascending grades of organic forms; and having appeared, retains throughout the character of a hollow muscle. Conversely, the organs which develop with great indirectness, are the organs of external relation; which, in the progress of organic forms, undergo various metamorphoses. Some light, too, is thus thrown on certain irregularities in the *order* of development of organs. If we contemplate those continuous actions and reactions which tend ever to establish a balance between an organic aggregate and its units; we shall see that the effect which the units composing any organ, produce on the organism as a whole, will depend, partly on the *permanence* of such organ, and partly on its proportional *mass*. The influence of any force, is a product of its *amount* multiplied into the *time* during which it has acted. Hence, a larger part of the aggregate acting for a shorter time, will impress itself on the physiological units, as much as a smaller part acting for a longer time; and may thus begin to show its influence in the developmental changes, as soon as, or even earlier than, a part that has existed for a greater period. Thus it becomes comprehensible why, in certain *Entozoa* which have immensely-developed generative systems, the rudiments of the generative systems are the first to become visible. And thus are also explicable, anomalies such as those pointed out by Prof. Agassiz—the appearance, in some cases, of traits characterizing the species, at an earlier period of development than traits characterizing the genus.

§ 132. So that while the embryologic law enunciated by Von Baer, is in harmony with the hypothesis of evolution, and is, indeed, a law which this hypothesis implies; the minor nonconformities to the law, are also interpretable by this hypothesis. Parallelism between the courses of development in species that had a common ancestry, is liable to be variously modified in correspondence with the later ancestral forms passed through after divergence of such species. The substitution of a direct for an indirect process of formation, which we have reason to believe will show itself, both in the unfolding of the entire organism and in the unfolding of particular organs, must obscure the embryologic history. And the parts influencing the whole in degrees varying with their masses, there results a further influence which, from the outset, must begin to modify the metamorphoses of each kind of embryo ; and cause it to show incipient divergences from embryos which had ancestral histories the same as its own. Thus we find three different causes conspiring in endless ways and degrees, to produce deviations from the general law —causes which are manifestly capable of producing, under special conditions, changes in apparent contradiction to this law.

## CHAPTER VI.

### THE ARGUMENTS FROM MORPHOLOGY.

§ 133. Leaving out of consideration the parallelism of development which characterizes organisms belonging to each group, that community of plan which exists among them when they are mature, is extremely remarkable and extremely suggestive. As before shown (§ 103), neither the supposition that these combinations of attributes which unite classes are fortuitous, nor the supposition that no other combinations were practicable, nor the supposition of adherence to predetermined typical plans, suffices to explain the facts. An instance will best prepare the reader for seeing the true meaning of these fundamental likenesses.

Under the immensely-varied forms of insects, greatly elongated like the dragon-fly, or contracted in shape like the lady-bird, winged like the butterfly, or wingless like the flea, we find this character in common—there are primarily twenty segments. These segments may be distinctly marked, or they may be so fused as to make it difficult to find the divisions between them. This is not all. It has been shown that the same number of segments is possessed by all the *Crustacea*. The highly-consolidated crab, and the squilla with its long, loosely-jointed divisions, are composed of the same number of somites. Though, in the higher crustaceans, some of these successive indurated rings, forming the exoskeleton, are never more than partially marked off from each other; yet they are indentifiable as homologous with segments, which, in other crustaceans, are definitely divided. What, now, can be the meaning of this community of structure among these hundreds of thousands of species filling the air, burrowing in the earth, swimming in the water, creeping about among the sea-weed, and having such enormous differences of size, outline, and substance, as that no community would be suspected between them? Why under the down-covered body of the moth and under the hard wing-cases of the beetle, should there be discovered the same number of divisions as in the calcareous framework of the lobster? It cannot be by *chance* that there exist just twenty segments in all these hundreds of thousands of species. There is no reason to think it was *necessary*, in the sense that no other number would have made a possible organism. And to say that it is the result of *design*—to say that the Creator followed this pattern throughout, merely for the purpose of maintaining the pattern—is to assign a motive which, if avowed by a human being, we should call whimsical. No rational interpretation of this and hosts of like morphological truths, can be given except by the hypothesis of evolution; and from the hypothesis of evolution they are corollaries. If organic forms have arisen from common stocks by perpetual divergences and redivergences—if they have continued to inherit, more or less clearly, the characters of ancestral races; then there will naturally result these communities of fundamental structure among extensive assemblages of creatures, that have severally become modified in countless ways and degrees, in adaptation to their respective modes of life. To this let it be added, that while the belief in an intentional adhesion to a pre-determined pattern throughout a whole group, is totally negatived by the occurrence of occasional deviations from the pattern; such deviations are reconcilable with the belief in evolution. As pointed out in the last chapter, there is reason to think that remote ancestral traits, will be obscured more or less according as the superposed modifications of structure, have or have not been great or long maintained. Hence, though the occurrence of articulate animals, such as spiders and mites, having fewer than twenty segments, is fatal to the supposition that twenty segments was decided on for the three groups of superior *Articulata;* it is not incongruous with the supposition, that some primitive race of articulate animals, bequeathed to these three groups this common typical character—a character which has nevertheless, in many cases, become greatly obscured, and in some of the most aberrant orders of these classes, quite lost.

§ 134. Besides these wide-embracing and often deeply-hidden homologies, which hold together different animals, there are the scarcely-less significant homologies between different organs of the same animal. These homologies, like the others, are obstacles to the supernatural interpretations, and supports of the natural interpretation.

One of the most familiar and instructive instances is furnished by the vertebral column. Snakes, which move sinuously through and over plants and stones, obviously need a segmentation of the bony axis from end to end; and inasmuch as flexibility is required throughout the whole length of the body, there is advantage in the comparative uniformity of this segmentation: the creature's movements would be impeded if, instead of a chain of vertebræ varying but little in their lengths, there existed in the middle of the series some long bony mass that would not bend. But in most of the higher *Vertebrata,* the mechanical actions and reactions demand that while some parts of the vertebral axis shall be flexible, other parts shall be inflexible. Inflexibility is especially requisite in that part of the vertebral column called the sacrum; which, in mammals and birds, forms a fulcrum exposed to the greatest strains which the skeleton has to bear. Now in both mammals and birds, this rigid portion of the vertebral column is not made of one long segment or vertebra, but of several segments fused together. In man there are five of these confluent sacral vertebræ; and in the ostrich tribe they number from seventeen to twenty. Why is this? Why, if the skeleton of each species was separately contrived, was this bony mass made by soldering together a number of vertebræ like those forming the rest of the column, instead of being made out of one simple piece? And why, if typical uniformity was to be maintained, does the number of sacral vertebræ vary within the same order of birds? Why, too, should the development of the sacrum be by the round-about process of first forming its separate constituent vertebræ, and then destroying their separateness? In the embryo of a mammal or bird, the substance of the vertebral column is, at the outset, continuous. The segments that are to become vertebræ, arise gradually in the midst of this originally-homogeneous axis. Equally in those parts of the spine which are to remain flexible, and in those parts which are to grow rigid, these segments are formed; and that part of the spine which is to compose the sacrum, having passed out of its original unity into disunity, by separating itself into segments, passes again into unity by the coalescence of these segments. To what end is this construction and re-construction? If, originally, the spine in vertebrate animals consisted from head to tail of separate moveable segments, as it does still in fishes and some reptiles—if, in the evolution of the higher *Vertebrata*, certain of these moveable segments were rendered less moveable with respect to each other, by the mechanical conditions to which they are exposed, and at length became relatively immoveable; it is comprehensible why the sacrum formed out of them, should continue ever after to show more or less clearly its originally-segmented structure. But on any other hypothesis, this segmented structure is inexplicable. "We see the same law in comparing the wonderfully complex jaws and legs in crustaceans," says Mr Darwin: referring to the well-known fact that those numerous lateral appendages which, in the lower crustaceans most of them serve as legs, and have like shapes, are, in the higher crustaceans, some of them represented by enormously-developed claws, and others by variously-modified foot-jaws. "It is familiar to almost every one," he continues, "that in a flower the relative position of the sepals, petals, stamens, and pistils, as well as their intimate structure, are intelligible on the view that they consist of metamorphosed leaves arranged in a spire. In monstrous plants we often get direct evidence of the possibility of one organ being transformed into another; and we can actually see in embryonic crustaceans and in many other animals, and in flowers, that organs, which when mature become extremely different, are at an early stage of growth exactly alike." * * * "Why should one crustacean, which has an extremely complex mouth formed of many parts, consequently always have fewer legs; or conversely, those with many legs have simpler mouths? Why should the sepals, petals, stamens, and pistils in any individual flower, though fitted for such widely-different purposes, be all constructed on the same pattern?"

To these and countless similar questions, the theory of evolution furnishes the only rational answer. In the course of that change from homogeneity to heterogeneity of structure, displayed in evolution under every form, it will necessarily happen that from organisms made up of numerous like parts, there will arise organisms made up of parts more and more unlike: which unlike parts will nevertheless continue to bear traces of their primitive likeness.

§ 135. One more striking morphological fact, near akin to some of the facts dwelt on in the last chapter, must be here set down—the frequent occurrence, in adult animals and plants, of rudimentary and useless organs, which are homologous with organs that are developed and useful in allied animals and plants. In the last chapter we saw that during the development of embryos, there often arise organs which disappear on being replaced by other organs discharging the same functions in different ways; and that in some cases, organs develop to certain points, and are then re-absorbed without performing any functions. But very generally, the partially-developed organs are retained throughout life.

The osteology of the higher *Vertebrata*, supplies abundant examples. Vertebral processes which, in one tribe, are fully formed and ossified from independent centres, are, in other tribes, mere tubercles not having independent centres of ossification. While in the tail of this animal, the vertebræ are severally composed of centrum and appendages, in the tail of that animal, they are simple osseous masses without any appendages; and in another animal, they have lost their individualities by coalescence with neighbouring vertebræ into a rudimentary tail. From the structures of the limbs, analogous facts are cited by comparative anatomists. The undeveloped state of certain metacarpal bones, characterizes whole groups of mammals. In one case we find the normal number of digits; and, in another case, a smaller number with an atrophied digit to make out the complement. Here is a digit with its full number of phalanges; and there a digit of which one phalange has been arrested in its growth. Still more remarkable are the instances of entire limbs being rudimentary; as in certain snakes, which have hind legs hidden beneath the integument. So, too, is it with the dermal appendages. Some of the smooth-skinned amphibia have scales buried in the skin. The seal, which is a mammal considerably modified in adaptation to an aquatic life, and which uses its feet mainly as paddles, has toes that still bear external nails; but the manatee, which is a much more transformed mammal, has nailless paddles, which, when the skin is removed, are said, by Humboldt, to display rudimentary nails at the ends of the imbedded digits. Nearly all birds are covered with developed feathers, severally composed of a shaft bearing fibres, each of which again bears a fringe of down. But in some birds, as in the ostrich, various stages of arrested development of the feathers may be traced; beginning with the unusually-elaborated feathers of the tail, and ending with those about the beak, which are reduced to simple hairs. Nor is this the extreme case. In the *Apteryx* we see the whole of the feathers reduced to a hair-like form. Again, the hair which commonly covers the body in mammals, is comparatively rudimentary over the greater part of the human body, and is in some parts reduced to mere down—down which nevertheless proves itself to be homologous with the hair of mammals in general, by occasionally developing into the original form. Numerous cases of aborted organs are given by Mr Darwin, of which a few may be here added. "Nothing can be plainer," he remarks, "than that wings are formed for flight, yet in how many insects do we see wings so reduced in size as to be utterly incapable of flight, and not rarely lying under wing-cases, firmly soldered together?" * * * "In plants with separated sexes, the male flowers often have a rudiment of a pistil; and Kölreuter found that by crossing such male plants with an hermaphrodite species, the rudiment of the pistil in the hybrid offspring was much increased in size; and this shows that the rudiment and the perfect pistil are essentially alike in nature." And then, to complete the proof that these undeveloped parts are marks of descent from races in which they were developed, there are not a few direct experiences of this relation. "We have plenty of cases of rudimentary organs in our domestic productions—as the stump of a tail in tailless breeds—the vestige of an ear in earless breeds—the re-appearance of minute dangling horns in hornless breeds of cattle."

Here, as before, the teleological doctrine fails utterly; for these rudimentary organs are useless, and occasionally even detrimental. The doctrine of typical plans is equally out of court; for while, in some members of a group, rudimentary organs completing the general type are traceable, in other members of the same group, such organs are unrepresented. There remains only the doctrine of evolution; and to this, these rudimentary organs offer no difficulties. On the contrary, they are among its most striking evidences.

§ 136. The general truths of morphology thus coincide in their implications. Unity of type, maintained under extreme dissimilarities of form and mode of life, is explicable as resulting from descent with modification; but is otherwise inexplicable. The likenesses disguised by unlikenesses, which the comparative anatomist discovers between various organs in the same organism, are worse than meaningless if it be supposed that organisms were severally framed as we now see them; but they fit in quite harmoniously with the belief, that each kind of organism is a product of accumulated modifications upon modifications. And the presence in all kinds of animals and plants, of functionally-useless parts corresponding to parts that are functionally-useful in allied animals and plants, while it is totally incongruous with the belief in a construction of each organism by miraculous interposition, is just what we are led to expect by the belief that organisms have arisen by progression.

## CHAPTER VII.

### THE ARGUMENTS FROM DISTRIBUTION.

§ 137. In §§ 105 and 106, we contemplated the phenomena of distribution in Space. The general conclusions reached, in great part based on the evidence brought together by Mr Darwin, were that, "on the one hand, we have similarly-conditioned, and sometimes nearly-adjacent, areas, occupied by quite different Faunas. On the other hand, we have areas remote from each other in latitude, and contrasted in soil as well as climate, which are occupied by closely-allied Faunas." Whence it was inferred that "as like organisms are not universally, or even generally, found in like habitats; nor very unlike organisms, in very unlike habitats; there is no manifest pre-determined adaptation of the organisms to the habitats." In other words, the facts of distribution in Space, do not conform to the hypothesis of design. At the same time we saw that "the similar areas peopled by dissimilar forms, are those between which there are impassable barriers; while the dissimilar areas peopled by similar forms, are those between which there are no such barriers;" and these generalizations appeared to be in harmony with the abundantly-illustrated truth, "that each species of organism tends ever to expand its sphere of existence—to intrude on other areas, other modes of life, other media."

By way of showing still more clearly the effects of this competition among races of organisms, let me here add some recently-published instances of the usurpations of areas, and changes of distribution hence resulting. In the *Natural History Review* for January, 1864, Dr Hooker quotes as follows from some New Zealand naturalists:—"You would be surprised at the rapid spread of European and other foreign plants in this country. All along the sides of the main lines of road through the plains, a *Polygonum* (*aviculare*), called 'Cow Grass,' grows most luxuriantly, the roots sometimes two feet in depth, and the plants spreading over an area from four to five feet in diameter. The dock (*Rumex obtusifolius* or *R. crispus*) is to be found in every river bed, extending into the valleys of the mountain rivers, until these become mere torrents. The sow-thistle is spread all over the country, growing luxuriantly nearly up to 6000 feet. The water-cress increases in our still rivers to such an extent, as to threaten to choke them altogether: * * * I have measured stems twelve feet long and three-quarters of an inch in diameter. In some of the mountain districts, where the soil is loose, the white clover is completely displacing the native grasses, forming a close sward. * * * In fact, the young native vegetation appears to shrink from competition with these more vigorous intruders." "The native (Maori) saying is, 'as the white man's rat has driven away the native rat, so the European fly drives away our own, and the clover kills our fern, so will the Maoris disappear before the white man himself.'"

Given this universal tendency of the superior to overrun the habitats of the inferior; let us consider what, on the hypothesis of evolution, will be the effects on the geographical relationships of species.

§ 138. A race of organisms cannot expand its sphere of existence, without subjecting itself to new external conditions. Those of its members which spread over adjacent areas, inevitably come in contact with circumstances partially different from their previous circumstances; and such of them as adopt the habits of other organisms, necessarily experience re-actions more or less contrasted with the reactions before experienced. Now if changes of organic structure are caused, directly or indirectly, by changes in the incidence of forces; there must result unlikenesses of structure between the divisions of a race which colonizes new habitats. Hence, in the absence of obstacles to migration, we may anticipate manifest kinships between the animals and plants of one area, and those of areas adjoining it. This inference corresponds with an induction before set down (§ 106). In addition to the illustrations of it already quoted from Mr Darwin, his pages furnish others. One is that species which inhabit islands are habitually allied to species which inhabit neighbouring main lands; and another is that the faunas of clustered islands show marked similarities. "Thus the several islands of the Galapagos Archipelago are tenanted," says Mr Darwin, "in a quite marvellous manner, by very closely related species; so that the inhabitants of each separate island, though mostly distinct, are related in an incomparably closer degree to each other than to the inhabitants of any other part of the world." Mr Wallace has traced "variation as specially influenced by locality" among the *Papilionidæ* inhabiting the East Indian Archipelago: showing how "the species and varieties of Celebes possess a striking character in the form of the anterior wings, different from that of the allied species and varieties of all the surrounding islands;" and how "tailed species in India and the western islands lose their tails as they spread eastward through the archipelago." During his travels on the Upper Amazons, Mr Bates found that "the greater part of the species of *Ithomiæ* changed from one locality to another, not further removed than 100 to 200 miles;" that "many of these local species have the appearance of being geographical varieties;" and that in some species "most of the local varieties are connected with their parent form by individuals exhibiting all the shades of variation."

Further general relationships are to be inferred. If races of organisms, ever being thrust by pressure of population into new habitats, undergo modifications of structure as they diverge more and more widely in space, it follows that, speaking generally, the widest divergences in Space will indicate the longest periods during which the descendants from a common stock have been subject to modifying conditions; and hence that, among organisms of the same group, the smaller constrasts of structure will be limited to the smaller areas. This we find: "varieties being," as Dr Hooker says in his *Flora of Tasmania*, "more restricted in locality than species, and these again than genera." Again, if races of organisms spread, and as they spread are altered by changing incident forces; it follows that where the incident forces vary greatly within given areas, the alterations will be more numerous than in equal areas which are less-variously conditioned. This, too, proves to be the fact. Dr Hooker points out that the most uniform regions have the fewest species; while in the most multiform regions the species are the most numerous.

§ 139. Let us consider next, how the hypothesis of evolution corresponds with the facts of distribution, not over different areas, but through different media. If all forms of organisms have descended from some primordial simplest form, it follows that, since this primordial simplest form must have inhabited some one medium out of the several media which organisms now inhabit, the peopling of other media by its descendants, implies migration from one medium to others—implies adaptations to media quite unlike the original medium. To speak specifically—water being the medium in which the lowest living forms exist, it is implied that the earth and the air have been colonized from the water. Great difficulties appear to stand in the way of this assumption. Ridiculing those who contend for the uniserial development of organic forms, who have, indeed, laid themselves open to ridicule by their many untenable propositions, Von Baer writes—"A fish, swimming towards the shore, desires to take a walk, but finds his fins useless. They diminish in breadth for want of use, and at the same time elongate. This goes on with children and grandchildren for a few millions of years, and at last who can be astonished that the fins become feet? It is still more natural that the fish in the meadow, finding no water, should gape after air, thereby, in a like period of time developing lungs; the only difficulty being that in the meanwhile, a few generations must manage without breathing at all." Though, as thus presented, the belief in a transition looks laughable; and though such derivation of terrestrial vertebrates by direct modification of the piscine type, is untenable; yet we must not therefore conclude that no migrations of the kind alleged can have taken place. The adage that "truth is stranger than fiction," applies quite as much to Nature in general as to human life. Besides the fact that there are certain fish which actually do "take a walk" without any very obvious reason; and besides the fact that sundry fish ramble about on land when impelled to do so by the drying-up of the waters inhabited by them; there is the still more astounding fact, that one kind of fish climbs trees. Few things seem more obviously impossible, than that a water-breathing creature without efficient limbs, should ascend eight or ten feet up the trunk of a palm; and yet the *Anabas scandens* does as much. To previous testimonies on this point, Capt. Mitchell has recently added others. Such remarkable cases of temporary changes of media, will prepare us for conceiving how, under special conditions, permanent changes of media may have taken place; and for considering how the doctrine of evolution is elucidated by them.

Both marine organisms and fresh-water organisms, are many of them left from time to time partially or completely without water; and the creatures which show the power to change their media temporarily or permanently, are in very many cases, of the kinds most liable to be thus deserted by their medium. Let us consider what the sea-shore shows us. Twice a-day the rise and the fall of the tide, covers and uncovers countless plants and animals, fixed and moving; and through the alternation of spring and neap tides, it results that the exposure of the organisms living low down on the beach, varies both in frequency and duration: while some of them are left dry only once a fortnight for a very short time, others a little higher up, are left dry during two or three hours at several ebb tides every fortnight. Then by small gradations we come to such as, living at the top of the beach, are bathed by salt-water only at long intervals; and still higher to some which are but occasionally splashed in stormy weather. What, now, do we find among the organisms thus subject to various regular and irregular alternations of media? Besides many plants and many fixed animals, we find numerous moving animals; some of which are confined to the lower zones of this littoral region, but others of which wander over the whole of it. Omitting the humbler animal forms, it will suffice to observe that each of the two great sub-kingdoms, *Mollusca* and *Articulata*, supplies examples of creatures having a wide excursiveness within this region. We have gasteropods which, when the tide is down, habitually creep snail-like over sand and sea-weed, even up as far as high-water mark. We have several kinds of crustaceans, of which the crab is the most conspicuous, running about on the wet beach, and sometimes rambling beyond the reach of the water. And then note the striking fact, that each of these forms thus habituated to changes of media, is allied to forms that are mainly or wholly terrestrial. On the West Coast of Ireland, marine gasteropods are found on the rocks three hundred feet above the sea, where they are only at long intervals wetted by the spray; and though between gasteropods of this class and land-gasteropods the differences are considerable, yet the land-gasteropods are more closely allied to them than to any other *Mollusca*. Similarly, the two highest orders of crustaceans have their species which live occasionally, or almost entirely, out of the water: there is a kind of lobster in the Mauritius which climbs trees; and there is the land-crab of the West Indies, which deserts the sea when it reaches maturity, and re-visits it only to spawn. Seeing, thus, how there are many kinds of marine creatures whose habitat habitually exposes them to changes of media; how some of the higher kinds so circumstanced, show a considerable adaptation to both media; and how these amphibious kinds are allied to kinds that are mainly or wholly terrestrial; we shall see that the migrations from one medium to another, which evolution pre-supposes, are by no means impracticable. With such evidence before us, the assumption that the distribution of the *Vertebrata* through media so different as air and water, may have been gradually effected in some analogous manner, would not be altogether unwarranted, even had we no clue to the process. We shall find, however, a tolerably distinct clue. Though rivers, and lakes, and pools, have no sensible tidal variations, they have their rises and falls, regular and irregular, moderate and extreme. Especially in tropical climates, we see them annually full for a certain number of months, and then dwindling away and drying up. This drying up may reach various degrees, and last for various periods: it may go to the extent only of producing a liquid mud, or it may reduce the mud to a hardened, fissured solid; it may last for a day or two or for months. That is to say, aquatic forms which are in one place annually subject to a slight want of water for a short time, are elsewhere subject to greater wants for longer times: we have gradations of transition, analogous to those which the tides furnish. Now it is well known that creatures inhabiting such waters, have, in various degrees, powers of meeting these contingences. The contained fish either bury themselves in the mud when the dry season comes, or ramble in search of other waters. This is proved by evidence from India, Guiana, Siam, Ceylon; and some of these fish, as the *Anabas scandens*, are known to survive for days out of the water. But the facts of greatest significance are furnished by an allied class of *Vertebrata,* almost peculiar to habitats of this kind. The *Amphibia* are not, like fish, habitually found in waters that are never partially or wholly dried up; but they nearly all inhabit waters which, at certain seasons, evaporate, in great measure or completely—waters in which most kinds of fish cannot exist. And what are the leading structural traits of these *Amphibia?* They have two respiratory systems—pulmonic and branchial—variously developed in different orders; and they have two or four limbs, also variously developed. Further the class *Amphibia* consists of two groups, in one of which this duality of the respiratory system is permanent, and the development of the limbs always incomplete; and in the other of which the branchiæ disappear as the lungs and limbs become fully developed. The lowest group, the *Perennibranchiata,* have organs homologous with the air-bladders of fishes, transformed in various degrees into lungs, until "in the *Siren,* the pulmonic respiration is more extensive and important than the branchial;" and to these creatures, having a habitat partially aërial and partially aquatic, there are at the same time supplied, in the shallow water covering soft mud, the mechanical conditions which render swimming difficult and rudimentary limbs useful. In the higher group, the *Caducibranchiata,* we find still more suggestive transformations. Having at first a structure resembling that which is permanent in the perennibranchiate amphibian, the larva of the caducibranchiate amphibian, pursues for a time a similar life; but eventually, the changes are carried further in the same direction: the respiration of air, originally supplementary to the respiration of water, predominates over it more and more, till it replaces it entirely; and an additional pair of legs is produced. This having been done, the creature either becomes, like the *Triton,* one which quits the water only occasionally; or, like the Frog, one which pursues a life mainly terrestrial, and returns to the water now and then. Finally, if we ask under what conditions this metamorphosis of a water-breather into an air-breather completes itself, the answer is—it completes itself at the time when the shallow pools inhabited by the larvæ, are being dried up by the summer's sun.*

See, then, how significant are the facts when thus brought together. There are particular habitats in which animals are subject to changes of media. In such habitats exist animals having, in various degrees, the power to live in both media, consequent on various phases of transitional organization. Near akin to these animals, there are some that, after passing their early lives in the water, acquire more completely the structures fitting them to live on land, to which they then migrate. Lastly, we have closely-allied creatures like the Surinam toad and the terrestrial salamander, which, though they belong by their structures to the class *Amphibia,* are not amphibious in their habits—creatures the larvæ of which do not pass their early lives in the water, and yet go through these same metamorphoses! Must we then think that the distribution of kindred organisms through different media, presents an insurmountable difficulty? On the contrary, with facts like these before us, the evolution-hypothesis supplies possible interpretations of many phenomena that are else unaccountable. Realizing the way in which such changes of media are in some cases gradually imposed by physical conditions, and in other cases voluntarily commenced and slowly increased in the search after food; we shall begin to understand how, in the course of evolution, there have arisen

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* While these pages are passing through the press, Dr Hooker has obliged me by pointing out, that "plants afford many excellent examples" of analogous transitions. He says that among true "water plants," there are found, in the same species, varieties which have some leaves submerged and some floating; other varieties in which they are all floating; and other varieties in which they are all submerged. Further, that many plants characterized by floating leaves, and which have all their leaves floating when they grow in deeper water, are found with partly aerial leaves when they grow in shallower water; and that elsewhere they occur in almost dry soil with all their leaves aerial.

those strange obscurations of one type by the externals of another type. When we see land-birds occasionally feeding by the water-side, and then learn that one of them, the water-ouzel, an "anomalous member of the strictly terrestrial thrush family, wholly subsists by diving—grasping the stones with its feet and using its wings under water"—we are enabled to comprehend how, under pressure of population, aquatic habits may be acquired by creatures organized for aërial life; and how there may eventually arise an ornithic type, in which the traits of the bird are very much disguised. Finding among mammals, some that in search of prey or shelter, have taken to the water in various degrees, we shall cease to be perplexed on discovering the mammalian structure hidden under a fish-like form, as it is in the *Cetacea*. Grant that there has ever been going on that re-distribution of organisms, which we see still resulting from their intrusions on one another's areas, media, and modes of life; and we have an explanation of those multitudinous cases in which homologies of structure are complicated with analogies. And while it accounts for the occurrence in one medium of organic types fundamentally organized for another medium, the doctrine of evolution accounts also for the accompanying unfitnesses. Either the seal has descended from some mammal which little by little became aquatic in its habits, in which case the structure of its hind limbs has a meaning; or else it was specially framed for its present habitat, in which case the structure of its hind limbs is incomprehensible.

§ 140. The facts respecting distribution in Time, which have more than any others been cited both in proof and in disproof of evolution, are too fragmentary to be conclusive either way. Were the geological record complete, or did it, as both Uniformitarians and Progressionists have habitually assumed, give us traces of the earliest organic forms; the evidence hence derived, for or against, would have had more weight than any other evidence. As it is, all we can do is to see whether such fragmentary evidence as remains, is congruous with the hypothesis.

Palæontology has shown that there is a "general relation between lapse of time and divergence of organic forms" (§ 107); and that "this divergence is comparatively slow and continuous, where there is continuity in the geological formations, but is sudden and comparatively wide, wherever there occurs a great break in the succession of strata." Now this is obviously what we should expect. The hypothesis implies structural changes that are not sudden but gradual. Hence, where conformable strata indicate a continuous record, we may expect to find successions of forms only slightly different from one another; while we may rationally look for considerable contrasts between the groups of forms fossilized in adjacent strata, where there is evidence of a great blank in the record.

The permanent disappearances of species, of genera, and of orders, which we saw to be a fact tolerably-well established, is also a fact for which the belief in evolution prepares us. If later organic forms have in all cases descended from earlier organic forms, and have diverged during their descent, both from their prototypes and from one another; then it obviously follows, that such of them as become extinct at any epoch, will never re-appear at a subsequent epoch; since there can never again arise a concurrence and succession of conditions, such as those under which each particular type was evolved.

Though comparisons of ancient and modern organic forms, prove that many types have persisted through enormous periods of time, without undergoing great changes; it was shown that such comparisons do not disprove the occurrence in organic forms, of changes great enough to produce what are called different types. The result of inductive inquiry we saw to be, that while a few modern higher types yield signs of having been developed from ancient lower types; and while there are many modern types which *may* have been thus developed, though we are without evidence that they have been so; yet that "any admissible hypothesis of progressive modification must be compatible with persistence without progression through indefinite periods." Now these results are quite congruous with the hypothesis of evolution. As rationally interpreted, evolution must in all cases be understood to result, directly or indirectly, from the incidence of forces. If there are no changes of conditions, entailing organic changes, organic changes are not to be expected. Only in organisms which fall under conditions, in conformity to which there arise additional modifications answering to additional needs, will there be that increased heterogeneity which characterizes higher forms. Hence, though the facts of palæontology cannot be held to prove evolution, yet they are in harmony with it; and some few of them yield it support.

§ 141. One general truth respecting distribution in Time, is, however, profoundly significant. If, instead of contemplating the relations among past forms of life taken by themselves, we contemplate the relations between them and the forms now existing; we find a connexion which is in perfect harmony with the belief in evolution, but quite irreconcilable with any other belief.

Note, first, how full of meaning is the close kinship that exists between the aggregate of organisms now living, and the aggregate of organisms which lived in the most recent geologic times. In the last-formed strata, nearly all the imbedded remains are those of species which still flourish. Strata a little older, contain a few fossils of species now extinct; though, usually, species greatly resembling extant ones. Of the remains found in strata of still earlier date, the extinct species form a larger per centage; and the differences between them and the allied species now living, are more marked. That is to say, the gradual change of organic types in Time, which we before saw is indicated by the geological record, is equally indicated by the relation between existing organic types and organic types of the epoch preceding our own. The evidence completely accords with the belief in a descent of present life from past life. Doubtless such a kinship is not incongruous with the doctrine of special creations. It may be argued that the introduction, from time to time, of new species better fitted to the somewhat changed conditions of the Earth's surface, would result in an apparent alliance between our living Flora and Fauna, and the Floras and Faunas that lately lived. No one can deny it. But on passing from the most general aspect of the alliance, to its more special aspects, we shall find this interpretation completely negatived.

For besides a close kinship between the aggregate of surviving forms and the aggregate of forms that have died out in recent geologic times; there is a peculiar connexion of like nature between present and past forms in each great geographical region. The instructive fact before cited from Mr Darwin, is the "wonderful relationship in the same continent between the dead and the living." This relationship is not explained by the supposition that new species have been at intervals supernaturally placed in each habitat, as the habitat became modified; since, as we saw, species are by no means uniformly found in the habitats to which they are best adapted. It cannot be said that the marsupials imbedded in recent Australian strata, having become extinct because of unfitness to some new external condition, the existing marsupials were then specially created to fit the modified environment; since sundry animals found elsewhere, are so much more completely in harmony with these new Australian conditions, that, when taken to Australia, they rapidly extrude the marsupials. While, therefore, the similarity between the existing Australian Fauna and the Fauna which immediately preceded it over the same area, is just that which the belief in evolution leads us to expect; it is a similarity which cannot be otherwise accounted for.

And so is it with parallel relations in New Zealand, in South America, and in Europe.

§ 142. Given, then, that pressure which species exercise on one another, in consequence of the universal overfilling of their respective habitats—given the resulting tendency to thrust themselves into one another's areas, and media, and modes of life, along such lines of least resistance as from time to time are found—given besides the changes in modes of life, hence arising, those other changes which physical alterations of habitats necessitate—given the structural modifications directly or indirectly produced in organisms by modified conditions; and the facts of distribution in Space and Time are accounted for. That divergence and re-divergence of organic forms, which we saw to be shadowed forth by the truths of classification and the truths of embryology, we see to be also shadowed forth by the truths of distribution. If that aptitude to multiply, to spread, to separate, and to differentiate, which the human races have in all times shown, be a tendency common to races in general, as we have ample reason to assume; then there will result that kind of relation among the species, and genera, and orders, peopling the Earth's surface, which we find exists. Those remarkable identities of type discovered between organisms inhabiting one medium, and strangely modified organisms inhabiting another medium, are at the same time rendered comprehensible. And the appearances and disappearances of species which the geological record shows us, as well as the connexions between successive groups of species from early eras down to our own, cease to be inexplicable.

## CHAPTER VIII.

### HOW IS ORGANIC EVOLUTION CAUSED?

§ 143. Already it has been necessary to speak of the causes of organic evolution in general terms; and now we are prepared for considering them specifically. The task before us is to deduce the leading facts of organic evolution, from those same first principles which evolution at large conforms to.

Before attempting this, however, it will be instructive to glance at the causes of organic evolution that have been from time to time alleged.

§ 144. The theory that plants and animals of all kinds were gradually evolved, seems to have been at first accompanied only by the vaguest conception of cause—or rather, by no conception of cause properly so called, but only by the blank form of a conception. One of the earliest who in modern times (1735) contended that organisms are indefinitely modifiable, and that through their modifications they have become adapted to various modes of existence, was De Maillet. But though De Maillet supposed all living beings to have arisen by a natural, continuous process, he does not appear to have had any definite idea of that which determines this process. In 1794, in his *Zoonomia*, Dr Darwin gave reasons (sundry of them valid ones) for believing that organized beings of every kind, have descended from one, or a few, primordial germs; and along with some observable causes of modification, which he points out as aiding the developmental process, he apparently ascribes it, in part, to a tendency given to such germ or germs when created. He suggests the possibility "that all warm-blooded animals have arisen from one living filament, which THE GREAT FIRST CAUSE endued with animality, with the power of acquiring new parts, attended with new propensities, directed by irritations, sensations, volitions, and associations; and thus possessing the faculty of continuing to improve by its own inherent activity." In this passage we see the idea to be, that evolution is pre-determined by some intrinsic proclivity. "It is curious," says Mr Charles Darwin, "how largely my grandfather, Dr Erasmus Darwin, anticipated the erroneous grounds of opinion, and the views of Lamarck." One of the anticipations was this ascription of development to some inherent tendency. To the "plan général de la nature, et sa marche uniforme dans ses opérations," Lamarck attributes "la progression évidente qui existe dans la composition de l'organisation des animaux;" and "la *gradation* régulière qu'ils devroient offrir dans la composition de leur organisation," he thinks is rendered irregular by secondary causes. Essentially the same in kind, though somewhat different in form, was the conception put forth in the *Vestiges of Creation;* the author of which contends "that the several series of animated beings, from the simplest and oldest up to the highest and most recent, are, under the providence of God, the results, *first*, of an impulse which has been imparted to the forms of life, advancing them, in definite times, by generation, through grades of organization terminating in the highest dicotyledons and vertebrata;" and that the progression resulting from these impulses, is modified by certain other causes. The broad general contrasts between lower and higher forms of life, are regarded by him as due to an innate aptitude to give birth to forms of more perfect structures. The last to re-enunciate this doctrine has been Prof. Owen; who asserts "the axiom of the continuous operation of creative power, or of the ordained becoming of living things." Though these highly-general expressions do not suggest any very definite idea, yet they imply the belief that organic progress is a result of some in-dwelling tendency to develop, supernaturally impressed on living matter at the outset—some ever-acting constructive force, which, independently of other forces, moulds organisms into higher and higher forms.

In whatever way it is formulated, or by whatever language it is obscured, this ascription of organic evolution to some aptitude naturally possessed by organisms, or miraculously imposed on them, is unphilosophical. It is one of those explanations which explains nothing—a shaping of ignorance into the semblance of knowledge. The cause assigned is not a true cause—not a cause assimilable to known causes—not a cause that can be anywhere shown to produce analogous effects. It is a cause unrepresentable in thought: one of those illegitimate symbolic conceptions which cannot by any mental process be elaborated into a real conception. In brief, this assumption of a persistent formative power, inherent in organisms, and making them unfold into higher forms, is an assumption no more tenable than the assumption of special creations: of which, indeed, it is but a modification; differing only by the fusion of separate unknown processes into a continuous unknown process.

§ 145. Along with this intrinsic tendency to progress, supposed to be primordially impressed on them, Dr Darwin held that animals have a capacity for being modified by processes which their own desires initiate. He speaks of powers as "excited into action by the necessities of the creatures which possess them, and on which their existence depends;" and more specifically he says that "from their first rudiment or primordium, to the termination of their lives, all animals undergo perpetual transformations; which are in part produced by their own exertions, in consequence of their desires and aversions, of their pleasures and their pains, or of irritations, or of associations; and many of these acquired forms or properties are transmitted to their posterity." While it embodies a belief for which a great deal is to be said, this passage involves the assumption that desires and aversions, existing before experiences of the actions to which they are related, were the originators of the actions, and therefore of the structural modifications caused by them. In his *Philosophie Zoologique*, Lamarck much more specifically asserts "le *sentiment intérieur*," to be in all creatures that have developed nervous systems, an independent cause of those changes of form which are due to the exercise of organs: distinguishing it from that simple *irritability* possessed by inferior animals, which cannot produce what we call a desire or emotion; and holding that these last, along with all "qui manquent de système nerveux, ne vivent qu'à l'aide des excitations qu'ils reçoivent de l'extérieur." Afterwards he says—"je reconnus que la nature, obligée d'abord d'emprunter des milieux environnans la *puissance excitatrice* des mouvemens vitaux et des actions des animaux imparfaits, sut, en composant de plus en plus l'organisation animale, transporter cette puissance dans l'intérieur même de ces êtres, et qu'à la fin, elle parvint à mettre cette même puissance à la disposition de l'individu." And still more definitely he contends that if one considers "la *progression* qui se montre dans la composition de l'organisation," * * * "alors on eût pu apercevoir comment les *besoins*, d'abord réduits à nullité, et dont le nombre ensuite s'est accru graduellement, ont amené le penchant aux actions propres à y satisfaire; comment les actions devenues habituelles et énergiques, ont occasionné le développement des organes qui les exécutent."

Now though this conception of Lamarck is more precisely stated, and worked out with much greater elaboration and wider knowledge of the facts, it is essentially the same as that of Dr Darwin; and along with the truth it contains, contains also the same error more distinctly pronounced. Merely noting that desires or wants, acting directly only on the nervo-muscular system, can have no immediate influence on very many organs, as the viscera, or such external appendages as hair and feathers; and observing, further, that even some parts which belong to the apparatus of external action, such as the bones of the skull, cannot be made to grow by increase of function called forth by desire; it will suffice to point out that the difficulty is not solved, but simply slurred-over, when needs or wants are introduced as independent causes of evolution. True though it is, as Dr Darwin and Lamarck contend, that desires, by leading to increased actions of motor organs, may induce further developments of such organs; and true as it probably is, that the modifications hence arising, are transmissible to offspring; yet there remains the unanswered question—Whence do these desires originate? The transferrence of the exciting power from the exterior to the interior, as described by Lamarck, begs the question. How comes there a wish to perform an action not before performed? Until some beneficial result has been felt from going through certain movements, what can suggest the execution of such movements? Every desire consists primarily of a mental representation of that which is desired, and secondarily excites a mental representation of the actions by which it is attained; and any such mental representations of the end and the means, imply antecedent experience of the end and antecedent use of the means. To assume that in the course of evolution there from time to time arose new kinds of actions dictated by new desires, is simply to remove the difficulty a step back.

§ 146. Changes of external conditions are named by Dr Darwin, as causes of modifications in organisms. Assigning, as evidence of original kinship, that marked similarity of type which exists among animals, he regards their deviations from one another, as caused by differences in their modes of life: such deviations being directly adaptive Enumerating various appliances for procuring food, he says they all "seem to have been gradually produced during many generations by the perpetual endeavour of the creatures to supply the want of food, and to have been delivered to their posterity with constant improvement of them for the purposes required." And the creatures possessing these various appliances, are considered as having been rendered unlike, by seeking for food in unlike ways. As illustrating the alterations wrought by changed circumstances, he names the acquired characters of domestic animals. Lamarck has elaborated the same view in detail: using for the purpose, with great ingenuity, his extensive knowledge of the animal kingdom. From a passage in the *Avertissement*, it would at first sight seem, that he looks upon direct adaptation to new conditions, as the chief cause of evolution. He says—"Je regardai comme certain que le *mouvement des fluides* dans l'intérieur des animaux, mouvement qui c'est progressivement accéléré avec la composition plus grande de l'organisation; et que l'*influence des circonstances* nouvelles, à mesure que les animaux s'y exposèrent en se répandant dans tous les lieux habitables, furent les deux causes générales qui ont amené les différens animaux à l'état où nous les voyons actuellement." But elsewhere, the view he expresses appears decidedly different from this. He asserts that "dans sa marche, la nature a commencé, et recommence encore tous les jours, par former les corps organisés les plus simples;" and that "les premières ébauches de l'animal et du végétal étant formées dans les lieux et les circonstances convenables, les facultés d'une vie commençante et d'un mouvement organique établi, ont nécessairement développé peu à peu les organes, et qu'avec le temps elles les ont diversifiés ainsi que les parties." And then, further on, he puts in italics this proposition:—"*La progression dans la composition de l'or-*

*ganisation subit, çà et là, dans la série générale des animaux, des anomalies opérées par l'influence des circonstances d'habitation, et par celle des habitudes contractées.*" These, and sundry other passages, joined with his general scheme of classification, make it clear that Lamarck conceived adaptive modification to be, not the cause of progression, but the cause of irregularities in progression. The inherent tendency which organisms have, to develop into more perfect forms, would, according to him, result in a uniform series of forms; but varieties in their conditions work divergences of structure, which break up the series into groups: groups which he nevertheless places in uni-serial order, and regards as still substantially composing an ascending succession.

§ 147. These speculations, crude as they may be considered, show much sagacity in their respective authors, and have done good service. Without embodying the truth in a definite shape, they contain adumbrations of it. Not directly, but by successive approximations, do mankind reach correct conclusions; and those who first think in the right direction, loose as may be their reasonings, and wide of the mark as their inferences may be, yield indispensable aid by framing provisional conceptions, and giving a bent to inquiry.

Contrasted with the dogmas of his age, the idea of De Maillet was a great advance. Before it can be ascertained how organized beings have been gradually evolved, there must be reached the conviction that they *have* been gradually evolved; and this conviction he reached. His wild notions as to the way in which natural agencies acted in the production of plants and animals, must not make us forget the merit of his intuition that animals and plants *were* produced by natural causes. In Dr Darwin's brief exposition, the belief in a progressive genesis of organisms, is joined with an interpretation having considerable definiteness and coherence. In the space of ten pages he not only indicates several of the leading classes of facts which support the hypothesis of evolution, but he does something towards elucidating the process of evolution. His reasonings show us an unconscious mingling of the belief in a supernaturally-impressed tendency to develop, with the belief in a development arising from the changing incidence of conditions. Probably had he pursued the inquiry further, this last belief would have grown at the expense of the first. Lamarck, in elaborating this general conception, has given greater precision to both its truth and its error. Asserting the same imaginary factors and the same real factors, he has traced out their supposed actions in detail; and has, in consequence, committed himself to a greater number of untenable positions. But while, in trying to reconcile the facts with a theory which is only an adumbration of the truth, he laid himself open to the criticisms of his contemporaries; he proved himself profounder than his contemporaries, by seeing that evolution, however caused, has been going on. If they were wise in not indorsing a theory which fails to account for a great part of the facts; they were unwise in ignoring that degree of congruity with the facts, which shows the theory to contain some fundamental verity.

Leaving out, however, the imaginary factors of evolution which these speculations allege, and looking only at the one actual factor which Dr Darwin and Lamarck assign as accounting for some of the phenomena; it is manifest from our present stand-point, that this, so far as it is a cause of evolution, is a proximate cause and not an ultimate cause. To say that functional adaptation to conditions, produces either evolution in general, or the irregularities of evolution, is to raise the further question—why is there a functional adaptation to conditions?—why do use and disuse generate appropriate changes of structure? Neither this nor any other interpretation of biologic evolution which rests simply on the basis of biologic induction, is an ultimate interpretation. The biologic induction must itself be interpreted. Only when the process of evolution of organisms, is affiliated on the process of evolution in general, can it be truly said to be explained. The thing required is to show that its various results are corollaries from first principles. We have to reconcile the facts with the universal laws of the re-distribution of matter and motion.

## CHAPTER IX.

### EXTERNAL FACTORS.

§ 148. WHEN illustrating the rhythm of motion (*First Principles*, § 94) it was pointed out that besides the daily and annual alternations in the quantities of light and heat which any portion of the Earth's surface receives from the Sun, there are alternations which require immensely-greater periods to complete. Reference was made to the fact, that "every planet, during a certain long period, presents more of its northern than of its southern hemisphere to the Sun at the time of its nearest approach to him; and then again, during a like period, presents more of its southern hemisphere than of its northern—a recurring co-incidence which, though causing in some planets no sensible alterations of climate, involves in the case of the Earth an epoch of 21,000 years, during which each hemisphere goes through a cycle of temperate seasons, and seasons that are extreme in their heat and cold." Further, it was pointed out that there is a variation of this variation. The slow rhythm of temperate and intemperate climates, which takes 21,000 years to complete, itself undergoes exaggeration and mitigation, during epochs that are far longer. The Earth's orbit slowly alters in form: now approximating to a circle; and now becoming more eccentric. During the period at which the Earth's orbit has least eccentricity, the temperate and intemperate climates which repeat their cycle in 21,000 years, are severally less temperate and less intemperate, than when, some one or two millions of years later, the Earth's orbit has reached its extreme of eccentricity.

Thus, besides those daily variations in the quantities of light and heat received by organisms, and responded to by variations in their functions; and besides the annual variations in the quantities of light and heat which organisms receive, and similarly respond to by variations in their functions; there are variations that severally complete themselves in 21,000 years and in some millions of years—variations to which there must also be a response in the changed functions of organisms. The whole vegetal and animal kingdoms, are subject to a quadruply-compounded rhythm in the incidence of the forces on which life primarily depends—a rhythm so involved in its slow working round, that at no time during one of these vast epochs, can the incidence of these forces be exactly the same as at any other time. To the direct effects so produced on organisms, have to be added much more important indirect effects. Changes of distribution must result. Certain redistributions are occasioned even by the annual variations in the quantities of the solar rays received by each part of the Earth's surface. The migrations of birds thus caused, are familiar. So too are the migrations of certain fishes: in some cases from one part of the sea to another; and in some cases from salt water to fresh water. Now just as the yearly changes in the amounts of light and heat falling on each locality, yearly extend and restrict the habitats of many organisms that are able to move about with some rapidity; so must these alternations of temperate and intemperate climates produce extensions and restrictions of habitats. These extensions and restrictions, though slow, will be universal—will affect the habitats of stationary organisms as well as those of locomotive ones. For if during an astronomic era, there is going on at any limit to a plant's habitat, a diminution of the winter's cold or summer's heat, which had before stopped its spread at that limit; then, though the individual plants are fixed, yet the species will move: the seeds of plants living at the limit, will produce individuals that survive beyond the limit. The gradual spread so effected, having gone on for some ten thousand years, the opposite change of climate will begin to cause retreat: the tide of each species will during the one half of a long epoch, slowly flow into new regions, and then will slowly ebb away from them. Further, this rise and fall in the tide of each species, will, during far longer intervals, undergo increasing rises and falls and then decreasing rises and falls. There will be an alternation of spring tides and neap tides, answering in its period to the changing eccentricity of the Earth's orbit.

These astronomical rhythms, therefore, entail on organisms unceasing changes in the incidence of forces in two ways. They directly subject them to variations of solar influences, in such a manner that each generation is somewhat differently affected in its functions; and they indirectly bring about complicated alterations in the environing agencies, by carrying each species into the presence of new physical conditions.

§ 149. The power of geological actions to modify everywhere the circumstances in which plants and animals are placed, is conspicuous. In each locality, denudation slowly uncovers different deposits; and slowly changes the exposed areas of deposits already uncovered. Simultaneously, the alluvial beds that are being formed, are qualitatively affected by these progressive changes in the natures and proportions of the strata denuded. The inclinations of surfaces and their directions with respect to the Sun, are at the same time altered; and the organisms existing on them are thus having their thermal conditions continually altered, as well as their drainage. Igneous action, too, complicates these gradual modifications. A flat region cannot be step by step thrust up into a protuberance, without unlike climatic changes being produced in its several parts, by their exposures to different aspects. Extrusions of trap, wherever they take place, revolutionize the localities; both over the areas covered, and over the areas on which their detritus is left. And where volcanoes are formed, the ashes they occasionally send out, modify the character of the soil throughout large surrounding tracts.

In like manner alterations in the Earth's crust, cause the ocean to be ever subjecting the organisms it contains to new combinations of conditions. Here the water is being deepened by subsidence, and there shallowed by upheaval. While the falling upon it of sediment brought down by neighbouring large rivers, is raising the sea-bottom in one place; in another, the habitual rush of the tide is carrying away the sediment previously deposited. The mineral character of the submerged surface on which sea-weeds grow and molluscs crawl, is everywhere occasionally changed: now by the bringing away from an adjacent shore some previously untouched strata; and now by the accumulation of organic remains, such as the shells of pteropods or of foraminifera. A further series of alterations in the circumstances of marine organisms, is entailed by changes in the movements of the water. Each modification in the outlines of neighbouring shores, makes the tidal streams vary their directions or velocities, or both. And the local temperature is from time to time raised or lowered, because some far-distant re-arrangement of the Earth's crust, has wrought a divergence in those circulating currents of warm and cold water which pervade the ocean.

These geologically-caused changes in the physical characters of each environment. occur in ever-new combinations, and with ever-increasing complexity. As already shown (*First Principles*, § 118), it follows from the law of the multiplication of effects, that during long periods, each tract of the Earth's surface increases in heterogeneity of both form and substance. Hence plants and animals of all kinds, are, in the course of generations, subject by these alterations in the crust of the

Earth, to sets of incident forces which differ from previous sets, both by changes in the proportions of the factors, and, occasionally, by the addition of new factors.

§ 150. Variations in the astronomical conditions joined with variations in the geological conditions, bring about variations in the meteorological conditions. Those extremely slow alternations of elevation and subsidence, which there is reason to believe take place over immense areas, here producing a continent where once there was a fathomless ocean, and there causing wide seas to spread where in a long past epoch there stood snow-capped mountains, gradually work great atmospheric changes. While yet the highest parts of an emerging surface of the Earth's crust, exist as a cluster of islands, the plants and animals which in course of time migrate to them, have climates that are peculiar to small tracts of land surrounded by large tracts of water. As, by successive upheavals, greater areas are exposed, there begin to arise sensible contrasts between the states of their peripheral parts and their central parts: the sea and land breezes, which daily moderate the extremes of temperature near the shores, cease to affect the interiors; and the interiors, less qualified too in their heat and cold by such ocean-currents as bathe the shores, acquire more decidedly the characters due to their latitudes. Along with the further elevations which unite the members of the archipelago into a continent, there come new meteorologic changes, as well as exacerbations of the old. The winds, which were comparatively uniform in their directions and periods when only islands existed, grow involved in their distribution, and widely-different in different parts of the continent. The quantities of rain which they discharge and of moisture which they absorb, vary everywhere according to the proximity to the sea and to surfaces of land having special characters.

Other complications result from variations of height above the sea: elevation producing a decrease of heat and consequently an increase in the precipitation of water—a precipitation that takes the shape of snow where the elevation is very great, and of rain where it is not so great. The gathering of clouds and descent of showers around mountain tops, are familiar to every tourist. Inquiries in the neighbouring valleys, prove that within distances of a mile or two the recurring storms differ in their frequency and violence. Nay, even a few yards off, the meteorologic conditions vary in such regions: as witness the way in which the condensing vapour keeps eddying round on one side of some high crag, while the other side is clear; or the way in which the snow-line runs irregularly to many different heights, in all the minor valleys and ravines and hollows of each mountain side.

Climatic variations that are thus geologically produced, being compounded with those which result from the slow astronomical changes; and no correspondence existing between the geologic and the astronomic rhythms; it results that the same plexus of actions never recurs. Hence the incident forces to which the organisms of every locality are exposed by atmospheric agencies, are ever passing into unparalleled combinations; and these are on the average ever becoming more complex.

§ 151. Besides changes in the incidence of inorganic forces, there are equally continuous, and still more involved, changes in the incidence of forces which organisms exercise on one another. As before pointed out (§ 105), the plants and animals inhabiting each locality, are held together in so entangled a web of relations, that any considerable modification which one species undergoes, acts indirectly on many other species; and eventually changes, in some degree, the circumstances of nearly all the rest. If an increase of heat, or modification of soil, or decrease of humidity, causes a particular kind of plant either to thrive or to dwindle; an unfavourable or favourable effect is wrought on all such competing kinds of plants, as are not immediately influenced in the same way. The animals which eat the seeds or browse on the leaves either of the plant primarily affected or those of its competitors, are severally altered in their states of nutrition and in their numbers; and this change presently tells on various predatory animals and parasites. And since each of these secondary and tertiary changes, becomes itself a centre of others; the increase or decrease of each species, produces waves of influence which spread and reverberate and re-reverberate, throughout the whole Flora and Fauna of the locality.

More marked and multiplied still, are the ultimate effects of those causes which make possible the colonization of neighbouring areas. Each intruding plant or animal, besides the new inorganic conditions to which it is subject, is subject to organic conditions considerably different from those to which it has been habituated. It has to compete with some organisms unlike those of its preceding habitat. It must preserve itself from enemies not before encountered. Or it may meet with a species over which it has some advantage greater than any that it had over the species it was previously in contact with. Even where migration does not bring it face to face with new competitors or new enemies or new prey, it inevitably experiences new proportions among these. Further, an expanding species is almost certain to invade more than one adjacent region. Spreading north or south, it will come among the plants and animals, here of a level district and there of a hilly one—here of an inland tract, and there of a tract bordered by the sea. And while different groups of its members will thus expose themselves to the actions and re-actions of different Floras and Faunas, these different Floras and Faunas will simultaneously have their organic conditions changed by the intruders.

This process becomes gradually more active and more complicated. Though in particular cases, a plant or animal may fall into simpler relations with the living things around, than those it was before placed in; yet it is manifest that, on the average, the organic environments of organisms have been increasing in heterogeneity. As the number of species with which each species is directly or indirectly implicated, multiplies, each species is oftener subject to changes in the organic actions which influence it. These more frequent changes severally grow more involved. And the corresponding reactions affect larger Floras and Faunas, in ways increasingly complex and varied.

§ 152. When the astronomic, geologic, meteorologic, and organic agencies that are at work on each species of organism, are contemplated as becoming severally more complicated in themselves, and at the same time as co-operating in ways that are always more or less new; it will be seen that throughout all time, there has been an exposure of organisms to endless successions of modifying causes which gradually acquire an intricacy that is scarcely conceivable. Every kind of plant and animal may be regarded as for ever passing into a new environment—as perpetually having its relations to external circumstances altered, either by their changes with respect to it when it remains stationary, or by its changes with respect to them when it migrates, or by both.

Yet a further cause of progressive alteration and complication in the incident forces, exists. All other things continuing the same, every additional faculty by which an organism is brought into relation with external objects, as well as every improvement in such faculty, becomes a means of subjecting the organism to a greater number and variety of external stimuli, and to new combinations of external stimuli. So that each advance in complexity of organization, itself becomes an added source of complexity in the incidence of external forces.

Once more, every increase in the locomotive powers of animals, increases both the multiplicity and the multiformity of the actions of things upon them, and of their reactions upon things. Doubling a creature's activity, quadruples the area that comes within the range of its excursions: thus augmenting in number and heterogeneity, the external agencies which act on it during any given interval.

By compounding the actions of these several orders of factors, there is produced a geometric progression of changes, increasing with immense rapidity. And there goes on an equally rapid increase in the frequency with which the combinations of the actions are altered, and the intricacies of their co-operations enhanced.

# CHAPTER X.

## INTERNAL FACTORS.

§ 153. We saw at the outset (§§ 10—16), that organic matter is built up of molecules so extremely unstable, that the slightest variation in their conditions destroys their equilibrium; and causes them either to assume altered structures or to decompose. But a substance which is beyond all others changeable by the actions and reactions of the forces liberated from instant to instant within its own mass, must be a substance that is beyond all others changeable by the forces acting on it from without. If their composition fits organic aggregates for undergoing with special facility and rapidity those re-distributions of matter and motion whence result individual organization and life; then their composition must make them similarly apt to undergo those permanent re-distributions of matter and motion which are expressed by changes of structure, in correspondence with permanent re-distributions of matter and motion in their environments.

Already in *First Principles,* when considering the phenomena of Evolution in general, the leading characters and causes of those changes which constitute organic evolution, were briefly traced. Under each of the derivative laws of force to which the passage from an incoherent, indefinite homogeneity to a coherent, definite heterogeneity, conforms, were given illustrations drawn from the metamorphoses of living bodies. Here it will be needful to contemplate the several resulting processes as going on at once, in both individuals and species.

§ 154. Our postulate being that organic evolution in general commenced with homogeneous organic matter, just as the evolution of individual organisms commences, we have first to remember that the state of homogeneity is an unstable state (*First Principles*, § 109). In any aggregate "the relations of outside and inside, and of comparative nearness to neighbouring sources of influence, imply the reception of influences that are unlike in quantity or quality, or both; and it follows that unlike changes will be produced in the parts thus dissimilarly acted upon." Further, "if any given whole, instead of being absolutely uniform throughout, consists of parts distinguishable from each other—if each of these parts, while somewhat unlike other parts, is uniform within itself; then, each of them being in unstable equilibrium, it follows that while the changes set up within it must render it multiform, they must at the same time render the whole more multiform than before;" and hence, "whether that state with which we commence be or be not one of perfect homogeneity, the process must equally be towards a relative heterogeneity." This loss of homogeneity which the special instability of organic aggregates fits them to display more promptly and variously than any other aggregates, must be shown in more numerous ways in proportion as the incident forces are more numerous. Every differentiation of structure being a result of some difference in the relations of the parts to the agencies acting on them, it follows that the more multiplied and more unlike the agencies, the more varied must be the differentiations wrought. Hence the gravitation from a state of homogeneity to a state of heterogeneity, will be conspicuously shown in proportion as the environment is complex. This transition from a uniform to a multiform state, must continue through successive individuals. Given a series of organisms, each of which is developed from a portion of a preceding organism, and the question is, whether, after exposure of the series for a million years to changed incident forces, one of its members will be the same as though the incident forces had only just changed. To say that it will, is implicitly to deny the persistence of force. In relation to any cause of divergence, the whole series of such organisms may be considered as fused together into a continuously-existing organism; and when so considered, it becomes manifest that a continuously-acting cause will go on working a continuously-increasing effect, until some counteracting cause prevents any further effect.

But now if any primordial organic aggregate, must, in itself and through its descendants, gravitate from uniformity to multiformity, in obedience to the more or less multiform forces acting on it; what must happen if these multiform forces are themselves ever undergoing slow variations and complications? Clearly the process, ever-advancing towards a temporary limit but ever having its limit removed, must go on unceasingly. On those structural changes wrought in the once homogeneous aggregate by an original set of incident forces, will be superposed further changes wrought by a modified set of incident forces; and so on throughout all time. Omitting for the present those circumstances which check and qualify its consequences, the instability of the homogeneous must be recognized an ever-acting cause of organic evolution, as of all other evolution.

While it follows that every organism, considered as an individual and as one of a series, tends thus to pass into a more heterogeneous state; it also follows that every species, considered as an aggregate of individuals, tends to do the like. Throughout the area it inhabits, the conditions can never be absolutely uniform: its members must, in different parts of its area, be exposed to different sets of incident forces. Still more decided must this difference of exposure be when its members spread into other habitats. Those expansive and repressive energies which set to each species a limit that perpetually oscillates from side to side of a certain mean, are, as we lately saw, frequently changed by new combinations of the external factors—astronomic, geologic, meteorologic, and organic. Hence there from time to time arise lines of diminished resistance, along which the species flows into new localities. Such portions of the species as thus migrate, are subject to circumstances markedly contrasted with its average circumstances. And from multiformity of the circumstances, must come multiformity of the species.

Thus the law of the instability of the homogeneous, has here a three-fold corollary. As interpreted in connexion with the ever-progressing, ever-complicating changes in external factors, it brings us to the conclusion that there must be a prevailing tendency towards greater heterogeneity in all kinds of organisms, considered both individually and in successive generations; as well as in each assemblage of organisms constituting a species; and, by consequence, in each genus, order, and class.

§ 155. When considering the causes of evolution in general, we further saw (*First Principles*, § 116), that the multiplication of effects aids continually to increase that heterogeneity into which homogeneity inevitably lapses. It was pointed out that since "the several parts of an aggregate are differently modified by any incident force;" and that since "by the reactions of the differently modified parts the incident force itself must be divided into differently modified parts;" it follows that "each differentiated division of the aggregate thus becomes a centre from which a differentiated division of the original force is again diffused. And since unlike forces must produce unlike results, each of these differentiated forces must produce, throughout the aggregate, a further series of differentiations." And to this it was added, that in proportion as the heterogeneity increases, the complications arising from this multiplication of effects grow more marked; since the more strongly contrasted the parts of an aggregate become, the more different must be their reactions upon incident forces, and the more unlike must be the secondary sets of effects which these modified incident forces initiate; and since every increase in the number of unlike parts increases the number of such differentiated incident forces, and such secondary sets of effects.

How this multiplication of effects conspires with the instability of the homogeneous, to work an increasing multiformity of structure in an organism, was shown at the time; and the foregoing pages contain further incidental illustrations. Under the head of Adaptation (§ 69), it was shown that a change in one function must act and re-act through ever-complicating perturbations on the rest; and that, eventually, all parts of the organism must be modified in their states. Suppose that the head of a mammal becomes very much more weighty—what must be the indirect results? The muscles of the neck are put to greater exertions; and its vertebræ have to bear additional tensions and pressures, caused both by the increased weight of the head, and the stronger contractions of the muscles that support and move the head. These muscles also affect their own attachments: several of the dorsal spines have augmented strains put on them; and the vertebræ to which they are fixed, are more severely taxed. Further, this heavier head and the more massive neck it necessitates, require a stronger fulcrum: the whole thoracic arch, and the fore limbs which support it, are subject to greater continuous stress and more violent occasional shocks. And the required strengthening of the fore-quarters cannot take place, without the centre of gravity being changed, and the hind limbs being differently reacted upon during locomotion. Any one who compares the outline of the bison with that of its congener, the ox, will clearly see how profoundly a heavier head affects the entire osseous and muscular systems. Besides this multiplication of mechanical effects, there is a multiplication of physiological effects. The vascular apparatus is modified throughout its whole structure, by each considerable modification in the proportions of the body. Increase in the size of any organ, implies a quantitative, and often a qualitative, reaction on the blood; and so alters the nutrition of all other organs. Such physiological correlations are exemplified in the many differences that accompany difference of sex. That the minor sexual peculiarities are brought about by the physiological actions and reactions, is shown both by the fact that they are commonly but faintly marked until the fundamentally distinctive organs are developed; and that when the development of these is prevented, the minor sexual peculiarities do not arise. No further proof is, I think, needed, that in any individual organism or its descendants, a new external action must, besides the primary internal change which it works, work sundry secondary changes, as well as tertiary changes still more multiplied. That tendency towards greater heterogeneity which is given to an organism by disturbing its environment, is helped by the tendency which every modification has to produce other modifications —modifications which must become more numerous in proportion as the organism becomes more complex. And then, lastly, among the indirect and involved manifestations of this tendency, we must not omit the innumerable small irregularities of structure that result from the crossing of dissimilarly-modified individuals. It was shown (§§ 89, 90) that what are called "spontaneous variations," are interpretable as results of miscellaneously compounding the changes wrought in different lines of ancestors by different conditions of life. These still more complex and multitudinous effects so produced, are thus further illustrations of the multiplication of effects.

Equally in the aggregate of individuals constituting a species, does multiplication of effects become the continual cause of increasing multiformity. The lapse of a species into divergent varieties, initiates fresh combinations of forces tending to work further divergences. The new varieties compete with the parent species in new ways; and so add new elements to its circumstances. They modify somewhat the conditions of other species existing in their habitat, or into whose habitat they have spread; and the modifications wrought in such other species, become additional sources of influence. The Flora and Fauna of every region are united by their entangled relations into a whole, of which no part can be affected without affecting the rest. Hence, each differentiation in a local assemblage of species, becomes the cause of further differentiations in such assemblage.

§ 156. One of the universal principles to which we saw that the re-distribution of matter and motion conforms, is that in any aggregate made up of mixed units, incident forces produce segregation—separate unlike units and unite like units; and it was shown that the increasing integration and definiteness which characterizes each part of an evolving organic aggregate, as of every other aggregate, results from this (*First Principles*, § 126). It remains here to be pointed out, that while the actions and reactions going on between organisms and their ever-changing environments, add to the heterogeneity of organic structures, they also give to the heterogeneity this growing distinctness. At first sight the reverse might be inferred. It might be argued that any new set of effects wrought in an organism by some new set of external forces, must tend more or less to obliterate the effects previously wrought—must produce confusion or indefiniteness. A little consideration, however, will dissipate this impression.

Doubtless the condition under which alone increasing definiteness of structure can be acquired by any part of an organism, either in an individual or in successive generations, is that such part shall be exposed to some set of tolerably-constant forces; and doubtless, continual change of circumstances interferes with this. But the interference can never be considerable. For the pre-existing structure of an organism prevents it from living under any new conditions except such as are congruous with the fundamental characters of its organization—such as subject its essential organs to actions substantially the same as before. Great changes must kill it. Hence, it can continuously expose itself and its descendants, only to those moderate changes which do not destroy the general harmony between the aggregate of incident forces and the aggregate of its functions. That is, it must remain under influences calculated to make greater the definiteness of the chief differentiations already produced. If, for example, we set out with an animal in which a rudimentary vertebral column with its attached muscular system has been established; it is clear that the mechanical arrangements have become thereby so far determined, that subsequent modifications are extremely likely, if not certain, to be consistent with the production of movement by the action of muscles on a flexible central axis. Hence, there will continue a general similarity in the play of forces to which the flexible central axis is subject; and so, notwithstanding the metamorphoses which the vertebrate type undergoes, there will be a maintenance of conditions favourable to increasing definiteness and integration of the vertebral column. Moreover, this maintenance of such conditions becomes secure in proportion as organization advances. Each further complexity of structure, implying some further complexity in the relations between an organism and its environment, must tend to specialize the actions and reactions between it and its environment—must tend to increase the stringency with which it is restrained within such environments as admit of those special actions and reactions for which its structure fits it; that is, must further guarantee the continuance of those actions and reactions to which its essential organs respond, and therefore the continuance of the segregating process.

How in each species, considered as an aggregate of individuals, there must arise stronger and stronger contrasts between those divergent varieties which result from the instability of the homogeneous and the multiplication of effects, needs only be briefly indicated. It has already been shown (*First Principles*, § 126), that in conformity to the universal law that mixed units are segregated by like incident forces, there are produced increasingly-definite distinctions among varieties, wherever there occur definitely-distinguished sets of conditions to which the varieties are respectively subject.

§ 157. Probably in the minds of some, the reading of this chapter has been accompanied by a running commentary, to the effect that the argument proves too much. The apparent implication is, that the passage from an indefinite, incoherent homogeneity to a definite, coherent heterogeneity in organic aggregates, must have been going on universally; whereas we find that in many cases there has been persistence without progression. This apparent implication, however, is not a real one.

For though every environment on the Earth's surface undergoes changes; and though usually the organisms which each environment contains, cannot escape certain resulting new influences; yet occasionally such new influences are escaped, by the survival of species in the unchanged parts of their habitats, or by their spread into neighbouring habitats which the change has rendered like their original habitats, or by both. Any alteration in the temperature of a climate or its degree of humidity, is unlikely to affect simultaneously the whole area occupied by a species; and further, it can scarcely fail to happen that the addition or subtraction of heat or moisture, will give to a part of some adjacent area, a climate like to that to which the species has been habituated. If, again, the circumstances of a species are modified by the intrusion of some foreign kind of plant or animal, it follows that since the intruders will probably not spread throughout its whole habitat, the species will, in one or more localities, remain unaffected by them. Especially among marine creatures, must there frequently occur cases in which modifying causes are continually eluded. Much more uniform as are the physical conditions to which the sea exposes its inhabitants, it becomes possible for such of them as live on widely-diffused food, to be widely distributed; and wide distribution generally prevents the members of a species from being all subject to the same cause. Our commonest cirrhiped, for instance, subsisting on minute creatures that are everywhere dispersed through the sea; needing only to have some firm surface on which to build up its shell; and in scarcely any danger from surrounding animals; is able to exist on shores so widely remote from one another, that nearly every change in the actions of incident forces, must fall within narrower areas than that which the species occupies. In nearly every case, therefore, a portion of the species will survive unmodified. Its easily-transported germs will take possession of such new habitats as have been rendered fitter by the change that has unfitted some parts of its original habitat. Hence, on successive occasions, while some parts of the species are slightly transformed, another part may continually escape transformation by migrating hither and thither, where the simple conditions needed for its existence recur in nearly the same combinations as before. And it will so become possible for it to survive, with comparatively trifling structural changes, throughout long geologic periods.

§ 158. The results to which we find ourselves led, are these.

In subordination to the different amounts and kinds of forces to which its different parts are exposed, every individual organic aggregate, like all other aggregates, tends to pass from its original indistinct simplicity towards a more distinct complexity. Unless we deny the persistence of force, we must admit that the gravitation of an organism's structure from an indefinitely homogeneous to a definitely heterogeneous state, must be cumulative in successive generations, if the forces causing it continue to act. And for the like reasons, the increasing assemblage of individuals arising from a common stock, is also liable to lose its original uniformity; and, in successive generations, to grow more pronounced in its multiformity.

These changes, which would go on to but a comparatively small extent were organisms exposed to constant external conditions, are kept up by the continual changes in external conditions, produced by astronomic, geologic, meteorologic, and organic agencies: the average result being, that on previous complications of structure wrought by previous incident forces, new complications are continually superposed by new incident forces. And hence simultaneously arises increasing heterogeneity in the structures of individuals, in the structures of species, and in the structures of the Earth's Flora and Fauna.

But while, in very many or in most cases, the ever-changing incidence of forces is ever adding to the complexity of organisms, and to the complexity of the organic world as a whole; it does this only where its action cannot be eluded. And since, by migration, it is possible for species to keep themselves under conditions that are tolerably constant; there must be a proportion of cases in which greater heterogeneity of structure is not produced.

Uniting these three propositions, we are brought to a conclusion which, so far as it goes, appears to be in harmony with the facts. We find progression to result, not from a special, inherent tendency of living bodies, but from a general average effect of their relations to surrounding agencies. While we are not called on to suppose that there exists in organisms any primordial impulse which makes them continually unfold into more heterogeneous forms; we see that a liability to be unfolded arises from the actions and reactions between organisms and their fluctuating environments. And we see that the existence of such a cause of development, presupposes the non-occurrence of development where this fluctuation of actions and reactions does not come into play.

To show, however, that there must arise a certain general tendency to the production of more heterogeneous aggregates, is not sufficient. It is quite conceivable that aggregates should be rendered more heterogeneous by changing incident forces, without having given to them that peculiar form of heterogeneity required for carrying on the functions of life. Hence it remains now to inquire, how the production and maintenance of this peculiar form of heterogeneity is insured.

# CHAPTER XI.

## DIRECT EQUILIBRATION.

§ 159. Every change is of necessity towards a balance of forces; and of necessity can never cease until a balance of forces is reached. When treating of equilibration under its general aspects (*First Principles,* Part II., Chap. xvi.), we saw that in every aggregate having compound movements, there tends continually to be established a moving equilibrium; since any unequilibrated force to which such an aggregate is subject, if not of a kind to overthrow the aggregate altogether, must continue modifying its state until an equilibrium is brought about. And we saw that the structure simultaneously reached must be "one presenting an arrangement of forces that counterbalance all the forces to which the aggregate is subject;" since, "so long as there remains a residual force in any direction—be it excess of a force exercised by the aggregate on its environment, or of a force exercised by its environment on the aggregate, equilibrium does not exist; and therefore the re-distribution of matter must continue."

It is essential that this truth should here be fully understood; and to the end of insuring a clear comprehension of it, some re-illustration is desirable. The case of the Solar System will best serve our purpose. An assemblage of bodies, each of which has its simple and compound motions, that severally alternate between two extremes, and the whole of which has its involved perturbations, that now increase and now decrease, is here presented to us. Suppose a new force were brought to bear on this moving equilibrium—say by the arrival of some wandering mass, or by an additional momentum given to one of the existing masses—what would be the result? If the strange body or the extra force were very large, it might so derange the entire system as to cause its collapse: by overthrow of its rhythmical movements, the moving equilibrium might rapidly be changed into a complete equilibrium. But what if the incident force, falling on the system from without, proved insufficient to overthrow it? There would then arise a set of perturbations which would, in the course of an enormous period, slowly work round into a modified moving equilibrium. The effects primarily impressed on the adjacent masses, and in a smaller degree on the remoter masses, would soon become complicated with the secondary effects impressed by the disturbed masses on one another; and these again with tertiary effects. Waves of perturbation would continue to be propagated throughout the entire system; until, around a new centre of gravity, there had been established a set of planetary motions more or less different from the preceding ones. All this would necessarily follow from the truth, that any new force brought to bear on a moving equilibrium, must gradually be used up in overcoming the forces that resist the divergence it generates: which antagonizing forces, being then no longer opposed, set up a counter-action, ending in a compensating divergence in the opposite direction, that is followed by a re-compensating divergence; and so on, until there is either established some additional rhythmical movement, or some equivalent modification of the pre-existing rhythmical movements. Now though instead of being, like the Solar System, in a state of *independent* moving equilibrium, an organism is in a state of *dependent* moving equilibrium (*First Principles*, § 130); yet this does not prevent the manifestation of the same law. Every animal daily obtains from without, a supply of force to replace the force which it expends; but this continual giving to its parts a new momentum, to make up for the momentum continually lost, does not interfere with the carrying on of actions and reactions like those just described. Here, as before, we have a definitely-arranged aggregate of parts, which we call organs, having their definitely-established actions and reactions, which we call functions. These rhythmical actions or functions, and the various compound rhythms resulting from their combinations, are in such adjustment as to balance the actions to which the organism is subject: there is a constant or periodic genesis of forces, which, in their kinds, amounts, and directions, suffice to antagonize the forces which the organism has constantly or periodically to bear. If then there exists this state of moving equilibrium among a definite set of internal actions, exposed to a definite set of external actions; what must result if any of the external actions are changed? Of course there is no longer an equilibrium. Some force which the organism habitually generates, is too great or too small to balance some incident force; and there arises a residuary force exerted by the environment on the organism, or by the organism on the environment. This residuary force—this unbalanced force, of necessity expends itself in producing some change of state in the organism. Acting directly on some organ and modifying its function, it indirectly modifies dependent functions, and remotely influences all the functions. As we have already seen (§§ 68, 69), if this new force is permanent, its effects must be gradually diffused throughout the entire system; until it has come to be equilibrated in working those structural rearrangements which produce an exactly counterbalancing force.

The bearing of this general truth on the question we are now dealing with, is obvious. Those modifications upon modifications, which the unceasing mutations of their environments have been all along generating in organisms, have been in each case modifications involved by the establishment of a new balance with the new combination of conditions. In every species throughout all geologic time, there has been perpetually going on a rectification of the equilibrium, that has been perpetually disturbed by the alteration of surrounding circumstances; and every further heterogeneity has been the addition of a structural change entailed by a new equilibration, to the structural changes entailed by previous equilibrations. There can be no other ultimate interpretation of the matter, since change can have no other goal. Any fresh force brought to bear on an aggregate in a state of moving equilibrium, must do one of two things: it must either overthrow the moving equilibrium altogether, or it must alter without overthrowing it; and the alteration must end in the establishment of a new moving equilibrium. Hence in organisms, death or restoration of the physiological balance, are the only alternatives.

This equilibration between the functions of an organism and the actions in its environment, may be either direct or indirect. The new incident force may either immediately call forth some counteracting force, and its concomitant structural change; or it may be eventually balanced by some otherwise-produced change of function and structure. These two processes of equilibration are quite distinct, and must be separately dealt with. We will devote this chapter to the first of them.

§ 160. Direct equilibration is that process currently known as *adaptation*. We have already seen (Part II., Chap. v.), that individual organisms become modified when placed in new conditions of life—so modified as to re-adjust the powers to the requirements; and though there is great difficulty in disentangling the evidence, we found reason for thinking (§ 82) that structural changes thus caused by functional changes are inherited. In the last chapter, it was argued that if, instead of the succession of individuals constituting a species, there were a continuously-existing individual, any such functional and structural divergence as we see produced by a new incident force, would necessarily go on increasing until the new incident force was counterpoised; and that the replacing of a continuously-existing individual by a succession of individuals, each formed out of the modified substance of its predecessor, will not prevent the like effect from being produced—the persistence of force negativing any other inference. Here we further find, that this limit towards which any such organic change advances, in the species as in the individual, is a new moving equilibrium adjusted to the new arrangement of external forces.

But now, what are the conditions under which alone, direct equilibration can occur? Are all the modifications that serve to re-fit organisms to their environments, directly adaptive modifications? And if otherwise, which are the directly adaptive and which are not? How are we to distinguish between them?

Manifestly, for any moving equilibrium to be gradually altered, it is needful, first, that some force shall operate upon it; and, second, that the force shall not be such as to overthrow it. If in the environment there exists some agency that would act advantageously on an organism were the organism a little modified, but which does not act on it in the absence of the required modification; it is clear that this agency cannot itself tend to produce the modification. On the other hand, if the external agency be of such kind, that individuals of the species whenever affected by it, are either killed or so injured that the production of vigorous offspring is much interfered with, there cannot be directly wrought in the species, any such alteration as will fit it to cope with this external agency. The only new incident forces which can work the changes of function and structure required to bring any animal or plant into equilibrium with them, are such incident forces as operate on this animal or plant, either continuously or frequently. They must be capable of appreciably changing that set of complex rhythmical actions and reactions constituting the life of the organism; and yet must not usually produce perturbations that are fatal. Let us see what are the limits to direct equilibration hence arising.

§ 161. In plants, organs engaged in nutrition, and exposed to variations in the amounts and proportions of matters and forces utilized in nutrition, may be expected to undergo corresponding variations. We find evidence that they do this. The "changes of habit" which are common in plants, when taken to places unlike in climate or soil to those before inhabited by them, are changes of parts in which the modified external actions directly produce modified internal actions. The characters of the stem and shoots as woody or succulent, erect or procumbent; of the leaves in respect of their sizes, thicknesses, and textures; of the roots in their degrees of development and modes of growth; are obviously in immediate relation to the characters of the environment. A permanent difference in the quantity of light or heat, affects, day after day, the processes going on in the leaves. Habitual rain or drought, alters all the assimilative actions, and appreciably influences the organs that carry them on. Some particular substance, by its presence in the soil, gives new qualities to some of the tissues; causing greater rigidity or flexibility, and so affecting the general aspect. Here, then, we have, in plants, changes tending to bring about in them, modified arrangements of functions and structures, in equilibrium with modified sets of external forces.

But now let us turn to other classes of organs possessed by plants—organs which are not at once affected in their actions by the variations of incident forces. Take first the organs of defence. Many plants are shielded against animals that would else devour them, by formidable thorns; and others, like the nettle, by stinging hairs. These must be counted among the appliances by which equilibrium is maintained between the actions in the organism and the actions in its environment; seeing that all other things remaining the same, if these defences were absent, the destruction by herbivorous animals would be so increased, that the number of young plants annually produced would not suffice, as it now does, to balance the mortality, and the species would therefore disappear. But these defensive appliances, though they aid in maintaining the balance between inner and outer actions, cannot have been directly called forth by the outer actions which they serve to neutralize; for these outer actions do not continuously affect the functions of the plant even in a general way, still less in the special way required. Suppose a species of nettle bare of poison-hairs, to be habitually eaten by some mammal intruding on its habitat; the agency of this mammal would have no direct tendency to develop poison-hairs in the plant; since the individuals devoured could not bequeath changes of structure, even were the actions of a kind to produce them; and since the individuals that perpetuated themselves, would be those on which the new incident force had not fallen. Another class of organs similarly circumstanced, are those of reproduction. Like the organs of defence, these are not, during the life of the individual plant, variably exercised by variable external actions; and therefore do not fulfil those conditions under which structural changes may be directly caused by changes in the environment. The generative apparatus contained in every flower, acts only once during its existence; and even then, the parts subserve their ends in a passive rather than an active way. Functionally-produced modifications are therefore out of the question. If a plant's anthers are so placed, that the insect which most commonly frequents its flowers, is sure to come in contact with the pollen, and to fertilize with it other flowers of the same species; and if this insect, dwindling away or disappearing from the locality, leaves behind no insects that have such shapes and habits as cause them to do the same thing efficiently, but only some which do it inefficiently; it is clear that the change of its conditions, has no immediate tendency to work in the plant any such structural change as shall bring about a new balance with its conditions. For the anthers, which, even when they discharge their functions, do it simply by standing in the way of the insect, are, under the supposed circumstances, left untouched by the insect; and this remaining untouched, cannot have the effect of so modifying the stamens as to bring the anthers into a position to be touched by some other insect. Only those individuals whose parts of fructification so far differed from the average form of the species, that some other insect could serve them as pollen-carrier, would be sufficiently prolific to have good chances of perpetuating themselves. And on their progeny, inheriting the deviation, there would act no external force directly calculated to make the deviation greater, and the adaptation more complete; since the new circumstances to which re-adaptation is required, are such as do not in the least alter the equilibrium of functions constituting the life of the individual plant.

§ 162. Among animals, adaptation by direct equilibration is similarly traceable, wherever, during the life of the individual, an external change generates some constant or repeated change of function. This is conspicuously the case with such parts of an animal as are immediately exposed to diffused influences, like those of climate, and with such parts of an animal as are occupied in its mechanical actions on the environment. Of the one class of cases, the darkening or lightening of the skin, that follows exposure to greater or less heat, may be taken as an instance; and with the other class of cases, we are made familiar by the increase and decrease which use and disuse cause in the organs of motion and manipulation. It is needless here to exemplify these: they were treated of in the Second Part of this work.

But in animals, as in plants, there are many indispensable offices fulfilled by parts, between which and the external conditions they respond to, there is no such action and reaction as can directly produce an equilibrium. This is especially manifest with dermal appendages. Some ground, perhaps, exists for the conclusion that the greater or less development of hairs, is in part immediately due to increase or decrease of demand on their passive function, as non-conductors of heat; but be this as it may, it is impossible that there can exist any such cause for those immense developments of hairs which we see in the quills of the porcupine, or those complex developments of them known as feathers. Such an enamelled armour as is worn by the *Lepidosteus*, is inexplicable as a direct result of any functionally-worked change. For purposes of defence, such an armour is as needful, or more needful, for hosts of other fishes; and did it result from any direct reaction of the organism against any offensive actions it was subject to, there seems no reason why other fishes should not have developed similar protective coverings. Of sundry reproductive appliances, the like may be said. The secretion of an egg-shell round the substance of an egg, in the oviduct of a bird, is quite inexplicable as a consequence of some functionally-wrought modification of structure, immediately caused by some modification of external conditions. The end fulfilled by the egg-shell, is that of protecting the contained mass against certain slight pressures and collisions, to which it is liable during incubation. How, by any process of direct equilibration, could it come to have the required thickness? or, indeed, how could it come to exist at all? Suppose this protective envelope to be too weak, so that some of the eggs a bird lays are broken or cracked. In the first place, the breakages or crackings are actions of a kind which cannot react on the maternal organism, in such way as to cause the secretion of thicker shells for the future: to suppose that they can, is to suppose that the bird understands the cause of the evil, and that the secretion of thicker or thinner shells can be controlled by its will. In the second place, such developing chicks as are contained in the shells which crack or break, are almost certain to die; and cannot, therefore, acquire any appropriately-modified constitutions: even supposing any conceivable relation could be shown, between the impression received and the change required. Meanwhile, such eggs as escape breakage, are not influenced at all by the requirement; and hence, on the birds developed from them, there cannot have acted any force tending to work the needful adjustment of functions. In no way, therefore, can a direct equilibration between constitution and conditions be here produced. Even in organs that can be modified by certain incident forces into correspondence with such incident forces, there are some re-adjustments which cannot be effected by the direct balancing of inner and outer actions. It is thus with the bones. The majority of the bones have to resist muscular strains; and it is a familiar fact that variations in the muscular strains, call forth, by reaction, variations in the strengths of the bones. Here there is direct equilibration. But though the greater massiveness acquired by bones subject to greater strains, may be ascribed to a counter-acting force evoked by a force brought into action; it is impossible that the acquirement of greater lengths by bones can be thus accounted for. It has been supposed that the elongation of the metatarsals in wading birds, has resulted from direct adaptation to conditions of life. To justify this supposition, however, it must be shown that the mechanical actions and reactions in the legs of a wading bird, differ from those in the legs of other birds; and that the differential actions are equilibrated by the extra lengths. There is not the slightest evidence of this. The metatarsals of a bird, have to bear no appreciable strains but those due to the superincumbent weight. Standing in the water does not appreciably alter these strains; and even if it did, an increase in the lengths of these bones would not fit them any better to meet the altered strains.

§ 163. The conclusion at which we arrive is, then, that there go on in all organisms, certain changes of function and structure that are directly consequent on changes in the incident forces—inner changes by which the outer changes are balanced, and the equilibrium restored. Such re-equilibrations, which are often conspicuously exhibited in individuals, we have reason to believe continue in successive generations; until they are completed by the arrival at structures fitted to the modified conditions. But, at the same time, we see that the modified conditions to which organisms may be adapted by direct equilibration, are conditions of certain classes only. That a new external action may be met by a new internal action, it is needful that it shall either continuously or frequently be borne by the individuals of the species, without killing or seriously injuring them; and shall act in such way as to affect their functions. And we find on examination, that many of the environing changes to which organisms have to be adjusted, are not of these kinds: being changes which either do not immediately affect the functions at all, or else affect them in ways that prove fatal.

Hence there must be at work some other process, which equilibrates the actions of organisms with the actions they are exposed to. Plants and animals that continue to exist, are necessarily plants and animals whose powers balance the powers that act on them; and as their environments change, the changes which plants and animals undergo, must necessarily be changes towards a re-establishment of the balance. Besides direct equilibration, there must therefore be an indirect equilibration. How this goes on we have now to inquire.

# CHAPTER XII.

## INDIRECT EQUILIBRATION.

§ 164. Besides those perturbations produced in the moving equilibrium of any organism by special disturbing forces, there are ever going on many other perturbations—some which are the still-reverberating effects of disturbing forces previously experienced by the individual, and others which are the still-reverberating effects of disturbing forces experienced by ancestral individuals; and the multiplied deviations of function so caused, imply multiplied deviations of structure. In § 155 there was re-illustrated the truth, set forth at length when treating of Adaptation (§ 69), that an organism in a state of moving equilibrium, cannot have extra function thrown on any organ, and extra growth produced in such organ, without there being entailed correlative changes throughout all other functions, and eventually throughout all other organs. And when treating of Variation (§ 90), we saw that individuals which have been made, by their different circumstances, to deviate functionally and structurally from the average type in different directions, will bequeath to their joint offspring, compound perturbations of function and compound deviations of structure, endlessly varied in their kinds and amounts. That is to say, besides the primary perturbations and deviations directly caused in organisms by altered actions in their environments, there are ever being indirectly caused, secondary and tertiary perturbations and deviations, which, when compounded with one another from generation to generation, work innumerable slight modifications in the moving equilibria and correlative structures throughout the species.

Now if the individuals of a species are thus necessarily made unlike, in countless ways and degrees—if the complicated sets of rhythms which we call their functions, though similar in their general characters, are dissimilar in their details—if in one individual the amount of action in a particular direction is greater than in any other individual, or if here a peculiar combination gives a resulting force which is not found elsewhere; then, among all the individuals, some will be less liable than others to have their equilibria overthrown by a particular incident force, previously unexperienced. Unless the change in the environment is of so violent a kind as to be universally fatal to the species, it must affect more or less differently the slightly different moving equilibria which the members of the species present. It cannot but happen that some will be more stable than others, when exposed to this new or altered factor. That is to say, it cannot but happen that those individuals whose functions are most out of equilibrium with the modified aggregate of external forces, will be those to die; and that those will survive whose functions happen to be most nearly in equilibrium with the modified aggregate of external forces.

But this survival of the fittest, implies multiplication of the fittest. Out of the fittest thus multiplied, there will, as before, be an overthrowing of the moving equilibrium wherever it presents the least opposing force to the new incident force. And by the continual destruction of the individuals that are the least capable of maintaining their equilibria in presence of this new incident force, there must eventually be arrived at an altered type completely in equilibrium with the altered conditions.

§ 165. This survival of the fittest, which I have here sought to express in mechanical terms, is that which Mr Darwin has called "natural selection, or the preservation of favoured races in the struggle for life." That there is going on a process of this kind throughout the organic world, Mr Darwin's great work on the *Origin of Species* has shown to the satisfaction of nearly all naturalists. Indeed, when once enunciated, the truth of his hypothesis is so obvious as scarcely to need proof. Though evidence may be required to show that natural selection accounts for everything ascribed to it, yet no evidence is required to show that natural selection has always been going on, is going on now, and must ever continue to go on. Recognizing this as an *à priori* certainty, let us contemplate it under its two distinct aspects.

That organisms which live, thereby prove themselves fit to live, in so far as they have been tried; while organisms which die, thereby prove themselves in some respects unfitted for living; are facts no less manifest, than is the fact that this self-acting purification of a species, must tend ever to insure adaptation between it and its environment. This adaptation may be either so *maintained* or so *produced.* Doubtless many who have looked at Nature with philosophic eyes, have observed that death of the worst and multiplication of the best, must result in the maintenance of a constitution in harmony with surrounding circumstances. That the average vigour of any race would be diminished, did the diseased and feeble habitually survive and propagate; and that the destruction of such, through failure to fulfil some of the conditions to life, leaves behind those which are able to fulfil the conditions to life, and thus keeps up the average fitness to the conditions of life; are almost self-evident truths. But to recognize "natural selection" as a means of preserving an already-established balance between the powers of a species and the forces to which it is subject, is to recognize it only in its simplest and most general mode of action. It is the more special mode of action with which we are here concerned. This more special mode of action, Mr Darwin has been the first to perceive. To him we owe the discovery that natural selection is capable of *producing* fitness between organisms and their circumstances; and he, too, has the merit of appreciating the immensely-important consequences that follow from this. He has worked up an enormous mass of evidence into an elaborate demonstration, that this "preservation of favoured races in the struggle for life," is an ever-acting cause of divergence among organic forms. He has traced out the involved results of the process with marvellous subtlety. He has shown how hosts of otherwise inexplicable facts, are fully accounted for by it. In brief, he has proved that the cause he alleges is a true cause; that it is a cause which we see habitually in action; and that the results to be inferred from it, are in harmony with the phenomena which the Organic Creation presents, both as a whole and in its details. Let us glance at a few of the more important interpretations which the hypothesis furnishes.

A soil possessing some ingredient in unusual quantity, may supply to a plant an excess of the matter required for a certain class of its tissues; and may cause all the parts formed of such tissues to be abnormally developed. Suppose that among these are the hairs clothing its surfaces, including those which grow on its seeds. Thus furnished with somewhat longer fibres, its seeds, when shed, are carried a little further by the wind before they fall to the ground. The young plants growing up from them, being rather more widely dispersed than those produced by other individuals of the same species, will be less liable to smother one another; and a greater number may therefore reach maturity and fructify. Supposing the next generation subject to the same peculiarity of nutrition, some of the seeds borne by its members will not simply inherit this increased development of hairs, but will carry it further; and these, still more advantaged in the same way as before, will, on the average, have still more numerous chances of continuing the race. Thus, by the survival, generation after generation, of those possessing these longer hairs, and the inheritance of successive increments of growth in the hairs, there may result a seed deviating greatly from the original. Other individuals of the same species, subject to the different physical conditions of other localities, may develop somewhat thicker or harder coatings to their seeds: so rendering their seeds less digestible by the birds that devour them. Such thicker-coated seeds, by escaping undigested more frequently than thinner-coated ones, will have additional chances of growing up and leaving offspring; and this process, acting in a cumulative manner through successive years, will produce a seed diverging in another direction from the ancestral type. Again, elsewhere, some modification in the physiologic actions of the plant, may lead to an unusual secretion of an essential oil in the seeds; which rendering them unpalatable to creatures that would otherwise feed on them, may diminish the destruction of the seeds, so giving an advantage to the variety in its rate of multiplication; and this incidental peculiarity proving a preservative, will, as before, be gradually increased by natural selection, until it constitutes another divergence. Now in these and countless analogous cases, we see that plants may become better adapted, or re-adapted, to the aggregate of surrounding agencies, not through any *direct* action of such agencies upon them, but through their *indirect* action—through the destruction by them of the individuals which are least congruous with them, and the survival of those which are most congruous with them. All these slight variations of function and structure, arising among the members of a species, serve as so many experiments; the great majority of which fail, but a few of which succeed. Just as we see that each plant bears a multitude of seeds, out of which some two or three happen to fulfil all the conditions required for reaching maturity, and continuing the race; so we see that each species is perpetually producing numerous slightly-modified forms, deviating in all directions from the average, out of which most fit the surrounding conditions no better than their parents, or not so well, but some few of which fit the conditions better; and doing so, are enabled the better to preserve themselves, and to produce offspring similarly capable of preserving themselves. Among animals the like process results in the like development of various structures which cannot have been affected by the performance of functions—their functions being purely passive. The thick shell of a mollusk, is inexplicable as a result of direct reactions of the organism against the external actions to which it is exposed; but it is quite explicable as a result of the survival, generation after generation, of individuals whose thicker coverings protected them against enemies. Similarly with such a dermal structure as that of the tortoise. Though we have evidence that the skin where it is continually exposed to pressure and friction may thicken, and so re-establish the equilibrium, by opposing a greater inner force to a greater outer force; yet we have no evidence that a coat of armour like that of the tortoise can be so produced. Nor, indeed, are the conditions under which only its production in such a manner could be accounted for, fulfilled; since the surface of the tortoise is not exposed to greater pressure and friction than the surfaces of other creatures. This massive carapace, and the strangely-adapted osseous frame-work which supports it, are unaccountable as results of evolution, unless through the process of natural selection. Thus, too, is it with the production of colours in birds and in insects; the formation of odoriferous glands in mammals; the growth of such excrescences as those of the camel. Thus, in short, is it with all those organs of animals, which do not play active parts in the compound rhythms of their functions.

Besides giving us explanations of structural characters that are otherwise unaccountable, Mr Darwin shows how natural selection explains peculiar relations between individuals in certain species. Such facts as the dimorphism of the primrose and other flowers, he proves to be quite in harmony with his hypothesis, though stumbling-blocks to all other hypotheses. While the production of neuters among bees and ants, is inexplicable as a result of direct adaptation, natural selection affords a feasible solution of it. The various differences that accompany difference of sex, sometimes slight, sometimes very great, are similarly accounted for. As before suggested (§ 79), natural selection appears capable of producing and maintaining the right proportion of the sexes in each species; and it requires but to contemplate the bearings of the argument, to see that the formation of different sexes may itself have been determined in the same way.

To convey here an adequate idea of Mr Darwin's doctrine, in the immense range of its applications, is of course impossible. The few illustrations just given, serving but dimly to indicate the many classes of phenomena interpreted by it, are set down simply to remind the reader what Mr Darwin's hypothesis is, and what are the else insoluble problems which it solves for us.

§ 166. But now, though it seems to me that we are thus supplied with a key to phenomena which are multitudinous and varied beyond all conception; it also seems to me that there is a moiety of the phenomena which this key will not unlock. Mr Darwin himself recognizes use and disuse of parts, as causes of modifications in organisms; and does this, indeed, to a greater extent than do some who accept his general conclusion. But I conceive that he does not recognize them to a sufficient extent. While he conclusively shows that the inheritance of changes of structure, caused by changes of function, is utterly insufficient to explain a great mass—probably the greater mass—of morphological phenomena; I think he leaves unconsidered a mass of morphological phenomena that are explicable as results of functionally-acquired modifications, transmitted and increased, and which are not explicable as results of natural selection.

By induction, as well as by inference from the hypothesis of natural selection, we know that there exists a balance among the powers of organs which habitually act together—such proportions among them, that no one has any considerable excess of efficiency. We see, for example, that throughout the vascular system, there is maintained an equilibrium between the powers, that is, the developments, of the component parts: in some cases, under excessive exertion, the heart gives way, and we have enlargement; in other cases the large arteries give way, and we have aneurisms; in other cases the minute blood-vessels give way—now bursting, now becoming chronically congested. That is to say, in the average constitution, no superfluous strength is possessed by any of the appliances for circulating the blood. Take, again, a set of motor organs. Great strain here causes the fibres of a muscle to tear. There the muscle does not yield but the tendon snaps. Elsewhere neither muscle nor tendon is damaged, but the bone breaks. Joining with these instances the general fact, that under the same adverse conditions, different individuals show their slight differences of constitution by going wrong some in one way and some in another; and that even in the same individual, similar adverse conditions will now affect one viscus and now another; it becomes manifest that though there cannot be maintained an accurate or absolute balance among the powers of the organs composing an organism, yet the excesses and deficiencies of power are extremely slight. That they must be extremely slight, is, as before said, a deduction from the hypothesis of natural selection. Mr Darwin himself argues "that natural selection is continually trying to economize in every part of the organization. If under changed conditions of life a structure before useful becomes less useful, any diminution, however slight, in its development, will be seized on by natural selection, for it will profit the individual not to have its nutriment wasted in building up an useless structure." In other words, if any muscle has more fibres than can be utilized, or if a bone be stronger than needful, no advantage results, but rather a disadvantage—a disadvantage which will decrease the chances of survival. Hence it becomes a corollary, that among any organs which habitually act in concert, an increase of one can be of no service unless there is a concomitant increase of the rest. The co-operative parts must vary together; otherwise variation will be detrimental. A stronger muscle must have a stronger bone to resist its contractions; must have stronger correlated muscles and ligaments to secure the neighbouring articulations; must have larger blood-vessels to bring it supplies; must have a more massive nerve to bring it stimulus, and some extra development of a nervous centre to supply this extra stimulus. The question arises, then,—does spontaneous variation occur simultaneously in all these co-operative parts? Have we any reason to think that they spontaneously increase or decrease together? The assumption that they do, seems to me untenable; and its untenability will, I think, become conspicuous if we take a case, and observe how extremely numerous and involved are the variations which must be supposed to occur together. In illustration of another point, we have already considered the modification required to accompany increased weight of the head. Instead of the bison, however, the moose deer, or the extinct Irish elk, will here best serve our purpose. In this species the male has enormously-developed horns, which are used for purposes of offence and defence. These horns, weighing upwards of a hundred-weight, are carried at great mechanical disadvantage—supported as they are along with the massive skull which bears them, at the extremity of the outstretched neck. Further, that these heavy horns may be of use in fighting, the supporting bones and muscles must be strong enough, not simply to carry them, but to put them in motion with the rapidity required for giving blows. Let us, then, ask how, by natural selection, this complex apparatus of bones and muscles can have been developed, *pari passu* with the horns? If we suppose the horns to have originally been of like size with those borne by other kinds of deer; and if we suppose that in certain individuals, they became larger by spontaneous variation; what would be the concomitant changes required to render their greater size useful? Other things equal, the blow given by a larger horn would be a blow given by a heavier mass moving at a smaller velocity: the momentum would be the same as before; and the area of contact with the body struck being somewhat increased, while the velocity was decreased, the injury done would be less. That the horns may become better weapons, the whole apparatus which moves them must be so strengthened as to impress more force on them, and to bear the more violent reactions of the blows given. The bones of the skull on which the horns are seated must be thickened; otherwise they will break. To render the thickening of these bones advantageous, the vertebræ of the neck must be further developed; and without the ligaments that hold together these vertebræ, and the muscles which move them, are also enlarged, nothing will be gained. Such modifications of the neck will be useless, or rather will be detrimental, if its fulcrum be not made capable of resisting intenser strains: the upper dorsal vertebræ and their spines must be strengthened, that they may withstand the more violent contractions of the neck-muscles; and like changes must be made on the scapular arch. Still more must there be required a simultaneous development of the bones and muscles of the fore-legs; since each of these extra growths in the horns, in the skull, in the neck, in the shoulders, adds to the burden which the fore-legs have to bear; unless this deer with its heavier horns, head, neck, and shoulders, had stronger fore-legs, it would not only suffer from loss of speed but would even fail in fight. Hence, to make larger horns of use, additional sizes must be acquired by numerous bones, muscles, and ligaments, as well as by the blood-vessels and nerves on which their actions depend. On calling to mind how the spraining of a single small muscle in the foot, incapacitates for walking, or how a permanent weakness in one of its ligaments will greatly diminish the power of a limb, it will be seen that unless all these many changes are simultaneously made, they may as well be none of them made—or rather, they had better be none of them made; since, the enlargements of some parts, by putting greater strains on connected parts, would render them relatively weaker if they remained unenlarged. Thus, then, to account by the hypothesis of natural selection, for such a structure as that of the moose deer, or the extinct Irish elk, we must suppose a spontaneous increase in the size of the horns, to be accompanied by a spontaneous increase in each of these numerous bones and muscles and ligaments directly and indirectly implicated in the use of the horns. Can we with any propriety do this? I think not. It would be a strong supposition that the vertebræ and muscles of the neck, spontaneously enlarged at the same time as the horns. It would be a still stronger supposition that the upper dorsal vertebræ not only at the same time spontaneously became more massive, but also spontaneously altered their proportions in appropriate ways, by the development of their immense neural spines. And it would be an assumption still more straining our powers of belief, that along with heavier horns there should spontaneously take place the required strengthenings of the scapular arch and the fore-legs.

Besides the multiplication of directly-coöperative organs, the multiplication of organs that do not coöperate, save in the degree implied by their combination in the same organism, seems to me a further hindrance to the development of special structures by natural selection alone. Where the life is comparatively simple, or where surrounding circumstances render some one function supremely important, the survival of the fittest may readily bring about the appropriate structural change, without any aid from the transmission of functionally-acquired modifications. But in proportion as the life grows complex—in proportion as a healthy existence cannot be secured by a large endowment of some one power, but demands many powers; in the same proportion do there arise obstacles to the increase of any particular power, by "the preservation of favoured races in the struggle for life." As fast as the faculties are multiplied, so fast does it become possible for the several members of a species to have various kinds of superiorities over one another. While one saves its life by higher speed, another does the like by clearer vision, another by keener scent, another by quicker hearing, another by greater strength, another by unusual power of enduring cold or hunger, another by special sagacity, another by special timidity, another by special courage; and others by other bodily and mental attributes. Now it is unquestionably true that, other things equal, each of these attributes, giving its possessor an extra chance of life, is likely to be transmitted to posterity. But there seems no reason to suppose that it will be increased in subsequent generations by natural selection. That it may be thus increased, the individuals not possessing more than average endowments of it, must be more frequently killed off than individuals highly endowed with it; and this can happen only when the attribute is one of greater importance, for the time being, than most of the other attributes. If those members of the species which have but ordinary shares of it, nevertheless survive by virtue of other superiorities which they severally possess; then it is not easy to see how this particular attribute can be developed by natural selection in subsequent generations. The probability seems rather to be, that by gamogenesis, this extra endowment will, on the average, be diminished in posterity—just serving in the long run to compensate the deficient endowments of other individuals, whose special powers lie in other directions; and so to keep up the normal structure of the species. The working out of the process is here somewhat difficult to follow; but it appears to me that as fast as the number of bodily and mental faculties increases, and as fast as the maintenance of life comes to depend less on the amount of any one, and more on the combined action of all; so fast does the production of specialities of character by natural selection alone, become difficult. Particularly does this seem to be so with a species so multitudinous in its powers as mankind; and above all does it seem to be so with such of the human powers as have but minor shares in aiding the struggle for life—the æsthetic faculties, for example.

It by no means follows, however, that in cases of this kind, and cases of the preceding kind, natural selection plays no part. Wherever it is not the chief agent in working organic changes, it is still, very generally, a secondary agent. The survival of the fittest must nearly always further the production of modifications which produce fitness; whether they be modifications that have arisen incidentally, or modifications that have been caused by direct adaptation. Evidently, those individuals whose constitutions or circumstances have facilitated the production in them of any structural change consequent on any functional change demanded by some new external condition, will be the individuals most likely to live and to leave descendants. There must be a natural selection of functionally-acquired peculiarities, as well as of incidental peculiarities; and hence such structural changes in a species as result from changes of habit necessitated by changed circumstances, natural selection will render more rapid than they would otherwise be.

There are, however, some modifications in the sizes and forms of parts, which cannot have been aided by natural selection; but which must have resulted wholly from the inheritance of functionally-produced alterations. The dwindling away of organs of which the undue sizes entail no appreciable evils, furnishes the best evidence of this. Take, for an example, that diminution of the jaws and teeth which characterizes the civilized races, as contrasted with the savage races.* How can the civilized races have been bene-

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* I am indebted to Mr Flower for the opportunity of examining the collection of skulls in the Museum of the College of Surgeons for verification of this. Un-

fited in the struggle for life, by the slight decrease in these comparatively-small bones? No functional superiority possessed by a small jaw over a large jaw, in civilized life, can be named as having caused the more frequent survival of small-jawed individuals. The only advantage which smallness of jaw might be supposed to give, is the advantage of economized nutrition; and this could not be great enough to further the preservation of men possessing it. The decrease of weight in the jaw and co-operative parts, that has arisen in the course of many thousands of years, does not amount to more than a few ounces. This decrease has to be divided among the many generations that have lived and died in the interval. Let us admit that the weight of these parts diminished to the extent of an ounce in a single generation (which is a large admission); it still cannot be contended that the having to carry an ounce less in weight, or the having to keep in repair an ounce less of tissue, could sensibly affect any man's fate. And if it never did this—nay, if it did not cause a *frequent* survival of small-jawed individuals where large-jawed individuals died; natural selection could neither cause nor aid diminution of the jaw and

fortunately the absence, in most cases, of some or many teeth, prevented me from arriving at that specific result which would have been given by weighing a number of the under jaws in each race. Simple inspection, however, disclosed a sufficiently-conspicuous difference. The under jaws of Australians and Negroes, when placed side by side with those of Englishmen, were visibly larger, not only relatively but absolutely. One Australian jaw only, did I observe, that was about of the same actual size as an average English jaw; and this (probably the jaw of a woman) belonging as it did to a much smaller skull, bore a much greater ratio to the whole body of which it formed part, than did an English jaw of the same actual size. In all the other cases, the under jaws of these inferior races (containing larger teeth than our own) were *absolutely* more massive than our own—often exceeding them in all dimensions; and *relatively* to the smaller skeletons of these inferior races, they were very much more massive. Let me add that the Australian and Negro jaws are thus strongly contrasted, not with all British jaws, but only with the jaws of the civilized British. An ancient British skull in the collection, possesses a jaw almost or quite as massive as those of the Australian skulls. And this is in harmony with the alleged relation between greater size of jaws and greater action of jaws, involved by the habits of savages.

its appendages. Here, therefore, the decreased action of these parts which has accompanied the growth of civilized habits (the use of tools and the disuse of coarse food), must have been the sole cause at work. During civilization this decrease of function has affected, more or less, all individuals. Through direct equilibration, diminished external stress on these parts, has resulted in diminution of the internal forces by which this stress is met. From generation to generation, this lessening of the parts consequent on functional decline has been inherited. And since the survival of individuals must always have been determined by more important structural traits, this trait can have neither been facilitated nor retarded by natural selection.

§ 167. Returning from these extensive classes of facts for which Mr Darwin's hypothesis does not account, to the still more extensive classes of facts for which it does account, and which are unaccountable on any other hypothesis; let us consider in what way this hypothesis is expressible in terms of the general doctrine of evolution. Already it has been pointed out that the evolving of modified types by "natural selection or the preservation of favoured races in the struggle for life," must be a process of equilibration, since it results in the production of organisms that are in equilibrium with their environments; and at the outset of this chapter, something was done towards showing how this continual survival of the fittest, may be understood as the progressive establishment of a balance between inner and outer forces. Here, however, we must consider the matter more closely. It remains to be shown that this process conforms to the same general mechanical principles as do all other equilibrations.

On previous occasions we have contemplated the assemblage of individuals composing a species, as an aggregate in a state of moving equilibrium. We have seen that its powers of multiplication give it an expansive force which is antagonized by other forces; and that through the rhythmical variations in these two sets of forces, there is maintained an oscillating limit to its habitat, and an oscillating limit to its numbers. On another occasion (§ 96) it was shown that the aggregate of individuals constituting a species, has a kind of general life, which, "like the life of an individual, is maintained by the unequal and ever-varying actions of incident forces on its different parts." We saw that "just as, in each organism, incident forces constantly produce divergences from the mean state in various directions, which are constantly balanced by opposite divergences indirectly produced by other incident forces; and just as the combination of rhythmical functions thus maintained, constitutes the life of the organism; so, in a species, there is through gamogenesis a perpetual neutralization of those contrary deviations from the mean state, which are caused in its different parts by different sets of incident forces; and it is similarly by the rhythmical production and compensation of these contrary deviations, that the species continues to live." Hence, to understand the way in which a species is affected by causes which destroy some of its units and favour the multiplication of others, we must consider it as a whole whose units are held together by complex forces that are ever balancing themselves and ever being disturbed—a whole whose moving equilibrium is continually being modified, and through which waves of perturbation are continually being propagated. Thus much premised, let us next call to mind in what way moving equilibria in general are changed. In the first place, the necessary effect wrought by a new incident force falling on any part of an aggregate with balanced motions, is to produce a new motion in the direction of least resistance. In the second place, the new incident force is gradually used up in overcoming the opposing forces, and when it is all expended the opposing forces produce a recoil—a reverse deviation that counter-balances the original deviation. Consequently, to consider whether the moving equilibrium of a species is modified in the same way as moving equilibria in general, is to consider whether, when exposed to a new force, a species yields in the direction of least resistance; and whether, by its thus yielding, there is generated in the species a compensating change in the opposite direction. We shall find that it does both these things.

For what, expressed in mechanical terms, is the effect wrought on a species by some previously-unknown enemy, that kills such of its members as fail in defending themselves? The disappearance of those individuals which meet the destroying forces by the smallest defensive forces, is tantamount to the yielding of the species as a whole at the places where the resistances are the least. Or if by some general influence, such as alteration of climate, the members of a species are subject to any increase of certain external actions that are ever tending to overthrow their equilibria, and which they are ever counter-balancing by the absorption of nutriment, which are the first to die? Those that are least able to generate the internal actions which antagonize these external actions. If the change be an increase of the winter's cold, then such members of the species as have unusual powers of getting food or of digesting food, or such as are by their constitutional aptitude for making fat, furnished with reserve stores of force, available in times of scarcity, or such as have the thickest coats and so lose least heat by radiation, survive; and their survival implies that in each of them the moving equilibrium of functions presents such an adjustment of internal forces, as prevents its overthrow by the modified aggregate of external forces. Conversely, the members that die, are, other things equal, those deficient in the power of meeting the new action by an equivalent counter-action. Thus, in all cases, a species considered as an aggregate in a state of moving equilibrium, has its state changed by the yielding of its fluctuating mass wherever this mass is weakest in the relation to the special forces acting on it. The conclusion is, indeed, a truism. But now, what must follow from the destruction of the least-resisting individuals and survival of the most-resisting individuals? On the moving equilibrium of the species as a whole, existing from generation to generation, the effect of this deviation from the mean state is to produce a compensating deviation. For if all such as are deficient of power in a certain direction are destroyed, what must be the influence on posterity? Had those which are destroyed lived and left offspring, the next generation would have had the same average balance of powers as preceding generations: there would have been a like proportion of individuals less endowed with this power, and individuals more endowed with this power. But the more-endowed individuals being alone left to continue the race, there must result a new generation characterized by a larger average endowment of this power. That is to say, on the moving equilibrium constituted by a species, an action producing change in a given direction, is followed, in the next generation, by a reaction producing an opposite change. Observe, too, that these effects correspond in their degrees of violence. If the alteration of some external factor is so great that it leaves alive only a few individuals, characterized by extreme endowments of the power required to antagonize it; then, in succeeding generations, there is a rapid multiplication of individuals similarly characterized by extreme endowments of this power —the force impressed calls out an equivalent conflicting force. Moreover, the change is temporary where the cause is temporary, and permanent where the cause is permanent. All that are deficient in the needful attribute having been killed off; and the survivors having the needful attribute in a comparatively high degree; there will descend from them, not only some possessing equal amounts of this attribute with themselves, but also some possessing less amounts of it. If the agency which proves fatal to them has not continued in action, such less-endowed individuals will multiply; and the species, after sundry oscillations, will return to its previous mean state. But if this agency be a persistent one, such less endowed individuals will be continually killed off; and eventually none but the highly-endowed individuals will be produced—a new moving equilibrium, adapted to the new environing conditions, will result.

It may be objected that this mode of expressing the facts, does not include the numerous cases in which a species becomes modified in relation to surrounding agencies that do not actively influence it—cases like that of the plant which acquires hooked seed-vessels, by which it lays hold of the skins of passing animals, and makes them the distributors of its seeds—cases in which the outer agency has no direct tendency at first to affect the species, but in which the species so alters itself as to take advantage of the outer agency. To cases of this kind, however, the same mode of interpretation applies on simply changing the terms. While, in the aggregate of influences amid which a species exists, there are some which tend to overthrow the moving equilibria of its members, there are others which facilitate the maintenance of their moving equilibria, and some which are capable of giving their moving equilibria increased stability: instance the spread into their habitat of some new kind of prey, which is abundant at seasons when other prey is scarce. Now what is the process by which the moving equilibrium in any species, becomes adapted to some additional external factor which furthers its maintenance? Instead of an increased resistance to be met and counter-balanced, there is here a diminished resistance; and the diminished resistance is equilibrated in the same way as the increased resistance. As, in the one case, there is a more frequent survival of those individuals whose peculiarities of constitution enable them best to resist the new adverse factor; so, in the other case, there is a more frequent survival of individuals whose peculiarities of constitution enable them to take advantage of the new favourable factor. In each member of the species, the balance of functions and correlated arrangement of structures, differ slightly from those existing in other members. To say that among all its members, one is better adapted than the rest to take advantage of some before-unused agency in the environment, is to say that its moving equilibrium is, in so far, more stably adjusted with respect to the aggregate of surrounding influences. And if, as a consequence, this individual maintains its moving equilibrium when others fail to do so, and produces offspring which do the like—that is, if individuals thus characterized multiply and supplant the rest; there is evidently, as before, a process by which an equilibration between the organism and its environment is effected, not immediately but mediately, through the continuous intercourse between the species as a whole and the environment.

§ 168. Thus we see that indirect equilibration does whatever direct equilibration cannot do. It is scarcely possible too much to emphasize the conclusion, that all these processes by which organisms are re-fitted to their ever-changing environments, must be equilibrations of one kind or other. As authority for this conclusion, we have not simply the universal truth that change of every order is towards equilibrium; but we have also the truth which holds throughout the organic world, that life itself is the maintenance of a moving equilibrium between inner and outer actions—the continuous adjustment of internal relations to external relations; or the maintenance of a correspondence between the forces to which an organism is subject and the forces which it evolves. For if the preservation of life is the preservation of such a moving equilibrium, it becomes a corollary that those changes which enable a species to live under altered conditions, are changes towards equilibrium with the altered conditions.

Hence, all such changes being equilibrations, their differences can be nothing but differences in the ways through which they result. If they are not effected immediately, they must be effected mediately. *A priori*, therefore, we may be certain that all processes of modification which do not come within the class of direct equilibrations, must come within the class of indirect equilibrations.

Examination of the facts confirms this conclusion. The external factors to which a species is exposed, are of two kinds. They are such as act continuously or frequently on the individuals; or they are such as do not act continuously or frequently on the individuals. To a factor which continuously or frequently acts on the individuals, the functions of the individuals re-adjust themselves—there is direct equilibration. While a factor which does not act continuously or frequently on the individuals, acts continuously on the species as a whole—either destroying such of the members as are least capable of resisting it, or fostering such of the members as are most capable of taking advantage of it. And by the abstraction, generation after generation, of those least in equilibrium with the new factor; or by the extra multiplication, generation after generation, of those most in equilibrium with the new factor; the species as a whole is eventually brought into complete equilibrium with the new factor—there is indirect equilibration.

## CHAPTER XIII.

### THE CO-OPERATION OF THE FACTORS.

§ 169. THUS the phenomena of organic evolution, may be interpreted in the same way as the phenomena of all other evolution. Those universal laws of the re-distribution of matter and motion, to which things in general conform, are conformed to by all living things; whether considered in their individual histories, in their histories as species, or in their aggregate history. However otherwise they may ordinarily be expressed, the truths of development as exhibited in the animal and vegetal kingdoms, prove to be expressible as manifestations of those abstract truths set forth in *First Principles*. Fully to see this, it will be needful for us to contemplate in their *ensemble*, the several processes separately described in the four preceding chapters.

If the forces acting on any aggregate remain the same, the changes produced by them in the aggregate will presently reach a limit, at which the constant outer forces are balanced by the constant inner forces; and thereafter no further metamorphosis will take place. Hence, that there may be continuous changes of structure in organisms, there must be continuous changes in the incident forces. This condition to the evolution of animal and vegetal forms, we find to be fully satisfied. The astronomic, geologic, and meteorologic changes that have been slowly but incessantly going on, and have been increasing in the complexity of their combinations, have been perpetually altering the circumstances of organisms; and organisms, as they have become more numerous in their kinds and higher in their kinds, have been perpetually altering one another's circumstances. Thus, for those progressive modifications upon modifications which organic evolution implies, we find a sufficient cause in the modifications after modifications, which every environment over the Earth's surface has been undergoing, throughout all geologic and pre-geologic times. The progressive inner changes for which we thus find a cause in the continuous outer changes, conform, so far as we can trace them, to that universal law of the instability of the homogeneous, which is manifested throughout evolution in general. We see that in organisms, as in all other things, the exposure of different parts to different kinds and amounts of incident forces, has necessitated their differentiation; and that for the like reason, aggregates of individuals have been lapsing into varieties, and species, and genera, and classes. We also see that in each type of organism, as in the aggregate of types, the multiplication of effects has continually aided this transition from a more homogeneous to a more heterogeneous state. And yet again, we see that that increasing segregation, and concomitant increasing definiteness, which characterizes the growing heterogeneity of organisms, has been insured by the necessary maintenance of them under combinations of forces not greatly unlike preceding combinations—by the continual destruction of those which expose themselves to aggregates of external actions markedly incongruous with the aggregates of their internal actions, and the survival of those subject only to comparatively small incongruities. Finally, we have found that each change of structure, superposed on preceding changes, has been a re-equilibration necessitated by the disturbance of a preceding equilibrium. The maintenance of life being the maintenance of a balanced combination of functions, it follows that individuals and species that have continued to live, are individuals and species in which the balance of functions has not been overthrown. Inevitably, therefore, survival through successive changes of conditions, implies successive adjustments of the balance to the new conditions. This deduction we find to be inductively verified. What is ordinarily called adaptation, is, when translated into mechanical terms, direct equilibration. And that process which, under the name of natural selection, Mr Darwin has shown to be an ever-acting means of fitting the structures of organisms to their circumstances, we find, on analysis, to be expressible in mechanical terms as indirect equilibration.

The actions that are here specified in succession, are in reality simultaneous; and they must be so conceived before organic evolution can be rightly understood. Some aid towards so conceiving them, will be given by the annexed table, representing the co-operation of the factors.

§ 170. Respecting this co-operation of these factors, it remains only to point out their respective shares in producing the total result; and the way in which the proportions of their respective shares vary as evolution progresses.

At first, changes in the amounts and combinations of external inorganic forces, astronomic, geologic, and meteorologic, were the only causes of the successive modifications undergone by organisms; and these changes have continued, and must still continue, to be causes of such modifications. As, however, through the diffusion of organisms, and the consequent differential actions of inorganic forces on them, there arose unlikenesses among organisms, producing varieties, species, genera, orders, classes, &c.; the actions of organisms on one another became new sources of organic modifications. And as fast as types have multiplied, and become more complex; so fast have the mutual actions of organisms come to be more influential factors in their respective evolutions. Until, eventually, as we see exemplified in the human race, they have come to be the chief factors.

Passing from the external causes of change to the internal

- Astronomic changes
- Geologic changes
- Meteorologic changes
  - alter the incidence of inorganic forces.
- Enemies
- Competitors
- Co-operators
- Prey
  - varying in number
- Enemies
- Competitors
- Co-operators
- Prey
  - varying in kind
    - alter the incidence of organic forces.
      - on each species : affecting
        - its individuals,
          - immediately through their functions ;
            - which, partially in the first generation, and completely in the course of generations, are directly equilibrated with the changed agencies.
            - which have their direct equilibration with the changed agencies, aided by indirect equilibration, through the more frequent survival of those in which the direct equilibration is most rapid.
          - mediately through the aggregate of individuals ;
            - positively—by aiding the multiplication of those whose moving equilibria happen to be most congruous with the changed agencies : thus, in the course of generations, indirectly equilibrating certain individuals with them.
            - negatively—by killing those whose moving equilibria are most incongruous with the changed agencies : thus, in the course of generations, indirectly equilibrating each of its surviving individuals with them
        - its aggregate of individuals,
          - by acting on it in some parts of the habitat more than in others ; and thus differentiating the species into local varieties.
          - by acting differently on slightly-unlike individuals in the same locality ;
            - and thus causing differentiations of the species into varieties, irrespective of locality.
            - and thus causing modification of the species as a whole, by abstracting a certain class of its units.

processes of change entailed by them, we see that these, too, have varied in their proportions—that which was originally the most important and almost the sole process, becoming gradually less important, if not at last the least important. Always there must have been, and always there must continue to be, a survival of the fittest: natural selection must have been in operation at the outset, and can never cease to operate. While yet organisms had comparatively feeble powers of co-ordinating their actions, and adjusting them to environing actions, natural selection worked almost alone in moulding and re-moulding organisms into fitness for their changing environments; and natural selection has remained almost the sole agency by which plants and inferior orders of animals have been modified and developed. The equilibration of organisms that are comparatively passive, is necessarily effected indirectly, by the action of incident forces on the species as a whole. But along with the gradual evolution of organisms having some activity, there grows up a kind of equilibration that is relatively direct. In proportion as the activity increases, direct equilibration plays a more important part. Until, when the nervo-muscular apparatus becomes greatly developed, and the power of varying the actions to fit the varying requirements becomes considerable, the share taken by direct equilibration rises into co-ordinate importance. We have seen reason to think that as fast as essential faculties multiply, and as fast as the number of organs that co-operate in any given function increases, indirect equilibration through natural selection, becomes less and less capable of producing specific adaptations; and remains fully capable only of maintaining the general fitness of constitution to conditions. Simultaneously, the production of adaptations by direct equilibration, takes the first place—indirect equilibration serving to facilitate it. Until at length, among the civilized human races, the equilibration becomes mainly direct: the action of natural selection being restricted to the destruction of those who are constitutionally too feeble to live, even with external aid. As the preservation of incapables is habitually secured by our social arrangements; and as very few except criminals are prevented by their inferiorities from leaving the average number of offspring (indeed the balance of fertility is probably in favour of the inferior); it results that survival of the fittest, can scarcely at all act in such way as to produce specialities of nature, either bodily or mental. Here the specialities of nature, chiefly mental, which we see produced, and which are so rapidly produced that a few centuries show a considerable change, must be ascribed almost wholly to direct equilibration.*

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* As having an instructive bearing on the question of the varieties of Man, let me here refer to a paper on "The Origin of the Human Races" read before the Anthropological Society, March 1st, 1864, by Mr Alfred Wallace—a gentleman well known among naturalists, as having independently thought out the hypothesis of natural selection, though at a later date, and less elaborately, than Mr Darwin. In this paper, Mr Wallace shows, very clearly I think, that along with the attainment of that degree of intelligence implied by the use of implements, clothing, &c., there arises a tendency for modifications of brain to take the place of modifications of body—still, however, regarding the natural selection of spontaneous variations, as the cause of the modifications. But if the foregoing arguments be valid, natural selection here plays but the secondary part of furthering the adaptations otherwise caused. It is true that, as Mr Wallace argues, and as I have myself briefly indicated (see *Westminster Review*, for April, 1852, pp. 496—501), the natural selection of races, leads to the survival of the more cerebrally-developed, while the less cerebrally-developed disappear. But though natural selection acts freely in the struggle of one society with another; yet, among the units of each society, its action is so interfered with, that there remains no adequate cause for the acquirement of mental superiority by one race over another, except the inheritance of functionally-produced modifications. This view, however, agrees equally well with Mr Wallace's conclusion, that at a certain stage of evolution, the brain begins to change much more than the body.

## CHAPTER XIV.

### THE CONVERGENCE OF THE EVIDENCES.

§ 171. Of the three classes of evidences that have been assigned, the *à priori*, which we took first, were partly negative, partly positive.

On considering the "General Aspects of the Special-creation-hypothesis," we discovered it to be worthless. Discredited by its origin, and wholly without any basis of observed fact, we found that it was not even a thinkable hypothesis; and while thus intellectually illusive, it turned out on examination to have moral implications quite at variance with the professed beliefs of those who hold it.

Contrariwise, the "General Aspects of the Evolution-hypothesis," begot the stronger faith in it the more nearly they were considered. By its lineage and its kindred, it was found to be as closely allied with the proved truths of modern science, as is the antagonist hypothesis with the proved errors of ancient ignorance. Instead of being a mere pseud-idea, we saw that it admitted of elaboration into a definite conception—so showing its legitimacy as an hypothesis. Instead of positing a purely fictitious process, the process which it alleges, we saw to be one that is actually going on around us. To which add, that morally considered, this hypothesis presents no irreconcilable incongruities.

Thus, even were we without further means of judging, there could be no rational hesitation which of the two views should be entertained.

§ 172. Further means of judging, however, we found to be afforded by bringing the two hypotheses face to face with the general truths established by naturalists. These inductive evidences were dealt with in four chapters.

"The Arguments from Classification" were these. Organisms fall into groups within groups; and this is the arrangement which we see results from evolution, where it is known to take place. Of these groups within groups, the great or primary ones are the most unlike, the sub-groups are less unlike, the sub-sub-groups still less unlike, and so on; and this, too, is a characteristic of groups demonstrably produced by evolution. Moreover, indefiniteness of equivalence among the groups, is common to those which we know have been evolved, and those here supposed to have been evolved. And then there is the further significant fact, that divergent groups are allied through their lowest rather than their highest members—a truth which the hypothesis of evolution implies.

Of "the Arguments from Embryology," the first and most striking is, that when the developments of embryos are traced from their common starting point, and their divergences and re-divergences symbolized by a genealogical tree, there is manifest a general parallelism between the arrangement of its primary, secondary, and tertiary branches, and the arrangement of the divisions and sub-divisions of our classifications—a general parallelism to be anticipated as a result of evolution. Nor do those minor deviations from this general parallelism, which at first sight look like difficulties, fail, on closer observation, to become additional supports; since those traits of a common ancestry which embryology reveals, are, if modifications have resulted from changed conditions, liable to be distorted or disguised in quite different ways and degrees in different lines of descendants

We next considered "the Arguments from Morphology." Leaving out those kinships among organisms disclosed by their developmental metamorphoses, the kinships which their adult forms show are profoundly significant. The remarkable unities of type which are found under such different externals, are inexplicable except as results of community of descent with non-community of modification. Again, each organism analyzed apart, shows us, in the likenesses obscured by unlikenesses of its component parts, a peculiarity of structure that can be ascribed only to the formation of a more heterogeneous organism out of a more homogeneous one. And once more, the habitual existence of rudimentary organs, homologous with organs that are developed in allied animals or plants, while it admits of no other rational interpretation, has a satisfactory interpretation given to it by the hypothesis of evolution.

Last of the inductive evidences, came "the Arguments from Distribution." While the phenomena of distribution in Space, prove to be unaccountable as results of designed adaptation of organisms to their habitats, they prove to be accountable as results of the competition of species, and the spread of the superior into the habitats of the inferior, followed by the changes which new conditions induce. Though the phenomena of distribution in Time, are so fragmentary that no positive conclusion can be drawn from them; yet all of them are reconcileable with the hypothesis of evolution, and some of them yield it strong support—especially the near relationship that exists between the living and extinct types of each great geographical area.

In each of these four groups, we thus found several arguments which point to the same conclusion; and the conclusion pointed to by the arguments of any one group, is that pointed to by the arguments of all the other groups. This coincidence of coincidences, would give to the induction a very high degree of probability, even were it not enforced by deduction.

§ 173. But the conclusion deductively reached, is in harmony with the inductive conclusion. Passing from the evidence that evolution has taken place, to the question—How has it taken place? we find in known agencies and known processes, adequate causes of its phenomena.

In astronomic, geologic, and meteorologic changes, ever in progress, ever combining in new and more involved ways, we have a set of inorganic factors to which all organisms are exposed; and in the varying and complicating actions of organisms on one another, we have a set of organic factors that alter with increasing rapidity. Thus, speaking generally, all members of the Earth's Flora and Fauna are continually passing into new environments—experience perpetual re-arrangements of external forces.

Each organic aggregate, whether considered individually or as a continuously-existing species, is modified afresh by each fresh distribution of external forces. To its pre-existing differentiations, new differentiations are added; and thus that lapse from a more homogeneous to a more heterogeneous state, which would have a fixed limit were the circumstances fixed, has its limit perpetually removed by the perpetual change of the circumstances. Meanwhile, that growing complexity of structure thus produced, must, in the average of cases, be accompanied by an increasing definiteness of structure; since only those organisms can survive which subject themselves to aggregates of forces that are not, in their essentials, greatly unlike those with which their structures correspond. And at the same time that progression is thus necessitated as a general result; yet, as change of structure arises only where there is change in the distribution of forces, it will not take place in organisms which elude changes in the distribution of forces, by migration or otherwise.

These modifications upon modifications which result in evolution structurally considered, are the accompaniments of those functional alterations continually required to re-equilibrate inner with outer actions. That moving equilibrium of inner actions corresponding with outer actions, which constitutes the life of an organism, must either be overthrown by a change in the outer actions, or must undergo perturbations that cannot end until there is a re-adjusted balance of functions and correlative adaptation of structures. Wherever the external changes are such as to be continuously or frequently operative on individuals, this direct equilibration must go on.

But where the external changes are either such as are fatal when experienced by the individuals, or such as act on the individuals in ways that do not affect the equilibrium of their functions; then the re-adjustment results through the effects produced on the species as a whole—there is indirect equilibration. By natural selection or survival of the fittest—by the preservation in successive generations of those whose moving equilibria happen to be least at variance with the requirements, there is eventually produced a changed equilibrium completely in harmony with the requirements.

And thus it results that those universal laws of the re-distribution of matter and motion, which are conformed to by evolution in general, are conformed to by organic evolution.

§ 174. Even were this the whole of the evidence assignable for the belief that organisms of all orders have been gradually evolved, this belief would have a warrant much higher than that of very many beliefs that are regarded as established. When we see that there are strong *à priori* probabilities in its favour, and wholly adverse to the antagonist hypothesis—when an examination of the facts which naturalists have accumulated, leads us to several groups of inductions which unite in supporting it—and when the characteristics which conspire to show that organic evolution has been going on, prove to be deducible from those universal actions known to work evolution of all other kinds; we have a combination of proofs which might suffice were there no more to be said.

But the evidence is far from exhausted. At the outset of the argument, it was remarked that the *ensemble* of vital phenomena presented by the organic world as a whole, cannot be properly dealt with apart from the *ensemble* of vital phenomena presented by each organism, in the course of its growth, development, and decay. The interpretation of either implies interpretation of the other; since the two are in reality parts of one process. Hence, the validity of any hypothesis respecting the one class of phenomena, may be tested by its congruity with phenomena of the other class. We are now about to pass to the more special phenomena of development, as displayed in the structures and functions of individual organisms. If the hypothesis that plants and animals have been progressively evolved, be true, it must furnish us with keys to these phenomena. We shall find that it does this; and by doing it, gives numberless additional vouchers for its truth.

END OF VOL. I.

# APPENDIX.

[*The following letter, originally written for publication in the* North American Review, *but declined by the Editor in pursuance of a general rule, and eventually otherwise published in the United States, I have thought well to append to this first volume of the* Principles of Biology. *I do this because the questions which it discusses are dealt with in this volume; and because the further explanations it furnishes seem needful to prevent misapprehensions.*]

## ON ALLEGED "SPONTANEOUS GENERATION," AND ON THE HYPOTHESIS OF PHYSIOLOGICAL UNITS.

*The Editor of the North American Review.*

SIR,

It is in most cases unwise to notice adverse criticisms. Either they do not admit of answers or the answers may be left to the penetration of readers. When, however, a critic's allegations touch the fundamental propositions of a book, and especially when they appear in a periodical having the position of the *North American Review*, the case is altered. For these reasons the article on "Philosophical Biology," published in your last number, demands from me an attention which ordinary criticisms do not.

It is the more needful for me to notice it, because its two leading objections have the one an actual fairness and the other an apparant fairness; and in the absence of explanations from me, they will be considered as substantiated even by many, or perhaps most, of those who have read the work itself—much more by those who have not read it. That to prevent the spread of misapprehensions I ought to say something, is further shown by the fact that the same two objections have already been made in England—the one by Dr. Child, of Oxford, in his *Essays on Physiological Subjects*, and the other by a writer in the *Westminster Review* for July, 1865.

In the note to which your reviewer refers, I have, as he says, tacitly repudiated the belief in "spontaneous generation;" and that I have done this in such a way as to leave open the door for the interpretation given by him is true. Indeed the fact that Dr. Child, whose criticism is a sympathetic one, puts the same construction on this note, proves that your reviewer has but drawn what seems to be a necessary inference. Nevertheless, the inference is one which I did not intend to be drawn.

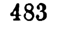
In explanation, let me at the outset remark that I am placed at a disadvantage in having had to omit that part of the System of Philosophy which deals with Inorganic Evolution. In the orginal programme will be found a parenthetic reference to this omitted part, which should, as there stated, precede the *Principles of Biology*.

Two volumes are missing. The closing chapter of the second, were it written, would deal with the evolution of organic matter—the step preceding the evolution of living forms. Habitually carrying with me in thought the contents of this unwritten chapter, I have, in some cases, expressed myself as though the reader had it before him; and have thus rendered some of my statements liable to misconstructions. Apart from this, however, the explanation of the apparent inconsistency is very simple, if not very obvious. In the first place, I do not believe in the "spontaneous generation" commonly alleged, and referred to in the note; and so little have I associated in thought this alleged "spontaneous generation" which I disbelieve, with the generation by evolution which I do believe, that the repudiation of the one never occurred to me as liable to be taken for repudiation of the other. That creatures having *quite specific structures* are evolved in the course of a few hours, without antecedents calculated to determine their specific forms, is to me incredible. Not only the established truths of Biology, but the established truths of science in general, negative the supposition that organisms having structures definite enough to identify them as belonging to known genera and species, can be produced in the absence of germs derived from antecedent organisms of the same genera and species. If there can suddenly be imposed on simple protoplasm the organization which constitutes it a *Paramœcium*, I see no reason why animals of greater complexity, or indeed of any complexity, may not be constituted after the same manner. In brief, I do not accept these alleged facts as exemplifying Evolution, because they imply something immensely beyond that which Evolution, as I understand it, can achieve. In the second place, my disbelief extends not only to the alleged cases of "spontaneous generation," but to every case akin to them. The very conception of spontaneity is wholly incongruous with the conception of Evolution. For this reason I regard as objectionable Mr. Darwin's phrase "spontaneous variation" (as indeed he does himself); and I have sought to show that there are always assignable causes of variation. No form of Evolution, inorganic or organic, can be spontaneous; but in every instance the antecedent forces must be adequate in their quantities, kinds, and distributions, to work the observed effects. Neither the alleged cases of "spontaneous generation," nor any imaginable cases in the least allied to them, fulfil this requirement.

If, accepting these alleged cases of "spontaneous generation," I had assumed, as your reviewer seems to do, that the evolution of organic life commenced in an analogous way; then, indeed, I should have left myself open to a fatal criticism. This supposed "spontaneous generation" habitually occurs in menstrua that contain either organic matter, or matter originally derived from organisms; and such organic matter, proceeding in all known cases from organisms of a higher kind, implies the pre-existence of such higher organisms. By what kind of logic, then, is it inferrible that organic life was initiated after a manner like that in which *Infusoria* are said to be now spontaneously generated? Where, before life commenced, were the superior organisms from which these lowest organisms obtained their organic matter? Without doubting that there are those who, as the reviewer says, "can penetrate deeper than Mr. Spencer has done into the idea of universal evolution," and who, as he contends, prove this by accepting the doctrine of "spontaneous generation"; I nevertheless think that I can penetrate deep enough to see that a tenable hypothesis respecting the origin of organic life must be reached by some other clue than that furnished by experiments on decoction of hay and extract of beef.

From what I do not believe, let me now pass to what I do believe. Granting that the formation of organic matter, and the evolution of life in its lowest forms, may go on under existing cosmical conditions; but believing it more likely that the formation of such matter and such forms, took place at a time when the heat of the Earth's surface was falling through those ranges of temperature at which the higher organic compounds are unstable; I conceive that the moulding of such organic matter into the simplest types, must have commenced with portions of protoplasm more minute, more indefinite, and more inconstant in their characters, than the lowest Rhizopods—less distinguishable from a mere fragment of albumen than even the *Protogenes* of Professor Haeckel. The evolution of specific shapes must, like all other organic evolution, have resulted from the actions and reactions between such incipient types and their environments, and the continued survival of those which happened to have specialities best fitted to the specialities of their environments. To reach by this process the comparatively well-specialized forms of ordinary *Infusoria*, must, I conceive, have taken an enormous period of time.

To prevent, as far as may be, future misapprehension, let me elaborate this conception so as to meet the particular objections raised. The reviewer takes for granted that a "first organism" must be assumed by me, as it is by himself. But the conception of a "first organism," in anything like the current sense of the words, is wholly at variance with conception of evolution; and scarcely less at variance with the facts revealed by the microscope. The lowest living things are not properly speaking organisms at all; for they have no distinctions of parts—no traces of organization. It is almost a misuse of language to call them "forms" of life: not only are their outlines, when distinguishable, too unspecific for description, but they change from moment to moment and are never twice alike, either in two individuals or in the same individual. Even the word "type" is applicable in but a loose way; for there is little constancy in their generic characters: according as the surrounding conditions determine, they undergo transformations now of one kind and now of another. And the vagueness, the inconstancy, the want of appreciable structure, displayed by the simplest of living things as we now see them, are characters (or absences of characters) which, on the hypothesis of Evolution, must have been still more decided when, as at first, no "forms," no "types," no "specific shapes," had been moulded. That "absolute commencement of organic life on the globe," which the reviewer says I "cannot evade the admission of," I distinctly deny. The affirmation of universal evolution is in itself the negation of an "absolute commencement" of anything. Construed in terms of evolution, every kind of being is conceived as a product of modifications wrought by insensible gradations on a pre-existing kind of being; and this holds as fully of the supposed "commencement of organic life" as of all subsequent developments of organic life. It is no more needful to suppose an "absolute commencement of organic life" or a "first organism," than it is needful to suppose an absolute commencement of social life and a first social organism. The assumption of such a necessity in this last case, made by early speculators with their theories of "social contracts" and the like, is disproved by the facts; and the facts, so far as they are ascertained, disprove the assumption of such a necessity in the first case. That organic matter was not produced all at once, but was reached through steps, we are well warranted in believing by the experiences of chemists. Organic matters are produced in the laboratory by what we may literally call *artificial evolution.* Chemists find themselves unable to form these complex combinations directly from their elements; but they succeed in forming them indirectly, by successive modifications of simpler combinations. In some binary compound, one element of which is present in several equivalents, a change is made by substituting for one of these equivalents an equivalent of some other element; so producing a ternary compound. Then another of the equivalents is replaced, and so on. For instance, beginning with ammonia, $N\,H_3$, a higher form is obtained by replacing one of the atoms of hydrogen by an atom of methyl, so producing methyl-amine, $N\,(C\,H_3\,H_2)$; and then, under the further action of methyl, ending in a further substitution, there is reached the still more compound substance dimethyl-amine, $N\,(C\,H_3)\,(C\,H_3)\,H$. And in this manner highly complex substances are eventually built up. Another characteristic of their method is no less significant. Two complex compounds are employed to generate, by their action upon one another, a compound of still greater complexity: different heterogeneous molecules of one stage, become parents of a molecule a stage higher in heterogeneity. Thus, having built up acetic acid out of its elements, and having by the process of substitution described above, changed the acetic acid into propionic acid, and propionic into butyric, of which the formula is $\left\{\begin{matrix} C\,(C\,H_3)\,(C\,H_3)\,H \\ C\,O\,(H\,O) \end{matrix}\right\}$;

this complex compound, by operating on another complex compound, such as the dimethyl-amine named above, generates one of still greater complexity, butyrate of dimethyl-amine  $\left\{\begin{matrix} C\,(C\,H_3)\,(C\,H_3)\,H \\ C\,O\,(H\,O) \end{matrix}\right\} N\,(C\,H_3)\,(C\,H_3)\,H$. See, then, the remarkable parallelism. The progress towards higher types of organic molecules is effected by modifications upon modifications; as throughout Evolution in general. Each of these modifications is a change of the molecule into equilibrium with its environment—an adaptation, as it were, to new surrounding conditions to which it is subjected; as throughout Evolution in general. Larger, or more integrated, aggregates (for compound molecules are such) are successively generated; as throughout Evolution in general. More complex or heterogeneous aggregates are so made to arise, one out of another; as throughout Evolution in general. A geometrically-increasing multitude of these larger and more complex aggregates so produced, at the same time results; as throughout Evolution in general. And it is by the action of the successively higher forms on one another, joined with the action of environing conditions, that the highest forms are reached; as throughout Evolution in general.

When we thus see the identity of method at the two extremes—when we see that the general laws of evolution, as they are exemplified in known organisms, have been unconsciously conformed to by chemists in the artificial evolution of organic matter; we can scarcely doubt that these laws were conformed to in the natural evolution of organic matter, and afterwards in the evolution of the simplest organic forms. In the early world, as in the modern laboratory, inferior types of organic substances, by their mutual actions under fit conditions, evolved the superior types of organic substances, ending in organizable protoplasm. And it can hardly be doubted that the shaping of organizable protoplasm, which is a substance modifiable in multitudinous ways with extreme facility, went on after the same manner. As I learn from one of our first chemists, Prof. Frankland, *protein* is capable of existing under probably at least a thousand isomeric forms; and, as we shall presently see, it is capable of forming, with itself and other elements, substances yet more intricate in composition, that are practically infinite in their varieties of kind. Exposed to those innumerable modifications of conditions which the Earth's surface afforded, here in amount of light, there in amount of heat, and elsewhere in the mineral quality of its aqueous medium, this extremely changeable substance must have undergone now one, now another, of its countless metamorphoses. And to the mutual influences of its metamorphic forms under favouring conditions, we may ascribe the production of the still more composite, still more sensitive, still more variously-changeable portions of organic matter, which, in masses more minute and simpler than existing *Protozoa*, displayed actions verging little by little into those called vital—actions which protein itself exhibits in a certain degree, and which the lowest known living things exhibit only in a greater degree. Thus, setting out with inductions from the experiences of organic chemists at the one extreme, and with inductions from the observations of biologists at the other extreme, we are enabled deductively to bridge the interval—are enabled to conceive how organic compounds were evolved, and how, by a continuance of the process, the nascent life displayed in these became gradually more pronounced. And this it is which has to be explained, and which the alleged cases of "spontaneous generation" would not, were they substantiated, help us in the least to explain.

It is thus manifest, I think, that I have not fallen into the alleged inconsistency. Nevertheless, I admit that your reviewer was justified in inferring this inconsistency; and I take blame to myself for not having seen that the statement, as I have left it, is open to misconstruction.

I pass now to the second allegation—that in ascribing to certain specific molecules, which I have called "physiological units," the aptitude to build themselves into the structure of the organism to which they are peculiar, I have abandoned my own principle, and have assumed something beyond the re-distribution of Matter and Motion. As put by the reviewer, his case appears to be well made out; and that he is not altogether unwarranted in so putting it, may be admitted. Nevertheless, there does not in reality exist the supposed incongruity.

Before attempting to make clear the adequacy of the conception which I am said to have tacitly abandoned as insufficient, let me remove that excess of improbability the reviewer gives to it, by the extremely-restricted meaning with which he uses the word mechanical. In discussing a proposition of mine he says:—

> "He then cites certain remarks of Mr. Paget on the permanent effects wrought in the blood by the poison of scarlatina and small-pox, as justifying the belief that such a 'power' exists, and attributes the repair of a wasted tissue to 'forces analogous to those by which a crystal reproduces its lost apex.' (Neither of which phenomena, however, is explicable by mechanical causes.)"

Were it not for the deliberation with which this last statement is made, I should take it for a slip of the pen. As it is, however, I have no course left but to suppose the reviewer unaware of the fact that molecular actions of all kinds are now not only conceived as mechanical actions, but that calculations based on this conception of them, bring out the results that correspond with observation. There is no kind of re-arrangement among molecules (crystallization being one) which the modern physicist does not think of, and correctly reason upon, in terms of forces and motions like those of sensible masses. Polarity is regarded as a resultant of such forces and motions; and when, as happens in many cases, light changes the molecular structure of a crystal, and alters its polarity, it does this by impressing, in conformity with mechanical laws, new motions on the constituent molecules. That the reviewer should present the mechanical conception under so extremely limited a form, is the more surprising to me because, at the outset of the very work he reviews, I have, in various passages, based inferences on those immense extensions of it which he ignores; indicating, for example, the interpretation it yields of the inorganic chemical changes effected by heat, and the organic chemical changes effected by light (*Principles of Biology*, § 13.)

Premising, then, that the ordinary idea of mechanical action must be greatly expanded, let us enter upon the question at issue—the sufficiency of the hypothesis that the structure of each organism is determined by the polarities of the special molecules, or physiological units, peculiar to it as a species, which necessitate tendencies towards special arrangements. My proposition and the reviewer's criticism upon it, will be most conveniently presented if I quote in full a passage of his from which I have already extracted some expressions. He says:—

> "It will be noticed, however, that Mr. Spencer attributes the possession of these 'tendencies,' or 'proclivities,' to natural inheritance from ancestral organisms; and it may be argued that he thus saves the mechanist theory and his own consistency at the same time, inasmuch as he derives even the 'tendencies' themselves ultimately from the environment. To this we reply, that Mr. Spencer, who advocates the nebular hypothesis, cannot evade the admission of an absolute commencement of organic life on the globe, and that the 'formative tendencies,' without which he cannot explain the evolution of a single individual, could not have been inherited by the first organism. Besides, by his virtual denial of spontaneous generation, he denies that the first organism was evolved out of the inorganic world, and thus shuts himself off from the argument (otherwise plausible) that its 'tendencies' were ultimately derived from the environment."

This assertion is already in great measure disposed of by what has been said above. Holding that, though not "spontaneously generated," those minute portions of protoplasm which first displayed in the feeblest degree that changeability taken to imply life, were evolved, I am *not* debarred from the argument that the "tendencies" of the physiological units are derived from the inherited effects of environing actions. If the conception of a "first organism" were a necessary one, the reviewer's objection would be valid. If there were an "absolute commencement" of life, a definite line parting organic matter from the simplest living forms, I should be placed in the predicament he describes. But as the doctrine of Evolution itself tacitly negatives any such distinct separation; and as the negation is the more confirmed by the facts the more we know of them; I do not feel that I am entangled in the alleged difficulty. My reply might end here; but as the hypothesis in question is one not easily conceived, and very apt to be misunderstood, I will attempt a further elucidation of it.

Much evidence now conspires to show that molecules of the substances we call elementary are in reality compound; and that, by the combination of these with one another, and re-combinations of the products, there are formed systems of systems of molecules, unimaginable in their complexity. Step by step as the aggregate molecules so resulting, grow larger and increase in heterogeneity, they become more unstable, more readily transformable by small forces, more capable of assuming various characters. Those composing organic matter transcend all others in size and intricacy of structure; and in them these resulting traits reach their extreme. As implied by its name *protein*, the essential substance of which organisms are built, is remarkable alike for the variety of its metamorphoses and the facility with which it undergoes them: it changes from one to another of its thousand isomeric forms on the slightest change of conditions. Now there are facts warranting the belief that though these multitudinous isomeric forms of protein will not unite directly with one another, yet they admit of being linked together by other elements with which they combine. And it is very significant that there are habitually present two other elements, sulphur and phosphorus, which have quite special powers of holding together many equivalents—the one being pentatomic and the other hexatomic. So that it is a legitmate supposition (justified by analogies) that an atom of sulphur may be a bond of union among half-a-dozen different isomeric forms of protein; and similarly with phosphorus. A moment's thought will show that, setting out with the thousand isomeric forms of protein, this makes possible a number of these combinations almost passing the power of figures to express. Molecules so produced, perhaps exceeding in size and complexity those of protein as those of protein exceed those of inorganic matter, may, I conceive, be the special units belonging to special kinds of organisms. By their constitution they must have a plasticity, or sensitiveness to modifying forces, far beyond that of protein; and bearing in mind not only that their varieties are practically infinite in number, but that closely allied forms of them, chemically indifferent to one another as they must be, may coexist in the same aggregate, we shall see that they are fitted for entering into unlimited varieties of organic structures.

The existence of such physiological units, peculiar to each species of organism, is not unaccounted for. They are evolved simultaneously with the evolution of the organisms they compose—they differentiate as fast as these organisms differentiate; and are made multitudinous in kind by the same actions which make the organism they compose multitudinous in kind. This conception is clearly representable in terms of the mechanical hypothesis. Every physicist will endorse the proposition that in each aggregate there tends to establish itself an equilibrium between the forces exercised by all the units upon each and by each upon all. Even in masses of substance so rigid as iron and glass, there goes on a molecular re-arrangement, slow or rapid according as circumstances facilitate, which ends only when there is a complete balance between the actions of the parts on the whole and the actions of the whole on the parts: the implication being that every change in the form or size of the whole, necessitates some redistribution of the parts. And though in cases like these, there occurs only a polar re-arrangement of the molecules, without changes in the molecules themselves; yet where, as often happens, there is a passage from the colloid to the crystalloid state, a change of constitution occurs in the molecules themselves. These truths are not limited to inorganic matter: they unquestionably hold of organic matter. As certainly as molecules of alum have a form of equilibrium, the octahedron, into which they fall when the temperature of their solvent allows them to aggregate, so certainly must organic molecules of each kind, no matter how complex, have a form of equilibrium in which, when they aggregate, their complex forces are balanced—a form far less rigid and definite, for the reason that they have far less definite polarities, are far more unstable, and have their tendencies more easily modified by environing conditions. Equally certain is it that the special molecules having a special organic structure as their form of equilibrium, must be reacted upon by the total forces of this organic structure; and that, if environing actions lead to any change in this organic structure, these special molecules, or physiological units, subject to a changed distribution of the total forces acting upon them will undergo modification—modification which their extreme plasticity will render easy. By this action and reaction I conceive the physiological units peculiar to each kind of organism, to have been moulded along with the organism itself. Setting out with the stage in which protein in minute aggregates, took on those simplest differentiations which fitted it for differently-conditioned parts of its medium, there must have unceasingly gone on perpetual re-adjustments of balance between aggregates and their units—actions and reactions of the two, in which the units tended ever to establish the typical form produced by actions and reactions in all antecedent generations, while the aggregate, if changed in form by change of surrounding conditions, tended ever to impress on the units a corresponding change of polarity, causing them in the next generation to reproduce the changed form—their new form of equilibrium.

This is the conception which I have sought to convey, though it seems unsuccessfully, in the *Principles of Biology;* and which I have there used to interpret the many involved and mysterious phenomena of Genesis, Heredity, and Variation. In one respect only am I conscious of having so inadequately explained myself, as to give occasion for a misinterpretation—the one made by the *Westminster* reviewer above referred to. By him, as by your own critic, it is alleged that in the idea of "inherent tendencies" I have introduced, under a disguise, the conception of "the archæus, vital principle, *nisus formativus*, and so on." This allegation is in part answered by the foregoing explanation. That which I have here to add, and did not adequately explain in the *Principles of Biology*, is that the proclivity of units of each order towards the specific arrangement seen in the organism they form, is not to be understood as resulting from their own structures and actions only; but as the product of these and the environing forces to which they are exposed. Organic evolution takes place only on condition that the masses of protoplasm formed of the physiological units, and of the assimilable materials out of which others like themselves are to be multiplied, are subject to heat of a given degree—are subject, that is, to the unceasing impacts of undulations of a certain strength and period; and, within limits, the rapidity with which the physiological units pass from their indefinite arrangement to the definite arrangement they presently assume, is proportionate to the strengths of the etherial undulations falling upon them. In its complete form, then, the conception is that these specific molecules, having the immense complexity above described, and having correspondently complex polarities which cannot be mutually balanced by any simple form of aggregation, have, for the form of aggregation in which all their forces are equilibrated, the structure of the adult organism to which they belong; and that they are compelled to fall into this structure by the co-operation of the environing forces acting on them, and the forces they exercise on one another—the environing forces being the source of the *power* which effects the re-arrangement, and the polarities of the molecules determining the *direction* in which that power is turned. Into this conception there enters no trace of the hypothesis of an "archæus or vital principle;" and the principles of molecular physics fully justify it.

It is, however, objected that "the living body in its development presents a long succession of *differing* forms; a continued series of changes for the whole length of which, according to Mr. Spencer's hypothesis, the physiological units must have an 'inherent tendency.' Could we more truly say of anything, 'it is unrepresentable in thought?'" I reply that if there is taken into account an element here overlooked, the process will not be found "unrepresentable in thought." This is the element of size or mass. To satisfy or balance the polarities of each order of physiological units, not only a certain structure of organism, but a certain size of organism is needed; for the complexities of that adult structure in which the physiological units are equilibrated, cannot be represented within the small bulk of the embryo. In many minute organisms, where the whole mass of physiological units required for the structure is present, the very thing *does* take place which it is above implied *ought* to take place. The mass builds itself directly into the complete form. This is so with *Acari*, and among the nematoid *Entozoa*. But among higher animals such direct transformations cannot happen. The mass of physiological units required to produce the size as well as the structure that approximately equilibrates them, is not all present, but has to be formed by successive additions—additions which in viviparous animals are made by absorbing, and transforming into these special molecules, the organizable materials directly supplied by the parent, and which in oviparous animals are made by doing the like with the organizable materials in the "food-yelk," deposited by the parent in the same envelope with the germ. Hence it results that, under such conditions, the physiological units which first aggregate into the rudiment of the future organism, do not form a structure like that of the adult organism, which, when of such small dimensions, does not equilibrate them. They distribute themselves so as partly to satisfy the chief among their complex polarities. The vaguely-differentiated mass thus produced cannot, however, be in equilibrium. Each increment of physiological units formed and integrated by it, changes the distribution of forces; and this has a double effect. It tends to modify the differentiations already made, bringing them a step nearer to the equilibrating structure; and the physiological units next integrated, being brought under the aggregate of polar forces exercised by the whole mass, which now approaches a step nearer to that ultimate distribution of polar forces which exists in the adult organism, are coerced more directly into the typical structure. Thus there is necessitated a series of compromises. Each successive form assumed is unstable and transitional: approach to the typical structure going on hand in hand with approach to the typical bulk.

Possibly I have not succeeded by this explanation, any more than by the original explanation, in making this process "representable in thought." It is manifestly untrue, however, that I have, as alleged, re-introduced under a disguise the conception of a "vital principle." That I interpret embryonic development in terms of Matter and Motion, cannot, I think, be questioned. Whether the interpretation is adequate, must be a matter of opinion; but it is clearly a matter of fact, that I have not fallen into the inconsistency asserted by your reviewer. At the same time I willingly admit that, in the absence of certain statements which I have now supplied, he was not unwarranted in representing my conception in the way that he has done.

But while I consider that what your reviewer has said on these two essential points, falls within the limits of legitimate criticism; I do not consider that he is justified in much that he says by implication respecting my general views.

In the first place, he conveys a totally wrong idea of the mode of interpretation he criticizes. He gives his readers no conception of the immense extensions which modern science has made of the "mechanical theory," now applied to the solution of all physical phenomena whatever; but he has deliberately restricted its applications in a way that produces an appearance of difficulty where no difficulty exists. The common uses of the words "mechanical" and "mechanist," are such as inevitably call up in all minds the notions of visible masses of matter acting on one another by measurable forces and producing sensible motions. In the absence of explanations or illustrations serving to enlarge the conception thus suggested, so as to bring within it the oscillations of the molecules of matter, and the undulations of the molecules of ether pervading all space, even the cultivated reader must carry with him an extremely crude and narrow idea of the "mechanist theory," and cannot fail to be struck with the seeming absurdity of interpreting vital phenomena in mechanical terms. But the reviewer says nothing to prevent misconceptions so arising. He gives no hint that heat, light, and electricity, are now all recognized as "modes of motion;" and that most of their phenomena are mechanically interpreted, while the rest are regarded as mechanically interpretable. He does not explain that the "mechanist" theory in its comprehensive form embraces actions such as those by which variations in the solar spots cause variations in our magnetic needles, and actions such as those through which Sirius tells us what substances are contained in his atmosphere. True he makes a passing reference to chemical changes as being included by me under the conception of mechanical; but he leaves this as a dead statement quite unintelligible to the general reader; and in the typical example he gives of my mode of interpretation (the development of vertebræ by transverse strains) he deliberately excludes the physio-chemical and chemical actions which I imply as co-operating, and describes me as attributing the effects entirely to the pressures and tensions caused by muscular movements! (See p. 408). Instead of the developed ideas of Matter and Motion everywhere implied throughout the *Principles of Biology*, the reviewer leads everyone to suppose that I bring to bear on biological problems nothing beyond the vulgar ideas of Matter and Motion, and leaves me responsible for the ludicrous incongruity!

That, however, which I regard as most reprehensible in his criticism is the way in which he persists in representing the *System of Philosophy* I am working out as a materialistic system. Already he has once before so represented it, and the injustice of so representing it has been pointed out. He knows that I have repeatedly and emphatically asserted that our conceptions of Matter and Motion are but symbols of an Unknowable Reality; that this Reality cannot be that which we symbolize it to be; and that as manifested beyond consciousness under the forms of Matter and Motion, it is the same as that which, in consciousness, is manifested as Feeling and Thought. Yet he continues to describe me as reducing everything to dead mechanism. If his statement on pp. 383-4 has any meaning at all, it means that there exists some "force operating *ab extra*," some "external power" distinguished by him as "mechanical," which is not included in that immanent force of which the universe is a manifestation; though whence it comes he does not tell us. This conception he speaks of as though it were mine; making it seem that I ascribe the moulding of organisms to the action of this "mechanical" "external power," which is distinct from the Inscrutable Cause of things. Yet he either knows, or has ample means of knowing, that I deny every such second cause: indeed he has himself classed me as an opponent of dualism. I recognize no forces within the organism, or without the organism, but the variously-conditioned modes of the universal immanent force; and the whole process of organic evolution is everywhere attributed by me to the co-operation of its variously-conditioned modes, internal and external. That this has been all along my general view, is clearly shown in the closing paragraph of *First Principles*, where I have said—

> "A Power of which the nature remains for ever inconceivable, and to which no limits in Time or Space can be imagined, works in us certain effects. These effects have certain likenesses of kind, the most general of which we class together under the names of Matter, Motion, and Force; and between these effects there are likenesses of connection, the most constant of which we class as laws of the highest certainty. Analysis reduces these several kinds of effect to one kind of effect; and these several kinds of uniformity to one kind of uniformity. And the highest achievement of Science is the interpretation of all orders of phenomena, as differently-conditioned manifestations of this one kind of effect, under differently-conditioned modes of this one kind of uniformity. But when Science has done this, it has done nothing more than systematize our experience; and has in no degree extended the limits of our experience. We can say no more than before, whether the uniformities are as absolutely necessary, as they have become to our thought relatively necessary. The utmost possibility for us, is an interpretation of the process of things as it presents itself to our limited consciousness; but how this process is related to the actual process, we are unable to conceive, much less to know. Similarly, it must be remembered that while the connection between the phenomenal order and the ontological order is for ever inscrutable; so is the connection between the conditioned forms of being and the unconditioned form of being for ever inscrutable. The interpretation of all phenomena in terms of Matter, Motion, and Force, is nothing more than the reduction of our complex symbols of thought, to the simplest symbols; and when the equation has been brought to its lowest terms the symbols remain symbols still. Hence the reasonings contained in the foregoing pages, afford no support to either of the antagonist hypotheses respecting the ultimate nature of

things. Their implications are no more materialistic than they are spiritualistic; and no more spiritualistic than they are materialistic. Any argument which is apparently furnished to either hypothesis, is neutralized by as good an argument furnished to the other. The Materialist, seeing it to be a necessary deduction from the law of correlation, that what exists in consciousness under the form of feeling, is transformable into an equivalent of mechanical motion, and by consequence into equivalents of all the other forces which matter exhibits; may consider it therefore demonstrated that the phenomena of consciousness are material phenomena. But the Spiritualist, setting out with the same data, may argue with equal cogency, that if the forces displayed by matter are cognizable only under the shape of those equivalent amounts of consciousness which they produce, it is to be inferred that these forces, when existing out of consciousness, are of the same intrinsic nature as when existing in consciousness; and that so is justified the spiritualistic conception of the external world, as consisting of something essentially identical with what we call mind. Manifestly, the establishment of correlation and equivalence between the forces of the outer and the inner worlds, may be used to assimilate either to the other; according as we set out with one or other term. But he who rightly interprets the doctrine contained in this work, will see that neither of these terms can be taken as ultimate. He will see that though the relation of subject and object renders necessary to us these antithetical conceptions of Spirit and Matter; the one is no less than the other to be regarded as but a sign of the Unknown Reality which underlies both."

This is the conception which your reviewer continues to speak of as "mechanical" and "mechanist;" without giving his readers any suspicion of the qualified sense in which only these words can be applied. If he thinks that by doing this he has represented the conception with fairness, or with any approach to fairness, I cannot agree with him.

I am, Sir,

Yours, &c.,

HERBERT SPENCER.

London, December 5, 1868.

# THE PRINCIPLES

OF

# BIOLOGY.

BY

## HERBERT SPENCER,

AUTHOR OF "SOCIAL STATICS," "THE PRINCIPLES OF PSYCHOLOGY,"
"ESSAYS: SCIENTIFIC, POLITICAL, AND SPECULATIVE,"
"FIRST PRINCIPLES," ETC.

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### Miscellaneous Writings.

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# PREFACE TO VOL. II.

THE proof sheets of this volume, like those of the last volume, have been looked through by Dr. Hooker and Prof. Huxley; and I have, as before, to thank them for their valuable criticisms, and for the trouble they have taken in checking the numerous statements of fact on which the arguments proceed. The consciousness that their many duties render time extremely precious to them, makes me feel how heavy is my obligation.

Part IV., with which this volume commences, contains numerous figures. Nearly one half of them are repetitions, mostly altered in scale and simplified in execution, of figures, or parts of figures, contained in the works of various Botanists and Zoologists. Among the authors whom I have laid under contribution, I may name Berkeley, Carpenter, Cuvier, Green, Harvey, Hooker, Huxley, Milne-Edwards, Ralfs, Smith. The remaining figures, numbering 150, are from original sketches and diagrams.

The successive instalments which compose this volume, were issued to the Subscribers at the following dates:—No. 13 (pp. 1—80) in January, 1865; No. 14 (pp. 81—160) in June, 1865; No. 15 (pp. 161—240) in December, 1865; No. 16 (pp. 241—320) in June, 1866; No. 17 (pp. 321—400) in November, 1866; and No. 18 (pp. 401—566) in March, 1867.

*London, March 23rd,* 1867.

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# PART IV.

# MORPHOLOGICAL DEVELOPMENT.

# CHAPTER I.

## THE PROBLEMS OF MORPHOLOGY.

§ 175. THE division of Morphology from Physiology, is one which may be tolerably-well preserved, so long as we do not carry our inquiries beyond the empirical generalizations of their respective phenomena; but it is one which becomes in great measure nominal, when the phenomena are to be rationally interpreted. It would be possible, after analyzing our Solar System, to set down certain general truths respecting the sizes and distances of its primary and secondary members, omitting all mention of their motions; and it would be possible to set down certain other general truths respecting their motions, without specifying their dimensions or positions, further than as greater or less, nearer or more remote. But on seeking to account for these general truths, arrived at by induction, we find ourselves obliged to consider simultaneously the relative sizes and places of the masses, and the relative amounts and directions of their motions. Similarly with organisms. Though we may frame sundry comprehensive propositions respecting the arrangements of their organs, considered as so many inert parts; and though we may establish several wide conclusions respecting the separate and combined actions of their organs, without knowing anything definite respecting the forms and positions of these organs; yet we cannot reach such a rationale of the facts as the hypothesis of Evolution aims at, without contemplating structures and functions in their mutual relations. Everywhere structures in great measure determine functions; and everywhere functions are incessantly modifying structures. In Nature, the two are inseparable co-operators; and Science can give no true interpretation of Nature, without keeping their co-operation constantly in view. An account of organic evolution, in its more special aspects, must be essentially an account of the inter-actions of structures and functions, as perpetually altered by changes of conditions.

Hence, when treating apart Morphological Development and Physiological Development, all we can do is to direct our attention mainly to the one or to the other, as the case may be. In dealing with the facts of structure, we shall consider the facts of function, only in such general way as is needful to explain the facts of structure; and conversely when dealing with the facts of function.

§ 176. The problems of Morphology fall into two distinct classes, answering respectively to the two leading aspects of Evolution. In things which evolve there go on two processes—increase of mass and increase of structure. Increase of mass is primary, and in simple evolution takes place almost alone. Increase of structure is secondary, accompanying or following increase of mass with more or less regularity, wherever evolution rises above that form which small inorganic bodies, such as crystals, present to us. The fundamental antagonism between Dissolution and Evolution consisting in this, that while the one is an integration of motion and disintegration of matter, the other is an integration of matter and disintegration of motion; and this integration of matter accompanying disintegration of motion, being a necessary antecedent to the differentiation of the matter so integrated; it follows that questions concerning the mode in which the parts are united into a whole, must be dealt with before questions concerning the mode in which these parts become modified.*

This is not obviously a morphological question. But an illustration or two will make it manifest, that fundamental differences may be produced between aggregates, by differences in the degrees of composition of the increments: the ultimate units of the increments being the same. Thus an accumulation of things of a given kind may be made by adding one at a time. Or the things may be tied up into bundles of ten, and the tens placed together. Or the tens may be united into hundreds, and a pile of hundreds formed. Such unlikenesses in the structures of masses, are habitually seen in our mercantile transactions. Articles which the consumer recognizes as single, the retailer keeps wrapped up in dozens, the wholesaler sends the gross, and the manufacturer supplies in packages of a hundred gross—that is, they severally increase their stocks by units of simple, of compound, and of doubly-compound kinds. Similarly result those differences of morphological composition which we have first to consider. An organism consists of units. These units may be aggregated into a mass by the addition of unit to unit. Or they may be united into groups, and the groups joined together. Or these groups of groups may be so combined as to form a doubly-compound aggregate. Hence there arise respecting each organic form, the question—is its composition of the first, second, third, or fourth order?—does it exhibit units of a singly-compounded kind only; or are these consolidated into units of a doubly-compounded kind, or a triply-compounded kind? And if it displays double or triple composition, the

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* It seems needful here to say, that allusion is made in this paragraph to a proposition respecting the ultimate natures of Evolution and Dissolution, which is contained in an essay on *The Classification of the Sciences*, published in March, 1864. When the opportunity comes, I hope to make the definition there arrived at, the basis of a re-organization of the second part of *First Principles*: giving to that work a higher development, and a greater cohesion, than it at present possesses.

homologies of its different parts become problems. Under the disguises induced by the consolidation of primary, secondary, and tertiary units, it has to be ascertained which answer to which, in their degrees of composition.

Such questions are more intricate than they at first appear; since, besides the obscurities caused by progressive integration, and those due to accompanying modifications of form, further obscurities result from the variable growths of units of the different orders. Just as an army may be augmented by recruiting in each company, without increasing the number of companies; or may be augmented by making up the full complement of companies in each regiment, while the number of regiments remains the same; or may be augmented by putting more regiments into each division, other things being unchanged; or may be augmented by adding to the number of its divisions without altering the components of each division; or may be augmented by two or three of these processes at once; so, in organisms, increase of mass may be due to growth in units of the first order, or in those of the second order, or in those of still higher orders; or it may be due to simultaneous growth in units of several orders. And this last mode of integration being the general mode, puts difficulties in the way of analysis. Just as the structure of an army would be made less easy to understand, if companies often outgrew regiments, or regiments became larger than brigades; so these questions of morphological composition, are complicated by the indeterminate sizes of the units of each kind—relatively-simple units frequently becoming far more bulky than relatively-compound units.

§ 177. The morphological problems of the second class, are those having for their subject-matter the changes of shape that accompany changes of aggregation. The most general questions respecting the structure of an organism, having been answered when it is ascertained of what units it is composed as a whole, and in its several parts; there come the more special questions concerning its form—form in the ordinary sense. After the contrasts caused by variations in the process of integration, we have to consider the contrasts caused by variations in the process of differentiation. To speak specifically—the shape of the organism as a whole, irrespective of its composition, has to be accounted for. Reasons have to be found for the unlikeness between its general outlines and the general outlines of allied organisms. And there have to be answered kindred inquiries respecting the proportions of its component parts:—Why, among such of these as are homologous with one another, have there arisen the differences that exist? And how have there been produced the contrasts between them and the homologous parts of organisms of the same type?

Very numerous are the heterogeneities of form that present themselves for interpretation under these heads. The ultimate morphological units combined in any group, may be differentiated individually, or collectively, or both: each of them may undergo changes of shape; or some of them may be changed and others not; or the group may be rendered multiform by the greater growth of some of its units than of others. Similarly with the compound units, arising by union of these simple units. Aggregates of the second order may be made relatively complex in form, by inequalities in the rates of multiplication of their component units in diverse directions; and among a number of such aggregates, numerous unlikenesses may be constituted by differences in their degrees of growth, and by differences in their modes of growth. Manifestly, at each higher stage of composition, the possible sources of divergence are multiplied still further.

That facts of this order can be accounted for in detail, is not to be expected—the data are wanting. All that we may hope to do, is to ascertain their general laws. How this is to be attempted we will now consider.

§ 178. The task before us is to trace throughout these phenomena the process of evolution; and to show how, as displayed in them, it conforms to those first principles which evolution in general conforms to. Two sets of factors have to be taken into account. Let us look at them.

The factors of the first class are those which tend directly to change an organic aggregate, in common with every other aggregate, from that more simple form which is not in equilibrium with incident forces, to that more complex form which is in equilibrium with them. We have to mark how, in correspondence with the universal law that the uniform lapses into the multiform, and the less multiform into the more multiform, the parts of each organism are ever becoming further differentiated; and we have to trace the varying relations to incident forces, by which further differentiations are entailed. We have to observe, too, how each primary modification of structure, induced by an altered distribution of forces, becomes a parent of secondary modifications—how, through the necessary multiplication of effects, change of form in one part brings about changes of form in other parts. And then we have also to note the metamorphoses constantly being induced by the process of segregation—by the gradual union of like parts exposed to like forces, and the gradual separation of like parts exposed to unlike forces. The factors of the second class which we have to keep in view throughout our interpretations, are the formative tendencies of organisms themselves—the proclivities inherited by them from antecedent organisms, and which past processes of evolution have bequeathed. We have seen it to be a necessary inference from various orders of facts (§§ 65, 84, 97,) that organisms are built up of certain highly-complex molecules, which we distinguished as physiological units—each kind of organism being built up of physiological units peculiar to itself. We found ourselves obliged to recognize in these physiological units, powers of arranging themselves into the forms of the organisms to which they belong; analogous to the powers which the molecules of inorganic substances have of aggregating into specific crystalline forms. We have consequently to regard this polarity of the physiological units, as producing, during the development of any organism, a combination of internal forces that expend themselves in working out a structure in equilibrium with the forces to which ancestral organisms were exposed; but not in equilibrium with the forces to which the existing organism is exposed, if the environment has been changed. Hence the problem in all cases, is, to ascertain the resultant of internal organizing forces, tending to reproduce the ancestral form, and external modifying forces, tending to cause deviations from that form. Moreover, we have to take into account, not only the characters of immediately-preceding ancestors, but also those of their ancestors, and ancestors of all degrees of remoteness. Setting out with rudimentary types, we have to consider how, in each successive stage of evolution, the structures acquired during previous stages, have been obscured by further integrations and further differentiations; or, conversely, how the lineaments of primitive organisms have all along continued to manifest themselves under the superposed modifications.

§ 179. Two ways of carrying on the inquiry suggest themselves. We may go through the several great groups of organisms, with the view of reaching, by comparison of parts, certain general truths respecting the homologies, the forms, and the relations of their parts; and then, having dealt with the phenomena inductively, may retrace our steps with the view of deductively interpreting the general truths reached. Or, instead of thus separating the two investigations, we may carry them on hand in hand—first establishing each general truth empirically, and then proceeding to the rationale of it. This last method will, I think, conduce to both brevity and clearness. Let us now thus deal with the first class of morphological problems.

# CHAPTER II.

## THE MORPHOLOGICAL COMPOSITION OF PLANTS.

§ 180. Evolution implies insensible modifications and gradual transitions, which render definition difficult—which make it impossible to separate absolutely the phases of organization from one another. And this indefiniteness of distinction, to be expected *à priori*, we are compelled to recognize *à posteriori*, the moment we begin to group morphological phenomena into general propositions. Thus, on inquiring what is the morphological unit, whether of plants or of animals, we find that the facts refuse to be included in any rigid formula. The doctrine that all organisms are built up of cells, or that cells are the elements out of which every tissue is developed, is but approximately true. There are living forms of which cellular structure cannot be asserted; and in living forms that are for the most part cellular, there are nevertheless certain portions which are not produced by the metamorphosis of cells. Supposing that clay were the only material available for building, the proposition that all houses are built of bricks, would bear about the same relation to the truth, as does the proposition that all organisms are composed of cells. This generalization respecting houses would be open to two criticisms: first, that certain houses of a primitive kind are formed, not out of bricks, but out of unmoulded clay; and second, that though other houses consist mainly of bricks, yet their chimney-pots, drain-pipes, and ridge-tiles do not result from combination or metamorphosis of bricks, but are made directly out of the original clay. And of like natures are the criticisms which must be passed on the generalization, that cells are the morphological units of organisms. To continue the simile, the truth turns out to be, that the primitive clay or protoplasm out of which organisms are built, may be moulded either directly, or with various degrees of indirectness, into organic structures. The physiological units which we are obliged to assume as the components of this protoplasm, must, as we have seen, be the possessors of those complex polarities which result in the structural arrangements of the organism. The assumption of such structural arrangements may go on, and, in many cases, does go on, by the shortest route; without the passage through what we call metamorphoses. But where such structural arrangements are reached by a circuitous route, the first stage is the formation of these small aggregates, which, under the name of cells, are currently regarded as morphological units.

The rationale of these truths appears to be furnished by the hypothesis of evolution. We set out with molecules one degree higher in complexity than those molecules of nitrogenous colloidal substance into which organic matter is resolvable; and we regard these somewhat more complex molecules as having the implied greater instability, greater sensitiveness to surrounding influences, and consequent greater mobility of form. Such being the primitive physiological units, organic evolution must begin with the formation of a minute aggregate of them—an aggregate showing vitality only by a higher degree of that readiness to change its form of aggregation, which colloidal matter in general displays; and by its ability to unite the nitrogenous molecules it meets with, into complex molecules like those of which it is composed. Obviously, the earliest forms must have been minute; since, in the absence of any but diffused organic matter, no form but a minute one could find nutriment. Obviously, too, it must have been structurelesss; since, as differentiations are producible only by the unlike actions of incident forces, there could have been no differentiations before such forces had had time to work. Hence, distinctions of parts like those required to constitute a cell, were necessarily absent at first. And we need not therefore be surprised to find, as we do find, specks of protoplasm manifesting life, and yet showing no signs of organization. A further stage of evolution is reached, when the very imperfectly integrated molecules forming one of these minute aggregates, become more coherent; at the same time as they pass into a state of heterogeneity, gradually increasing in its definiteness. That is to say, we may look for the assumption by them, of some distinctions of parts, such as we find in cells, and in what are called unicellular organisms. They cannot retain their primordial uniformity; and while in a few cases they may depart from it but slightly, they will, in the great majority of cases, acquire a very decided multiformity—there will result the comparatively integrated and comparatively differentiated *Protophyta* and *Protozoa*. The production of minute aggregates of physiological units, being the first step; and the passage of such minute aggregates into more consolidated and more complex forms, being the second step; it must naturally happen that all higher organic types, subsequently arising by further integrations and differentiations, will everywhere bear the impress of this earliest phase of evolution. From the law of heredity, considered as extending to the entire succession of living things during the Earth's past history, it follows, that since the formation of these small, simple organisms, must have preceded the formation of larger and more complex organisms, the larger and more complex organisms must inherit their essential characters. We may anticipate that the multiplication and combination of these minute aggregates or cells, will be conspicuous in the early developmental stages of plants and animals; and that throughout all subsequent stages, cell-production and cell-differentiation will be dominant characteristics. The physiological units peculiar to each higher species, will, speaking generally, pass through this form of aggregation on their way towards the final arrangement they are to assume; because those primordial physiological units from which they are remotely descended, aggregated into this form. And yet, just as in other cases we found reasons for inferring (§ 131), that the traits of ancestral organization may, under certain conditions, be partially or wholly obliterated, and the ultimate structure assumed without passing through them; so, here, it is to be inferred that the process of cell-formation may, in some cases, be passed over. Thus the hypothesis of evolution prepares us for those two radical modifications of the cell-doctrine, which the facts oblige us to make. It leads us to expect that as structureless portions of protoplasm must have preceded cells in the process of general evolution; so, in the special evolution of each higher organism, there will be an habitual production of cells out of structureless blastema. And it leads us to expect that though, generally, the physiological units composing a structureless blastema, will display their inherited proclivities by cell-development and metamorphosis; there will nevertheless occur cases in which the tissue to be formed, is formed by direct transformation of the blastema.

Interpreting the facts in this manner, we may recognize that large amount of truth which the cell-doctrine contains, without committing ourselves to the errors involved by the sweeping assertion of it. We are enabled to understand how it happens that organic structures are usually cellular in their composition, at the same time that they are not universally so. We are shown that while we may properly continue to regard the cell as the morphological unit, we must constantly bear in mind that it is such, only in a greatly-qualified sense.*

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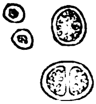
* Let me here refer those who are interested in this question, to Prof. Huxley's criticism on the cell-doctrine, published in the *Medico-Chirurgical Review* in 1853.

§ 181. These aggregates of the lowest order, each formed of physiological units united into a group that is structurely single, and cannot be divided without destruction of its individuality, may, as above implied, exist as independent organisms. The assumption to which we are committed by the hypothesis of evolution, that such so-called uni-cellular plants, were at first the only kinds of plants, is in harmony with the fact that habitats not occupied by plants of higher orders, commonly contain these protophytes in great abundance and great variety. The various species of *Protococcus*, of *Desmidiaceæ*, and *Diatomaceæ*, supply examples of morphological units living and propagating separately, under numerous modifications of form and structure. Figures 1, 2, and 3, represent a few of the commonest types.



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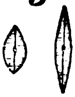

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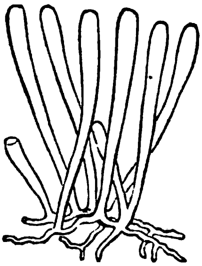
Mostly, simple plants are too small to be individually visible without the microscope. But, in some cases, these vegetal aggregates of the first order, grow to appreciable sizes. In the mycelium of some fungi, we have single cells developed into long branched filaments, or ramified tubules, that are of considerable lengths. An analogous structure characterizes certain tribes of *Algæ*, of which *Codium adhærens*, Fig. 4, may serve as an example. In *Hydrogastrum*, another alga, Fig. 5, we have a structure which is described as



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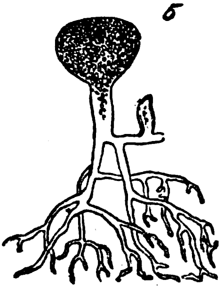

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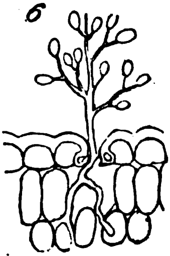

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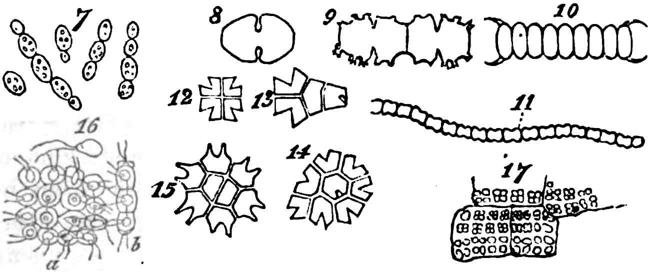
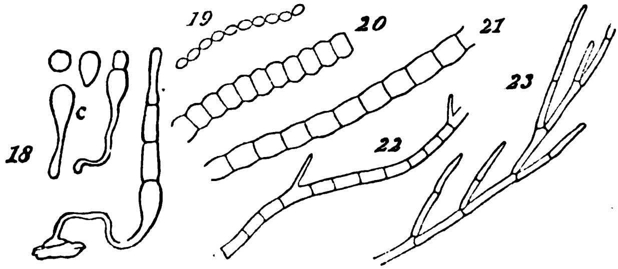
simulating a perfect plant, with root, stem, bud, and fruit, all produced by the branching of a single cell. And among fungi, the genus *Botrytis*, Fig. 6, furnishes an illustration of allied kind. Here, though the size attained is much greater than that of many organisms which are morphologically compound, we are compelled to consider the morphological composition as simple; since the whole can no more be separated into minor wholes, than can the branched vascular system of an animal. In these cases, we have considerable bulk attained, not by a number of aggregates of the first order being united into an aggregate of the second order; but by the continuous growth of an aggregate of the first order.

§ 182. The transition to higher forms begins in a very unobtrusive manner. Among these aggregates of the first order, an approach towards that union by which aggregates of the second order are produced, is indicated by mere juxtaposition. Protophytes multiply rapidly; and their rapid multiplication sometimes causes crowding. When, instead of floating free in the water, they form a thin film on a moist surface, or are imbedded in a common matrix of mucus; the mechanical obstacles to dispersion result in a kind of feeble integration, vaguely shadowing forth a combined group. Somewhat more definite combination is shown us by such plants as *Palmella botryoides*. Here the members of a family of cells, arising by the spontaneous fission of a parent-cell, remain united by slender threads of that jelly-like substance which envelops their surfaces. In some *Diatomaceæ*, several individuals, instead of completely separating, hold together by their angles; and in other *Diatomaceæ*, as the *Bacillaria*, a variable number of units cohere so slightly, that they are continually moving in relation to one another.

This formation of aggregates of the second order, faintly indicated in feeble and variable unions like the above, may be traced through phases of increasing permanence and definiteness, as well as increasing extent. In the yeast-plant, Fig. 7, we have cells which may exist singly, or joined into groups of several; and which have their shapes scarcely at all modified by their connexion. Among the *Desmidiaceæ*, it happens in many cases, that the two individuals produced by division of a parent-individual, part as soon as they are fully formed; but in other cases, instead of parting they compose a group of two. Allied kinds show us how, by subsequent fissions of the adherent individuals and their progeny, there result longer groups; and in some species, a continuous thread of them is thus produced. Figs. 8, 9, 10, 11, exhibit these several stages. Instead of linear aggregation, some of the *Desmidiaceæ* illustrate central aggregation; as shown in Figs. 12, 13, 14, 15. Other instances of central aggregation are furnished by such protophytes as the *Gonium pectorale*, Fig. 16 (*a* being the front view, and *b* the edge view), and the *Sarcina ventriculi*, Fig. 17. Further, we have that spherical mode of aggregation of which the *Volvox globator* furnishes a familiar instance.



Thus far, however, the individuality of the secondary aggregate is feebly pronounced: not simply in the sense that it is small; but also in the sense that the individualities of the primary aggregates are very little subordinated. But on seeking further, we find transitions towards forms in which the compound individuality is more dominant, while the simple individualities are more obscured. Obscuration of one kind, accompanies mere increase of size in the secondary aggregate: in proportion to the greater number of the morphological units held together in one mass, becomes their relative insignificance as individuals. We see this in the irregularly-spreading lichens that form patches on rocks; and in such creeping fungi as grow in films or laminæ on decaying wood and the bark of trees. In these cases, however, the integration of the component cells is of an almost mechanical kind. The aggregate of them is scarcely more individuated than a lump of inorganic matter: as witness the way in which the lichen extends its curved edges in this or that direction, as the surface favours; or the way in which the fungus grows round and imbeds the shoots and leaves that lie in its way, just as so much plastic clay might do. Though here, in the augmentation of mass, we see a progress towards the evolution of a higher type; we have as yet none of that definiteness required to constitute a compound unit, or true aggregate of the second order. Another kind of obscuration of the morphological units, is brought about by their more complete coalescence into the form of some structure made by their union. This is well exemplified among the *Confervæ*, and their allies. In Fig. 18, there are represented the stages of a growing *Mougeotia genuflexa*, in which this merging of the simple individualities into the compound individuality, is shown in the history of a single plant; and in Figs. 19, 20, 21, 22, 23, are represented a series of species from this group, and that of *Cladophora*, in which we see a progressing integration. While in the lower types, the primitive spheroidal forms of the cells are scarcely



altered; in the higher types, the cells are so fused together as to constitute cylinders divided by septa. Here, however, the indefiniteness is still great: there are no specific limits to the length of any thread thus produced; and none of that differentiation of parts required to give a decided individuality to the whole.

To constitute something like a true aggregate of the second order, capable of serving as a compound unit, that may be combined with others like itself into still higher aggregates, there must exist both mass and definiteness.

§ 183. An approach towards plants which unite these characters, may be traced in such forms as *Bangia ciliaris*, Fig. 24. The multiplication of cells here takes place, not in a longitudinal direction only, but also in a transverse direction; and the transverse multiplication being greater towards the middle of the frond, there results a difference between the middle and the two extremities—a character which, in a feeble way, unites all the parts into a whole. Even this slight individuation is, however, very indefinitely marked; since, as shown by the figures, the lateral multiplication of cells does not go on in a precise manner.

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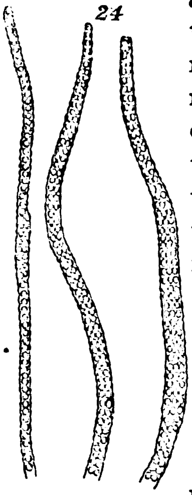
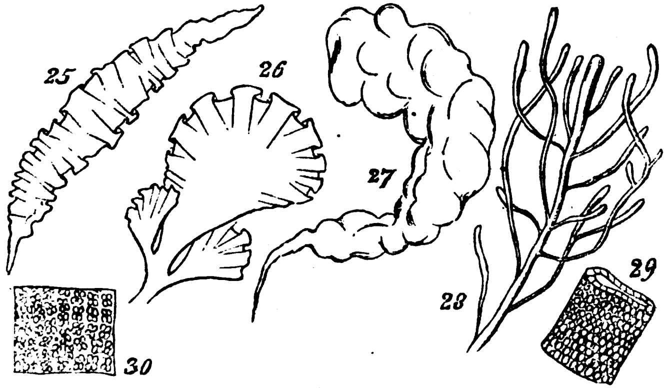


From some such type as this there appear to arise, by slight differences in the modes of growth, two closely-allied groups of plants, having individualities somewhat more pronounced. If, while the cells multiply longitudinally, their lateral multiplication goes on in one direction only, there results a flat surface, as in *Ulva linza*, Fig. 25; or where the lateral multiplication is less uniform in its rate, in types like Fig. 26. But where the lateral multiplication occurs in two directions transverse to one another, a hollow frond may be produced—sometimes irregularly spheroidal, and sometimes irregularly tubular; as in *Enteromorpha intestinalis*, Fig. 27. And occasionally, as in *Enteromorpha compressa*, Fig. 28, this tubular frond becomes branched. Figs. 29 and 30 are magnified portions of such fronds; showing the simple cellular aggregation which allies them with the preceding forms.

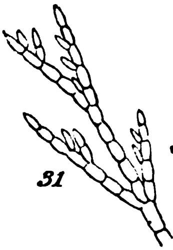


In the common *Fuci* of our coasts, other and somewhat higher stages of this integration are displayed. We have fronds preserving something like constant breadths; and dividing dichotomously with approximate regularity. Though the sub-divisions so produced, are not to be regarded at all as separate fronds, but only as extensions of one frond, they foreshadow a higher degree of composition; and by the comparatively methodic way in which they are united, give to the aggregate a more definite, as well as a more complex, individuality. Many of the higher lichens exhibit an analogous advance. While in the lowest lichens, the different parts of the thallus are held together only by being all attached to the supporting surface, in the higher lichens the thallus is so far integrated that it can support itself by attachment to such surface at one point only. And then, in still more developed kinds, we find the thallus assuming a dichotomously-branched form, and so gaining a more specific character as well as greater size.

Where, as in types like these, the morphological units show an inherent tendency to arrange themselves in a manner that is so far constant as to give characteristic proportions, we may say that there is a recognizable compound individuality. Considering the Thallogens that grow in this way, apart from their kinships, and wholly with reference to their morphological composition, we might not inaptly describe them as pseudo-foliar.

§ 184. Another mode in which aggregation is so carried on as to produce a compound individuality of considerable definiteness, is variously displayed among other families of *Algæ*. When the cells, instead of multiplying longitudinally alone, and instead of all multiplying laterally as well as longitudinally, multiply laterally only at particular places; they produce a branched structure.

Indications of this mode of aggregation occur among the *Confervæ* and simple plants akin to them, as shown in Figs. 22, 23. Though, in some of the more developed *Algæ* which exhibit the ramified arrangement in a higher degree, the component cells are, like those of the lower *Algæ*, united together end to end, in such way as but little to obscure their separate forms, as in *Cladophora Hutchinsiæ*, Fig. 31; they nevertheless evince greater subordination to the whole of which they are parts, by arranging themselves more method-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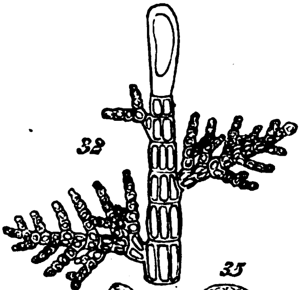
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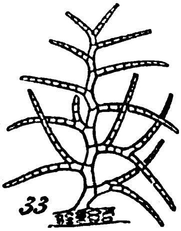
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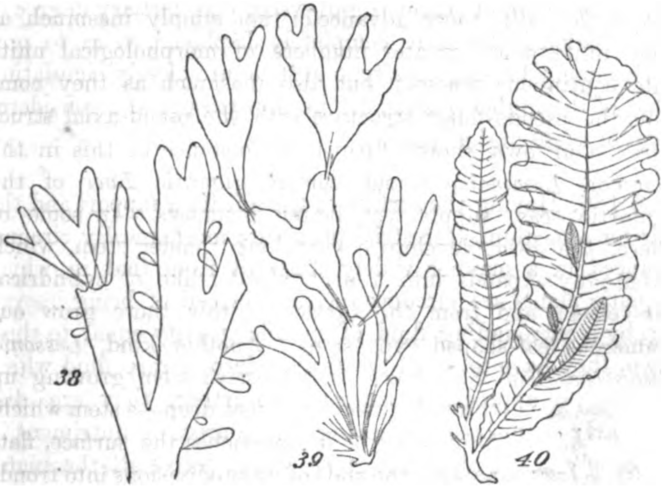
ically. Still further pronounced becomes the compound individuality, when, while the component cells of the branches unite completely into jointed cylinders, the component cells of the stem begin to multiply laterally, so as to form an axis distinguished by its relative thickness and complexity. Such types of structures are indicated by Figs. 32, 33—figures representing small portions of plants which are quite tree-like in their entire outlines. On examining Figs. 34, 35, 36, which show the structures of the stems in these types, it will be seen, too, that the component cells in becoming more coherent, have undergone changes of form which obscure their individualities more than before: not only are they much elongated, but they are so compressed as to be prismatic rather than cylindrical. This structure, besides displaying integration of the morphological units carried on in two directions instead of one; and besides displaying this higher integration in the greater merging of the individualities of the morphological units in the general individuality; also displays it in the more pronounced subordination of the branches and branchlets to the main stem. This differentiation and consolidation of the stem, brings all the secondary growths into more marked dependence; and so renders the individuality of the aggregate more decided.

We might not inappropriately call this type of structure pseud-axial. It simulates that of the higher plants in certain leading characters. We see in it a primary axis along which development may continue indefinitely, and from which there bud out, laterally, secondary axes of like nature, bearing like tertiary axes; and this is the mode of growth with which Phænogams make us familiar. But the resemblance goes no further; for these pseud-axes are devoid of those lateral appendages—those leaves or foliar organs—which true axes bear, and the bearing of which ordinarily constitutes them true axes.

§ 185. Some of the larger *Algæ* supply examples of an integration still more advanced: not simply inasmuch as they unite much greater numbers of morphological units into continuous masses; but also inasmuch as they combine the pseudo-foliar structure with the pseud-axial structure. Our own shores furnish an instance of this in the common *Laminaria;* and certain gigantic *Fuci* of the Antartic seas, supply yet better instances. In some of these, the germ develops a very long slender stem, which eventually expands into a large bladder-like or cylindrical air-vessel; and from the surface of this there grow out numerous leaf-shaped expansions. Another kind, *Lessonia fuscescens,* Fig. 37, shows us a massive stem growing up through water many feet deep—a stem which, bifurcating as it approaches the surface, flattens out the ends of its subdivisions into fronds like ribands. These, however, are not true foliar appendages, since they are merely expanded continuations of the stem. The whole plant, great as is its size, and made up though it seems to be of many groups of morphological units, united into a compound group by their marked subordination to a connecting mass, is nevertheless a single thallus. The aggregate is still an aggregate of the second order.

But among certain of the highest *Algæ,* we *do* find something more than this union of the pseud-axial with the pseudo-foliar structure. In addition to pseud-axes of comparative complexity; and in addition to pseudo-folia that are like leaves, not only in their general shapes, but in having mid-ribs and even veins; there are the beginnings of a higher stage of integration. Figs. 38, 39, and 40, show some of the steps. In *Rhodymenia palmata,* Fig. 38, the parent-frond is comparatively irregular in shape, and without a mid-rib; and along with this very imperfect integration, we see that the secondary fronds growing from

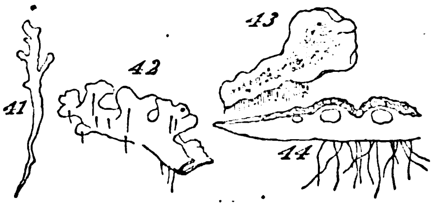


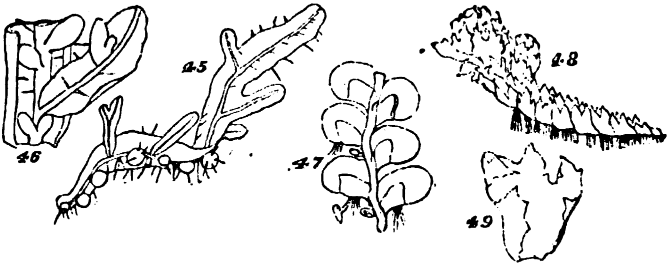
the edges are distributed very much at random, and are by no means specific in their shapes. A considerable advance is displayed by *Phyllophora rubens*, Fig. 39. Here the frond, primary, secondary, or tertiary, betrays some approach towards regularity in both form and size; by which, as also by its partially-developed mid-rib, there is established a more marked individuality; and at the same time, the growth of the secondary fronds no longer occurs anywhere on the edge, in the same plane as the parent frond, but from the surface at specific places. *Delesseria sanguinea*, Fig. 40, illustrates a much more definite arrangement of the same kind. The fronds of this plant, quite regularly shaped, have their parts decidedly subordinated to the whole; and from their mid-ribs grow other fronds, which are just like them. Each of these fronds is an organized group of those morphological units which we distinguish as aggregates of the first order. And in this case, two or more such aggregates of the second order, well individuated by their forms and structures, are united together; and the plant composed of them is thus rendered, in so far, an aggregate of the third order.

Just noting that in certain of the most-developed *Algæ*, as the *Sargassum*, or common gulf-weed, this tertiary degree of composition is far more completely displayed, so as to produce among Thallogens a type of structure closely simulating that of the higher plants, let us now pass to the consideration of these higher plants.

§ 186. Having the surface of the soil for a support and the air for a medium, terrestrial plants are mechanically circumstanced in a manner widely different from that in which aquatic plants are circumstanced. Instead of being buoyed up by a surrounding fluid of specific gravity equal to their own, they have to erect themselves into a rare fluid which yields no appreciable support. Further, they are dissimilarly conditioned in having two sources of nutriment in place of one. Unlike the *Algæ*, which derive all the materials for their tissues from the water bathing their entire surfaces, and use their roots only for attachment; most of the plants which cover the Earth's surface, absorb part of their food through their imbedded roots and part through their exposed leaves. These two marked unlikenesses in the relations to surrounding conditions, profoundly affect the respective modes of growth. We must duly bear them in mind while studying the further advance of composition.

The class of plants to which we now turn—that of Acrogens—is nearly related by its lower members to the classes above dealt with: so much so, that some of the inferior liverworts are quite licheniform, and are often mistaken for lichens. Passing over these, let us recommence our analysis with such members of the class, as repeat those indications of progress towards a higher composition, which we have just observed among the more-developed *Algæ*. The *Jungermanniaceæ* furnish us with a series of types, clearly indicating the transition from an aggregate of the second order to an aggregate of the third order. Figs. 41, and 42, indicate the structure among the lowest of this group. Here there is but an incomplete development of the second order of aggregate. The frond grows as irregularly as the thallus of a lichen: it is indefinite in size and outline, spreading hither or thither as the conditions favour. Moreover, it lacks the differentiations required to subordinate its parts to the whole: it is uniformly cellular, having neither mid-rib nor veins; and it puts out rootlets indifferently from all parts of its under-surface. In Fig 43, *Jungermannia epiphylla*, we have an advance on this type. There is here, as shown in the transverse section, Fig. 44, a thickening of the frond along its central portion, producing something like an approach towards a mid-rib; and from this the rootlets are chiefly given off. The outline, too, is much less irregular; whence results greater distinctness of the individuality. A further step is displayed in *Jungermannia furcata*, Fig. 45. The frond of this plant, comparatively well integrated by the distribution of its substance around a decided mid-rib, and by its comparatively-definite outlines, produces secondary fronds—there is what is called proliferous growth; and, occasionally, as shown in Fig. 46, representing an enlarged portion, the growth is doubly-proliferous. In these cases, however, the tertiary aggregate, so far as it is formed, is but very feebly integrated; and its integration is but temporary. For not only do these younger fronds that bud out from the mid-ribs of older fronds, develop rootlets of their own; but as soon as they are well grown and adequately rooted, they dissolve their connexions with the parent-fronds, and become quite independent. From these transitional forms we pass, in the higher *Jungermanniaceæ*, to forms composed of many fronds that are permanently united by a continuous stem. A more-developed ag-





gregate of the third order is thus produced. But though, along with increased definiteness in the secondary aggregates, there is here an integration of them so extensive and so regular, that they are visibly subordinated to the whole they form; yet the subordination is really very incomplete. In some instances, as in *J. complanata*, Fig. 47, the leaflets develop roots from their under surfaces, just as the primitive frond does; and in the majority of the group, as in *J. capitata*, Fig. 48, roots are given off all along the connecting stem, at the spots where the leaflets or frondlets join it: the result being, that though the connected frondlets form a physical whole, they do not form, in any decided manner, a physiological whole; since successive portions of the united series, carry on their functions independently of the rest. Finally, the most developed members of the group, present us with tertiary aggregates that are physiologically as well as physically integrated. Not lying prone like the kinds thus far described, but growing erect, the stem and attached leaflets become dependent upon a single root or group of roots; and being so prevented from carrying on their functions separately, are made members of a compound individual—there arises a definitely-established aggregate of the third degree of composition.

The facts as arranged in the above order, are suggestive. Minute aggregates, or cells, the grouping of which we traced in § 182, showed us analogous phases of indefinite union, which appeared to lead the way towards definite union. We see here among compound aggregates, as we saw there among simple aggregates, the establishment of a specific form, and a size that falls within moderate limits of variation. This passage from less definite extension to more definite extension, seems in the one case, as the other, to be accompanied by the result, that growth exceeding a certain rate, ends in the formation of a new aggregate, rather than an enlargement of the old. And on the higher stage, as on the lower, this process, irregularly carried out in the simpler types, produces in them unions that are but temporary; while in the more-developed types, it proceeds in a systematic way, and ends in the production of a permanent aggregate that is doubly compound.

Must we then conclude, that as cells, or morphological units, are integrated into a unit of a higher order, which we call a thallus or frond; so, by the integration of fronds, there is evolved a structure such as the above-delineated species possess? Whether this is the interpretation to be given of these plants, we shall best see when considering whether it is the interpretation to be given of plants that rank above them. Thus far we have dealt only with the Cryptogamia. We have now to deal with the Phanerogamia or Phænogamia.

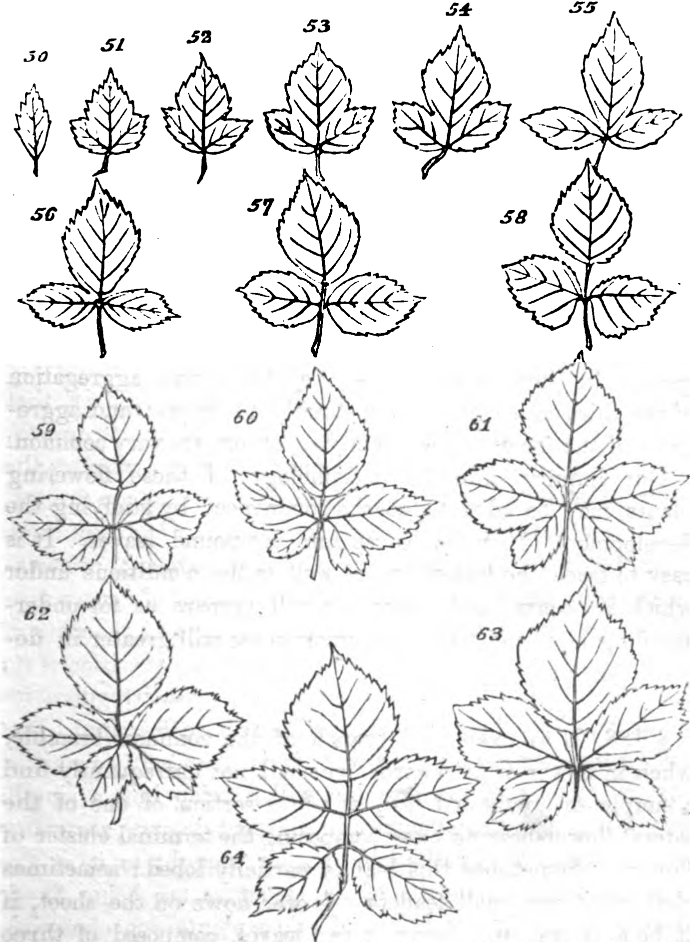
# CHAPTER III.

## THE MORPHOLOGICAL COMPOSITION OF PLANTS, CONTINUED.

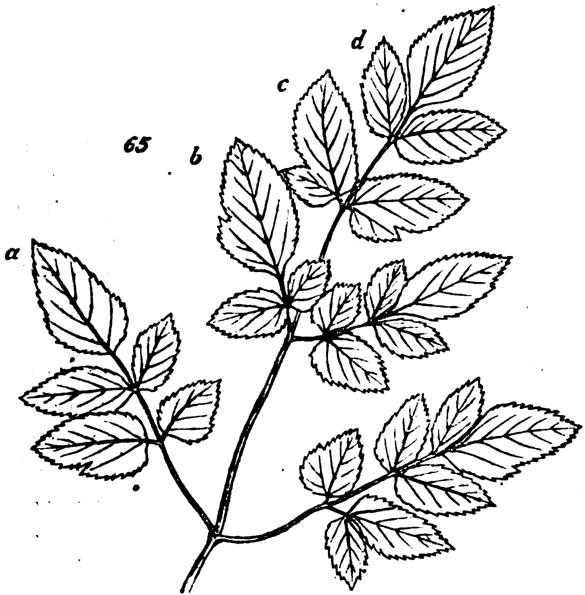
§ 187. That advanced composition arrived at in the Acrogens, is carried still further in the Endogens and Exogens. In these most-elevated vegetal forms, aggregation of the third order is always distinctly displayed; and aggregates of the fourth, fifth, sixth, &c., orders are very common.

Our inquiry into the morphology of these flowering plants, may be advantageously commenced by studying the development of simple leaves into compound leaves. It is easy to trace the transition, as well as the conditions under which it occurs; and tracing it will prepare us for understanding how, and when, metamorphoses still greater in degree, take place.

§ 188. If we examine a branch of the common bramble, when in flower or afterwards, we shall not unfrequently find a simple or undivided leaf, at the insertion of one of the lateral flower-bearing axes, composing the terminal cluster of flowers. Sometimes this leaf is partially lobed; sometimes cleft into three small leaflets. Lower down on the shoot, if it be a lateral one, occur larger leaves, composed of three leaflets; and in some of these, two of the leaflets may be lobed more or less deeply. On the main stem, the leaves, usually still larger, will be found to have five leaflets. Supposing the plant to be a well-grown one, it will furnish all gradations between the simple, very small leaf, and the large composite leaf, containing sometimes even seven leaflets. Figs. 50 to 64, represent leading stages of the transition.



What determines this transition? Observation shows that the quintuple leaves occur where the materials for growth are supplied in greatest abundance; that the leaves become less and less compound, in proportion to their remoteness from the main currents of sap; and that where an entire absence of divisions or lobes is observed, it is on leaves within the flower-bunch: at the place, that is, where the forces that cause growth are nearly equilibrated by the forces that oppose growth; and where, as a consequence, gamogenesis is about to set in (§ 78). Additional evidence that the degree of nutrition determines the degree of composition of the leaf, is furnished by the relative sizes of the leaves. Not only, on the average, is the quintuple leaf much larger in its total area than the triple leaf; but the component leaflets of the one, are usually much larger than those of the other. The like contrasts are still more marked between triple leaves and simple leaves. This connexion of decreasing size with decreasing composition, is conspicuous in the series of figures: the differences shown, being not nearly so great as may be frequently observed. Confirmation may be drawn from the fact, that when the leading shoot is broken or arrested in its growth, the shoots it gives off (provided they are given off after the injury), and into which its checked currents of sap are thrown, produce leaves of five leaflets, where ordinarily leaves of three leaflets occur. Of course incidental circumstances, as variations in the amounts of sunshine, or of rain, or of matter supplied to the roots, are ever producing changes in the state of the plant as a whole; and by thus affecting the nutrition of its leaf-buds at the times of their formation, cause irregularities in the relations of size and composition above described. But taking these causes into account, it is abundantly manifest that a leaf-bud of the bramble, will develop into a simple leaf or into a leaf compounded in different degrees, according to the quantity of assimilable matter brought to it at the time when the rudiments of its structure are being fixed. And on studying the habits of other plants—on observing how annuals that have compound leaves, usually bear simple leaves at the outset, when the assimilating surface is but small; and how, when compound-leaved plants in full growth bear simple leaves in the midst of compound ones, the relative smallness of such simple leaves shows that the buds from which they arose were ill-supplied with sap; it will cease to be doubted that a foliar organ may be metamorphosed into a group of foliar organs, if furnished, at the right time, with a quantity of matter greater than can be readily organized round a single centre of growth. An examination of the transitions through which a compound leaf passes into a doubly-compound leaf, as seen in the various intermediate forms of leaflets in Fig. 65, will further enforce this conclusion.



Here we may advantageously note, too, how in such cases, the leaf-stalk undergoes concomitant changes of structure. In the bramble-leaves above described, it becomes compound simultaneously with the leaf—the veins become mid-ribs while the mid-ribs become petioles. Moreover, the secondary stalks, and still more the main stalks, bear thorns similar in their shapes, and approaching in their sizes, to those on the stem;

besides simulating the stem in colour and texture. In the petioles of large compound leaves, like those of the common *Heracleum*, we still more distinctly see both internal and external approximations in character to axes. Nor are there wanting plants whose large, though simple, leaves, are held out far from the stems, by foot-stalks that are, near the ends, sometimes so like axes, that the transverse sections of the two are indistinguishable; as instance the *Calla Ethiopica*.

One other fact respecting the modifications which leaves undergo, should be set down. Not only may leaf-stalks assume to a great degree the characters of stems, when they have to discharge the functions of stems, by supporting many leaves or very large leaves; but they may assume the characters of leaves, when they have to undertake the functions of leaves. The Australian Acacias furnish a remarkable illustration of this. Acacias elsewhere found, bear pinnate leaves; but the majority of those found in Australia, bear what appear to be simple leaves. It turns out, however, that these are merely leaf-stalks flattened out into foliar shapes: the laminæ of the leaves being undeveloped. And the proof is, that in young plants, showing their kinships by their embryonic characters, these leaf-like petioles bear true leaflets at their ends. A metamorphosis of like kind occurs in *Oxalis bupleurifolia*, Fig. 66. The fact most deserving of notice, however, is, that these leaf-stalks, in usurping the general aspects and functions of leaves, have also usurped their structures: though their venation is not like that of the leaves they replace, yet they have veins, and in some cases mid-ribs.

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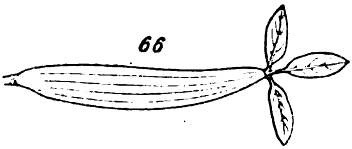

Reduced to their most general expression, the truths above shadowed forth are these:—That group of morphological units, or cells, which we see integrated into the compound unit called a leaf, has, in each higher plant, a typical form; due to the special arrangement of these cells around a mid-rib and veins. If the multiplication of morphological units, at the time when the leaf-bud is taking on its main outlines, exceeds a certain limit, these units begin to arrange themselves round secondary centres, or lines of growth, in such ways as to repeat, in part or wholly, the typical form: the larger veins become transformed into imperfect mid-ribs of partially independent leaves; or into complete mid-ribs of quite separate leaves. And as there goes on this transition from a single aggregate of cells to a group of such aggregates, there simultaneously arises, by similarly-insensible steps, a distinct structure which supports the several aggregates thus produced, and unites them into a compound aggregate. These phenomena should be carefully studied; since they give us a key to more involved phenomena.

§ 189. Thus far we have dealt with leaves ordinarily so called: briefly indicating the homologies between the parts of the simple and the compound. Let us now turn to the homologies among foliar organs in general. These have been made familiar to readers of natural history, by popularized outlines of "The Metamorphosis of Plants"—a title, by the way, which is far too extensive; since the phenomena treated of under it, form but a small portion of those it properly includes.

Passing over certain vague anticipations that have been quoted from ancient writers, and noting only that some clearer recognitions were reached by Joachim Jung, a Hamburg professor, in the middle of the 17th century; we come to the *Theoria Generationis*, which Wolff published in 1759, and in which he gives a definite form to the conceptions that have since become current. Specifying the views of Wolff, Dr Masters writes,—"After speaking of the homologous nature of the leaves, the sepals and petals, an homology consequent on their similarity of structure and identity of origin, he goes on to state that the 'pericarp is manifestly composed of several leaves, as in the calyx, with this difference only, that the leaves which are merely placed in close contact in the calyx, are here united together;' a view which he corroborates by referring to the manner in which many capsules open and separate 'into their leaves.' The seeds, too, he looks upon as consisting of leaves in close combination. His reasons for considering the petals and stamens as homologous with leaves, are based upon the same facts as those which led Linnæus, and, many years afterwards, Goethe, to the same conclusion. 'In a word,' says Wolff, 'we see nothing in the whole plant, whose parts at first sight differ so remarkably from each other, but leaves and stem, to which latter the root is referrible.'" It appears that Wolff, too, enunciated the now-accepted interpretation of compound fruits: basing it on the same evidence as that since assigned. In the essay of Goethe, published thirty years after, these relations among the parts of flowering plants were traced out in greater detail, but not in so radical a way; for Goethe did not, as did Wolff, verify his hypothesis by dissecting buds in their early stages of development. Goethe appears to have arrived at his conclusions independently. But that they were original with him, and that he gave a more variously-illustrated exposition of them than had been given by Wolff, does not entitle him to anything beyond a secondary place, among those who have established this important generalization.

Were it not that these pages may be read by some to whom Biology, in all its divisions, is a new subject of study, it would be needless to name the evidence on which this now-familiar generalization rests. For the information of such it will suffice to say, that the fundamental kinship existing among all the foliar organs of a flowering plant, is shown by the transitional forms which may be traced between them, and by the occasional assumption of one another's forms. "Floral leaves, or bracts, are frequently only to be distinguished from ordinary leaves by their position at the base of the flower; at other times the bracts gradually assume more and more of the appearance of the sepals." The sepals, or divisions of the calyx, are not unlike undeveloped leaves: sometimes assuming quite the structures of leaves. In other cases, they acquire partially or wholly the colours of the petals—as, indeed, the bracts and uppermost stem-leaves occasionally do. Similarly, the petals show their alliances to the foliar organs lower down on the axis, and to those higher up on the axis: on the one hand, they may develop into ordinary leaves that are green and veined; and, on the other hand, as so commonly seen in double flowers, they may bear anthers on their edges. All varieties of gradation into neighbouring foliar organs, may be witnessed in stamens. Flattened and tinted in various degrees, they pass insensibly into petals, and through them prove their homology with leaves; into which, indeed, they are transformed in flowers that become wholly foliaceous. The style, too, is occasionally changed into petals or into green leaflets; and even the ovules are now and then seen to take on leaf-like forms. Thus we have clear evidence that in Phænogams, all the appendages of the axis are homologues: they are all modified leaves.

Wolff established, and Goethe further illustrated, another general law of structure in flowering plants. Each leaf commonly contains in its axil, a bud, similar in structure to the terminal bud. This axillary bud may remain undeveloped; or it may develop into a lateral shoot like the main shoot; or it may develop into a flower. If a shoot bearing lateral flowers be examined, it will be found that the internode, or space which separates each leaf with its axillary flower from the leaf and axillary flower above it, becomes gradually less towards the upper end of the shoot. In some plants, as in the fox-glove, the internodes constitute a regularly-diminishing series. In other plants, the series they form suddenly begins to diminish so rapidly, as to bring the flowers into a short spike—instance the common orchis. And again, by a still more sudden dwarfing of the internodes, the flowers are brought into a cluster; as they are in the cowslip. On contemplating a clover-flower, in which this clustering has been carried so far as to produce a compact head; and on considering what must happen if, by a further arrest of axial development, the foot-stalks of the florets disappear; it will be seen that there must result a crowd of flowers, seated close together on the end of the axis. And if, at the same time, the internodes of the upper stem-leaves also remain undeveloped, these stem-leaves will be grouped into a common calyx or involucre: we shall have a composite flower, such as the thistle. Hence, to modifications in the developments of foliar organs, have to be added modifications in the developments of axial organs. Comparisons disclose the gradations through which axes, like their appendages, pass into all varieties of size, proportion, and structure. And we learn that the occurrence of these two kinds of metamorphosis, in all conceivable degrees and combinations, furnishes us with a proximate interpretation of morphological composition in Phænogams.

I say a proximate interpretation, because there remain to be solved certain deeper problems; one of which at once presents itself to be dealt with under the present head. Leaves, petals, stamens, &c., being shown to be homologous foliar organs; and the part to which they are attached, proving to be an indefinitely-extended axis of growth, or axial organ; we are met by the questions,—What is a foliar organ? and What is an axial organ? The morphological composition of a Phænogam is undetermined, so long as we cannot say to what lower structures leaves and shoots are homologous; and how this integration of them originates. To these questions let us now address ourselves.

§ 190-1. Already, in § 78, reference has been made to the occasional development of foliar organs into axial organs: the special case there described, being that of a fox-glove, in which some of the sepals were replaced by flower-buds.

The observation of these and some analogous monstrosities, raising the suspicion that the distinction between foliar organs and axial organs is not absolute, led me to examine into the matter; and the result has been the deepening of this suspicion into a conviction. Part of the evidence is given in Appendix A

Some time after having reached this conviction, I found on looking into the literature of the subject, that analogous irregularities have suggested to other observers, beliefs similarly at variance with the current morphological creed. Difficulties in satisfactorily defining these two elements, have served to shake this creed in some minds. To others, the strange leaf-like developments which axes undergo in certain plants, have afforded reasons for doubting the constancy of this distinction which vegetal morphologists usually draw. And those not otherwise rendered sceptical, have been made to hesitate by such cases as that of the Nepaul-barley; in which the glume, a foliar organ, becomes developed into an axis, and bears flowers. In his essay—"Vegetable Morphology: its History and Present Condition,"* whence I have already quoted, Dr Masters indicates sundry of the grounds for thinking, that there is no impassable demarcation between leaf and stem. Among other difficulties which meet us if we assume that the distinction is absolute, he asks—"What shall we say to cases such as those afforded by the leaves of *Guarea* and *Trichilia*, where the leaves after a time assume the condition of branches and develop young leaflets from their free extremities, a process less perfectly seen in some of the pinnate-leaved kinds of *Berberis* or *Mahonia*, to be found in almost every shrubbery?"

A class of facts on which it will be desirable for us here to dwell a moment, before proceeding to deal with the matter deductively, is presented by the *Cactaceæ*. In this remarkable group of plants, deviating in such varied ways from the ordinary phænogamic type, we find many highly instructive

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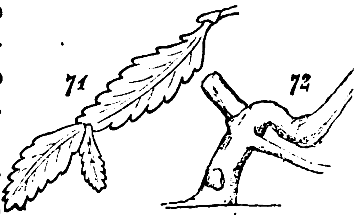
* See *British and Foreign Medico-Chirurgical Review* for January, 1862.

modifications of form and structure. By contemplating the changes here displayed within the limits of a single order, we shall greatly widen our conception of the possibilities of metamorphosis in the vegetal kingdom, taken as a whole. Two different, but similarly-significant, truths are illustrated. First, we are shown how, of these two components of a flowering plant, commonly regarded as primordially distinguished, one may assume, throughout numerous species, the functions, and to a great degree the appearance, of the other. Second, we are shown how, in the same individual, there may occur a re-metamorphosis—the usurped function and appearance being maintained in one part of the plant, while in another part, there is a return to the ordinary appearance and function. We will consider these two truths separately. Some of the *Euphorbiaceæ*, which simulate Cactuses, show us the stages through which such abnormal structures are arrived at. In *Euphorbia splendens*, the lateral axes are considerably swollen at their distal ends, so as often to be club-shaped: still, however, being covered with bark of the ordinary colour, and still bearing leaves. But in kindred plants, as *Euphorbia neriifolia*, this swelling of the lateral axes is carried to a far greater extent; and, at the same time, a green colour and a fleshy consistence have been acquired: the typical relations nevertheless being still shown, by the few leaves that grow out of these soft and swollen axes. In the *Cactaceæ*, which are thus resembled by plants not otherwise allied to them, we have indications of a parallel transformation. Some kinds, not commonly brought to England, bear leaves; but in the species most familiar to us, the leaves are undeveloped and the axes assume their functions. Passing over the many varieties of form and combination which these green succulent growths display, we have to note that in some genera, as in *Phyllocactus*, they become flattened out into foliaceous shapes, having mid-ribs and something approaching to veins. So that here, and in the genus *Epiphyllum*, which has this character still more marked, the plant appears to be composed of fleshy leaves growing one upon another. And then, in *Rhipsalis*, the same parts are so leaf-like that an uncritical observer would regard them as leaves. These which are axial organs in their homologies, have become foliar organs in their analogies. When, instead of comparing these strangely-modified axes in different genera of Cactuses, we compare them in the same individual, we meet with transformations no less striking. Where a tree-like form is produced by the growth of these foliaceous shoots, one on another; and where, as a consequence, the first-formed of them become the main stem that acts as support to secondary and tertiary stems; they lose their green, succulent character, acquire bark, and become woody—in resuming the functions of axes they resume the structures of axes, from which they had deviated. In Fig. 71 are shown some of the leaf-like axes of *Rhipsalis rhombea* in their young state; while Fig. 72 represents the oldest portion of the same plant, in which the foliaceous characters are quite obliterated, and there has resulted an ordinary stem-structure. One further fact is to be noted. At the same time that their leaf-like appearances are lost, the axes also lose their separate individualities. As they become stem-like, they also become integrated; and they do this so effectually, that their original points of junction, at first so strongly marked, are effaced, and a consolidated trunk is produced.



Joined with the facts previously specified, these facts help us to conceive how, in the evolution of flowering plants in general, the morphological components that were once distinct, may become extremely disguised. We may rationally expect that during so long a course of modification, much greater changes of form, and much more decided fusions of parts, have taken place. Seeing how, in an individual plant, the single leaves pass into compound leaves, by the development of their veins into mid-ribs while their mid-ribs begin to simulate axes; and seeing that leaves ordinarily exhibiting definitely-limited developments, occasionally produce other leaves from their edges; we are led to suspect the possibility of still greater changes in foliar organs. When, further, we find that within the limits of one natural order, petioles usurp the functions and appearances of leaves, at the same time that in other orders, as in *Ruscus*, lateral axes so completely simulate leaves that their axial nature would never have been supposed, did they not bear flowers on their mid-ribs or edges; and when, among Cactuses, we perceive that such metamorphoses and re-metamorphoses take place with great facility; our suspicion that the morphological elements of Phænogams admit of profound transformations, is deepened. And then, on discovering how frequent are the monstrosities that do not seem satisfactorily explicable without admitting the development of foliar organs into axial organs; we become ready to entertain the hypothesis, that during the evolution of the phænogamic type, the distinction between leaves and axes has arisen by degrees.

With our pre-conceptions loosened by such facts, and carrying with us the general idea which such facts suggest, let us now consider in what way the typical structure of a flowering plant may be interpreted.

§ 192. To proceed methodically, we must seek a clue to the structures of Endogens and Exogens, in the structures of those inferior plants that approach to them—Acrogens. The various divisions of this class present, along with sundry characters which ally them with Thallogens, other characters by which the phænogamic structure is shadowed forth. While some of the inferior *Hepaticæ* or Liverworts, severally consist of little more than a thallus-like frond; among the higher members of this group, and still more among the

Mosses and Ferns, we find a distinctly marked stem.* Some Acrogens have foliar expansions that are indefinite in their forms; and some have quite definitely-shaped leaves. Roots are possessed by all the more developed genera of the class; but there are other genera, as *Sphagnum*, which have no roots. Here the fronds are thallus-like, in being formed of only a single layer of cells; and there a double layer gives them a more leaf-like character—a difference exhibited between closely-allied genera of one order, the Mosses. Equally varied are the developments of the foliar-organs in their detailed structures: now being without mid-ribs or veins; now having mid-ribs but no veins; now having both mid-ribs and veins. Where stem and leaves exist, their imperfect differentiation is shown by the fact, that in many cases the stem is covered by an epidermis containing stomata. Nor must we omit the similarly-significant circumstance, that whereas in the lower Acrogens, the reproductive elements are immersed here and there in the thallus-like frond; they are, in the higher orders, seated in well-specialized and quite distinct fructifying organs, having analogies with the flowers of Phænogams. Thus, many facts imply that if the phænogamic type is to be analyzed at all, we must look among the Acrogens for its morphological components, and the manner of their integration.

Already we have seen among the lower Cryptogamia, how

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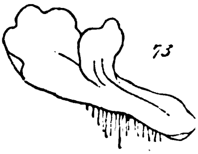
* Schleiden, who chooses to regard as an axis, that which Mr Berkeley, with more obvious truth, calls a mid-rib, says:—"The flat stem of the Liverworts presents many varieties, consisting frequently of one simple layer of thin-walled cells, or it exhibits in its axis the elements of the ordinary stem." This passage exemplifies the wholly gratuitous hypotheses which men will sometimes espouse, to escape hypotheses they dislike. Schleiden, with the positiveness characteristic of him, asserts the primordial distinction between axial organs and foliar organs. In the higher Acrogens, he sees an undeniable stem. In the lower Acrogens, clearly allied to them by their fructification, there is no structure having the remotest resemblance to a stem. But to save his hypothesis, Schleiden calls that "a flat stem," which is very obviously a structure in which stem and leaf are not differentiated. He is the more to be blamed for this unphilosophical assumption, since he is merciless in his strictures on the unphilosophical assumptions of other botanists.

as they become integrated and definitely limited, aggregates acquire the habit of budding out other aggregates, on reaching certain stages of growth. Cells produce other cells endogenously or exogenously; and fronds give origin to other fronds from their edges or surfaces. We have seen, too, that the new aggregates so produced, whether of the first order or the second order, may either separate or remain connected. Fissiparously-multiplying cells in some cases fly asunder, while in other cases they unite into threads or laminæ or masses; and fronds originating proliferously from other fronds, sometimes when mature disconnect themselves from their parents, and sometimes continue attached to them. Whether they do or do not part, is clearly determined by their nutrition. If the conditions are such that they can severally thrive better by separating after a certain development is reached, it will become their habit then to separate; since natural selection will favour the propagation of those which separate most nearly at that time. If, conversely, it profits the species for the cells or fronds to continue longer attached, which it can only do if their growth and subsequent powers of multiplication are thereby increased; it must happen, through the continual survival of the fittest, that longer attachment will become an established characteristic; and by persistence in this process, permanent attachment will result, when permanent attachment is advantageous. That disunion is really a consequence of relative innutrition, and union a consequence of relative nutrition, is clear, *à posteriori*. On the one hand, the separation of the new individuals, whether in germs or as developed aggregates, is a decaying away of the connecting tissue; and this implies that the connecting tissue has ceased to perform its function as a channel of nutriment. On the other hand, where, as we see among Phænogams, there is about to take place a separation of new individuals in the shape of germs, at the point where the nutrition is the lowest, a sudden increase of nutrition will cause the impending separation to be arrested; and the fructifying elements will revert towards the ordinary form, and develop in connexion with the parent. Turning to the Acrogens, we find among them, many indications of this transition from discontinuous development to continuous development. Thus the Liverworts give origin to new plants by cells which they throw off from their surfaces; as, indeed, we have seen that much higher plants do. "According to Bischoff," says Schleiden, "both the cells of the stem (*Jungermannia bidentata*) and those of the leaves (*J. exsecta*) separate themselves as propagative cells from the plant, and isolated cells shoot out and develop while still connected with the parent plant into small cellular bodies (*J. violacea*), which separate from the plant, and grow into new plants, as in *Mnium androgynum* among the Mosses." Now in the way above explained, these propagative cells and proliferous buds, may continue developing in connexion with the parent, to various degrees before separating; or the buds which are about to become fructifying organs, may similarly, under increased nutrition, develop into young fronds. As Sir W. Hooker says of the male fructification in *Jungermannia furcata*,—"It has the appearance of being a young shoot or innovation (for in colour and texture I can perceive no difference) rolled up into a spherical figure." On finding in this same plant, that sometimes the proliferously-produced frond, buds out from itself another frond before separating from the parent, as shown in Fig. 46; it becomes clear that this long-continued connexion, may readily pass into permanent connexion. And when we see how, even among Phænogams, buds may either detach themselves as bulbils, or remain attached and become shoots; we can scarcely doubt that among inferior plants, less definite in their modes of organization, such transitions must continually occur.

Let us suppose, then, that Fig. 73 is the frond of some primitive Acrogen, similar in general characters to *Jungermannia epiphylla*, Fig. 43; bearing, like it, the fructifying buds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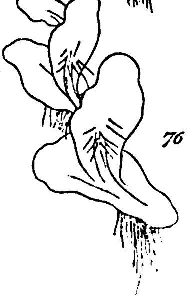
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on its upper surface, and having a slightly-marked mid-rib and rootlets. And suppose that, as shown, a secondary frond is proliferously produced from the mid-rib, and continues attached to it. Evidently, the ordinary discontinuous development, can thus become a continuous development, only on condition that there is an adequate supply, to the secondary frond, of such materials as are furnished by the rootlets: the remaining materials being obtainable by itself from the air. Hence, that portion of the mid-rib lying between the secondary frond and the chief rootlets, having its function increased, will increase in bulk. An additional consequence will be, a greater concentration of the rootlets—there will be extra growth of those which are most serviceably placed. Observe, next, that the structure so arising, is likely to be maintained. Such a variation implying, as it does, circumstances especially favourable to the growth of the plant, will give to the plant extra chances of leaving descendants; since the area of frond supported by a given area of the soil, being greater than in other individuals, there may be a greater production of spores. And then, among the more numerous descendants thus secured by it, the variation will give advantages to those in which it recurs. Such a mode of growth having, in this manner, become established, let us ask what is next likely to result. If it becomes the habit of the primary frond to bear a secondary frond from its mid-rib, this secondary frond, composed of physiological units of the same kind, will inherit the habit; and supposing that the supply of mineral matters obtained by the rootlets suffices for the full development of the secondary frond, there is a likelihood that the growth from it of a tertiary frond, will become an habitual characteristic of the variety. Along with the establishment of such a tertiary frond, as shown in Fig. 74, there must arise a further development of mid-rib in the primary frond, as well as in the secondary frond—a development which must bring with it a greater integration of the two; while, simultaneously, extra growth will take place in such of the rootlets as are most directly connected with this main channel of circulation. Without further explanation it will be seen, on inspecting Figs. 75 and 76, that there may in this manner result an integrated series of fronds, placed alternately on opposite sides of a connecting vascular structure. That this connecting vascular structure will, as shown in the figures, become more distinct from the foliar surfaces as these multiply, is no unwarranted assumption; for we have seen in compound-leaved plants, how, under analogous conditions, mid-ribs become developed into separate supporting parts, which acquire some of the characters of axes while assuming their functions. And now mark how clearly the structure thus built up by integration of proliferously-growing fronds, corresponds with the structure of the more-developed *Jungermanniaceæ*. Each of the fronds successively produced, repeating the characters of its parent, will bear roots; and will bear them in homologous places, as shown. Further, the united mid-ribs having but very little rigidity, will be unable to maintain an erect position. Hence there will result the recumbent, continuously-rooted stem, which these types exhibit. Nay, the parallelism is more complete than the figures show. To avoid confusion, the fronds thus supposed to be progressively integrated, have been represented as simple. But, as shown in Fig. 45, these lower types ordinarily have fronds which divide dichotomously, in such way that one division is larger than the other; and this is just the character of the successive leaves in the higher types. As shown in Fig. 47, each leaf is usually composed of two unequal lobes.

A natural concomitant of the mode of growth here described, is, that the stem, while it increases longitudinally, increases scarcely at all transversely: hence the name Acrogens. Clearly the transverse development of a stem, is the correlative, partly of its function as a channel of circulation, and partly of its function as a mechanical support. That an axis may lift its attached leaves into the air, implies thickness and solidity proportionate to the mass of such leaves; and an increase of its sap-vessels, also proportionate to the mass of such leaves, is necessitated when the roots are all at one end and the leaves at the other. But in the generality of Acrogens, these conditions, under which arises the necessity for transverse growth of the axis, are absent, wholly or in great part. The stem habitually creeps below the surface, or lies prone upon the surface; and where it grows in a vertical or inclined direction, does this by attaching itself to a vertical or inclined object. Moreover, throwing out rootlets, as it mostly does, at intervals throughout its length, it is not called upon in any considerable degree, to transfer nutritive materials from one of its ends to the other. Hence this peculiarity which gives their name to the Acrogens, is a natural accompaniment of the low degree of specialization reached in them. And that it is an incidental and not a necessary peculiarity, is demonstrated by two converse facts. On the one hand, in those higher Acrogens which, like the tree-ferns, lift large masses of foliage into the air, there is just as decided a transverse expansion of the axis as in Exogens. On the other hand, in those Exogens which, like the common Dodder, gain support and nutriment from the surfaces over which they creep, there is no more lateral expansion of the axis than is habitual among Acrogens. Concluding, as we are thus fully justified in doing, that the lateral expansion accompanying longitudinal extension, which is a general characteristic of Endogens and Exogens as distinguished from Acrogens, is nothing more than a concomitant of their usually-vertical growth;* let us now go on to consider how vertical growth originates, and what are the structural changes it involves.

§ 193. Plants depend for their prosperity mainly on air and light: they dwindle where they are smothered, and thrive where they can expand their leaves into free space and sunshine. Those kinds which assume prone positions, consequently labour under disadvantages in being habitually interfered with by one another—they are mutually shaded and mutually injured. Such of them, however, as happen, by variations in mode of growth, to get at all above the rest, are more likely to flourish and leave offspring than the rest. That is to say, natural selection will favour the more upright-growing forms: individuals with structures that lift them above the rest, are the fittest for the conditions; and by the continual survival of the fittest, such structures must become established. There are two essentially-different ways in which the integrated series of fronds above described, may be modified so as to acquire the stiffness needful for maintaining perpendicularity. We will consider them separately.

A thin layer of substance gains greatly in power of resisting a transverse strain, if it is bent round so as to form a tube—witness the difference between the pliability of a sheet of paper when outspread, and the rigidity of the same sheet of paper when rolled up. Engineers constantly recognize

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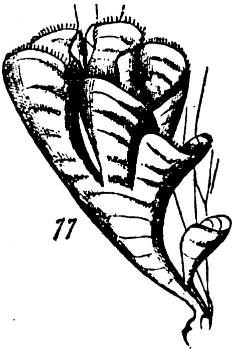
* I am indebted to Dr Hooker for pointing out further facts supporting this view. In his *Flora Antarctica*, he describes the genus *Lessonia* (see Fig. 37) and especially *L. ovata*, as having a mode of growth simulating that of the Exogens. The tall vertical stem thickens as it grows, by the periodical addition of layers to its periphery. Among lichens, too, it seems that there is an analogous case. That even Thallogens should thus, under certain conditions, present a transversely-increasing axis, shows that there is nothing absolute in the character which gives the names to the two highest classes of plants, in contradistinction to the class nearest to them.



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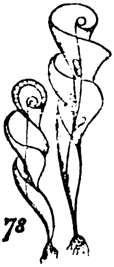

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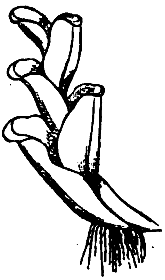
this truth, in devising appliances by which the greatest strength shall be obtained at the smallest cost of material; and among organisms, we see that natural selection habitually establishes structures conforming to the same principle, wherever lightness and stiffness are to be combined. The cylindrical bones of mammals and birds, and the hollow shafts of feathers, are examples. The lower plants, too, furnish cases where the strength needful for maintaining an upright position, is acquired by this rolling up of a flat thallus or frond. In Fig. 77, we have an *Alga* which approaches towards a tubular distribution of substance; and which has a consequent rigidity. Sundry common forms of lichen, having the thallus folded into a branched tube, still more decidedly displaying the connexion between this structural arrangement and this mechanical advantage. And from the particular class of plants we are here dealing with—the Acrogens—a type is shown in Fig. 78, *Riella helicophylla*, similarly characterized by a thin frond that is made stiff enough to stand, by an incurving which, though it does not produce a hollow cylinder, produces a kindred form. If, then, as we have seen, natural selection or survival of the fittest, will favour such among these recumbent Acrogens, as are enabled, by variations of their structures, to maintain raised postures; it will favour the formation of fronds that curve round upon themselves, and curve round upon the fronds growing out of them. What, now, will be the result should such a modification take place in the group of proliferous fronds represented in Fig. 76? Clearly, the result will be a structure like that shown in Fig. 79. And if this inrolling becomes more complete, a form like *Jungermannia cordifolia*.

represented in Fig. 80, will be produced.



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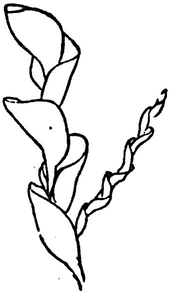

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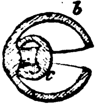
When the successive fronds are thus folded round so completely that their opposite edges meet, these opposite edges will be apt to unite: not that they will grow together after being formed, but that they will develop in connexion; or, in botanical language, will become "adnate." That foliar surfaces which, in their embryonic state, are in close contact, often join into one, is a familiar fact. It is habitually so with sepals or divisions of the calyx. In all campanulate flowers it is so with petals. And in some tribes of plants it is so with stamens. We are therefore well-warranted in inferring, that under the conditions above described, the successive fronds or leaflets will, by union of their remote edges, first at their points of origin, and afterwards higher up, form sheaths inserted one within another, and including the axis. This incurving of the successive fronds, ending in the formation of sheaths, may be accompanied by different sets of modifications. Supposing Fig. 81 to be a transverse section of such a type (*a* being the mid-rib, and *b* the expansion of an older frond; while *c* is a younger frond proliferously developed within it), there may begin two divergent kinds of changes, leading to two contrasted structures. If, while frond continues to grow out of frond, the series of united mid-ribs continues to be the channel of circulation between the uppermost fronds and the roots—if, as a consequence, the compound mid-rib, or rudimentary axis, continues to increase in size laterally; there will arise the series of transitional forms represented by the transverse sections 82, 83, 84, 85; ending in the production of a solid axis, everywhere wrapped round by the foliar surface of the frond, as an outer layer or sheath. But if, on the other hand, circumstances favour a form of plant which maintains its uprightness at the smallest cost of substance—if the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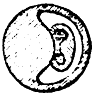
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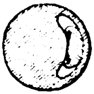
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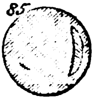
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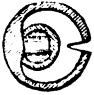
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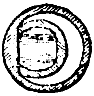
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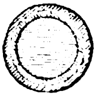
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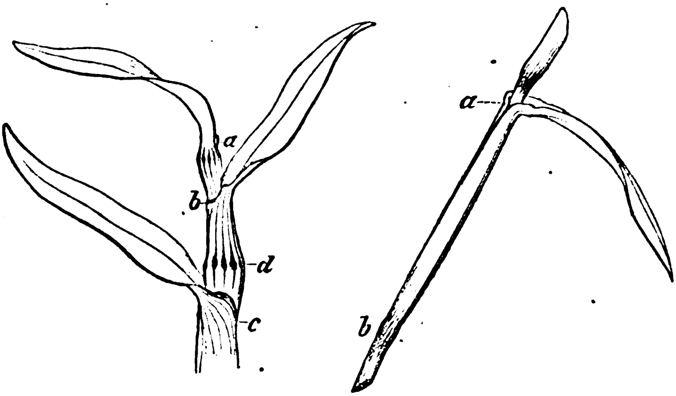
vascular bundles of each succeeding mid-rib, instead of remaining concentrated, become distributed all round the tube formed by the infolded frond; then the structure eventually reached, through the transitional forms 86, 87, 88, 89, will be a hollow cylinder. And now observe how the two structures thus produced, correspond with two kinds of Endogens. Fig. 90 represents a species of *Dendrobium*, in which we see clearly how each leaf is but a continuation of the external layer of a solid axis—a sheath such as would result from the infolded edges of a frond becoming adnate; and on examining how the sheath of each leaf includes the one above it, and how the successive sheaths include the axis, it will be manifest that the relations of parts are just such as exist in the united series of fronds shown in Fig. 79—the successive nodes answering to the successive points of origin of the fronds. Conversely, the stem of a grass, Fig. 91, displays just such relations of parts, as would result from the development of the type shown in Fig. 79, if instead of the mid-ribs thickening into a solid axis, the matter composing them became evenly distributed round the foliar surfaces, at the same time that the incurved edges of the foliar surfaces united. The arrangements of the tubular axis and its appendages, thus resulting, are still more instructive than those of the solid axis. For while, even more clearly than in the *Dendrobium*, we see at the point *b*, a continuity of structure between the substance of the axis below the node, and the substance of the sheath above the node; we see that this sheath, instead of having its edges united as in *Dendrobium*, has them simply overlapping, so as to form an incomplete hollow cylinder which may be taken off and unrolled;



and we see that were the overlapping edges of this sheath, united all the way from the node *a* to the node *b*, it would constitute a tubular axis, like that which precedes it or like that which it includes. And then, giving an unexpected conclusiveness to the argument, it turns out that in one family of grasses, the overlapping edges of the sheaths *do* unite: thus furnishing us with a demonstration that tubular structures *are* produced by the incurving and joining of foliar surfaces; and that so, hollow axes may be interpreted as above, without making any assumption unwarranted by fact. One further correspondence between the type thus ideally constructed, and the endogenous type, must be noted. If, as already pointed out, the transverse growth of an axis arises, when the axis comes to be a channel of circulation between all the roots at one of its extremities and all the leaves at the other; and if this lateral bulging must increase, as fast as the quantity of foliage to be brought in communication with the roots increases—especially if such foliage has at the same time to be raised high above the earth's surface; what must happen to a plant constructed in the manner just described? The elder fronds or foliar organs, ensheathing those within them, as well as the incipient axis serving as a bond of union, are at first of such circumference only as suffices to inclose these undeveloped parts. What, then, will take place when the inclosed parts grow—when the axis thickens while it elongates? Evidently the earliest-formed sheaths, not being large enough for the swelling axis, must burst; and evidently each of the later-formed sheaths must, in its turn, do the like. There must result a gradual exfoliation of the successive sheaths, like that indicated as beginning in the above figure of *Dendrobium;* which, at *a*, shows the bud of the undeveloped parts just visible above the enwrapping sheaths, while at *b*, and *c*, it shows the older sheaths in process of being split open. That is to say, there must result the mode of growth which helps to give the name Endogens to this class.

The other way in which an integrated series of fronds may acquire the rigidity needful for maintaining an erect position, has next to be considered. If the successive fronds do not acquire such habit of curling as may be taken advantage of by natural selection, so as to produce the requisite stiffness; then, the only way in which the requisite stiffness appears producible, is by the thickening and hardening of the fused series of mid-ribs. The incipient axis will not, in this case, be inclosed by the rolled-up fronds; but will continue exposed. Survival of the fittest will favour the genesis of a type, in which those portions of the successive mid-ribs that enter into the continuous bond, become more bulky than the disengaged portions of the mid-ribs: the individuals which thrive and have the best chances of leaving offspring, being, by the hypothesis, individuals having axes stiff enough to raise their foliage above that of their fellows. At the same time, under the same influences, there will tend to result an elongation of those portions of the mid-ribs, which become parts of the incipient axis; seeing that it will profit the plant to have its leaves so far removed from one another, as to prevent mutual interferences. Hence, from the recumbent type, there will evolve, by indirect equilibration, (§ 167) such modifications as are shown in Figs. 92, 93, 94: the first of which is a slight advance on the ideal type represented in Fig. 76, arising in the way described; and the others of which are actual plants—*Jungermannia Hookeri*, and *J. decipiens*. Thus the higher Acrogens show us how, along with an assumption of the upright attitude, there does go on, as we see there must go on, a separation of the leaf-producing parts from the root-producing parts; a greater development of that connecting portion of the successive fronds, by which they are kept in communication with the roots, and raised above the ground; and a consequent increased differentiation of such connecting portion from the parts attached to it. And this lateral bulging of the axis, directly or indirectly consequent on its functions as a support

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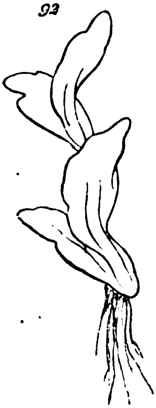

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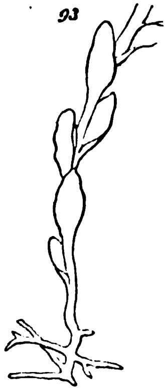

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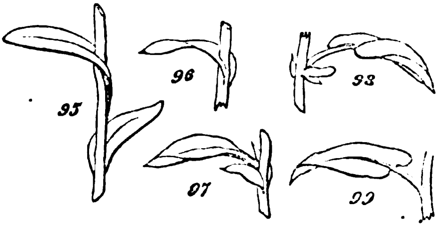
and a channel, being here unrestrained by the early-formed fronds folded round it, goes on without the bursting of these. Hence arises a leading character of what is called exogenous growth—a growth which is, however, still habitually accompanied by exfoliation, in flakes, of the outermost layer, continually being cracked and split by the accumulation of layers within it. And now if we examine plants of the exogenous type, we find among them many displaying the stages of this metamorphosis. In Fig. 95, is shown a form in which the continuity of the axis with the mid-rib of the leaf, is manifest—a continuity that is conspicuous in the common thistle. Here the foliar expansion, running some distance down the axis, makes the included portion of the axis a part of its mid-rib; just as in the ideal types above drawn. By the greater growth of the internodes, which are very variable, not only in different plants but in the same plant, there results a modification like that delineated in Fig. 96. And then, in such forms as Fig. 97, there is shown the arrangement that arises when, by more rapid development of the proximal portion of the mid-rib, the distal part of the foliar surface is separated from the part which embraces the axis: the wings of the mid-rib still serving, however, to connect the two portions of the foliar surface. Such a separation is, as pointed out in § 188, an habitual occurrence; and in some compound leaves, an actual tearing of the inter-veinous tissue, is caused by extra growth of the mid-rib. Modifications like this, and the further one in Fig. 98, we may expect to be established by survival of the fittest, among



those plants which produce considerable masses of leaves; since the development of mid-ribs into footstalks, by throwing the leaves further away from the axes, will diminish the shading of the leaves, one by another. And then, among plants of bushy growth, in which the assimilating surfaces become still more liable to intercept one another's light, natural selection will continue to give an advantage to those which carry their assimilating surfaces at the ends of the petioles, and do not develop assimilating surfaces close to the axis, where they are most shaded. Whence will result a disappearance of the stipules and the foliar fringes of the mid-ribs; ending in the production of the ordinary stalked leaf, Fig. 99, which is characteristic of trees. Meanwhile, the axis thickens in proportion to the number of leaves it has to carry, and to put in communication with the roots; and so there comes to be a more marked contrast between it and the petioles, severally carrying a leaf each.*

§ 194. When, in the course of the process above sketched out, there has arisen such community of nutrition among the fronds thus integrated into a series, that the younger ones are aided by materials which the older ones have elaborated; the younger fronds will begin to show, at earlier and earlier periods of development, the structures about to originate from them. Abundant nutrition will abbreviate the intervals between the successive prolifications; so that eventually, while each frond is yet imperfectly formed, the rudiment of the next will begin to show itself. All embryology justifies this inference. The analogies it furnishes lead us to expect that when this serial arrangement becomes organic, the growing part of the series will show the general relations of

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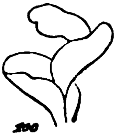
* Since this paragraph was put in type, I have observed that in some varieties of *Cineraria*, as probably in other plants, a single individual furnishes all these forms of leaves—all gradations between unstipulated leaves on long petioles, and leaves that embrace the axis. It may be added that the distribution of these various forms, is quite in harmony with the rationale above given.

the forthcoming parts, while they are very small and unspecialized. What will in such case be the appearances they assumed? We shall have no difficulty in perceiving what it will be, if we take a form like that shown in Fig. 92, and dwarf its several parts at the same time that we generalize them. Figs. 100, 101, 102, and 103, will show the result; and in Fig. 104, which is the bud of an exogen, we see how clear is the morphological correspondence: *a* being the rudiment of a foliar organ beginning to take shape; *b* being the almost formless rudiment of the next foliar organ; and *c* being the quite-undifferentiated part whence the rudiments of subsequent foliar organs are to arise.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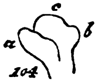

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And now we are prepared for entering on a still-remaining question respecting the structure of Phænogams—what is the origin of axillary buds? As the synthesis at present stands, it does not account for these; but on looking a little more closely into the matter, we shall find that the axillary buds are interpretable in the same manner as the terminal buds. So to interpret them, however, we must return to that process of proliferous growth with which we set out, for the purpose of observing some facts not before named. *Delesseria hypoglossum*, Fig. 105, represents a seaweed of the same genus as one outlined in Fig. 40; but of a species in which proliferous growth is carried much further. Here, not only does the primary frond bud out many secondary fronds from its mid-rib; but most of the secondary fronds similarly bud out several tertiary fronds; and even by some of the tertiary fronds, this prolification is repeated. Besides being shown that the budding out of several fronds from one frond, may become habitual; we are also shown that it may become a habit inherited by the fronds so produced, and also by the fronds they produce: the manifestation of the tendency, being probably limited only by failure of nutrition. That under fit conditions, an analogous mode of growth will occur in fronds of the acrogenic type, like those we set out with, is shown by the case of *Jungermannia furcata*, Figs. 45, 46, in which such compound prolification is partially displayed. Let us suppose then, that the frond *a*, Fig. 106, produces not only a single secondary frond *b*, but also another such secondary frond, *b'*. Let us suppose, further, that the frond *b* is in like manner doubly proliferous: producing both *c* and *c'*. Lastly, let us suppose that in the second frond *b'* which *a* produces, as well as in the second frond *c'* which *b* produces, the doubly-proliferous habit is manifested. If, now, this habit grows organic—if it becomes, as it naturally will become, the characteristic of a plant of luxuriant growth, the unfolding parts of which can be fed by the unfolded parts; it will happen with each lateral series, as with the main series, that its successive components will begin to show themselves at earlier and earlier stages of development. And in the same way that, by dwarfing and generalizing


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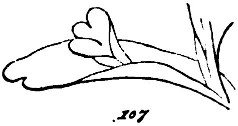
the original series, we arrive at a structure like that of the terminal bud; by dwarfing and generalizing a lateral series, as shown in Figs. 107—110, we arrive at a structure answering in nature and position to the axillary bud.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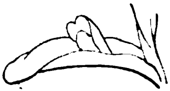
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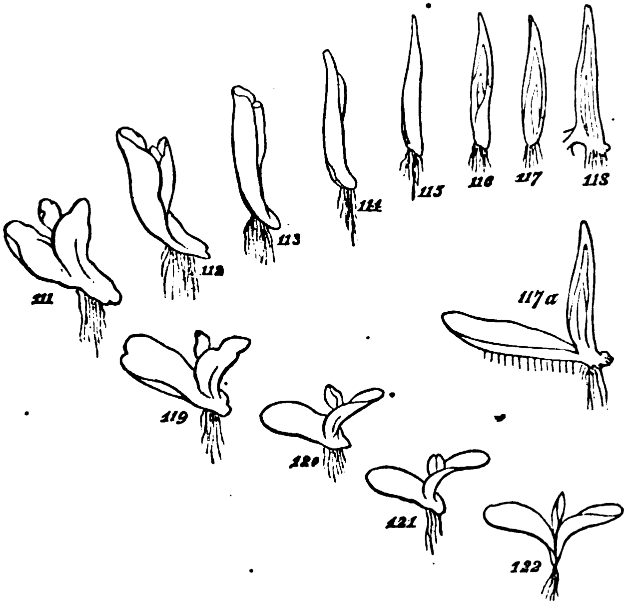
Facts confirming these interpretations, are afforded by the structure and distribution of buds. The phænogamic axis in its primordial form, being an integrated series of folia; and the development of that part by which these folia are held together at considerable distances from one another, taking place afterwards; it is inferable from the general principles of embryology, that in its rudimentary stages, the phænogamic axis will have its foliar parts much more clearly marked out than its axial parts. This we see in every bud. Every bud consists of the rudiments of leaves packed together without any appreciable internodal spaces; and the internodal spaces begin to increase with rapidity, only when the foliar organs have been considerably developed. Moreover, where nutrition is defective, and arrest of development takes place—that is, where a flower is formed—the internodes remain undeveloped: the process of unfolding ceases before the later-acquired characters of the phænogamic axis are assumed. Lastly, as the hypothesis leads us to expect, axillary buds make their appearances later than the foliar organs which they accompany; and where, as at the ends of axes, these foliar organs show failure of chlorophyll, the axillary buds are not produced at all. That these are inferable traits of structure, will be manifest on contemplating Figs. 106—110; and on observing, first, that the doubly-proliferous tendency of which the axillary bud is a result, implies abundant nutrition; and on observing, next, that the original place of secondary prolification, is such that the foliar surface on which it occurs, must grow to some extent before the bud appears.

On thus looking at the matter—on contemplating afresh the ideal type shown in Fig. 106, and noting how, by the conditions of the case, the secondary prolifications must cease before that primary prolification which produces the main axis; we are enabled to reconcile all the phenomena of axillary gemmation. We see harmony among the several facts—first, that the axillary bud becomes a lateral, leaf-bearing axis if there is abundant material for growth; second, that its development is arrested, or it becomes a flower-bearing axis, if the supply of sap is but moderate; third, that it is absent when the nutrition is failing. We are no longer committed to the gratuitous assumption, that in the phænogamic type, there must exist an axillary bud to each foliar organ; but we are led to conclude, *à priori*, that which we find, *à posteriori*, that axillary buds are as normally absent in flowers as they are normally present lower down the axis. And then, to complete the argument, we are prepared for the corollary that axillary prolification may naturally arise even at the ends of axes, provided the failing nutrition which causes the dwarfing of the foliar organs to form a flower, be suddenly changed into such high nutrition as to transform the components of the flower into appendages that are green, if not otherwise leaf-like—a condition under which only, this phenomenon is proved to occur.

§ 195. One more question presents itself, when we contrast the early stages of development in the two classes of Phænogams; and a further answer supplied by the hypothesis, gives to the hypothesis a further probability. It is characteristic of an endogen, to have a single seed-leaf or cotyledon; and it is characteristic of an exogen, to have at least two cotyledons, if not more than two. That is to say, the monocotyledonous mode of germination everywhere coexists with the endogenous mode of growth; and along with the exogenous mode of growth, there always goes either a dicotyledonous or polycotyledonous germination. Why is this? Such correlations cannot be accidental—cannot be meaningless. A true theory of the phænogamic types, in their origin and divergence, should account for the connexion of these traits. Let us see whether the foregoing theory does this.

The higher plants, like the higher animals, bequeath to their offspring more or less of nutriment and structure. Superior organisms of either kingdom do not, as do all inferior organisms, cast off their progeny in the shape of minute portions of protoplasm, unorganized and without stocks of material fit for them to organize; but they either deposit along with the germs they cast off, certain quantities of albumenoid substance, fit for them to appropriate while they develop themselves, or else they continue to supply such substance while the germs partially-develop themselves before their detachment. Among plants, this constitutes the distinction between seeds and spores. Every seed contains a store of food to serve the young plant during the first stages of its independent life; and usually, too, before the seed is detached, the young plant is so far advanced in structure, that it bears to the attached stock of nutriment much the same relation that the young fish bears to the appended yelk-bag at the time of leaving the egg. Sometimes, indeed, the development of chlorophyll gives the seed-leaves a bright green, while the seed is still contained in the parent-pod. This early organization of the phænogam, must be supposed rudely to indicate the type out of which the phænogamic type arose. . On the foregoing hypothesis, the seed-leaves therefore represent the primordial fronds—which, indeed, they simulate in their simple, cellular, unveined structures. And the question here to be asked is—do the different relations of the parts in young endogens and exogens correspond with the different relations of the primordial fronds, severally implied by the endogenous and the exogenous modes of growth? We shall find that they do.

Starting, as before, with the proliferous form shown in Fig. 111, it is clear that if the strength required for maintaining the vertical attitude, is obtained by the rolling up of the fronds, the primary frond will more and more conceal the secondary frond within it. At the same time, the secondary frond must continue to be dependent on the first for its nutrition; and being produced within the first, must be prevented by defective supply of light and air, from ever becoming synchronous in its development with the first. Hence, this infolding which leads to the endogenous mode of growth, implies that there must always continue such pre-eminence of the first-formed frond or its representative, as to make the germination monocotyledonous. Figs. 111 to 115, show the transitional forms that would result from the infolding of the fronds. In Fig. 116, a vertical section of the form represented in Fig. 115, are exhibited the relations of the succes-



sive fronds to each other. The modified relations that would result, if the nutrition of the embryo admitted of anticipatory development of the successive fronds, is shown in Fig. 117. And how readily the structure may pass into that of the monocotyledonous germ, will be seen on inspecting Fig. 118; which is a vertical section of an actual monocotyledon at an early stage—the incomplete lines at the left of its root, indicating its connexion with the seed.* Contrariwise, where the strength required for maintaining an upright attitude is not obtained by the rolling up of the fronds, but by the strengthening of the continuous mid-rib, the second frond, so far from being less favourably circumstanced than the first, becomes in some respects even more favourably circumstanced: being above the other, it gets a greater share of light, and it is less restricted by surrounding obstacles. There is nothing, therefore, to prevent it from rapidly gaining an equality with the first. And if we assume, as the truths of embryology entitle us to do, an increasing tendency towards anticipation in the development of subsequent fronds—if we assume that here, as in other cases, structures which were originally produced in succession, will, if the nutrition allows and no mechanical dependence hinders, come to be produced simultaneously; there is nothing to prevent the passage of the type represented in Fig. 111, into that represented

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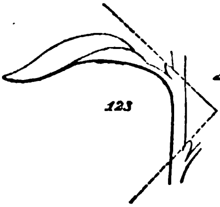
* Since these figures were put on the block, it has occurred to me that the relations would be still clearer, were the primary frond represented as not taking part in these processes of modification, which have been described as giving rise to the erect form; as, indeed, the rooting of its under surface will prevent it from doing in any considerable degree. In such case, each of the Figs. 111 to 117, should have a horizontal rooted frond at its base, homologous with the pro-embryo among Acrogens. This primary frond would then more manifestly stand in the same relation to the rest, as the cotyledon does to the plumule—both by position, and as a supplier of nutriment. Fig. 117 *a*, which I am enabled to add, shows that this would complete the interpretation. Of the dicotyledonous series, it is needful to add no further explanation than that the difference in habit of growth, will permit the second frond to root itself as well as the first; and so to become an additional source of nutrition, similarly circumstanced to the first and equal with it.

in Fig. 122. Or rather, there is everything to facilitate it; seeing that natural selection will continually favour the production of a form in which the second frond grows in such way as not to shade the first, and in such way as allows the axis readily to assume a vertical position.

Thus, then, is interpretable the universal connexion between monocotyledonous germination and endogenous growth; as well as the similarly-universal connexion between exogenous growth and the development of two or more cotyledons. That it explains these fundamental relations, adds very greatly to the probability of the hypothesis.

§ 196. While we are in this manner enabled to discern the kinship that exists between the higher vegetal types themselves, as well as between them and the lower types; we are at the same time supplied with a rationale of those truths which vegetal morphologists have established. Those homologies which Wolff indicated in their chief outlines and Goethe followed out in detail, have a new meaning given to them when we regard the phænogamic axis as having been evolved in the way described. Forming the modified conception which we are here led to do, respecting the units of which a flowering plant is composed, we are no longer left without an answer to the question—What is an axis? And we are helped to understand the naturalness of those correspondences which the successive members of each shoot display. Let us glance at the facts from our present standpoint.

The unit of composition of a Phænogam, is such portion of a shoot as answers to one of the primordial fronds. This portion is neither one of the foliar appendages nor one of the internodes; but it consists of a foliar appendage together with the preceding internode, including the axillary bud where this is developed. The parts intercepted by the dotted lines in Fig. 123, constitute such a segment; and the true homology is between this and any other foliar organ with the portion of the axis below it. And now observe how, when we take this for the unit of composition, the metamorphoses which the phænogamic axis displays, are inferable from known laws of development. Embryology teaches us that arrest of development shows itself first in the absence of those parts that have arisen latest in the course of evolution; that if defect of nutrition causes an earlier arrest, parts that are of more ancient origin abort; and that the part alone produced when the supply of materials fails near the outset, is the primordial part. We must infer, therefore, that in each segment of a Phænogam, the foliar organ, which answers to the primordial frond, will be the most constant element; and that the internode and the axillary bud, will be successively less constant. This we find. Along with a smaller size of foliar surface implying lower nutrition, it is usual to see a much-diminished internode and a less-pronounced axillary bud, as in Fig. 124. On approaching the flower, the axillary bud disappears; and the segment is reduced to a small foliar surface, with an internode which is in most cases very short if not absent, as in 125 and 126. In the flower itself, axillary buds and internodes are both wanting: there remains only a foliar surface (127), which, though often larger than the immediately preceding foliar surface, shows failing nutrition by absence of chlorophyll. And then, in the quite terminal organs of fructification (129), we have the foliar part itself reduced to a mere rudiment. Though these progressive degenerations are by no means regular, being in many cases varied by adaptation to particular requirements, yet it cannot, I think, be questioned,



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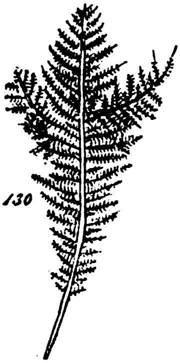
that the general relations are as described, and that they are such as the hypothesis leads us to expect. Nor are we without a kindred explanation of certain remaining traits of foliar organs in their least-developed forms. Petals, stamens, pistils, &c., besides reminding us of the primordial fronds by their diminished sizes, and by the want of those several supplementary parts which the preceding segments possess, also remind us of them by their histological characters: they consist of simple cellular tissue, scarcely at all differentiated. The fructifying cells, too, which here make their appearance, are borne in ways like those in which the lower Acrogens bear them—at the edge of the frond, or at the end of a peduncle, or immersed in the general substance; as in Figs. 128 and 129. Nay, it might even be said that the colours assumed by these terminal folia, call to mind the plants out of which we conclude that Phænogams have been evolved; for it is said of the fronds of the *Jungermanniaceæ*, that "though under certain circumstances of a pure green, they are inclined to be shaded with red, purple, chocolate, or other tints."

As thus understood, then, the homologies among the parts of the phænogamic axis are interpretable, not as due to a needless adhesion to some typical form or fulfilment of a predetermined plan; but as the inevitable consequences of the mode in which the phænogamic axis originates.

§ 197. And now it remains only to observe, in confirmation of the foregoing synthesis, that it at once explains for us various irregularities. When we see leaves sometimes producing leaflets from their edges or extremities, we recognize in the anomaly, a resumption of an original mode of growth: fronds frequently do this. When we learn that a flowering plant, as the *Drosera intermedia*, has been known to develop a young plant from the surface of one of its leaves, we are at once reminded of the proliferous growths and fructifying organs in the Liverworts. The occasional production of bulbils by Phænogams, ceases to be so surprising when we find it to be habitual among the inferior Acrogens; and when we see that it is but a repetition, on a higher stage, of that self-detachment which is common among proliferously-produced fronds. Nor are we any longer without a solution of that transformation of foliar organs into axial organs, which not uncommonly takes place. How this last irregularity of development is to be accounted for, we will here pause a moment to consider. Let us first glance at our data.

The form of every organism, we have seen, must depend on the structures of its physiological units. Any group of such physiological units will tend to arrange itself into the complete organism, if it is uncontrolled and placed in fit conditions. Hence the development of fertilized germs; and hence the development of those self-detached cells which characterize some plants. Conversely, physiological units which form a small group involved in a larger group, and are subject to all the forces of the larger group, will become subordinate in their structural arrangements to the larger group—will be co-ordinated into a part of the major whole, instead of co-ordinating themselves into a minor whole. This antithesis will be clearly understood on remembering how, on the one hand, a small detached part of a hydra soon moulds itself into the shape of an entire hydra; and how, on the other hand, the cellular mass that buds out in place of a lobster's lost claw, gradually assumes the form of a claw—has its parts so moulded as to complete the structure of the organism: a result which we cannot but ascribe to the forces which the rest of the organism exerts upon it. Consequently, among plants, we may expect that whether any portion of protoplasm moulds itself into the typical form around an axis of its own, or is moulded into a part subordinate to another axis, will depend on the relative mass of its physiological units—the accumulation of them that has taken place before the assumption of any structural arrangement. A few illustrations will make clear the validity of this inference. In the compound leaf, Fig. 65, the several lateral growths *a, b, c, d,* are manifestly homologous; and on comparing a number of such leaves together, it will be seen that one of these lateral growths may assume any degree of complexity, according to the degree of its nutrition. Every fern leaf exemplifies the same general truth still better. Whether each sub-frond remains an undeveloped wing of the main frond, or whether it organizes itself into a group of frondlets borne by a secondary rib, or whether, going further, as it often does, it gives rise to tertiary ribs, is clearly determined by the supply of materials for growth; since such higher developments are habitually most marked at points where the nutrition is greatest; namely, next the stem. But the clearest evidence is afforded among the *Algæ*, which, not drawing nutriment from roots, have their parts much less mutually dependent; and are therefore capable of showing more clearly, how any part may remain an appendage or may become the parent of appendages, according to circumstances. In the annexed Fig. 130, representing a branch of *Ptilota plumosa*, we see how a wing grows into a wing-bearing branch, if its nutrition passes a certain point. This form, so strikingly like that of the feathery crystallizations of many inorganic substances, proves to us that, as in such crystallizations, the simplicity or complexity of structure at any place, depends on the quantity of matter that has to be polarized at that place in a given time.[*]



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[*] How the element of time modifies the result, is shown by the familiar fact that crystals rapidly formed are small; and that they become larger when they are formed more slowly. If the quantity of molecules contained in a solution is relatively great, so that the mutual polarities of the molecules crowded together in every place throughout the solution are intense, there arises a crystalline aggregation around local axes; whereas, in proportion as the local action of molecules on one another is rendered less intense by their wider dispersion, they become

Hence, then, we are not without an interpretation of those over-developments which the phænogamic axis occasionally undergoes. Fig. 104, represents the phænogamic bud in its rudimentary state. The lateral process *b*, which ordinarily becomes a foliar appendage, differs very little from the terminal process *c*, which is to become an axis—differs mainly in having, at this period when its form is being determined, a smaller bulk. If while thus undifferentiated, its nutrition remains inferior to that of the terminal process, it becomes moulded into a part that is subordinate to the general axis. But if, as sometimes happens, there is supplied to it such an abundance of the materials needful for growth, that it becomes as large as the terminal process; then we may naturally expect it to begin moulding itself round an axis of its own: a foliar organ will be replaced by an axial organ. And this result will be especially liable to occur, when the growth of the axis has been previously undergoing that arrest which leads to the formation of a flower; that is, when, from defect of materials, the terminal process has almost ceased to increase, and when some concurrence of favourable causes, brings a sudden access of sap, which reaches the lateral processes before it reaches the terminal process.

§ 198. The general conclusion to which these various lines of evidence converge, is, then, that the shoot of a flowering plant is an aggregate of the third degree of composition. Taking as aggregates of the first order, those small masses of protoplasm which ordinarily assume the forms under which they are known as cells; and considering as aggregates of the second order, those assemblages of such cells which, in the lower cryptogamia, compose the various kinds of thallus; then that structure, common to the higher cryptogams and to phænogams, in which we find a series of such groups

relatively more subordinate to the forces exerted on them by the larger aggregates of molecules that are at greater distances, and thus are left to arrange themselves round fewer axes into larger crystals.

of cells bound up into a continuous whole, must be regarded as an aggregate of the third order. The inference drawn from analysis, and verified by a synthesis that corresponds in a remarkable manner with the facts, is, that those compound parts which, in Endogens and Exogens, are called axes, have really arisen by integration of such simple parts as in lower plants are called fronds. Here, on a higher level, appears to have taken place a repetition of the process already observed on lower levels. The formation of those small groups of physiological units which compose the lowest protophytes, is itself a process of integration; and the consolidation of such groups into definitely-circumscribed and coherent cells, is a completing of the process. In those coalescences, variously carried on, by which many such cells are joined into threads, and discs, and solid or flattened-out masses, we see these morphological units aggregating into units of a compound kind—the different phases of the transition being exemplified by groups of various sizes, various degrees of cohesion, and various degrees of definiteness. Once more do we now find evidences of a like process on a larger scale: the compound groups are again compounded. And, as before, there are not wanting types of organization by which the stages of this higher integration are shadowed forth. From fronds that occasionally produce other fronds from their surfaces, we pass to those that habitually produce them. From those that do so in an indefinite manner, to those that do so in a definite manner. And from those that do so singly, to those that do so doubly and triply through successive generations of fronds. Even within the limits of a sub-class, we find gradations between fronds irregularly proliferous, and groups of such fronds united into a regular series.

Nor does the process end here. The flowering plant is rarely uniaxial—it is nearly always multiaxial. From its primary shoot, there grow out secondary shoots of like kind. Though occasionally among Phænogams, and frequently among the higher Cryptogams, the germs of new axes detach themselves under the form of bulbils, and develop separately instead of in connexion with the parent axis; yet in most Phænogams, the germ of each new axis maintains its connexion with the parent axis: whence results a group of axes —an aggregate of the fourth order. Every tree, by the production of branch out of branch, shows us this integration repeated over and over again: forming an aggregate having a degree of composition too complex to be any longer defined.

# CHAPTER IV.

## THE MORPHOLOGICAL COMPOSITION OF ANIMALS.

§ 199. WHAT was said in § 180, respecting the ultimate structure of organisms, holds more manifestly of animals than of plants. That throughout the vegetal kingdom the cell is the morphological unit, is a proposition admitting of a better defence, than the proposition that the cell is the morphological unit throughout the animal kingdom. The qualifications with which, as we saw, the cell-doctrine must be taken, are qualifications thrust upon us more especially by the facts which zoologists have brought to light. It is among the *Protozoa* that there occur numerous cases of vital activity displayed by specks of protoplasm; and from the minute anatomy of all creatures above these, up to the *Teleozoa*, are drawn the numerous proofs that non-cellular tissues may arise by direct metamorphosis of structureless colloidal substance.

Our survey of morphological composition throughout the animal kingdom, must therefore begin with those undifferentiated aggregates of physiological units, out of which are formed what we call, with considerable license, morphological units.

§ 200. In that division of the *Protozoa* distinguished as *Rhizopoda*, are presented, under various modifications, these minute portions of living organic matter, so little differentiated, if not positively undifferentiated, that animal individuality can scarcely be claimed for them. Figs. 131, 132, and 133, represent certain nearly-allied types of these—*Amœba*, *Actinophrys*, and *Lieberkühnia*. The viscid jelly or sarcode, comparable in its physical properties to white of egg, out of which one of these creatures is mainly formed, shows us in various ways, the feebleness with which the component physiological units are integrated—shows us this by its very slight cohesion, by the extreme indefiniteness and mutability of its form, and by the absence of a limiting membrane. Though unqualified adherents of the cell-doctrine assert that the *Amœba* has an investment, yet since this investment, compared by Dujardin to the film which forms on the surface of paste, does not prevent the taking of solid particles into the mass of the body, and does not, in such kindred forms as Fig. 133, prevent the pseudopodia from coalescing when they meet, it cannot be anything deserving the name of a cell-wall. A considerable portion of the body, however, in *Difflugia*, Fig. 134, has a denser coating; so that the protrusion of the pseudopodia is limited to one part of it. And in the solitary *Foraminifera*, like *Gromia*, the sarcode is covered over most of its surface by a delicate calcareous shell, pierced with minute holes, through which the slender pseudopodia are thrust. The *Gregarina* exhibits an advance in integration, and a consequent greater definiteness. Figs. 135 and 136, exemplifying this type, show the complete membrane in which the substance of the creature is contained. Here there has arisen what may be properly called a cell: under its solitary form this animal is truly unicellular. Its embryology has considerable significance. After passing through a certain quiescent, "encysted" state, its interior breaks up into small portions, which, after their exit, assume


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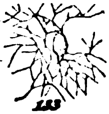
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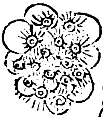
forms like that of the *Amœba;* and from this young condition in which they are undifferentiated, they pass into that adult condition in which they have limiting membranes. If this development of the individual *Gregarina* typifies the mode of evolution of the species, it yields further support to the belief, that homogeneous fragments of sarcode existed earlier than any of the structures which are properly called cells. Among aggregates of the first order, there are some much more highly developed. These are the *Infusoria;* constituting the most numerous of the *Protozoa,* in species as in individuals. Figs. 137, 138, and 139, are examples. In them we find, along with greater definiteness, a considerable heterogeneity. The sarcode of which the body consists, has an indurated outer layer, bearing cilia and sometimes spines; there is an opening serving as mouth, a permanent œsophagus, and a cavity or cavities, temporarily formed in the interior of the sarcode, to serve as one or more stomachs; and there is a comparatively specific arrangement of these and various minor parts.

Thus in the animal kingdom, as in the vegetal kingdom, there exists a class of minute forms having this peculiarity, that no one of them is separable into a number of visible components homologous with one another—no one of them can be resolved into minor individualities. Its proximate units are those physiological units of which we conclude every organism consists. The aggregate is an aggregate of the first order.

§ 201. Among plants are found types indicating a transition from aggregates of the first order to aggregates of the second order; and among animals we find analogous types. But the stages of progressing integration are not here so distinct. The reason probably is, that the simplest animals, having individualities much less marked than those of the simplest plants, do not afford us the same facilities for observation. In proportion as the limits of the minor individualities are indefinite, the formation of major individualities out of them, naturally leaves less conspicuous traces.

Be this as it may, however, in such types of *Protozoa* as the *Thalassicollæ,* we find that though there is reason to regard the aggregate as an aggregate of the second order, yet its divisibility into minor individualities like those just described, is by no means manifest. Fig. 140, representing *Sphærozoum punctatum*, one of this group, illustrates the difficulty. Only by some license of interpretation, can we regard the "cellæform bodies" contained in it, as the morphological units of the animal. The jelly-like mass in which they are imbedded, shows no signs of being divisible into portions having each a cell or nucleus for its centre.[*] Comparison of the various forms assumed by creatures of this type, suggests, contrariwise, that the homogeneous sarcode is primary, and its included structures secondary. Among the *Foraminifera,* we find evidence of the coalescence of aggregates of the first order, into aggregates of the second order. There are solitary Foraminifers, allied to the creature represented in Fig. 134. Certain ideal types of combination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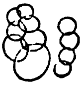
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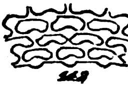
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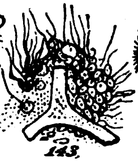
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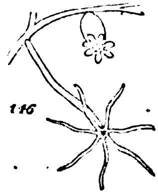
[*] This statement seems at variance with the figure; but the figure is very inaccurate. Its inaccuracy curiously illustrates the vitiation of evidence. When I saw the drawing on the block, I pointed out to the draughtsman, that he had made the surrounding curves much more obviously related to the contained bodies, than they were in the original (in Dr Carpenter's *Foraminifera*); and having looked on while he in great measure remedied this defect, thought no further care was needed. Now, however, on seeing the figure in the printer's proof, I find that the engraver, swayed by the same supposition as the draughtsman that such a relation was meant to be shown, has made his lines represent it still more decidedly than those of the draughtsman before they were corrected. Thus, vague linear representations, like vague verbal ones, are apt to grow more definite when repeated. Hypothesis warps perceptions as it warps thoughts.

among them, are shown in Fig. 141. And setting out from these, we may ascend in various directions to kinds compounded to an immense variety of degrees in an immense variety of ways. In all of them, however, the separability of the major individuality into minor individualities, is very incomplete. The portion of sarcode contained in one of these calcareous chambers, gives origin to an external bud; and this presently becomes covered, like its parent, with calcareous matter: the position in which each successive chamber is so produced, determining the form of the compound shell. But the portions of sarcode thus budded out one from another, do not become distinctly individualized. Fig. 142, representing the living net-work which remains when the shell of an Orbitolite has been dissolved, shows the continuity that exists among the occupants of its aggregated chambers. Still, the occupant of each chamber may fairly be considered as homologous with a solitary Foraminifer; and if so, the Orbitolite is an aggregate of the second order: this indefinite marking-off of its morphological units, being the obverse of the fact that the individualities of their prototypes are feebly pronounced. Forms of essentially the same kind are aggregated in another manner among the *Spongidæ*. The fibres of a living sponge are clothed with gelatinous substance, which is separable into *Amœba*-like creatures, capable of moving about by their pseudopodia when detached. These nucleated portions of sarcode, which are the morphological units of the sponge, lining all its channels and chambers, subsist on the nutritive particles brought to them by the currents of water that are drawn in through the superficial pores, and sent out through the larger openings—currents produced by ciliated units, such as are shown in Fig. 143. So that, in the words of Prof. Huxley, "the sponge represents a kind of subaqueous city, where the people are arranged about the streets and roads, in such a manner, that each can easily appropriate his food from the water as it passes along." In the compound *Infusoria*, the component units remain quite distinct. Being, as aggregates of the first order, much more definitely organized, their union into aggregates of the second order does not destroy their original individualities. Among the *Vorticellæ*, of which two kinds are delineated in Figs. 144 and 145, there are various illustrations of this: the members of the community being sometimes appended to a single stem; sometimes attached by long separate stems to a common base; and sometimes massed together.

Thus far, these aggregates of the second order exhibit but indefinite individualities. The integration is physical; but not physiological. Though, in the *Thalassicollæ*, there is a shape that has some symmetry; and though, in the *Foraminifera*, the formation of successive chambers proceeds in such methodic ways, as to produce quite-regular and tolerably-specific shells; yet no more in these than in the Sponges or the compound *Vorticellæ*, do we find such co-ordination as gives the whole a life predominating over the lives of its parts. We have not yet reached an aggregate of the second order, so individuated as to be capable of serving as a unit in still higher combinations. But in the class *Cœlenterata*, this advance is displayed. The common *Hydra*, habitually taken as the type of the lowest division of this class, has specialized parts performing mutually-subservient functions; and thus exhibiting a total life distinct from the lives of the units. Fig. 146 represents one of these creatures in its contracted state and in its expanded state; while Fig. 147 is a rude diagram from memory showing the wall of this creature's sack-like body as seen in section under the microscope: *a* and *b* being the outer and inner cellular layers; while in the central space between them, is that nucleated substance, or sarcode, or protoplasm, in which the cells originate. But this lowly-organized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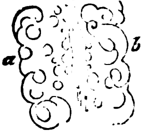
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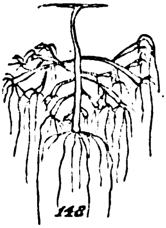
tissue of the *Hydra*, illustrates a phase of integration in which the lives of the minor aggregates are only partially-subordinated to the life of the major aggregate formed by them. For a *Hydra's* substance is separable into *Amœba*-like portions, capable of moving about independently. Prof. Green quotes Ecker, Lewes, and Jäger, in proof that "this animal exhibits, at certain seasons of the year, a tendency to break up into particles of a sarcode aspect, which retain for a long time an independent vitality." And if we bear in mind how analogous are the extreme extensibility and contractility of a *Hydra's* body and tentacles, to the properties displayed by the sarcode among Rhizopods; we may infer that probably the movements and other actions of a *Hydra*, are due to the half-independent co-operation of the *Amœba*-like individuals composing it.

§ 202. A truth which we before saw among plants, we here see repeated among animals—the truth that as soon as the integration of aggregates of the first order into aggregates of the second order, produces compound wholes so specific in their shapes and sizes, and so mutually dependent in their parts, as to have distinct individualities; there simultaneously arises the tendency in them to produce, by gemmation, other such aggregates of the second order. The approach towards definite limitation in an organism, is, by implication, an approach towards a state in which growth passing a certain point, results, not in the increase of the old individual, but in the formation of a new individual. Thus it happens that the common polype buds out other polypes, some of which very shortly do the like, as shown in Fig. 148: a process paralleled by the fronds of sundry *Algæ*, and by those of the lower *Jungermanniaceæ*. And just as, among these last plants, the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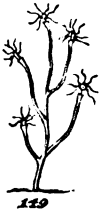
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proliferously-produced fronds, after growing to certain sizes and developing rootlets, detach themselves from their parent-fronds; so among these animals, separation of the young ones from the bodies of their parents, ensues when they have acquired tolerably complete organizations.

There is reason to think that the parallel holds still further. Within the limits of the *Jungermanniaceæ*, we found that while some genera exhibit this discontinuous development, other genera exhibit a development that is similar to it in all essential respects, save that it is continuous. And here within the limits of the *Hydrozoa,* we find, along with this genus in which the gemmiparous individuals are presently cast off, other genera in which they are not cast off, but form a permanent aggregate of the third order. Figs. 149 and 150, exemplify these compound *Hydrozoa*—one of them showing this mode of growth so carried out as to produce a single axis; and the other showing how, by repetitions of the process, lateral axes are produced. Integrations characterizing certain higher genera of the *Hydrozoa,* which swim or float instead of being fixed, are indicated by Figs. 151 and 152: the first of them representing the type of a group in which the polypes growing from an axis, or cœnosarc, are drawn through the water by the rhythmical contractions of the organs from which they hang; and the second of them representing a *Physalia* the component polypes of which are united into a cluster, attached to an air-vessel. It should be added that in the Rhizostomes, the integration is carried so far, that the individualities of the polypes are almost lost in that of the aggregate they form.

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A parallel series of illustrations might be drawn from that second division of the *Cœlenterata*, known as the *Actinozoa*. Here, too, we have a group of species—the Sea-anemonies—the individuals of which are solitary. Here, too, we have agamogenetic multiplication: occasionally by gemmation, but more frequently by that modified process called spontaneous fission. And here, too, we have compound forms resulting from the arrest of this spontaneous fission before it is complete. To give examples is needless; since they would but show, in more varied ways, the truth already made sufficiently clear, that the compound *Cœlenterata* are aggregates of the third order, produced by integration of aggregates of the second order such as we have in the *Hydra*. As before, it is manifest that on the hypothesis of evolution, these higher integrations will insensibly arise, if the separation of the gemmiparous polypes is longer and longer postponed; and that an increasing postponement will result by survival of the fittest, if it profits the group of individuals to remain united instead of dispersing.

§ 203. The like relations exist, and imply that the like processes have been gone through, among those more highly-organized animals called *Molluscoida*. We have solitary individuals, and we have variously-integrated groups of individuals: the chief difference between the evidence here furnished, and that furnished in the last case, being the absence of a type obviously linking the solitary state with the aggregated state.

It is now an accepted belief that the creatures named *Brachiopoda*, very abundant in the so-called palæozoic times, but at present comparatively rare, are akin in structure to the *Polyzoa;* widely as they differ from them in size. If we cannot fairly say that by union of many Brachiopods there would be produced a compound animal like a Polyzoon; yet we may fairly say that were a small imperfectly-developed Brachiopod united with others like itself, a Polyzoon would result. This integration of aggregates of the second order, is carried on among the *Polyzoa* in divers ways, and with different degrees of completeness. The little patches of minute cells, shown as magnified in Fig. 153, so common on the fronds of sea-weeds and the surfaces of rocks at low-water mark, display little beyond mechanical combination. The adjacent individuals, though severally originated by gemmation from the same germ, have but little physiological dependence. In kindred kinds, however, as shown in Figs. 154 and 155, one of which is a magnified portion of the other, the integration is somewhat greater: the co-operation of the united individuals being shown in the production of those tubular branches which form their common support, and establish among them a more decided community of nutrition.


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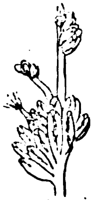
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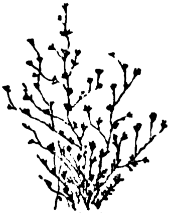
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Among the Ascidians, another order of the *Molluscoida*, this general law of morphological composition is once more displayed. Each of these creatures subsists on the nutritive particles contained in the water which it draws in through one orifice and sends out through another; and it may thus subsist either alone, or in connexion with others that are in some cases loosely aggregated and in other cases closely aggregated. Fig. 156, *Phallusia mentula*, is one of the solitary forms. A type in which the individuals are united by a stolon that gives origin to them by successive buds, is shown in *Perophora*, Fig. 157. Among the *Botryllidæ*, of which one


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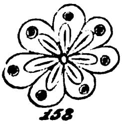
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kind is drawn on a small scale in Fig. 159, and a portion of the same on a larger scale in Fig. 158, there is a combination of the individuals into annular clusters, which are themselves imbedded in a common gelatinous matrix. And in this group there are integrations even a stage higher, in which several such clusters of clusters grow from a single base. Here the compounding and re-compounding, appears to be carried further than anywhere else in the animal kingdom.

Thus far, however, among these aggregates of the third order, we see what we before saw among the simpler aggregates of the second order—we see that the component individualities are but to a very small extent subordinated to the individuality made up of them. In nearly all the forms indicated, the mutual dependence of the united animals is so slight, that they are more fitly comparable to societies, of which the members co-operate in securing certain common benefits. There is scarcely any specialization of functions among them. Only in the last type described do we see a number of individuals so completely combined as to simulate a single individual. And even here, though there appears to be an intimate community of nutrition, there is no physiological integration beyond that implied in several mouths and stomachs having a common vent.

§ 204. We come now to an extremely interesting question. Does there exist in other sub-kingdoms composition of the third degree, analogous to that which we have found so prevalent among the *Cœlenterata* and the *Molluscoida?* The question is not whether elsewhere there are tertiary aggregates produced by the branching or clustering of secondary aggregates, in ways like those above traced; but whether elsewhere there are aggregates which, though otherwise unlike in the arrangement of their parts, nevertheless consist of parts so similar to one another that we may suspect them to be united secondary aggregates. The various compound types above described, in which the united animals maintain their individualities so distinctly that the individuality of the aggregate remains vague, are constructed in such ways that the united animals carry on their several activities with scarcely any mutual hindrance. The members of a branched *Hydrozoon* such as is shown in Fig. 149 or Fig. 150, are so placed that they can all spread their tentacles and catch their prey as well as though separately attached to stones or weeds. Packed side by side on a flat surface or forming a tree-like assemblage, the associated individuals among the *Polyzoa* are not unequally conditioned; or if one has some advantage over another in a particular case, the mode of growth and the relations to surrounding objects are so irregular as to prevent this advantage re-appearing with constancy in successive generations. Similarly with the Ascidians growing from a stolon or those forming an annular cluster: each of them is as well placed as every other for drawing in the currents of sea-water from which it selects its food. In these cases the mode of aggregation does not expose the united individuals to multiform circumstances; and therefore is not calculated to produce among them any structural multiformity. For the same reason no marked physiological division of labour arises among them; and consequently no combination close enough to disguise their several individualities. But under converse conditions we may expect converse results. If there is a mode of integration which necessarily subjects the united individuals to unlike sets of incident forces, and does this with complete uniformity from generation to generation, it is to be inferred that the united individuals will become unlike. They will severally assume such different functions as their different positions enable them respectively to carry on with the greatest advantage to the assemblage. This heterogeneity of function arising among them, will be followed by heterogeneity of structure; as also by that closer combination which the better enables them to utilize one another's functions. And hence, while the originally-like individuals are rendered unlike, they will have their homologies further obscured by their progressing fusion into an aggregate individual of a higher order.

These converse conditions are in nearly all cases fulfilled where the successive individuals arising by continuous development are so budded-off as to form a linear series. I say in nearly all cases, because there are some types in which the associated individuals, though joined in single file, are not thereby rendered very unlike in their relations to the environment; and therefore do not become differentiated and integrated to any considerable extent. I refer to such Ascidians as the *Salpidæ*. These creatures float passively in the sea, attached together in strings. Being placed side by side and having mouths and vents that open laterally, each of them is as well circumstanced as its neighbours for absorbing and emitting the surrounding water; nor have the individuals at the two extremities any marked advantages over the rest in these respects. Hence in this type, and in the allied type *Pyrosoma,* which has its component individuals built into a hollow cylinder, linear aggregation may exist without the minor individualities becoming obscured and the major individuality marked: the conditions under which a differentiation and integration of the component individuals may be expected, are not fulfilled. But where the chain of individuals produced by gemmation, is either habitually fixed to some solid body by one of its extremities or moves actively through the water or over submerged stones and weeds, the several members of the chain become differently conditioned in the way above described; and may therefore be expected to become unlike while they become united. A clear idea of the contrast between these two linear arrangements and their two diverse results, will be obtained by considering what happens to a row of soldiers, when changed from the ordinary position of a single rank to the position of Indian file. So long as the men stand shoulder to shoulder, they are severally able to use their weapons in like ways with like efficiency; and could, if called on, similarly perform various manual processes directly or indirectly conducive to their welfare. But when on the word of command "right face," they so place themselves that each has one of his neighbours before him and another behind him, nearly all of them become incapacitated for fighting and for many other actions. They can walk or run one after another, so as to produce movement of the file in the direction of its length; but if the file has to oppose an enemy or remove an obstacle lying in the line of its march, the front man is the only one able to use his weapons or hands to much purpose. And manifestly such an arrangement could become advantageous only if the front man possessed powers peculiarly adapted to his position, while those behind him facilitated his actions by carrying supplies, &c. This simile, grotesque as it seems, serves to convey better perhaps than any other could do, a clear idea of the relations that must arise in a chain of individuals arising by gemmation, and continuing permanently united end to end. Such a chain can arise by natural selection, only on condition that combination is more advantageous than separation; and for it to be more advantageous, the anterior members of the series must become adapted to functions facilitated by their positions, while the posterior members become adapted to functions which their positions permit. Hence, survival of the fittest must tend continually to establish types in which the connected individuals are more unlike one another, at the same time that their several individualities are more disguised by the integration consequent on their mutual dependence.

Such being the anticipations warranted by the general laws of evolution, we have now to inquire whether there are any animals which fulfil them. Very little search suffices; for structures of the kind to be expected are abundant. In that great division of the animal kingdom called *Annulosa*, especially if the *Annuloida* be regarded as part of it, we find a variety of types having the looked-for characters. Let us contemplate some of them.

§ 205. An adult Annelid is composed of segments which repeat one another in their details as well as in their general shapes. Dissecting one of the lower orders, such as is shown in Fig. 160, proves that the successive segments, besides having like locomotive appendages, like branchiæ, and sometimes even like pairs of eyes, also have like internal organs. Each has its enlargement of the alimentary canal; each its contractile dilatation of the great blood-vessel; each its portion of the double nervous cord, with ganglia when these exist; each its branches from the nervous and vascular trunks answering to those of its neighbours; each its similarly answering set of muscles; each its pair of openings through the body-wall; and so on throughout, even to the organs of reproduction. That is to say, every segment is in great measure a physiological whole—every segment contains most of the organs essential to individual life and multiplication: such essential organs as it does not contain, being those which its position as one in the midst of a chain, prevents it from having or needing. If we ask what is the meaning of these homologies, no adequate answer is supplied by any current hypothesis. That this "vegetative repetition" is carried out to fulfil a predetermined plan, was shown to be quite an untenable notion (§§ 133, 134). On the one hand, we found nothing satisfactory in the conception of a Creator who prescribed to him-

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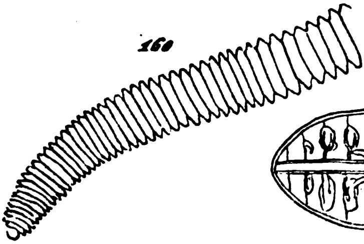

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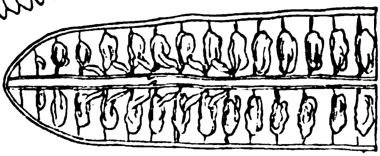
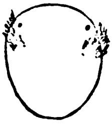


self a certain unit of composition for all creatures of a particular class, and then displayed his ingenuity in building up a great variety of forms without departing from the "archetypal idea." On the other hand, examination made it manifest that even were such a conception worthy of being entertained, it would have to be relinquished; since in each class there are numerous deviations from the supposed "archetypal idea." Still less can these traits of structure be accounted for teleologically. That certain organs of nutrition and respiration and locomotion are repeated in each segment of a dorsibranchiate annelid, may be regarded as functionally advantageous for a creature following its mode of life. But why should there be a hundred or even two hundred pairs of ovaries? This is an arrangement at variance with that physiological division of labour which every organism profits by—is a less advantageous arrangement than might have been adopted. That is to say, the hypothesis of a designed adaptation fails to explain the facts. Contrariwise, these structural traits are just such as might naturally be looked for, if these annulose forms have arisen by the integration of simpler forms. Among the various compound animals already glanced at, it is very general for the united individuals to repeat one another in all their parts—reproductive organs included. Hence if, instead of a clustered or branched integration, such as the *Cœlenterata* and *Molluscoida* exhibit, there occurs a longitudinal integration; we may expect that the united individuals will habitually indicate their original independence by severally bearing germ-producing or sperm-producing organs.

The reasons for believing one of these creatures to be an aggregate of the third order, are greatly strengthened when we turn from the adult structure to the mode of development. Among the *Dorsibranchiata* and *Tubicolæ*, the embryo leaves the egg in the shape of a ciliated gemmule, not much more differentiated than that of a polype. As shown in Fig. 162, it is a nearly globular mass; and its interior consists of untransformed cells. The first appreciable change is an elongation and a simultaneous commencement of segmentation. The segments multiply by a modified gemmation, which takes place from the hinder end of the penultimate segment. And considerable progress in marking out these divisions is made before the internal organization begins. Figs. 163, 164, 165, represent some of these early stages. In Annelids of other orders, the embryo assumes the segmented form while still in the egg. But it does this in just the same manner as before. Indeed, the essential identity of the two modes of development is shown by the fact that the segmentation within the egg is only partially carried out: in all these types the segments continue to increase in number for some time after birth. Now this process is as like that by which compound animals in general are formed, as the different conditions of the case permit. When new individuals are budded-out laterally, their unfolding is not hindered—there is nothing to disguise either the process or the product. But gemmæ produced one from another in the same straight line, and remaining connected, restrict one another's developments; and that the resulting segments are so many gemmiparously-produced individuals, is necessarily less obvious.



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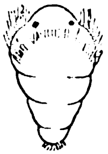

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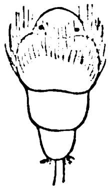

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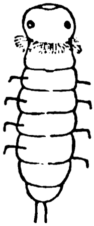

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§ 206. Evidence remains which adds very greatly to the weight of that already assigned. Thus far we have studied only the individual annulose animal; considering what may be inferred from its mode of evolution and final organization.

We have now to study annulose animals in general. Comparison of them will disclose various phases of progressive integration of the kind to be anticipated.

Among the simpler *Annuloida*, as in the *Nemertidæ* and in some kinds of *Planaria*, transverse fission occurs. A portion of a *Planaria* separated by spontaneous constriction, becomes an independent individual. Sir J. G. Dalyell found that in some cases numerous fragments artificially separated, grew into perfect animals. In these annuloids which thus remind us of the lowest *Hydrozoa* in their powers of agamogenetic multiplication, the individuals produced one from another, do not continue connected. As the young ones laterally budded-off by the *Hydra* separate when complete, so do the young ones longitudinally budded-off by the *Planaria*. Fig. 166 indicates this. But there are allied types which show us a more or less persistent union of homologous parts, or individuals, similarly arising by longitudinal gemmation. The cestoid *Entozoa* furnish illustrations. Without dwelling on the fact that each segment of a *Tænia*, like each separate *Planaria*, is an independent hermaphrodite, or on the fact that both develop their ova by the peculiar method of forming germinal vesicles in one canal and surrounding them with yelk that is secreted in another canal; and without specifying the sundry common structural traits which add probability to the suspicion that there is some kinship between the individuals of the one order and the segments of the other; it will suffice to point out that the two types are so far allied as to demand their union under the same subclass title. And recognizing this kinship, we see significance in the fact that in the one case the longitudinally-produced gemmæ separate as complete individuals, and in the other continue united as segments in smaller or larger numbers and for shorter or longer periods. In *Tænia echinococcus*, represented in Fig. 167, we have a species in which the number of segments thus united does not exceed four. In *Echinobothrium typus* there are eight or ten; and in cestoids generally they are numerous.* A considerable hiatus occurs between this phase of integration and the next higher phase which we meet with; but it is not greater than the hiatus between the types of the *Annuloida* and the *Annelida*, which present the two phases. Though it is doubtful whether separation of single segments occurs among the *Annelida*, yet very often we find strings of segments, arising by repeated longitudinal budding, which after reaching certain lengths undergo spontaneous fission: in some cases doing this so as to form two or more similar strings of segments constituting independent individuals; and in other cases doing it so that the segments spontaneously separated are but a small part of the string. Thus a *Syllis*, Fig. 168, after reaching a certain length, begins to transform itself into two individuals: one of the posterior segments develops into a head, and simultaneously narrows its connexion with the preceding segments, from which it


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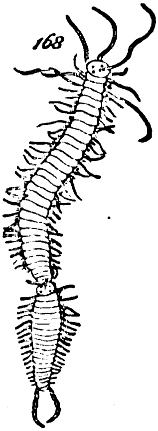
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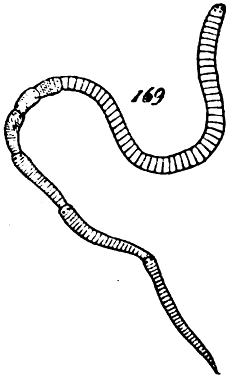
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* I find that the reasons for regarding the segment of a *Tænia* as answering to an individual of the second order of aggregation, are much stronger than I supposed when writing the above. Van Beneden says:—"Le Proglottis (segment) ayant acquis tout son développement, se détache ordinairement de la colonie et continue encore à croître dans l'intestin du même animal; il change même souvent de forme et semble doué d'une nouvelle vie; ses angles s'effacent, tout le corps s'arrondit, et il nage comme une Planaire au milieu des muscosités intestinales."

eventually separates. Still more remarkable is the extent to which this process is carried in certain kindred types; which exhibit to us several individuals thus being simultaneously formed out of groups of segments. Fig. 169, copied (omitting the appendages) from one contained in a memoir by M. Milne-Edwards, represents six worms of different ages in course of development: the terminal one being the eldest, the one having the greatest number of segments, and the one that will first detach itself; and the successively anterior ones, with their successively smaller numbers of segments, being successively less advanced towards fitness for separation and independence. Here among groups of segments we see repeated what in the previous cases occurs with single segments. And then in other Annelids we find that the string of segments arising by gemmation from a single germ becomes a permanently united whole: the tendency to any more complete fission than that which marks out the segments, being lost; or, in other words, the integration having become relatively complete. Leaving out of sight the question of alliance among the types above grouped together, that which it here concerns us to notice is, that longitudinal gemmation does go on; that it is displayed in that primitive form in which the gemmæ separate as soon as produced; that we have types in which such gemmæ hang together in groups of four, or in groups of eight and ten, from which however the gemmæ successively separate as individuals; that among higher types we have long strings of similarly-formed gemmæ which do not become individually independent, but separate into organized groups; and that from these we advance to forms in which all the gemmæ remain parts of a single individual. One other significant class of facts must be added. A few cases have been pointed out, one of them quite recently, in which Annelids multiply by lateral gemmation. M. Pagenstecher alleges this of the *Exogone gemmifera:* describing a certain number of the segments of the body as severally bearing on their dorsal surfaces a bud on each side. And M. L. Vaillant, after citing this observation of M. Pagenstecher, gives an account of a species of *Syllis* in which a great number of buds were borne by a single segment. That the longitudinally-produced gemmæ which compose an Annelid, should thus have, one of them or several of them, the power of laterally budding-off gemmæ, from which no doubt other annelids arise, gives further support to the hypothesis that, primordially, the segments were independent individuals. And it suggests this belief the more strongly because, in certain types of *Cœlenterata*, we see that longitudinal and lateral gemmation *do* occur together, where the longitudinally-united gemmæ are demonstrably independent individuals.

§ 207. It would add to the probability of this conclusion could we identify the type out of which the annulose type may have arisen by the process of integration. I believe there may be pointed out such a type—a type which, by a slight modification carrying somewhat further an habitual mode of development, would produce not only a unit of composition for the annulose type, but also as a bond uniting it with the other types, and these with one another. It is undesirable, however, here to enter upon the numerous explanations involved by opening the question of these relationships; both because it would necessitate a long digression, encumbering too much the general argument, and because, being highly speculative, it would be impolitic to let the general argument be even apparently implicated by it.

But even supposing it impossible now to identify the unit of composition of the annulose type, the foregoing evidence still goes far towards showing that an annulose animal is an aggregate of the third order. This repetition of segments, sometimes numbering several hundreds, like one another in all their organs even down to those of reproduction, while it is otherwise unaccountable, is fully accounted for if these segments are homologous with the separate individuals of some lower type. The gemmation by which these segments are produced, is as similar as the conditions allow, to the gemmation by which compound animals in general are produced. As among plants and as among demonstrably-compound animals, we see that the only thing required for the formation of a permanent chain of gemmiparously-produced individuals, is that by remaining associated, such individuals will have advantages greater than are to be gained by separation. Further, by comparison of the annuloid and lower annulose forms, we discover a number of those transitional phases of integration which the hypothesis leads us to expect. And, lastly, the differences among these united individuals or successive segments, are not greater than the differences in their positions and functions explain—not greater than such differences are known to produce among other united individuals: witness sundry compound *Hydrozoa.*

Indirect evidence of much weight has still to be given. Thus far we have considered only the less-developed *Annulosa.* The more integrated and more differentiated types of the class remain. If in them we find a carrying further of the processes by which the lower types are here supposed to have been evolved, we shall have additional reason for believing them to have been so evolved. If we find that in these superior orders the individualities of the united segments are much less pronounced than in the inferior, we shall have grounds for suspecting that in the inferior the individualities of the segments are less pronounced than in those lost forms which initiated the annulose sub-kingdom.

## CHAPTER V.

### THE MORPHOLOGICAL COMPOSITION OF ANIMALS, CONTINUED.

§ 208. INSECTS, Arachnids, Crustaceans, and Myriapods, are all members of that higher division of the *Annulosa* called *Articulata* or *Arthropoda*. Though in these creatures the formation of segments may be interpreted as a disguised gemmation; and though in some of them the number of segments increases by this modified budding after leaving the egg, as among the higher Annelids; yet the process is not nearly so dominant: the segments are usually much less numerous than we find them in the types last considered. In most cases, too, the segments are in a greater degree differentiated one from another, at the same time that they are severally more differentiated within themselves. Nor is there any instance of spontaneous fission taking place in the series of segments composing an articulate animal. On the contrary, the integration, always great enough permanently to unite the segments, is frequently carried so far as to hide very completely the individualities of some or many of them; and occasionally, as among the *Acari*, the consolidation, or the arrest of segmentation, is so decided as to leave scarcely a trace of the articulate structure: the type being in these cases indicated chiefly by the presence of those characteristically-formed limbs, which give the alternative name *Arthropoda* to all the higher *Annulosa*. Omitting the parasitic orders, which, as in other cases, are aberrant members of their sub-kingdom, comparisons between the different orders prove that the higher are strongly distinguished from the lower, by the much greater degree in which the individuality of the tertiary aggregate dominates over the individualities of those secondary aggregates called segments or "somites," of which it is composed. The successive Figs. 170—176, representing (without their limbs) a Julus, a Scolopendra, an isopodous Crustacean, and four kinds of decapodous Crustaceans, ending with a Crab, will convey at a glance an idea of the way in which that greater size and heterogeneity reached by the higher types, is accompanied by an integration which, in the extreme cases, almost obliterates all traces of composite structure. In the Crab the posterior segments, usually folded underneath the shell, alone preserve their primitive distinctness: so completely confluent are the rest, that it seems absurd to say that a Crab's carapace is composed of as many segments as there are pairs of limbs, foot-jaws, and antennæ attached to it; and were it not that during early stages of the Crab's development the segmentation is faintly marked, the assertion might be considered illegitimate.


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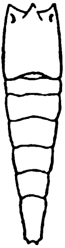
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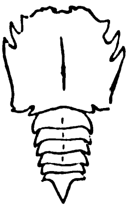
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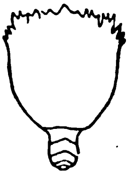
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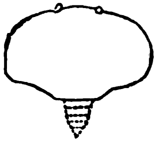
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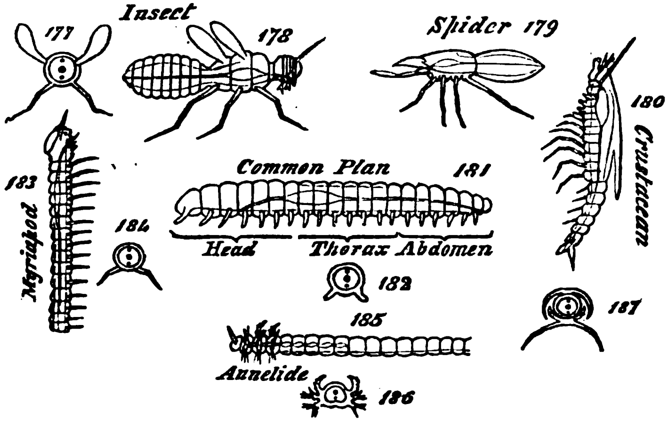
That all articulate animals are thus composed from end to end of homologous segments, is, however, an accepted doctrine among naturalists. It is a doctrine that rests on careful observation of three classes of facts—the correspondences of parts in the successive "somites" of an adult articulate animal; the still more marked correspondences of such parts as they exist in the embryonic or larval articulate animal; and the maintenance of such correspondences in some types, which are absent in types otherwise near akin to them. The nature of the conclusion which these evidences unite in supporting, will best be shown by the annexed copies from the lecture-diagrams of Prof. Huxley; exhibiting the typical structures of a Myriapod, an Insect, a Spider, and a Crustacean, with their relations to a common plan, as interpreted by him.



Treating of these homologies, Prof. Huxley says "that a striking uniformity of composition is to be found in the heads of, at any rate, the more highly organized members of these four classes, and that, typically, the head of a Crustacean, an Arachnid, a Myriapod, or an Insect, is composed of six somites (or segments corresponding with those of the body) and their appendages, the latter being modified so as to serve the purpose of sensory and manducatory organs." And omitting the Myriapods, he also finds among these groups the further unity that in most of them the entire animal contains twenty of these homologous segments.

Thus even in the higher *Annulosa,* the much greater consolidation and much greater heterogeneity do not obliterate the evidence of the fact, that the organism is an aggregate of the third order. Beyond all question it is divisible into a number of proximate units, each of which has essentially the same structure as its neighbours, and each of which is an aggregate of the second order, in so far as it is an organized combination of those aggregates of the first order which we call morphological units or cells. And that these segments or somites, which make up an annulose animal, were originally aggregates of the second order having independent individualities, is an hypothesis which gathers further support from the contrast between the higher and the lower articulate types, as well as from the contrast between the *Articulata* in general and the inferior *Annulosa.* For if that masking of the individualities of the segments which we find distinguishes the higher forms from the lower, has been going on from the beginning, as we may fairly assume; it is to be inferred that the individualities of the segments in the lower forms, were originally more marked than they now are. Reversing those processes of change by which the most developed *Annulosa* have arisen from the least developed; and applying in thought this reversed process to the least developed, as they were described in the last Chapter; we are brought to the conception of attached segments that are completely alike, and have their individualities in no appreciable degree subordinated to that of the chain they compose. From which there is but a step to the conception of gemmiparously-produced individuals which severally part one from another as soon as they are formed.

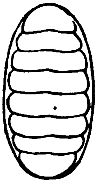
§ 209. We must now return to a point whence we diverged some time ago. As before explained under the head of Classification, organisms do not admit of uni-serial arrangement, either in general or in detail; but everywhere form groups within groups. Hence, having traced the phases of morphological composition up to the highest forms in any sub-kingdom, we find ourselves at the extremity of a great branch, from which there is no access to another great branch, except by going back to some place of bifurcation low down in the tree.

The nearest relatives of the *Mollusca* are those molluscoid forms treated of early in the last Chapter. A Brachiopod or a solitary Ascidian, though widely unlike a Mussel or a Snail or a Cuttle-fish, is nearer akin to them than is any cœlenterate animal or annulose animal or vertebrate animal. One of the leading distinctions, however, between the *Molluscoida* and the *Mollusca,* considered as groups, is that whereas the *Molluscoida* are very frequently, or indeed generally, compound, the *Mollusca* are invariably single. No true Mollusk multiplies by gemmation, either continuous or discontinuous; but the product of every fertilized germ is a single individual.

It is a significant fact that here, where for the first time we have homogenesis holding throughout an entire sub-kingdom, we have also throughout an entire sub-kingdom no case in which the organism is divisible into two, three, or more, like parts. There is neither any such clustering or branching as a cœlenterate or molluscoid animal usually displays; nor is there any trace of that segmentation which characterizes the *Annulosa.* Among these animals in which no single egg produces several individuals, no individual is separable into several homologous divisions. This connexion will be seen to have a probable meaning, on remembering that it is the converse of the connexion which obtains among the *Annulosa,* considered as a group.

A Mollusk, then, is an aggregate of the second order. Not only in the adult animal is there no sign of a multiplicity of like parts that have become obscured by integration; but there is no sign of such multiplicity in the embryo. And this unity is just as conspicuous in the lowest Lamellibranch as in the highest Cephalopod.

It may be well to note, however, more especially because it illustrates a danger of misinterpretation presently to be guarded against, that there are certain Mollusks which simulate the segmented structure. Externally a *Chiton*, Fig. 188, appears to be made up of divisions substantially like those of the creature Fig. 189; and one who judged only by externals, would say that the creature Fig. 190 differs as much from the creature Fig. 189, as this does from the preceding one. But the truth is, that while 190 and 189 are closely-allied types, 189 differs from 188 much more widely than a man does from a fish. And the radical distinction between them is this; that whereas in the Crustacean the segmentation is carried transversely through the whole mass of the body, so as to render the body more or less clearly divisible into a series of parts that are similarly composed; in the Mollusk the segmentation is limited to the shell which it carries on its upper surface, and leaves its body as completely undivided as is that of a common slug. Were the body cut through at each of the divisions, the section of it attached to each portion of the shell would be unlike all the other sections. Here the segmentation has a purely functional derivation—is adaptive instead of genetic. The similarly-formed and similarly-placed parts, are not homologous in the same sense as are the appendages of a phœnogamic axis or the limbs of an insect.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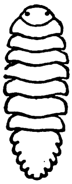
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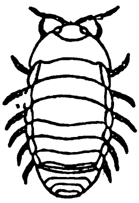
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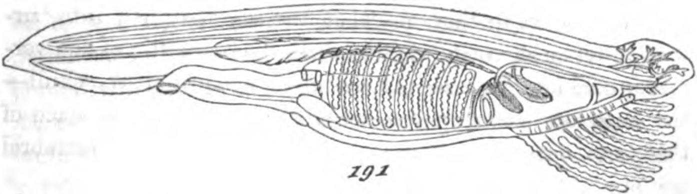
§ 210. In studying the remaining and highest sub-kingdom of animals, it is important to recognize this radical difference in meaning between that likeness of parts which is produced by likeness of modifying forces, and that likeness of parts which is due to primordial identity of origin. On our recognition of this difference depends the view we take of certain doctrines that have long been dominant, and have still a wide currency.

Among the *Vertebrata,* as among the *Mollusca,* homogenesis is universal. The two sub-kingdoms are like one another and unlike the remaining sub-kingdoms in this, that in all the types they severally include, a single fertilized ovum produces only a single individual. It is true that as the eggs of certain Gasteropods occasionally exhibit spontaneous fission of the vitelline mass, which may or may not result in the formation of two individuals; so among vertebrate animals we now and then meet with double monsters, which appear to imply such a spontaneous fission imperfectly carried out. But these anomalies serve to render conspicuous the fact, that in both these sub-kingdoms the normal process is the integration of the whole germ-mass into a single organism, which at no phase of its development displays any tendency to separate into two or more parts.

Equally as throughout the *Mollusca* there holds throughout the *Vertebrata,* the correlative fact, that not even in its lowest any more than in its highest types, is the body divisible into homologous segments. The vertebrate animal, under its simplest as under its most complex form, is like the molluscous animal in this, that you cannot cut it into transverse slices, each of which contains a digestive organ, a respiratory organ, a reproductive organ, &c. The organs of the least-developed fish as well as those of the most-developed mammal, form but a single physiological whole; and they show not the remotest trace of having ever been divisible into two or more physiological wholes. That segmentation which the vertebrate animal usually exhibits throughout part of its organization, is the same in origin and meaning as the segmentation of a *Chiton's* shell; and no more implies in the vertebrate animal a composite structure, than do the successive pairs of branchiæ of the *Doto* or the transverse rows of branchiæ in the *Eolis,* imply composite structure in the molluscous animal. To some this will seem a very questionable proposition; and had we no evidence beyond that which adult vertebrate animals of developed types supply, it would be a proposition not easy to substantiate. But abundant support for it is to be found in the structure of the vertebrate embryo, and in the comparative morphology of the *Vertebrata* in general.

Embryologists teach us that the primordial relations of parts are most clearly displayed in the early stages of evolution; and that they generally become partially or completely disguised in its later stages. Hence, were the vertebrate animal on the same level as the annulose animal in degree of composition—did it similarly consist of segments which are homologous in the sense that they are the proximate units of composition; we ought to find this fundamental fact most strongly marked at the outset. As in the annelid-embryo, the first conspicuous change is the elongation and division into segments, by constrictions that encircle the whole body; and as in the articulate embryo, the blastoderm becomes marked out transversely into pieces which extend themselves round the yelk before the internal organization has made any appreciable progress; so in the embryo of every vertebrate animal, had it an analogous composition, the first decided change should be a segmentation implicating the entire mass. But it is not so. Sundry important differentiations occur before any divisions begin to show themselves. There is the defining of that elongated, elevated area with its longitudinal groove, which becomes the seat of subsequent changes; there is the formation of the notochord lying beneath this groove; there is the growth upwards of the boundaries of the groove into the dorsal laminæ, which rapidly develop and fold over in the region of the head. Rathke, as quoted and indorsed by Prof. Huxley, describes the subsequent changes as follows:—"The gelatinous investing mass, which, at first, seems only to constitute a band to the right and to the left of the notochord, forms around it, in the further course of development, a sheath, which ends in a point posteriorly. Anteriorly, it sends out two processes which underlie the lateral parts of the skull, but very soon coalesce for a longer or shorter distance. Posteriorly, the sheath projects but little beyond the notochord; but, anteriorly, for a considerable distance, as far as the infundibulum. It sends upwards two plates, which embrace the future central parts of the nervous system laterally, probably throughout their entire length." All this precedes segmentation. Considered under its broadest aspects, the process is directly opposed to the process among the *Annulosa*. Whereas among the *Annulosa* the first step is the resolution of the germ-mass or of the blastoderm into segments, which may or may not afterwards become integrated; in the *Vertebrata* the first step is the marking out on the blastoderm of an integrated structure within which segments subsequently appear. When these do appear, they are for some time limited to the middle region of the spinal axis; and no more then than ever after, do they implicate the general mass of the body in their transverse divisions. On the contrary, before segmentation has made much progress the rudiments of the vascular system are laid down in a manner showing not the remotest trace of any primordial correspondence of its parts with the divisions of the axis. No less at variance with the belief that the vertebrate animal is essentially a series of homologous parts, is the heterogeneity which exists among these parts on their first appearance. Though in the head of an adult articulate animal there is little sign of divisibility into segments like those of the body; yet such segments, with their appropriate ganglia and appendages, are easily identifiable in the articulate embryo. But in the vertebrata this antithesis is exactly reversed. At the time when segmentation has become decided in the dorsal region of the spine, there is no trace of segments in the parts that are to form the skull—nothing whatever to suggest that the skull is being formed out of divisions homologous with vertebræ. And minute observation no more discloses any such homology than does general appearance. "Remak," says Prof. Huxley, "has more fully proved than any other observer, the segmentation into 'urwirbel,' or proto-vertebræ, which is characteristic of the vertebral column, stops at the occipital margin of the skull—the base of which, before ossification, presents no trace of that segmentation which occurs throughout the vertebral column."

Consider next the evidence supplied by comparative morphology. In preceding sections (§§ 206, 208,) it has been shown that among annulose animals, the divisibility into homologous parts is most clearly demonstrable in the lowest types. Though in decapodous Crustaceans, in Insects, in Arachnids, there is difficulty in identifying some or many of the component somites; and though when identified they display only partial correspondences; yet on descending to Annelids, the composition of the entire body out of such somites becomes conspicuous, and the homology between each somite and its neighbours is shown by the repetition of one another's structural details, as well as by their common gemmiparous origin: indeed, in some cases we have the homology directly demonstrated by seeing a somite of the body transformed into a head. If, then, a vertebrate animal had a segmental composition of kindred nature, we ought to find it most clearly marked in the lowest *Vertebrata*, and most disguised in the highest *Vertebrata*. But here, as before, the fact is just the reverse. Among the *Vertebrata* of developed type, such segmentation as really exists remains conspicuous—is but little obscured even in parts of the spinal column formed out of integrated vertebræ. Whereas in the undeveloped vertebrate type, segmentation is scarcely at all traceable. The *Amphioxus*, Fig. 191, is not only without ossified vertebræ; not only is it without cartilaginous representatives of them; but it is even without anything like distinct membranous divisions. The spinal column exists as a continuous notochord: the only signs of incipient segmentation being given by its membranous sheath, in the upper part of which "quadrate masses of somewhat denser tissue seem faintly to represent neural spines." Moreover, throughout sundry groups of fishes and amphibians, the segmentation remains very imperfect: only certain peripheral appendages of the vertebræ becoming defined and solidified, while in place of the bodies of the vertebræ there still continues the undivided notochord. Thus, instead of being morphologically composed of vertebral segments, the vertebrate animal in its primitive form is entirely without vertebral segments; and vertebral segments begin to appear only as we advance towards developed forms. Once more, evidence equally adverse to the current hypothesis meets us on observing that the differences between the parts supposed to be homologous, are as great at first as at last. Did the vertebrate animal primordially consist of homologous segments from snout to tail; then the segments said to compose the skull ought, in the lowest *Vertebrata*, to show themselves much more like the remaining segments than they do in the highest *Vertebrata*. But they do not. Fishes have crania made up of bones that are no more clearly arrangeable into segments like vertebræ, than are the cranial bones of the highest mammal. Nay, indeed, the case is much stronger: the simplest fish possessing a skeleton, has a cranium composed of cartilage that is not segmented at all!



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Besides being inconsistent with the leading truths of Embryology and Comparative Morphology, the hypothesis of Goethe and Oken is inconsistent with itself. The facts brought forward to show that there exists an archetypal vertebra; and that the vertebrate animal is composed of archetypal vertebræ arranged in a series, and severally modified to fit their positions—these facts, I say, so far from proving as much, suffice, when impartially considered, to disprove it. No assigned nor any conceivable attribute of the supposed archetypal vertebra is uniformly maintained. The parts composing it are constant neither in their number, nor in their relative positions, nor in their modes of ossification, nor in the separateness of their several individualities when present. There is no fixity of any one element, or connexion, or mode of development, which justifies even a suspicion that vertebræ are modelled after an ideal pattern. To substantiate these assertions here would require too much space, and an amount of technical detail wearisome to the general reader. The warrant for them will be found in a criticism on the osteological works of Prof. Owen, originally published in the *British and Foreign Medico-Chirurgical Review* for Oct. 1858. This criticism I add in the Appendix, for the convenience of those who may wish to study the question more fully. (See Appendix B.)

Everything, then, goes to show that the segmental composition which characterises the apparatus of external relation in most vertebrata, is not primordial or genetic, but functionally determined or adaptive. Our inference must be that the vertebrate animal is an aggregate of the second order, in which a relatively superficial segmentation has been produced by mechanical intercourse with the environment. We shall hereafter see that this conception leads us to a consistent interpretation of the facts—shows us why there has arisen such unity in variety as exists in every vertebral column, and why this unity in variety is displayed under countless modifications in different skeletons.

§ 211. Glancing back at the facts brought together in these two chapters, it seems probable that there has gone on among animals a process parallel to that which we saw reason to think has gone on among plants. Minute aggregates of those physiological units which compose living protoplasm, exist as *Protozoa:* some of them incoherent, indefinite, and almost homogenous; and others of them more coherent, definite, and heterogenous. By union of these nucleated particles of sarcode, are produced various indefinite aggregates of the second order—Sponges, Thalassicollæ, Foraminifers, &c.; in which the compound individuality is scarcely enough marked to subordinate the primitive individualities. But in other types, as the *Hydra*, the lives of the morphological units are in a considerable degree, though not wholly, merged in the life of the integrated whole they form. As the primary aggregate when it passes a certain size undergoes fission or gemmation; so does the secondary aggregate. And as on the lower stage so on the higher, we see cases in which the gemmiparously-produced individuals part as soon as formed, and other cases in which they continue united, though in great measure independent. This massing of secondary aggregates into tertiary aggregates, is variously carried on among the *Hydrozoa*, the *Actinozoa*, and the *Molluscoida*. In most of the types so produced, the component individualities are very little subordinated to the individuality of the mass they form —there is only physical unity and not physiological unity; but in certain of the oceanic *Hydrozoa*, the individuals are so far differentiated and combined as very much to mask them. Forms showing us clearly the transition to well-developed individuals of the third order, are not to be found. Nevertheless, in the great sub-kingdom *Annulosa*, there are traits of structure, development, and mode of multiplication, which go far to show that its members are such individuals of the third order; and in the relations to external conditions involved by the mode of union, we find an adequate cause for that obscuration of the secondary individualities which we must suppose has taken place. The two other great sub-kingdoms *Mollusca* and *Vertebrata*, between the lower members of which there are suggestive points of community, present us only with aggregates of the second order, that have in many cases become very large and very complex. We find in them no trace of the union of gemmiparously-produced individuals. Neither the molluscous nor the vertebrate animal shows the faintest trace of a segmentation affecting the totality of its structure; and we see good grounds for concluding that such segmentation as exceptionally occurs in the one and usually occurs in the other, is superinduced.

# CHAPTER VI.

## MORPHOLOGICAL DIFFERENTIATION IN PLANTS.

§ 212. WHILE in the course of their evolution plants and animals have displayed progressive integrations, there have at the same time been progressive differentiations of the resulting aggregates, both as wholes and in their parts. These differentiations and the interpretations of them, form the second class of morphological problems.

We commence as before with plants. We have to consider, first, the several kinds of modification in shape they have undergone; and, second, the relations between these kinds of modification and their factors. Let us glance at the leading questions that have to be answered.

§ 213. Irrespective of their degrees of composition, plants may, and do, become changed in their general forms. Are their changes capable of being formulated? The inquiry which meets us at the outset is—does a plant's shape admit of being expressed in any universal terms?—terms that remain the same for all genera, orders, and classes.

After plants considered as wholes, have to be considered their proximate components, which vary with their degrees of composition, and in the highest plants are what we call branches. Is there any law traceable among the contrasted shapes of different branches in the same plant? Do the relative developments of parts in the same branch conform to any law? And are these laws, if they exist, allied with one another and with that to which the shape of the whole plant conforms?

Descending to the components of these components, which in developed plants we distinguish as leaves, there meet us kindred questions respecting their relative sizes, their relative shapes, and their shapes as compared with those of foliar organs in general. Of their morphological differentiations, also, it has to be asked whether they exemplify any truth that is exemplified by the entire plant and by its larger parts.

Then, a step lower, we come down to those morphological units of which leaves and fronds consist; and concerning these arise parallel inquiries touching their divergencies from one another and from cells in general.

The problems thus put together in several groups cannot of course be rigorously separated. Evolution pre-supposes transitions which make all such classings more or less conventional; and adherence to them must be subordinate to the needs of the occasion.

§ 214. In studying the causes of the morphological differentiations thus grouped and prospectively generalized, we shall have to bear in mind several orders of forces which it will be well briefly to specify.

Growth tends inevitably to initiate changes in the shape of any aggregate, by changing both the amounts of the incident forces and the forces which the parts exert on one another. With the mechanical actions this is obvious: matter that is sensibly plastic cannot be increased in mass without undergoing a change in its proportions, consequent on the diminished ratio of its cohesive force to the force of gravitation. With the physiological actions it is equally obvious: increase of size, other things equal, alters the relations of the parts to the material and dynamical factors of nutrition; and by so affecting differently the nutrition of different parts, initiates further changes of proportions.

Similarly in any composite plant, the proximate units as fast as they accumulate are subjected to mutual influences that are unlike one another and are continually changing. The earlier-formed units become mechanical supporters of the later-formed units, and so experience modifying forces from which the later-formed units are exempt. Further, these elder units simultaneously begin to serve as channels through which materials are carried to and from the younger units—another cause of differentiation that goes on increasing in intensity. Once more, there arise ever-strengthening contrasts between the amounts of light which fall upon the youngest or outermost units and the eldest or innermost units; whence result structural contrasts of yet another kind. Evidently, then, along with the progressive integration of cells into fronds, of fronds into axes, and of axes into plants still more composite, there come into play sundry causes of differentiation which act on the whole and on each of its parts, whatever their grade. The forces to be overcome, the forces to be utilized, and the matters to be appropriated, do not remain the same in their proportions and modes of action for any two members of the aggregate: be they members of the first, second, third, or any other order.

§ 215. Nor are these the only kinds and causes of heterogeneity which we have to consider. Beyond the more general changes produced in the relative sizes and shapes of plants and their parts by progressive aggregation, there are the more particular changes determined by the more particular conditions.

Plants as wholes assume unlike attitudes towards their environments; they have many ways of articulating their parts with one another; they have many ways of adjusting their parts towards surrounding agencies. These are causes of special differentiations additional to those general differentiations that result from increase of mass and increase of composition. In each part considered individually, there arises a characteristic shape consequent on that relative position towards external and internal forces, which the mode of growth entails. Every member of the aggregate presents itself in a more or less peculiar way towards the light, towards the air, and towards its point of support; and according to the relative homogeneity or heterogeneity in the incidence of the agencies thus brought to bear on it, will be the relative homogeneity or heterogeneity of its shape.

§ 216. Before passing from this *à priori* view of the morphological differentiations which necessarily accompany morphological integrations, to an *à posteriori* view of them, it seems needful to specify the meanings of certain descriptive terms we shall have to employ.

Taking for our broadest division among forms, the regular and the irregular, we may divide the latter into those which are wholly irregular and those which, being but partially irregular, suggest some regular form to which they approach. By slightly straining the difference between them, two current words may be conveniently used to describe these subdivisions. The entirely irregular forms we may class as *asymmetrical*—literally as forms without any equality of dimensions. The forms which approximate towards regularity without reaching it, we may distinguish as *unsymmetrical*—a word which, though it asserts inequality of dimensions, has been associated by use rather with such slight inequality as constitutes an observable departure from equality.

Of the regular forms there are several classes, differing in the number of directions in which equality of dimensions is repeated. Hence results the need for names by which symmetry of several kinds may be expressed.

The most regular of figures is the sphere: its dimensions are the same from centre to surface in all directions; and if cut by any plane through the centre, the separated parts are equal and similar. This is a kind of symmetry which stands alone, and will be hereafter spoken of as *spherical symmetry.*

When a sphere passes into a spheroid, either prolate or oblate, there remains but one set of planes that will divide it into halves which are in all respects alike; namely, the planes in which its axis lies, or which have its axis for their line of intersection. Prolate and oblate spheroids may severally pass into various forms without losing this property. The prolate spheroid may become egg-shaped or pyriform, and it will still continue capable of being divided into two equal and similar parts by any plane cutting it down its axis; nor will forming constrictions round it deprive it of this property. Similarly with the oblate spheroid. The transition from a slight oblateness like that of an orange to an oblateness reducing it nearly to a flat disc, does not alter its divisibility into like halves by every plane passing through its axis. And clearly the moulding of any such flattened oblate spheroid into the shape of a plate, leaves it as before, symmetrically divisible by all planes at right angles to its surface and passing through its centre. This species of symmetry is called *radial symmetry.* It is familiarly exemplified in such flowers as the daisy, the tulip, and the dahlia.

From spherical symmetry, in which we have an infinite number of axes through each of which may pass an infinite number of planes severally dividing the aggregate into equal and similar parts; and from radial symmetry, in which we have a single axis through which may pass an infinite number of planes severally dividing the aggregate into equal and similar parts; we now turn to *bilateral symmetry,* in which the divisibility into equal and similar parts becomes very limited. Noting, for the sake of completeness, that there is a sextuple bilateralness in the cube and its derivative forms, which admit of division into equal and similar parts by planes passing through the three diagonal axes and by planes passing through the three axes that join the centres of the surfaces, let us limit our attention to the three kinds of bilateralness which here concern us. The first of these is *triple bilateral symmetry.* This is the symmetry of a figure having three axes at right angles to one another, through each of which there passes a single plane that divides the aggregate into corresponding halves. A common brick will serve as an example; and of objects not quite so simple, the most familiar is that modern kind of spectacle-case which is open at both ends. This may be divided into corresponding halves along its longitudinal axis, by cutting it through in the direction of its thickness or by cutting it through in the direction of its breadth; or it may be divided into corresponding halves by cutting it across the middle. Of objects which illustrate *double bilateral symmetry,* may be named one of those boats built for moving with equal facility in either direction, and therefore made alike at stem and stern. Obviously such a boat is separable into equal and similar parts by a vertical plane passing through stem and stern; and it is also separable into equal and similar parts by a vertical plane cutting it amidships. To exemplify *single bilateral symmetry* it needs but to turn to the ordinary boat of which the two ends are unlike. Here there remains but the one plane passing vertically through stem and stern, on the opposite sides of which the parts are symmetrically disposed.

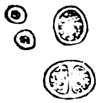
These several kinds of symmetry as placed in the foregoing order, imply increasing heterogeneity. The greatest uniformity in shape is shown by the divisibility into like parts in an infinite number of infinite series of ways; and the greatest degree of multiformity consistent with any regularity, is shown by the divisibility into like parts in only a single way. Hence, in tracing up organic evolution as displayed in morphological differentiations, we may expect to pass from the one extreme of spherical symmetry, to the other extreme of single bilateral symmetry. This expectation we shall find to be completely fulfilled.

# CHAPTER VII.

## THE GENERAL SHAPES OF PLANTS.

§ 217. Among protophytes those which are by general consent regarded as the simplest, are the *Protococci.* As shown in Fig. 1, they are globular cells presenting no obvious differentiation save that between inner and outer parts. Their uniformity of figure coexists with a mode of life involving the uniform exposure of all their sides to incident forces. The *Protococcus nivalis,* which colours red the snow through which it spreads with such marvellous rapidity, is subject to no constant contrasts in the amounts of light, heat, air, or moisture, on its upper and lower surfaces. For though each individual may have its external parts differently related to environing agencies, yet the new individuals produced by spontaneous fission have no means of maintaining parallel relations of position among their parts. On the contrary, the indefiniteness of the attitudes into which successive generations fall, must prevent the rise of any unlikeness between one portion of the surface and another. Spherical symmetry continues because, on the average of cases, incident forces are equal in all directions.

Other orders of *Protophyta* have much more special forms, along with much more special attitudes: their homologous parts maintaining, from generation to generation, unlike relations to incident forces. The *Desmidiaceæ* and



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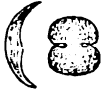

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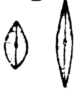

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*Diatomaceæ,* of which Figs. 2 and 3 show examples, severally include genera characterized by triple bilateral symmetry. A *Navicula* is divisible into corresponding halves by a transverse plane and by two longitudinal planes—one cutting its valves at right angles and the other passing between its valves. The like is true of those numerous transversely-constricted forms of *Desmidiaceæ,* exemplified by the second of the individuals represented in Fig. 2. If now we ask how a *Navicula* is related to its environment, we see that its mode of life exposes it to three different sets of forces: each set being resolvable into two equal and opposite sets. A *Navicula* moves in the direction of its length, with either end foremost. Hence, on the average, its ends are subject to like actions from the agencies to which its motions subject it. Further, either end while moving, exposes its right and left sides to amounts of influence which in the long run must be equal. If, then, the two ends are not only like one another, but have corresponding right and left sides, the symmetrical distribution of parts answers to the symmetrical distribution of forces. Passing to the two edges and the two flat surfaces, we similarly find a clue to their likenesses and differences in their respective relations to the things around them. These locomotive protophytes move through the entangled masses of fragments and fibres produced by decaying organisms and confervoid growths. The interstices in such matted accumulations are nearly all of them much longer in one dimension than in the rest—form crevices rather than regular meshes. Hence, a small organism will have much greater facility of insinuating itself through this *débris,* in which it finds nutriment, if its transverse section is flattened instead of square or circular. And while we see how, by survival of the fittest, a flattened form is likely to be acquired by diatoms having this habit; we also see that likeness will be maintained between the two flat surfaces and between the two edges. For, on the average, the relations of the two flat surfaces to the sides of the openings through which the diatom passes, will be alike; and so, too, on the average, will be the relations of the two edges. In desmids of the type exemplified by the second individual in Fig. 2, a kindred equalization of dimensions is otherwise insured. There is nothing to keep one of the two surfaces uppermost rather than the other; and hence, in the long succession of individuals, the two surfaces are sure to be similarly exposed to light and agencies in general. When to this is added the fact that spontaneous fission occurs transversely in a constant way, it becomes manifest that the two ends, while they are maintained in conditions like one another, are maintained in conditions unlike those of the two edges. Here then, as before, triple bilateral symmetry in form, coexists with a triple bilateral symmetry in the average distribution of actions.

Still confining our attention to aggregates of the first order, let us next note what results when the two ends are permanently subject to different conditions. The fixed unicellular plants, of which examples are given in Figs. 4, 5, and 6, severally illustrate the contrast in shape that arises between the part that is applied to the supporting surface and the part that extends into the surrounding medium. These two parts which are the most unlike in their relations to incident forces, are the most unlike in their forms. Ob-

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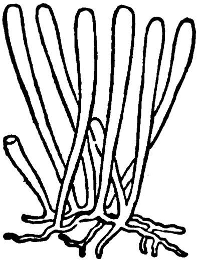

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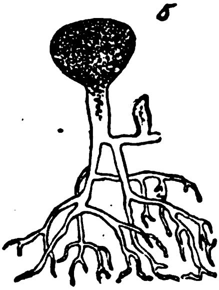

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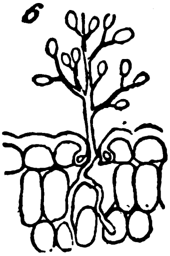


serve, next, that the part which lifts itself into the water or air, is more or less decidedly radial. Each upward growing tubule of *Codium adhærens*, Fig. 4, has its parts disposed with some regularity around its axis; the upper stem and spore-vessel of *Hydrogastrum*, Fig. 5, display a lateral growth that is approximately equal in every direction; and the branches of the *Botrytis*, Fig. 6, shoot out with an approach to evenness on all sides. Plants of this low type are naturally very variable in their modes of growth: each individual being greatly modified in form by its special circumstances. But they nevertheless show us a general likeness between parts exposed to like forces, as well as a general unlikeness between parts exposed to unlike forces.

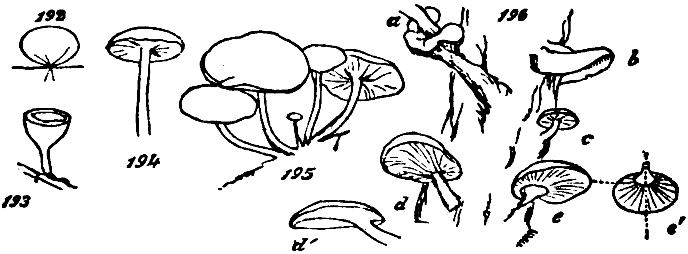
Respecting the forms of these aggregates of the first order, it has only to be added that they are asymmetrical where there is total irregularity in the incidence of forces. We have an example in the indefinitely contorted and branched shape of a fungus-cell, growing as a mycelium among the particles of soil or through the interstices of organic tissue.

§ 218. Re-illustrations of the general truths which the forms of these vegetal aggregates of the first order display, are furnished by vegetal aggregates of the second order. The equalities and inequalities of growth in different directions, prove to be similarly related to the equalities and inequalities of environing actions in different directions.

Of spherical symmetry, an instance occurs in the *Volvox globator*. The ciliated cells, here so united as to produce a small, mulberry-shaped, hollow ball, cause, by the movements of their cilia, a simultaneous rotation of the ball and progress of it through the water. There is nothing to determine the axis of rotation or the direction of rotation. And if the axis and direction of rotation continually vary, as we may conclude that they do, then the different members of the aggregate severally occupy in their turns like positions towards surrounding agencies; and so are not made to lose their homogeneity of form and distribution.

Vegetal aggregates of the second order are usually fixed: locomotion is exceptional. Fixity implies that the surface of attachment is differently circumstanced from the free surface. Hence we may expect to find, as we do find, that among these rooted aggregates of the second order, as among those of the first order, the primary contrast of shape is between the adherent part and the loose part. Sea weeds variously exemplify this. In some the fronds are very irregular and in some tolerably regular; in some the form is pseudo-foliar and in some pseud-axial; but differing though they do in these respects, they agree in having the end which is attached to a solid body unlike the other end. The same truth is seen in such secondary aggregates as the common fungi, or rather in their immensely-developed organs of fructification. A puff-ball, Fig. 192, presents no other obvious unlikeness of parts than that between its under and upper surfaces. So too with the stalked kinds that frequent our woods and pastures. In the types which Figs. 193, 194, 195, delineate, the unlikenesses between the rooted ends and the expanded ends, as well as between the under and upper surfaces of the expanded ends, are obviously related to this fundamental contrast of conditions. Nor is this relation less clearly displayed in the sessile fungi which grow out from the sides of trees, as shown at *a*, *b*, Fig. 196. That which is common to this and the preceding types, is the contrast between the attached end and the free end.

From what these forms have in common, let us turn to that which they have not in common, and observe the causes of the want of community. A puff-ball shows us in the simplest way, the likeness of parts accompanying likeness of conditions, along with the unlikeness of parts accompanying unlikeness of conditions. For while, if we cut vertically through its centre, we find a difference between top and bottom, if we cut horizontally through its centre, we find no differences among its several sides. Being, on the average of cases, similarly related to the environment all round, it remains the same all round. The radial symmetry of the mushroom and other vertically-growing fungi, illustrates this connexion of cause and effect still better. But now mark what happens in the group of *Agaricus xylophilus*, shown in Fig. 195. Radially symmetrical as is the type, and radially symmetrical as are those centrally-placed individuals which are equally crowded all round, we see that the peripheral individuals, dissimilarly circumstanced on their outer sides and on their sides next the group, have partially changed their radial symmetry into bilateral symmetry. It is no longer possible to make two corresponding halves by *any* vertical plane cutting down through the pileus and the stem; but there is only *one* vertical plane that will thus produce corresponding halves—the plane on the opposite sides of which the relations to the environment are alike. And then mark that the divergence from all-sided symmetry towards two-sided symmetry, here caused in the individual by special circumstances, is characteristic of the race where the habits of the race constantly involve two-sidedness of conditions. Besides being exemplified by such comparatively undifferentiated types as *Boletus*, Fig. 196, *a*, *b*, this truth is exemplified by members of the genus just named. In *Agaricus horizontalis*, Fig. 196, *c*, we have a departure from radial symmetry that is conspicuous only in the form of the stem. A more decided bilateralness exists in *A. palmatus*,



shown in elevation at *d* and in section at *d′*. And *A. flabelliformis*, of which *e* and *é* are different views, exhibits complete bilateralness—a bilateralness in which there is the greatest likeness of the parts that are most similarly conditioned, and the greatest unlikeness of the parts that are most dissimilarly conditioned.

Among plants of the second order of composition, it will suffice to note one further class of facts which are the converse of the foregoing and have the same implications. These are the facts showing that along with habitual irregularity in the relations to external forces, there is habitual irregularity in the mode of growth. Besides finding such facts among Thallogens, as in the tubers of underground fungi and in the creeping films of sessile lichens, which severally show us variations of proportions obviously caused by variations in the amounts of the influences on their different sides, we also among Acrogens of inferior types, find irregularities of form along with irregularities in environing actions. The fronds of the *Marchantiaceæ* or such *Jungermanniaceæ* as are shown in Figs. 41, 42, 43, illustrate the way in which each lowly-organized aggregate of the second order, not individuated by the mutual dependence of its parts, has its form determined by the balance of facilities and resistances which each portion of the frond meets with as it spreads.

§ 219. Among plants that display integration of the third degree, and among plants still further compounded, these same truths are equally manifest. In the forms of such plants we see primary contrasts and secondary contrasts, which, no less clearly than the foregoing, are related to contrasts of conditions.

That flowering plants from the daisy up to the oak, have in common the fundamental unlikeness between the upward growing part and the downward growing part; and that this most marked unlikeness corresponds with the most marked unlikeness between the two parts of their environment, soil and air; are facts too conspicuous to be named were they not important items in the argument. More instructive, perhaps, because less familiar, is the fact that we miss this extreme contrast in flowering plants which have not their higher and lower portions exposed to conditions so extremely contrasted. A parasite like the Dodder, growing in entangled masses upon other plants, from which it sucks the juices, is not thus divisible into two strongly-distinguished halves.

Leaving out of consideration the difference between the supporting part and the supported part in phænogams, and looking at the supported part only, we observe between its form and the habitual incidence of forces, a relation like that which we observed in the simpler plants. Phænogams that are practically if not literally uniaxial, and those which develop their lateral axes only in the shape of axillary flowers, when uninterfered with ordinarily send up vertical axes round which the leaves and flowers are disposed with a more or less decided radial symmetry. Gardens and fields supply us with such instances as the Tulip and the Orchis; and on a larger scale the Palms and the Aloes are fertile in examples. The exceptions, too, are instructive. Besides the individual divergences that arise from special interferences, there are to be traced general divergences where the habits of the plants expose them to general interferences in anything approaching to constant ways. Plants which, like the Foxglove, have spikes of flowers that are borne on flexible footstalks, have their flowers habitually bent round to one face of the stem: an unlikeness of distribution probably caused by unlikeness in the relation to the sun's rays. The wild Hyacinth, too, with stem so flexible that its upper part droops, shows us how a consequent difference in the action of gravity on the flowers, causes them to deviate from their typically radial arrangement towards a bilateral arrangement.

Much more conspicuous are the segeneral and special relations of form to general and special actions in the environment, among phænogams that are multiaxial. That when standing alone, and in positions where the winds do not injure them or adjacent objects shade them, shrubs and trees develop with tolerable evenness on all sides, is an obvious truth. Equally obvious is the truth that, when growing together in a wood, and mutually interfered with on all sides, trees still show obscurely radial distributions of parts; though, under such conditions, they have tall taper stems with branches directed upwards—a difference of shape clearly due to the different incidence of forces. And almost equally obvious is the truth, that a tree of this same kind growing at the edge of the wood, has its outer branches well-developed and its inner branches comparatively ill-developed. Fig. 197, which very inaccurately represents this difference, will serve to make it manifest that while one of the peripheral trees can be cut into something like two similar halves by a vertical plane directed towards the centre of the wood—a plane on each side of which the conditions are alike—it cannot be cut into similar halves by any other plane. A like divergence from an indefinitely-radial symmetry towards an indefinitely-bilateral symmetry, occurs in trees that have their conditions made bilateral by growing on inclined surfaces. Two of the common forms observable in such cases are given in Fig. 198. Here there is divisibility into parts that are tolerably similar, by a vertical plane running directly down the hill; but not by any other plane. Then, further, there is the bilateralness, similar in general meaning though differently caused, which we see in trees exposed to strong prevailing winds. Almost every

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sea-coast has abundant examples of stunted trees which, like the one shown in Fig. 199, have been made to deviate from their ordinary equal growth on all sides of a vertical axis, to a growth that is equal only on the opposite sides of a vertical plane directed towards the wind's eye.

From among vegetal aggregates of the third order, we have now only to add examples of the entirely asymmetrical form that accompanies an entirely irregular distribution of incident forces. Creeping plants furnish such examples. They show us, alike when climbing up vertical or inclined surfaces or trailing along the ground, that their branches grow hither and thither as the balance of forces aids or opposes; and the general outline is without symmetry of any kind, because the environing influences have no kind of regularity in their arrangement.

§ 220. Along with some unfamiliar facts, I have here set down facts that are so familiar as to seem scarcely worth noting. It is because these facts have become meaningless to perceptions deadened by infinite repetitions of them, that it is needful here to point out their meaning. Not alone for its intrinsic importance has the unlikeness between the attached ends and the free ends been traced among plants of all degrees of integration. Nor is it simply because of the significance they have in themselves, that instances have been given of those different varieties of symmetry and asymmetry which the free ends of plants equally display: be they plants of the first, second, third, or any higher order. Neither has the only other purpose been that of showing how, in the radial symmetry of some vegetal aggregates and the single bilateral symmetry of others, there are traceable the same ultimate principles as in the spherical symmetry and triple bilateral symmetry of certain minute plants first described. But the main object has been to present under their simplest aspects, those general laws of morphological differentiation which are fulfilled by the component parts of each plant.

If organic form is determined by the distribution of forces, and the approach in every case towards an equilibrium of inner actions with outer actions; then this relation between forms and forces must hold alike in the organism as a whole, in its proximate units, and in its units of lower orders. Formulas which express the shapes of entire plants in terms of surrounding conditions, must be formulas which also express the shapes of their several parts in terms of surrounding conditions. If, therefore, we find that a plant as a whole is radially symmetrical or bilaterally symmetrical or asymmetrical, according as the incident forces affect it equally on all sides of an axis or affect it equally only on the opposite sides of one plane or affect it equally in no two directions; then, we may expect that each member of a plant will display radial symmetry where environing influences are alike along many radii, bilateral symmetry where there is bilateralness of environing influences, and unsymmetry or asymmetry where there is partial or entire departure from a balance of surrounding actions.

To show that this expectation is borne out by the facts, will be the object of the following four chapters. Let us begin with the largest parts into which plants are divisible; and proceed to the successively smaller parts.

# CHAPTER VIII.

## THE SHAPES OF BRANCHES.

§ 221. Aggregates of the first order supply a few examples of forms ramified in an approximately-regular manner, under conditions which subject their parts to approximately-regular distributions of forces. Some unicellular *Algæ*, becoming elaborately branched, assume very much the aspects of small trees; and show us in their branches analogous relations of forms to forces. *Bryopsis plumosa* may be instanced. Fig. 200 represents the end of one of its lateral ramifications, above and beneath which come others of like characters. Here it will be seen that the attached and free ends differ; that the two sides are much alike; and that they are unlike the upper and under surfaces, which resemble one another.

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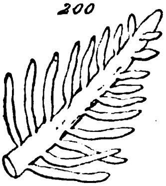
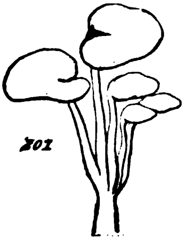


§ 222. Fig. 201 shows us how in an aggregate of the second order, each proximate component is modified by its relations to the rest; just as we before saw a whole fungus of the same type modified by its relations to environing objects. If a branch of the fungus here figured, be compared with one of the fungi clustered together in Fig. 195, or, still better, with one of the laterally-



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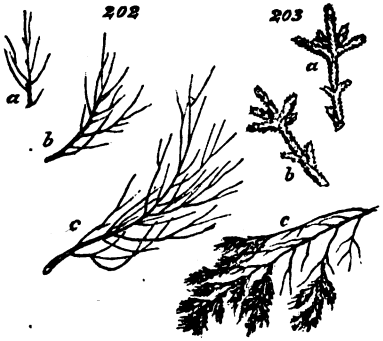
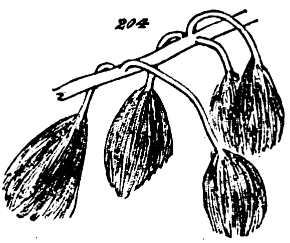
growing fungi shown in Fig. 196, there will be perceived a kindred transition from radial to bilateral symmetry, occurring under kindred conditions. The portion of the pileus next to the side of attachment is undeveloped in this branched form as in the simple form; and in the one case as in the other, the stem is modified towards the side of attachment. A division into similar halves, which, as shown in Fig. 196 *é*, might be made of the whole fungus by a vertical plane passing through the centre of the pileus and the axis of the supporting body, might here be made of the branch, by a vertical plane passing through the centre of its pileus and the axis of the main stem. Among aggregates of this order, the *Algæ* furnish cases of kindred nature. In the branches of *Lessonia*, Fig. 37, may be observed a substantially-similar relationship: their inner parts being less developed than their outer parts, while their two sides are developed in approximately equal degrees, they are rendered bilateral.

§ 223. These few cases introduce us to the more familiar but more complex cases which plants of the third degree of aggregation present. At *a, b, c,* Fig. 202, are sketched three





homologous parts of the same tree: *a* being the leading shoot; *b* a lateral branch near the top, and *c* a lateral branch lower down. There is here a double exemplification. While the branch *a*, as a whole, has its branchlets arranged with tolerable regularity all round, in correspondence with its equal exposure on all sides, each branchlet shows by its curve as much bilateral symmetry as its simple form permits. The branch *b*, dissimilarly circumstanced on the side next the main stem and on the side away from it, has an approximate bilateralness as a whole, while the bilateralness of its branchlets varies with their respective positions. And in the branch *c*, having its parts still more differently conditioned, these traits of structure are still more marked. Extremely strong contrasts of this kind occur in trees having very regular modes of growth. The uppermost branches of a Spruce-fir have radially arranged branchlets: each of them, if growing vigorously, repeats the type of the leading shoot, as shown in Fig. 203, *a*, *b*. But if we examine branches lower and lower down the tree, we find the vertically-growing branchlets bear a less and less ratio to the horizontally-growing ones; until, towards the bottom, the radial arrangement has wholly merged into the bilateral. Shaded and confined by the branches above them, these eldest branches develop their offshoots in those directions where there is most space and light: becoming finally quite flattened and fan-shaped, as shown at Fig. 203, *c*. And on remembering that each of these eldest branches, when first it diverged from the main stem, was radial, we see not only that between the upper and lower branches does this contrast in structure hold, but also that each branch is transformed from the radial to the bilateral by the progressive change in its environment. Other forces besides those which aid or hinder growth, conspire to produce this two-sided character in lateral branches. The annexed Fig. 204, sketched from an example of the *Pinus Coulterii* at Kew, shows very clearly how, by mere gravitation, the once radially-arranged branchlets may be so bent as to produce in the branch as a whole a decided bilateralness. A full-grown *Araucaria*, too, exhibits in its lower branches modifications similarly caused; and in each of such branches there may be remarked the further fact, that its upward-bending termination has a partially-modified radialness, at the same time that its drooping lateral branchlets give to the part nearer the trunk a completely bilateral character.

Now in these few instances, which are typical of countless instances that might be given, we see, as we saw in the case of the fungi, that the same thing is true of the parts in their relations to the whole and to one another, which is true of the whole in its relations to the environment at large. Entire trees become bilateral instead of radial, when exposed to forces that are equal only on opposite sides of one plane; and in their branches, parallel changes of form occur under parallel changes of conditions.

§ 224. There remains to be said something respecting the distribution of leaves. How a branch carries its leaves constitutes one of its characters as a branch; and is to be considered apart from the characters of the leaves themselves. The principles hitherto illustrated we shall here find illustrated still further.

The leading shoot and all the upper twigs of a fir-tree, have their pin-shaped leaves evenly distributed all round, or placed radially;* but as we descend, we find them beginning to assume a bilateral distribution; and on the lower, horizontally-growing branches, their distribution is quite bilateral. Between the Irish and English kinds of Yew, there is a contrast of like significance. The branches of the one, shooting up as they do almost vertically, are clothed with leaves all round; while those of the other, which spread laterally, bear their leaves on the two sides. In trees with better-developed leaves, the same principle is more or less manifest in proportion as the leaves are more or less enabled by their structures to maintain fixed positions. Where the foot-stalks

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* Here and throughout, the word *radial* is applied equally to the spiral and the whorled structures. These, as being alike on all sides, are similarly distinguished from arrangements that are alike on two sides only.

are long and slender, and where, consequently, each leaf, according to its weight, the flexibility and twist of its foot-stalk, and the direction of the branch it grows from, falls into some indefinite attitude, the relations are obscured. But where the foot-stalks are stiff, as in the Laurel, it will be found, as before, that from the topmost and upward-growing branches the leaves diverge on all sides; while the undermost branches, growing out from the shade of those above, have their leaves so turned as to bring them into rows horizontally spread out on the two sides of each branch.

A kindred truth, having like implications, comes into view when we observe the relative sizes of leaves on the same branch, where their sizes differ. Fig. 205 represents a branch of a Horse-chesnut, taken from the lowermost fringe of the tree, where the light has been to a great extent intercepted from all but the most protruded parts. Beyond the fact that the leaves are bilaterally distributed on this drooping branch, instead of being distributed symmetrically all round, as on one of the ascending shoots, we have here to note the fact that there is unequal development on the upper and lower sides. Each of the compound leaves acquires a foot-stalk and leaflets that are large in proportion to the supply of light; and hence, as we descend towards the bottom of the tree, the clusters of leaves display increasing contrasts. How marked these contrasts become will be seen on comparing *a* and *b*, which form one pair of leaves that are normally equal, or *c* and *d*, which form another pair normally equal.

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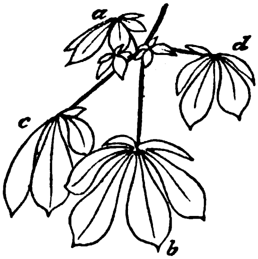

Let us not omit to note, while we have this case before us, the proof it affords that these differences of development are in a considerable degree determined by the different conditions of the parts after they have been unfolded. Though those inequalities of dimensions whence the differentiations of form result, are in many cases largely due to the inequalities in the circumstances of the parts while in the bud (which are however representative of inequalities in ancestral circumstances); yet these are clearly not the sole causes of the unlikenesses that eventually arise. For the leaf-buds whence the larger leaves in Fig. 205 were developed, instead of being at first more favourably circumstanced than the others, were less favourably circumstanced. So that this bilateralness that results from the unequal sizes of the leaves, must be considered as wholly due to the differential actions that come into play after the leaves have assumed their typical structures.

§ 225. How in the arrangement of their twigs and leaves, branches tend to lapse from forms that are approximately symmetrical to forms that are quite asymmetrical, need not be demonstrated: it is sufficiently conspicuous. But it may be well to point out how the tendency to do this further enforces our argument. The comparatively regular budding-out of secondary axes and tertiary axes, does not usually produce an aggregate which maintains its regularity, for the simple reason that many of the axes abort. Terminal buds are some of them destroyed by birds; others are burrowed into by insects; others are nipped by frost; others are broken off or injured during gales of wind. The environment of each branch and its branchlets is thus ever being varied on all sides: here, space being left vacant by the death of some shoot that would ordinarily have occupied it; and there, space being trenched on by the lateral growth of some adjacent branch that has had its main axis broken. Hence the asymmetry or heterogeneity of form which the branch assumes, is caused by the asymmetrical distribution of incident forces—a result and a cause that go on ever complicating.

§ 226. One conspicuous trait in the shapes of branches has still to be named. Their proximal or attached ends differ from their distal or free ends, in the same way that the lower ends of trees differ from their upper ends. This fact, like the fact to which it is here paralleled, has had its significance obscured by its extreme familiarity. But it shows in a striking way how the most differently-conditioned parts become the most strongly contrasted in their structures. A phænogamic axis is made up of homologous segments, marked off from one another by the nodes; and a compound branch consists of groups of such segments. The earliest-formed segments, alike of the tree and of each branch, serve as mechanical supports and channels for sap to the successive generations of segments that grow out of them; and become more and more shaded by their progeny as these increase. Hence the progressively-increasing contrasts. If the trunk of a tree were sawn horizontally into a series of slabs, each some two inches thick or thereabouts; if each of the main branches were similarly divided transversely, and the like were done with all the branches borne by it, down to their ultimate twigs, which would be severally cut across at each internode; then, morphologically considered, any one of these slabs would be the homologue of any internode of an ultimate twig, with its leaf and axillary bud. In the immense contrast between these oldest and youngest units of composition, we should have exhibited the cumulative result of continuous differentiation caused by continuous action of modifying forces—the one unit having been originally just like the other.

§ 227. Thus, then, it is with the proximate parts of plants as it is with plants as wholes. The radial symmetry, the bilateral symmetry, and the asymmetry, which branches display in different trees, in different parts of the same tree, and at different stages of their own growths, prove to be all consequent on the ways in which they stand towards the entire plexus of surrounding actions. The principle that the growths are unequal in proportion as the relations to the environment are unequal, serves to explain all the leading traits of structure.

# CHAPTER IX.

## THE SHAPES OF LEAVES.

§ 228. Next in the descending order of composition come compound leaves. The relative sizes and distributions of their leaflets, as affecting their forms as wholes, have to be considered in their relations to conditions. Figs. 206, 207, represent leaves of the common *Oxalis* and of the *Marsilea*, in which radial symmetry is as completely displayed as the small number of leaflets permits. This equal development of the leaflets on all sides, occurs where the foot-stalks, growing up vertically from creeping or underground stems, are so long that the leaves either do not interfere with one another or do it in an inconstant way: the leaflets are not differently conditioned on different sides, as they are where the foot-stalks grow out in the ordinary manner. How unlikeness of position influences the leaflets is clearly shown in a Clover-leaf, Fig. 208, which deviates from the Oxalis-leaf but slightly towards bilateralness, as it deviates from it but slightly in the attitude of its petiole; which is a little inclined away from the others borne by the same procumbent axis. A familiar example of an almost-radial symmetry along with almost equal relations to surrounding conditions, occurs in the root-leaves of the Lupin, Fig. 209, *b*. Here though we have lateral divergence from a vertical axis, yet the long foot-stalks preserve nearly erect positions, and carry their leaves to such distances from the axis, that the development of the leaflets on the side next the axis is not much hindered. Still the interference of the leaves with one another is, on the average, somewhat greater on the proximal side than on the distal side; and hence the interior leaflets are rather less than the exterior leaflets. In further proof of which influence, let it be added that, as shown in the figure, at *a,* the leaves growing out of the flowering-stem deviate towards the two-sided form more decidedly. Two-sidedness is much greater where there is a greater relative proximity of the inner leaflets to the axis, or where the foot-stalk approaches towards a horizontal position. The Horse-chesnut, Fig. 205, already instanced as showing how the arrangements and sizes of leaves are determined by the incidence of forces, serves also to show how the incidence of forces determines the relative sizes and arrangements of leaflets. Fig. 210, which shows a leaf of the *Bombax,* further illustrates this relation of structure to conditions.

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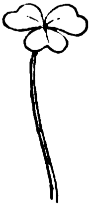

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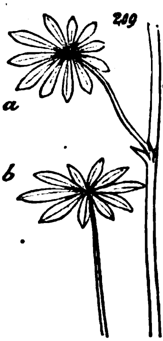

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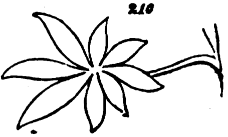

Compound leaves that are completely bilateral, present us with modifications of form exemplifying the same general truth in another way. In them the proximal and distal parts have none of that resemblance which we see in those intermediate forms just described: the portion next the axis and the portion furthest from the axis are entirely different; and the only likeness is between the wings or leaflets on opposite sides of the main foot-stalk or midrib. On turning back to Fig. 65, it will be seen that the compound leaf there drawn to exemplify another truth, serves also to exemplify this truth: the homologous parts *a*, *b*, *c*, *d*, while they are unlike one another, are, in their main proportions, severally like the parts with which they are paired. And here let us not overlook a characteristic which is less conspicuous but not less significant. Each of the lateral wings has winglets that are larger on the one side than on the other; and in each case the two sides are dissimilarly conditioned. Even in the several components of each wing may be traced a like divergence from symmetry, along with a like inequality in the relations to the rest: the proximal half of each leaflet is habitually larger than the distal half. In the leaves of the Bramble, previously figured, kindred facts are presented. How far such differences of development are due to the positions of the parts in the bud; how far the respective spaces available for the parts when unfolded affect them; and how far the parts are rendered unlike by unlikenesses in their relations to light; it is difficult to say. Probably these several factors operate in all varieties of proportion. That the habitual shading of some parts by others largely aids in causing these divergences from symmetry, is very instructively shown by the compound leaves of the Cow-parsnip. Fig. 211 represents one of these. While the leaf as a whole is bilaterally symmetrical, each of the wings has an unsymmetrical bilateralness: the side next the axis being larger than the remoter side. How does this happen? Fig. 212,

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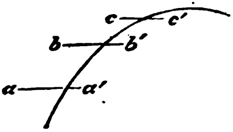
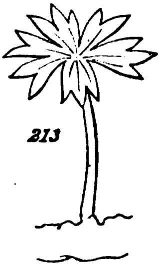


which is a diagrammatic section down the midrib of the leaf, showing its inclined attitude and the positions of the wings *a*, *b*, *c*, will make the cause clear. As the wings overlap like the bars of a Venetian blind, each intercepts some light from the one below it; and the one below it thus suffers more on its distal side than on its proximal side. Hence the smaller development of the distal side. That this is the cause is further shown by the proportion that is maintained between the degree of obscuration and the degree of non-development; for this unlikeness is greater between the two sides *a* and *a′*, than between *b* and *b′*, or *c* and *c′*, at the same time that the interference is greater in the lower wings than in the upper. Of course in this case and in the kindred cases hereafter similarly interpreted, it is not meant that this differentiation is consequent solely, or even chiefly, on the differential actions experienced by the individual plant. Though there is good reason to believe that the rate of growth in each part of each leaf is affected by the incidence of light, yet contrasts so marked and so systematic as these are not explicable without taking into account the inheritance of modifications either functionally caused or caused by spontaneous variation. Clearly, the tendency will be towards the preservation of a plant which distributes its chlorophyll in the most economical way; and hence there will always be a gravitation towards a form in which shaded parts of leaves are undeveloped.

§ 229. From compound leaves to simple ones, we find transitions in leaves of which the divisions are partial instead of total; and in these we see, with equal clearness, the relations between forms and positions that have been traced thus far. Fig. 213 is the leaf of a Winter-aconite, in which, round a vertical petiole, there is a radial distribution of half-separated leaflets. The *Cecropia*-leaf, Fig. 214, shows us a two-sided development of the parts beginning to modify, but not obliterating, the all-sided arrangement; and this mixed symmetry occurs under conditions that are intermediate. A more marked degree of the same relation is presented in the leaf of the Lady's Mantle, Fig. 215. And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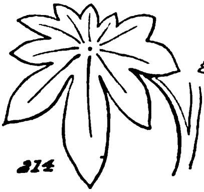
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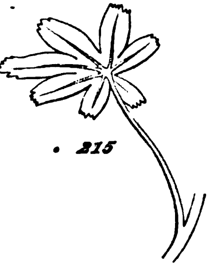
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then in the Sycamore and the Vine, we have a cleft type of leaf in which a decided bilateralness of form co-exists with a decided bilateralness of conditions.

The quite simple leaves to which we now descend, exhibit, very distinctly, a parallel series of facts. Where they grow up on long and completely-independent foot-stalks, without definite subordination to some central vertical axis, the leaves of water-plants are symmetrically peltate. Of this the sacred Indian-bean, Fig. 216, furnishes an example. Here there is only a trace of bilateralness in the venation of the leaf, corresponding to the very small difference of the conditions on the proximal and distal sides. In the *Victoria regia*, Fig. 217, the foot-stalks, though radiating almost horizontally from a centre, are so long as to keep the leaves quite remote from one another; and in it each leaf is almost symmetrically peltate, with a bilateralness indicated only by a seam over the line of the foot-stalk. The leaves of the *Nymphæa*, Fig. 218, more closely clustered, and having less room transversely than longitudinally, exhibit a marked advance to the two-sided form; not only in the excess of the length over the breadth, but in the existence of a cleft,

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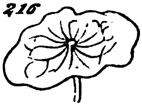
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where in the *Victoria regia* there is merely a seam. Among land-plants similar forms are found under analogous conditions. The common *Hydrocotyle*, Fig. 219, which sends up direct from its roots a few almost upright leaf-stalks, has these surmounted by peltate leaves; which leaves, however, diverge slightly from radial symmetry in correspondence with the slight contrast of circumstances which their grouping involves. Another case is supplied by the *Nasturtium*, Fig. 220, which combines the characters—a creeping stem, long leaf-stalks growing up at right angles to it, and unsymmetrically peltate leaves, of which the least dimension is, on the average, towards the stem. But perhaps the most striking illustration is that furnished by the *Cotyledon umbilicus*, Fig. 221, in which different kinds of symmetry occur in the leaves of the same plant, along with differences in their relations to conditions. The root-leaves, *a*, that grow up on vertical petioles before the flower-stalk makes its appearance, are symmetrically peltate; while the leaves which subsequently grow out of the flower-stalk, *b*, are at the bottom transitionally bilateral, and higher up completely bilateral.

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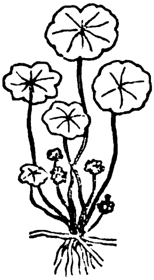

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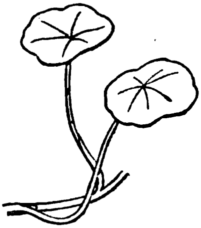

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That the bilateral form of leaf is the ordinary form, corresponds with the fact that, ordinarily, the circumstances of the leaf are different in the direction of the plant's axis from what they are in the opposite direction, while transversely the circumstances are alike. It is needless to give diagrams to illustrate this extremely familiar truth. Whether they are broad or long, oval or heart-shaped, pointed or obtuse, the leaves of most trees and plants will be remembered by all as having the ends by which they are attached unlike the free ends, while the two sides are alike. And it will also be remembered that these equalities and inequalities of development correspond with the equalities and inequalities in the incidence of forces.

§ 230. A confirmation that is interesting and important, is furnished by the cases in which leaves present unsymmetrical forms in positions where their parts are unsymmetrically related to the environment. A considerable deviation from bilateral symmetry may be seen in a leaf which habitually so carries itself, that the half on the one side of the midrib is more shaded than the other half. The drooping branches of the Lime, exemplified in Fig. 222, show us leaves so arranged and so modified. On examining their attitudes and their relations one to another, it will be found that each leaf is so inclined that the half of it next the shoot grows over the shoot and gets plenty of light; while the other half so hangs down that it comes a good deal into the shade of the preceding leaf. The result is that having leaves which fall into these positions, the species profits by a large development of the exposed halves; and by survival of the fittest acting along with the direct effect of extra exposure, this modification becomes established. How unquestionable is the connexion between the relative positions of the halves and their relative developments, will be admitted on observing a


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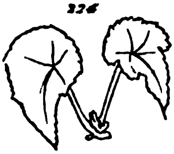
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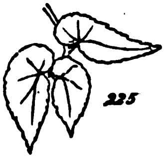
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converse case. Fig. 223 represents a shoot of *Goldfussia glomerata.* Here the leaves are so set on the stem that the inner half of each leaf is shaded by the subsequently-formed leaf, while its outer half is not thus shaded; and here we find the inner half less developed than the outer half. But the most conclusive evidence of this relation between unsymmetrical form and unsymmetrical distribution of surrounding forces, is supplied by the genus *Begonia;* for in it we have a manifest proportion between the degree of the alleged effect and the degree of the alleged cause. These plants produce their leaves in pairs, in such a way that the connate leaves interfere with one another, much or little according as the foot-stalks are short or long; and the result is a correlative divergence from symmetry. In *Begonia nelumbiæfolia,* which has petioles so long that the connate leaves are not kept close together, there is but little deviation from a bilaterally-peltate form; whereas, accompanying the comparatively marked and constant proximity in *B. pruinata,* Fig. 224, we see a more decidedly unsymmetrical shape; and in *B. mahringii,* Fig. 225, the modification thus caused is pushed so far as to destroy the peltate structure.*

§ 231. Again, then, we are taught the same truth. Here, as before, we see that homologous units of any order become

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* We may note that some of these leaves, as those of the Lime, furnish indications of the ratio which exists between the effects of individual circumstances and those of typical tendencies. On the one hand, the leaves borne by these drooping branches of the Lime are with hardly an exception unsymmetrical more or less decidedly, even in positions where the causes of unsymmetry are not in action: a fact showing us the repetition of the type irrespective of the conditions. On the other hand, the degree of deviation from symmetry is extremely variable, even on the same shoot: a fact proving that the circumstances of the individual leaf are highly influential in modifying its form. But the most striking evidence of this direct modification is afforded by the suckers of the Lime. Growing, as these do, in approximately upright attitudes, the leaves they bear do not stand to one another in the way above described, and the causes of unsymmetry are not in action; and here, though there is a general leaning to the unsymmetrical form, a large proportion of the leaves become quite symmetrical.

differentiated in proportion as their relations to incident forces become different. And here, as before, we see that in each unit, considered by itself, the differences of dimension are greatest in those directions in which the parts are most differently conditioned; while there are no differences between the dimensions of the parts that are not differently conditioned.*

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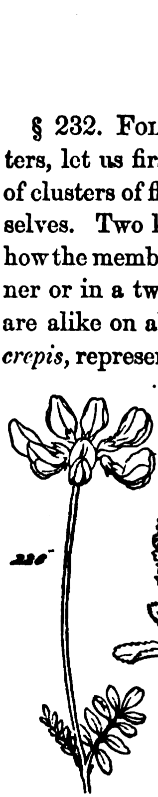
* It was by an observation on the forms of leaves, that I was first led to the views set forth in the preceding and succeeding chapters on the morphological differentiation of plants and animals. In the year 1851, during a country ramble in which the structures of plants had been a topic of conversation with a friend—Mr G. H. Lewes—I happened to pick up the leaf of a buttercup, and drawing it by its foot-stalk through my fingers so as to thrust together its deeply-cleft divisions, observed that its palmate and almost radial form was changed into a bilateral one; and that were the divisions to grow together in this new position, an ordinary bilateral leaf would result. Joining this observation with the familiar fact that leaves, in common with the larger members of plants, habitually turn themselves to the light, it occurred to me that a natural change in the circumstances of the leaf might readily cause such a modification of form as that which I had produced artificially. If, as they often do with plants, soil and climate were greatly to change the habit of the buttercup, making it branched and shrub-like; and if these palmate leaves were thus much overshadowed by each other; would not the inner segments of the leaves grow towards the periphery of the plant where the light was greatest, and so change the palmate form into a more decidedly bilateral form? Immediately I began to look round for evidence of the relation between the forms of leaves and the general characters of the plants they belonged to; and soon found some signs of connexion. Certain anomalies, or seeming anomalies, however, prevented me from then pursuing the inquiry much further. But consideration cleared up these difficulties; and the idea afterwards widened into the general doctrine here elaborated. Occupation with other things prevented me from giving expression to this general doctrine until Jan. 1859; when I published an outline of it in the *Medico-Chirurgical Review.*

## CHAPTER X.

### THE SHAPES OF FLOWERS.

§ 232. Following an order like that of preceding chapters, let us first note a few typical facts respecting the forms of clusters of flowers, apart from the forms of the flowers themselves. Two kindred kinds of *Leguminosæ* will serve to show how the members of clusters are distributed in an all-sided manner or in a two-sided manner, according as the circumstances are alike on all sides or alike on only two sides. In *Hippocrepis*, represented in Fig. 226, the flowers growing at the end of a vertical stem, are arranged round it in radial symmetry. Contrariwise in *Melilotus*, Fig. 227, where the axillary stem bearing the flowers is so placed in relation to the main stem, that its outer and inner sides are differently conditioned, the flowers are all on the outer side: the cluster is bilaterally symmetrical, since it may be cut into approximately equal and similar groups by a vertical plane passing through the main axis.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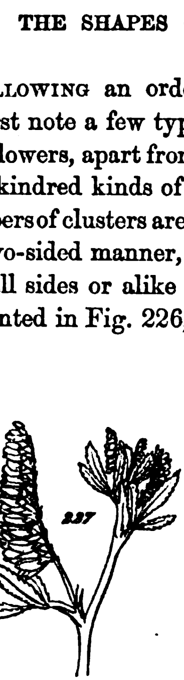
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Plants of this same tribe furnish clusters of intermediate characters having intermediate conditions. Among these, as among the clusters which other types present, may be found some in which conformity to the general law is not obvious. The discussion of these apparent anomalies would carry us too much out of our course. A clue to the explanation of them will, I believe, be found in the explanation presently to be given of certain kindred anomalies in the forms of individual flowers.

§ 233. The radially-symmetrical form is common to all individual flowers that have vertical axes. In plants which are practically if not literally uniaxial, and bear their flowers at the ends of upright stalks, so that the faces open horizontally, the petals are disposed in an all-sided way. Crocuses, Tulips, and Poppies are familiar examples of this structure occurring under these conditions. A Ranunculus flower, Fig. 228, will serve as a typical one. Similarly, flowers which have peduncles flexible enough to let them hang directly downwards, and are not laterally incommoded, are also radial; as in the *Fuchsia*, Fig. 229, as in *Cyclamen*, *Hyacinth*, &c. These relations of form to position are, I believe, uniform. Though some flowers carried at the ends of upright or downright stems have oblique shapes, it is only when they have inclined axes or are not equally conditioned all round. No solitary flower having an axis habitually vertical, presents a bilateral form. This is as we should expect, since flowers which open out their faces horizontally, whether facing upwards or downwards, are, on the average, similarly affected on all sides.

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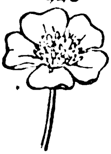

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At first it seems that flowers thus placed should alone be radial; but further consideration discloses conditions under which this type of symmetry may exist in flowers otherwise placed. Remembering that the radial form is the primitive form—that, morphologically speaking, it results from the contraction into a whorl, of parts that are originally arranged in the same spiral succession as the leaves; we must expect it to continue wherever there are no forces tending to change it. What now must be the forces tending to change it? They must be forces which do not simply affect differently the different parts of an individual flower; but they must be forces which affect in like contrasted ways the homologous parts of other individual flowers, both on the same plant and on surrounding plants of the same species. A permanent modification can be expected only in cases where, by inheritance, the effect of the modifying causes accumulates. That it may accumulate the flowers must keep themselves so related to the environment, that the homologous parts may generation after generation be subjected to like differentiating forces. Hence, among a plant's flowers which maintain no uniformity in the relations of their parts to surrounding influences, the radial form will continue. Let us glance at the several causes which entail this variability. When flowers are borne on many branches, which have all inclinations from the vertical to the horizontal—as are the flowers of the Apple, the Plum, the Hawthorn—they are placed in countless different attitudes. Consequently, any spontaneous variation in shape which might be advantageous were the attitude constant, is not likely to be advantageous; and any functionally-produced modification in one flower is likely to be neutralized in offspring by some opposite functionally-produced modification in another flower. It is quite comprehensible, therefore, that irregularly-branched plants should thus preserve their laterally-borne flowers from undergoing permanent deviations from their primitive radial symmetry. Fig. 230, representing a blossoming twig of the Blackthorn, will illustrate this. Again, upright panicles such as that of the Saxifrage, shown in Fig. 231, and irregular terminal groups of flowers otherwise named, furnish conditions under which there is similarly an


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absence of determinate relations between the parts of the flowers and the incident forces; and hence an absence of bilateralness. This inconstancy of relative position is produced in various other ways—by extreme flexibility of the peduncles, as in the Blue-bell; by the tendency of the peduncles to curl to a greater or less extent in different directions, as in *Pyrola;* by special twisting of the peduncles, differing in degree in different individuals, as in *Convolvulus;* by extreme flexibility of the petals, as in *Lythrum.* Elsewhere the like general result arises from a progressive change of attitude; as in *Myosotis,* the stem of which as it unfolds causes each flower to undergo a transition from an upward position of the mouth to a lateral position; or as in most *Cruciferæ,* where the like effect follows from an altered direction of the peduncle.

There are, however, certain seemingly anomalous cases where radial sympathy is maintained by laterally-placed flowers, which keep their parts in relative positions that are tolerably constant. The explanation of these exceptions is not manifest. It is only when we take into account certain incident actions liable to be left unremembered, that we find a probable solution. It will be most convenient to postpone the consideration of these cases until we have reached the general rule to which they are exceptions.

§ 234. Transitions varying in degree from the radial towards the bilateral, are common in flowers that are borne at the ends of branches or axes which are inclined in tolerably constant ways. We may see this in sundry garden flowers such as *Petunia,* or such as *Tydæa* and *Achimenes* shown in Figs. 232 and 233. If these plants be examined, it will be perceived that the mode of growth makes the flower unfold in a partially one-sided position; that its parts of attachment have rigidity

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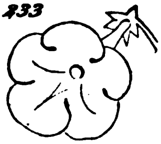

sufficient to prevent this attitude from being very much interfered with; and that though the individual flowers vary somewhat in their attitudes, they do not vary to the extent of neutralizing the differentiating conditions—there remains an average divergence from a horizontal unfolding of the flower, to account for its divergence from radial symmetry.

We pass insensibly from forms like these, to forms having bilateral symmetry strongly pronounced. Some such forms occur among flowers that grow at the ends of upright stems; as in *Pinguicula*, and in the Violet tribe. But this happens only where in successive generations the flower unfolds its parts sideways in constant relative positions. And in the immense majority of flowers that have well-marked two-sided forms, the habitual exposure of the different parts to different sets of forces, is effectually secured by the mode of placing. As illustrations I may name the genera—*Orchis, Utricularia, Salvia, Salix, Delphinum, Mentha, Teucrium, Ajuga, Ballota, Galeopsis, Lamium, Stachys, Glechoma, Marrubium, Calamintha, Clinopodium, Melittis, Prunella, Scutellaria, Bartsia, Euphrasia, Rhinanthus, Melampyrum, Pedicularis, Linaria, Digitalis, Orobanche, Fumaria, &c.*; to which may be added, all the Grasses and all the *Papilionaceæ*. In most of these cases the flowers, being sessile on the sides of upright stems, are kept in quite fixed attitudes; and in the other cases the peduncles are very short, or else stiff enough to secure general uniformity in the positions. A few of the more marked types are shown in Figs. 234 to 241.

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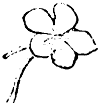
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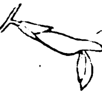
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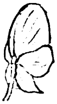

Very instructive evidences here meet us. Sometimes within the limits of one genus we find radial flowers, bilateral flowers, and flowers of intermediate characters. The genus *Begonia* may be instanced. In *B. rigida* the flowers, various in their attitudes, are in their more conspicuous characters radial: though there is a certain bilateralness in the calyx, the five petals are symmetrically disposed all round. *B. Wagneriana* furnishes two forms of flowers: on the same individual plant may be found radial flowers like Fig. 242, and others like Fig. 243 that are merging into the bilateral. More decided is the bilateralness in *B. albo-coccinea*, Fig. 244; and still more in *B. nitida*, Fig. 245. While in *B. jatrophæfolia*, Fig. 246, the change reaches its extreme by the disappearance of the lateral petals. On examining the modes of growth in these several species, they will be seen to explain these changes in the manner alleged. Even more conclusive are the nearly-allied transformations occurring in artificially-produced varieties of the same species. *Gloxinia* may be named in illustration. In Fig. 247 is represented one of the ordinary forms, which shows us bilateralness of shape along with a mode of growth that renders the conditions alike on the two sides while different above and below. But in *G. erecta*, Fig. 248, we have the flower assuming an upright attitude, and at the same time assuming the radial type. This is not to be interpreted as a production of radial symmetry out of bilateral symmetry, under the action of the appropriate conditions. It is rather to be taken as a case of what is termed "peloria"—a reversion to the primitive radial type, from which the bilateral modification had been derived. The significant inference to be drawn from it is, that this primitive radial type had an upright attitude; and

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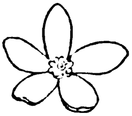

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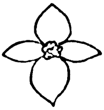

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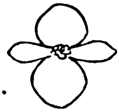

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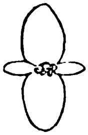

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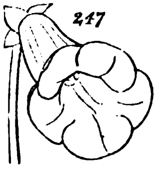

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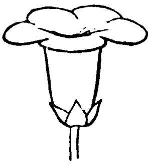

that the derivation of a bilateral type from it, occurred along with the assumption of an inclined attitude.

We come now to a group of cases above referred to, in which radial symmetry continues to co-exist with that constant lateral attitude ordinarily accompanied by the two-sided form. Two examples will suffice: one a very large flower, the Hollyhock, and the other a very small flower, the Agrimony. Why does the radial form here remain unchanged? and how does its continuance consist with the alleged general law?

Until quite recently I have been unable to find any probable answers to these questions. When the difficulty first presented itself, I could think of no other possible cause for the anomaly, than that the parts of the Hollyhock-flower, unfolding spirally as they do, might have different degrees of spiral twist in different flowers, and might thus not be unfolded in sufficiently-constant positions. But this seemed a very questionable interpretation; and one which did not obviously apply to the case of the Agrimony. It was only on inquiring what are the special causes of modifications in the forms of flowers, that a more feasible explanation suggested itself; and this would probably never have suggested itself, had not Mr Darwin's investigations into the fertilization of Orchids led me to take into account an unnoticed agency.

The actions which affect the forms of leaves, affect much less decidedly the forms of flowers; and the forms of flowers are influenced by actions that do not influence the forms of leaves. Partly through the direct action of incident forces and partly through the indirect action of natural selection, leaves get their parts distributed in ways that most facilitate their assimilative functions, under the circumstances in which they are placed; and their several types of symmetry are thus explicable. But in flowers, the petals and fructifying organs of which do not contain chlorophyll, the tendency to grow most where the supply of light is greatest, is less decided, if not absent; and a shape otherwise determined is hence less liable to alter in consequence of altered relations to sun and air. Gravity, too, must be comparatively ineffective in causing modifications: the smaller sizes of the parts, as well as their modes of attachment, giving them greater relative rigidity. Not, indeed, that these incident forces of the inorganic world are here quite inoperative. Fig. 249, representing a species of *Campanula*, shows that the developments of individual flowers are somewhat modified by the relations of their parts to general conditions. But the fact to be observed is, that the extreme transformations which flowers undergo are not likely to be thus caused: some further cause must be sought. And if we bear in mind the functions of flowers, we shall find in their adaptations to their functions, under conditions that are extremely varied, an adequate cause for the different types of symmetry, as well as for the exceptions to them. Flowers are parts in which fertilization is effected; and the active agents of this fertilization are insects—bees, moths, butterflies, &c. Mr Darwin has shown in many cases, that the forms and positions of the essential organs of fructification, are such as to facilitate the actions of insects in transferring pollen from the anthers of one flower to the pistil of another — an arrangement produced by natural selection. And here we shall find reason for concluding, that the forms and positions of those subsidiary parts which give the general shape to the flower, similarly arise by the survival of individuals which have the subsidiary parts so adjusted as to aid this fertilizing process—the deviations from radial symmetry being among such adjustments. The reasoning is as follows. So long as the axis of a flower is vertical and the conditions are similar all round, a bee or butterfly alighting on it, will be as likely to come from one side as from another; and hence, hindrance rather than facilitation would result if the several sides of the flower did not afford it equally

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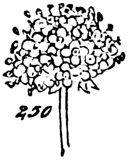
free access. In like manner, flowers which are distributed over a plant in such ways that their discs open out on planes of all directions and inclinations, will have no tendency to lose their radial symmetry; since, on the average, no part of the periphery is differently related to insect-agency from any other part. But flowers so fixed as to open out sideways in tolerably-constant attitudes, have their petals differently related to insect-agency. A bee or butterfly coming to a laterally-growing flower, does not settle on it in one way as readily as in another; but almost of necessity settles with the axis of its body inclined upwards towards the stem of the plant. Hence, the side-petals of a flower so fixed, habitually stand to the alighting insect in relations different from those in which the upper and lower petals stand; and the upper and lower petals differ from one another in their relations to it. If, then, there so arises an habitual attitude of the insect towards the petals, there must be some particular arrangement of the petals that will be most convenient to the insect—will most facilitate its entrance into the flower. Thus we see in many cases, that a long undermost petal or lip, by enabling the insect to settle in such way as to bring its head opposite to the opening of the tube, aids its fertilizing agency. But whatever be the special modifications of the corolla which facilitate the actions of the particular insects concerned, all of them will conduce to bilateral symmetry; since they will be alike for the two sides but unlike for the top and bottom. And now we are prepared for understanding the exceptions. Flowers growing sideways can become thus adapted by survival of the fittest, only if they are of such sizes and structures that insect-agency can affect them in the way described. But in the plants named above, this condition is not fulfilled. A Hollyhock-flower is so open, as well as so large, that its petals are not in any appreciable degree differently related to the insects which visit it. On the other hand, the flower of the Agrimony is so small, that unless visited by insects of a corresponding size which settle as bees and butterflies settle, its parts will not be affected in the alleged manner. That all anomalies of this kind can at once be satisfactorily explained, is scarcely to be expected: the circumstances of each case have to be studied. But it seems not improbable that they are all due to causes of the kind indicated.

§ 235. We have already glanced at clusters of flowers for the purpose of considering their shapes as clusters. We must now return to them to observe the modifications undergone by their component flowers. Among these occur illustrations of great significance.

An example of transition from the radial to the bilateral form in clustered flowers of the same species, is furnished by the cultivated *Geraniums,* called by florists *Pelargoniums.* Some of these bearing somewhat small terminal clusters of flowers, which are closely packed together, with their faces almost upwards, have radially-symmetrical flowers. But among other varieties having terminal clusters of which the members are mutually thrust on one side by crowding, the flowers depart very considerably from the radial shape towards the bilateral shape. A like result occurs under like conditions in Rhododendrons and Azaleas. The *Verbena,* too, furnishes an illustration of radial flowers rendered slightly two-sided by the slight two-sideness of their relations to other flowers in the cluster. And among the *Cruciferæ,* a kindred case occurs in the cultivated Candytuft.

Evidence of a somewhat different kind, is offered us by clustered flowers in which the peripheral members of the clusters differ from the central members; and this evidence is especially conclusive where we find allied species that do not exhibit the deviation, at the same time that they do not fulfil the conditions under which it may be expected. Thus, in *Scabiosa succisa,* Fig. 250, which bears its numerous small flowers in a hemispherical knob, the component flowers, similarly circumstanced, are all equal and all radial; but in

*Scabiosa arvensis*, Fig. 251, in which the numerous small flowers form a flattened disk, only the confined central ones are radial: round the edge the flowers are much larger, and conspicuously bilateral.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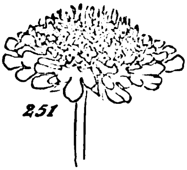
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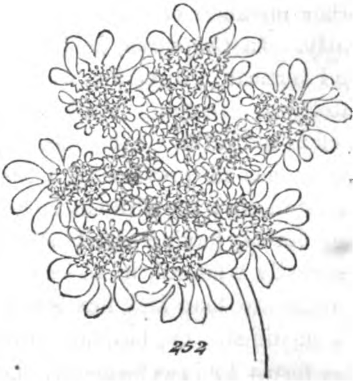
But the most remarkable and most conclusive proofs of these relations between forms and positions, are those given by the clustered flowers called *Umbelliferæ*. In some cases, as where the component flowers have all plenty of room, or where the surface of the umbel is more or less globular, the modifications are not conspicuous; but where, as in *Viburnum, Chærophyllum, Anthriscus, Torilis, Caucalis, Daucus, Tordylium,* &c., we have flowers clustered in such ways as to be differently conditioned, we find a number of modifications that are marked and varied in proportion as the differences of conditions are marked and varied. In *Chærophyllum*, where the flowers of each umbellule are closely placed so as to form a flat surface, but where the umbellules are wide apart and form a dispersed umbel, the umbellules do not differ from one another; though among the flowers of each umbellule there are decided differences—the central flowers being small and radial, while the peripheral ones are large and bilateral. But in other genera, where not only the flowers of each umbellule but also the umbellules themselves are closely clustered into a flat surface, the umbellules themselves become contrasted; and many remarkable secondary modifications arise. In an umbel of *Heracleum*, for instance, there are to be noted the facts:—first, that the external umbellules are larger than the internal ones; second, that in each umbellule the central flowers are less developed than the peripheral ones; third, that this greater development of the peripheral flowers is most marked in the outer umbellules; fourth, that it is most marked on the outer sides of the outer umbellules; fifth, that while the interior flowers of each umbellule are radial, the exterior ones are bilateral; sixth, that this bilateralness is most marked in the peripheral flowers of the peripheral umbellules; seventh, that the flowers on the outer side of these peripheral umbellules are those in which the bilateralness reaches a maximum; and eighth, that where the outer umbellules touch each other, the flowers, being unsymmetrically placed, are unsymmetrically bilateral.* The like modifications are displayed, though not in so clearly-traceable a way, in an umbel of *Tordylium*, Fig. 252. Considering how obviously these various forms are related to the various conditions, we should be scarcely able, even in the absence of all other facts, to resist the conclusion that the differences in the conditions are the causes of the differences in the forms.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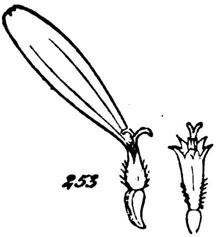
Composite flowers furnish evidence so nearly allied to that which clustered flowers furnish, that we may fitly glance at them under the same head. Such a common type of this order as the Sun-flower, exemplifies the extremely marked difference that arises in many of these plants between the closely-packed internal florets, each similarly circumstanced on all sides, and the external florets, not similarly circumstanced on all sides. In Fig. 253, representing the inner and outer florets of a Daisy, the contrast is marked between the small radial corolla of the one and the larger bilateral corolla of the other. In many cases, however, this contrast is less marked: the inner florets having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* I had intended here to insert a figure exhibiting these differences; but as the Cow-parsnip does not flower till July, and as I can find no drawing of the umbel which adequately represents its details, I am obliged to take another instance.

also their outward-growing prolongations—a difference possibly related to some difference in the habits of the insects that fertilize them. Nevertheless, these composite flowers which have inner florets with strap-shaped corollas outwardly directed, equally conform to the general principle; both in the radial arrangement of the assemblage of florets, and in the bilateral shape of each floret; which has its parts alike on the two sides of a line passing from the centre of the assemblage to the circumference. Certain other members of this order fulfil the law somewhat differently. In *Centaurea,* for instance, the inner florets are small and vertical in direction, while the outer florets are large and lateral in direction. And here may be remarked, in passing, a clear indication of the effect which great flexibility of the petals has in preventing a flower from losing its original radiate form; for while in *C. cyanus,* the large outward-growing florets, having short, stiff divisions of the corolla, are decidedly bilateral, in *C. scabiosa,* where the divisions of the corolla are long and flexible, the radial form is scarcely at all modified. On bearing in mind the probable relations of the forms to insect-agency, the meaning of this difference will not be difficult to understand.

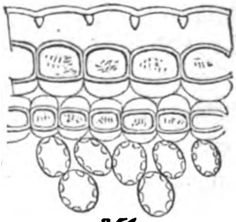
§ 236. In extremely-varied ways there are thus re-illustrated among flowers, the general laws of form which leaves and branches and entire plants disclose to us. Composed as each cluster of flowers is of individuals that are originally similar; and composed as each flower is of homologous foliar organs; we see both that the like flowers become unlike and the like parts of each flower become unlike, where the positions involve unlike incidence of forces. The symmetry remains radial where the conditions are equal all round; shows deviation towards two-sidedness where there is slight two-sidedness of conditions; becomes decidedly bilateral where the conditions are decidedly bilateral; and passes into an unsymmetrical form where the relations to the environment are unsymmetrical.

## CHAPTER XI.

### THE SHAPES OF VEGETAL CELLS.

§ 237. We come now to aggregates of the lowest order. Already something has been said (§ 217) concerning the forms of those morphological units which exist as independent plants. But it is here requisite briefly to note the modifications undergone by them where they become components of larger plants.

Of the numerous cell-forms which are found in the tissues of the higher plants, it will suffice to give, in Fig. 254, representing a section of the surface of a leaf, a single example. In this it will be seen that the epidermis cells *c*, covered by the secreted external layer *a*, and separated from the layer of cells below them by the masses of inter-cellular substance *b*, have differentiations of form clearly related to differences in the incidence of forces. Their divergences from primordial sphericity are such as correspond with the unlikenesses in the circumstances of their respective sides. Similarly with the layers below them. And throughout the more complex modifications which the cells of other tissues exhibit, the like correspondence holds.



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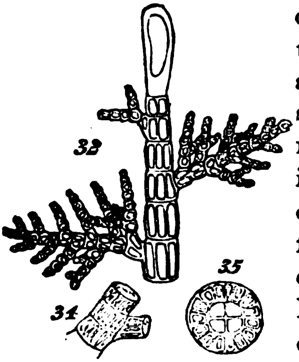
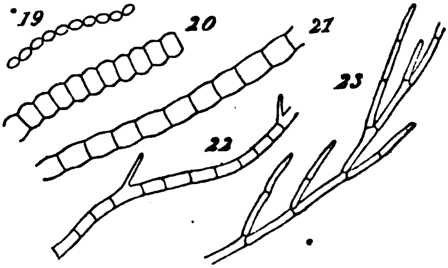
Among plants of a lower order of aggregation, we have already seen how cells become metamorphosed as they become integrated into masses having definite organizations. The



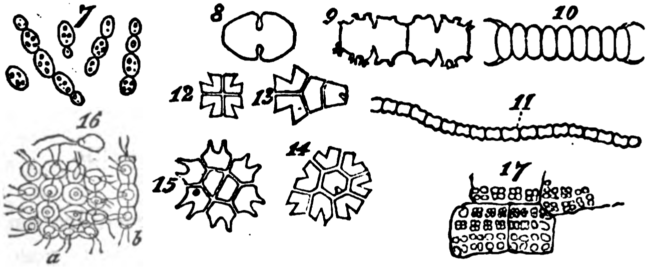
higher *Algæ*, exemplified in Figs. 32, 34, 35, show this very clearly. Here the departure from the simple cell-form to the form of an elongated prism, is manifestly subordinated to the contrasts in the relations of the parts. And it is interesting to observe how, in one of the branches of Fig. 32, we pass from the small, almost-spherical cells which terminate the branchlets, to the large, much-modified cells which join the main stem, through gradations obviously related in their changed forms to the altered actions their positions expose them to.

More simply, but quite as conclusively, do the inferior *Algæ*, of which Figs. 19—23 are examples, show us how



cells pass from their original spherical symmetry into radial symmetry, as they pass from a state in which they are similarly-conditioned on all sides, to a state in which two of their opposite sides or ends are conditioned in ways that are like one another, but unlike the ways in which all other sides are conditioned.

Still more instructive are the morphological differentiations of those protophytes in which the first steps towards a higher degree of integration are shown. Fig. 9 represents one of the transitional forms of *Desmidiaceæ*. In it we see that the two inner halves by which the individuals are united, differ somewhat from the two outer halves. So, too, of the type exemplified by Fig. 10, it is to be noted that besides the difference between the transverse and longitudinal dimensions, which the component units display in common, the two end units differ from the rest: they have appendages which the rest have not. Once more, where the integration is carried on in such ways as to produce not strings but clusters, there arise contrasts and correspondences just such as might be looked for. All the four members of the group shown in Fig. 12, are similarly conditioned; and each of them has a bilateral shape answering to its bilateral relations. In Fig. 14 we have a number of similarly-bilateral individuals on the circumference, including a central individual differing from the rest by having the bilateral character nearly obliterated. And then, in Fig. 15, we have two central components of the group, deviating more decidedly from those that surround them.



These few typical facts, which must be taken like the few typical facts grouped in each of the foregoing chapters as indicating a mass of evidence too great to be here detailed, will sufficiently show that from the most complex vegetal types down to the most simple, the laws of morphological differentiation remain the same.

# CHAPTER XII.

## CHANGES OF SHAPE OTHERWISE CAUSED.

§ 238. Besides the more special causes of modification in the shapes of plants and of their parts, certain more general causes must be briefly noticed. These may be described as consequences of variations in the total quantities of the matters and forces furnished to plants by their environments. Some of the changes of form so produced are displayed by plants as wholes, and others only by their parts. We will glance at them in this order.

§ 239. It is a familiar fact that luxuriant shoots have relatively-long internodes; and, conversely, that a shoot dwarfed from lack of sap, has its nodes closely clustered: the result being that the lateral axes, where these are developed, become in the one case far apart and in the other case near together. Fig. 255 represents a branch to the parts of which the longer and shorter internodes so resulting give differential characters. A whole tree being in many cases simultaneously thus affected by states of the earth or the air, all parts of it may have such variations impressed on them; and, indeed, such variations, following more or less regularly the changes of the seasons, give to many trees manifest traits of structure. In Fig. 256, a shoot of *Phyllocactus*

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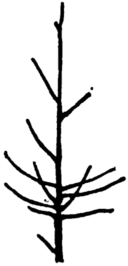

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*crenatus*, we have an interesting example of a variation essentially of the same nature, little as it appears to be so. For each of the lateral indentations is here the seat of an axillary bud; and these we see are separated by internodes which, becoming broader as they become longer, and narrower as they become shorter, produce changes of form that correspond with changes in the luxuriance of growth.

To complete the statement it must be added that these variations of nutrition often determine the development or non-development of lateral axes; and by so doing cause still more marked structural differences. The Fox-glove may be named as a plant which illustrates this truth.

§ 240. From the morphological differentiations caused by unlikenesses of nutrition which the whole plant feels, we pass now to those which are thus caused in some of its parts and not in others. Among such are the contrasts between flowering axes, and the axes that bear leaves only. It has already been shown in § 78, that the belief expressed by Wolff in a direct connexion between fructification and innutrition, is justified inductively by many facts of many kinds. Deductively too, in § 79, we saw reason to conclude that such a relation would be established by survival of the fittest; seeing that it would profit a species for its members to begin sending off migrating germs from the ends of those axes which innutrition prevented from further agamogenetic multiplication. Once more, when considering the nature of the phænogamic axis, we found support for this belief in the fact that the components of a flower exhibit a reversion to that type from which the phænogamic type has probably arisen—a reversion which the laws of embryology would lead us to look for where innutrition had arrested development.

Hence, then, we may properly count those deviations of structure which constitute inflorescence, as among the morphological differentiations produced by local innutrition. I do not mean that the detailed modifications which the essential and subservient organs of fructification display, are thus accounted for: we have seen reason to think them otherwise caused. But I mean that the morphological characters which distinguish gamogenetic axes in general from agamogenetic axes, such as non-development of the internodes, and dwarfing of the foliar organs, are primarily results of failure in the supply of some material required for further growth.*

§ 241. Another trait which has to be noticed under this head, is the spiral, or rather the helical, arrangement of parts. The successive nodes of a phænogam habitually bear their appendages in ways implying more or less twist in the substance of the axis; and in climbing plants the twist is such as to produce a corkscrew shape. This structure is ascribable to differences of interstitial nutrition. Taking a shoot that is growing vertically, it is clear that if the molecules are added with perfect equality on all sides, there will be no tendency towards any kind of lateral deviation; and the successively-produced parts will be perpendicularly over one

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* It is but just to the memory of Wolff, here to point out that he was immensely in advance of Goëthe in his rationale of these metamorphoses. Whatever greater elaboration Goëthe gave to the theory considered as an induction, seems to me more than counter-balanced by the irrationality of his deductive interpretation; which unites mediæval physiology with Platonic philosophy. A dominant idea with him is that leaves exist for the purpose of carrying off crude juices—that "as long as there are crude juices to be carried off, the plant must be provided with organs competent to effect the task;" that while "the less pure fluids are got rid of, purer ones are introduced;" and that "if nourishment is withheld, that operation of nature (flowering) is facilitated and hastened; the organs of the nodes (leaves) become more refined in texture, the action of the purified juices becomes stronger, and the transformation of parts having now become possible, takes place without delay." This being the proximate explanation, the ultimate explanation is, that Nature wishes to form flowers—that when a plant flowers it "attains the end prescribed to it by nature;" and that so "nature at length attains her object." Instead of vitiating his induction by a teleology that is as unwarranted in its assigned object as in its assigned means, Wolff ascribes the phenomena to a cause which, whether sufficient or not, is strictly scientific in its character. Variation of nutrition is unquestionably a "true cause" of variation in plant-structure. We have here no imaginary action of a fictitious agency; but an ascertained action of a known agency.

another. But any inequality in the rate of growth-on the different sides of the shoot, will destroy this straightness in the lines of growth. If the greatest and least rates of molecular increase happens to be on opposite sides, the shoot must assume a curve of single curvature; but in every other case of unequal molecular increase, a curve of double curvature will result. Now it is a corollary from the instability of the homogeneous, that the rates of growth on all sides of a shoot can never be exactly alike; and it is to be also inferred from the same general law, that the greatest and least rates of growth will not occur on exactly opposite sides of the shoot, at the same time that equal rates of growth are preserved by the two other sides. Hence, there must almost inevitably arise more or less of twist; and the appendages of the internodes will so be prevented from occurring perpendicularly one over another.

A deviation of this kind, necessarily initiated by physical causes in conformity with the general laws of evolution, is likely to be made regular and decided by natural selection. For under ordinary circumstances, a plant will profit by having its axis so twisted as to bring the appended leaves into positions that prevent them from shading one another. And, manifestly, modifications in the forms, sizes, and insertions of the leaves, may, under the same agency, lead to adapted modifications of the twist. We must therefore ascribe this common characteristic of phænogams, primarily to local differences of nutrition, and secondarily to survival of the fittest.

It is proper to add that there are some Monocotyledons, as *Urania speciosa,* in which this character does not occur. What conditions of existence they are that here hold this natural tendency in check, it is not easy to see.*

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* The *Natural History Review* for July, 1865, contained an article on the doctrine of morphological composition set forth in the foregoing Chaps. I. to III. In this article, which unites exposition and criticism in a way that is unhappily not common with reviewers, it is suggested that the spiral structure may be caused by natural selection. When this article appeared, the foregoing five pages were standing over in type, as surplus from No. 14, issued in June, 1865.

# CHAPTER XIII.

## MORPHOLOGICAL DIFFERENTIATION IN ANIMALS.

§ 242. THE general considerations which preluded our inquiry into the shapes of plants and their parts, equally serve, so far as they go, to prelude an inquiry into the shapes of animals and their parts. Among animals, as among plants, the formation of aggregates greater in bulk or higher in degree of composition, or both, is accompanied by changes of form in the aggregates as wholes as well as by changes of form in their parts; and the processes of morphological differentiation conform to the same general laws in the one kingdom as in the other.

It is needless to recapitulate the several kinds of modification to be explained, and the several factors that cooperate in working them. In so far as these are common to plants and animals, the preceding chapters have sufficiently familiarized them. Nor is it needful to specify afresh the several types of symmetry and their descriptive names; for what is true of them in the one case is true of them in the other. There is, however, one new and all-important factor which we shall have now to take into account; and about this a few preliminary remarks are requisite.

§ 243. This new factor is motion—motion of the organism in relation to surrounding objects, or of the parts of the organism in relation to one another, or both. Though there are plants, especially of the simpler kinds, which move, and though a few of the simpler animals do not move; yet movements are so exceptional and unobtrusive in the one kingdom, while they are so general and conspicuous in the other, that the broad distinction commonly made is well warranted. What, among plants, is an inappreciable cause of morphological differentiation, becomes, among animals, the chief cause of morphological differentiation.

Animals that are rooted or otherwise fixed, of course present traits of structure nearest akin to those we have been lately studying. The motions of parts in relation to one another and to the environment, being governed by the mode of aggregation and mode of fixing, we are presented with morphological differentiations similar in their general characters to those of plants, and showing us parallel kinds of symmetry under parallel conditions. But animals which move from place to place are subject to an additional class of actions and reactions. These actions and reactions affect them in various ways according to their various modes of movement. Let us glance at the several leading relations between shape and motion which we may expect to find.

If an organism advances through a homogeneous medium with one end always foremost, that end, being exposed to forces unlike those to which the other end is exposed, may be expected to become unlike it; and supposing this to be the only constant contrast of conditions, we may expect an equal distribution of the parts round the axis of movement—a radial symmetry. If in addition to this habitual attitude of the ends, one surface of the body is always uppermost and another always lowermost, there arise between the top and bottom dissimilarities of conditions, while the two sides remain similarly conditioned. Hence it is inferable that such an organism will be divisible into similar halves by a vertical plane passing through its axis of motion—will have a bilateral symmetry. We may presume that this symmetry will deviate but little from double bilateralness where the upper and under parts are not exposed to strongly-contrasted influences; while we may rationally look for single bilateral symmetry of a decided kind, in creatures having dorsal and ventral parts conversant with very unlike regions of the environment: as in all cases where the movement is over a solid surface. If the movement, though over a solid surface, is not constant in direction, but takes place as often on one side as on another, radial symmetry may be again looked for; and if the motions are still more variously directed—if they are not limited to approximately-plane surfaces, but extend to surfaces that are distributed all around with a regular irregularity—an approach of the radial towards the spherical symmetry is to be anticipated. Where the habits are such that the intercourse between the organism and its environment, does not involve an average equality of actions and reactions on any two or more sides, there may be expected either total irregularity or some divergence from regularity.

The like general relations between forms and incident forces are inferable in the component parts of animals, as well as in the animals as wholes. It is needless, however, to occupy space by descriptions of these. Let us now pass to the facts, and see how they confirm, *à posteriori*, the conclusions here reached *à priori*.

# CHAPTER XIV.

## THE GENERAL SHAPES OF ANIMALS.

§ 244. CERTAIN of the *Protozoa* are quite indefinite in their shapes, and quite inconstant in those indefinite shapes which they have—the relations of their parts are indeterminate both in space and time. In one of the simpler Rhizopods, at least during the active stage of its existence, no permanent distinction of inside and outside is established; and hence there can arise no established correspondence between the shape of the outside and the distribution of environing actions. But when the relation of inner and outer becomes fixed, either over part of the mass or over the whole of it, we have kinds of symmetry that correspond with the habitual incidence of forces. An *Amœba* in becoming encysted, which we may regard as the production in it of a differentiation between superficial parts and central parts, passes from an indefinite, ever-changing form into a spherical form; and the order of symmetry which it thus assumes, is in harmony with the average equality of the actions on all its sides. In *Difflugia*, Fig. 134, and still better in *Arcella*, we have an indefinitely-radial symmetry occurring where the conditions are different above and below but alike all around. Among the *Gregarinida* the spherical symmetry and symmetry passing from that into the radial, are such as appear to be congruous with the simple circumstances of these creatures in the intestines of insects.

But the relations of these lowest types to their environments are comparatively so indeterminate, and our knowledge of their actions so scanty, that little beyond negative evidence can be expected from the study of them.

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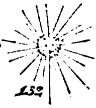

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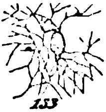

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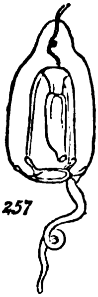
The like may be said of the *Infusoria.* These are more or less irregular. In some cases where the line of movement through the water is tolerably definite and constant we have a form that is approximately radial—externally at least. But usually, as shown in Figs. 137, 138, 139, there is either an unsymmetrical or an asymmetrical shape. And when one of these creatures is watched under the microscope, the congruity of this shape with the incidence of forces is manifest. For the movements are conspicuously varied and indeterminate—movements which do not expose any two or more sides of the mass to approximately equal sets of actions.

§ 245. Among aggregates of the second order, as among aggregates of the first order, we find that of those possessing any definite shapes the lowest are spherical or spheroidal. Such are the *Thalassicollæ.* These gelatinous bodies which float passively in the sea, and present in turn all their sides to the same influences, have their parts disposed with approximate regularity all around a centre. In some orders of *Foraminifera,* as for instance the Nummulites, we have secondary aggregates the parts of which are spirally arranged, approximately in harmony with the radial relations of the society to the environment; but we have other types in which the congregated units are distributed in ways not easily definable, and having to the environment relations that are obscure. Further, among these secondary aggregates in which the units, only physically integrated, have not had their individualities merged into an individuality of a higher order, must be named the compound *Infusoria*. The cluster of *Vorticellæ* in Fig. 144, will sufficiently exemplify them; and the striking resemblance borne by its individuals to those of a radially-arranged cluster of flowers, will show how, under analogous conditions, the general principles of morphological differentiation are similarly illustrated in the two kingdoms.

§ 246. Radial symmetry is usual in those aggregates of the second order that have their parts sufficiently differentiated and integrated to give individualities to them as wholes. The *Cœlenterata* offer numerous examples of this. Solitary polypes—hydroid or helianthoid—mostly stationary, and when they move, moving with any side foremost, do not by locomotion subject their bodies to habitual contrasts of conditions. Seated with their mouths upwards or downwards, or else at all degrees of inclination, the individuals of a species taken together, are subject to no mechanical actions affecting some parts of their discs more than other parts. And this indeterminateness of attitude similarly prevents their relations to prey from being such as subject some of their prehensile organs to forces unlike those to which the rest are subject. The fixed end is differently conditioned from the free end, and the two are therefore different; but around the axis running from the fixed to the free end the conditions are alike in all directions, and the form therefore is radial. Again, among many of the simple free-swimming *Hydrozoa*, the same general truth is exemplified under other circumstances. In a common *Medusa*, advancing through the water by the rhythmical contractions of its disc, the mechanical reactions are the same on all sides; and as, from accidental causes, every part of the edge of the disc comes upwards in its turn, no part is permanently affected in a different way from the rest. Hence the radial form continues.

In others of this same group, however, there occur forms which show us an incipient bilateralness; and help us to see how a more decided bilateralness may arise. Sundry of the *Medusidæ* are proliferous, giving origin to gemmæ from the body of the central polypite or from certain points on the edge of the disc; and this budding, unless it occurs equally on all sides, which it does not and is unlikely to do, must tend to destroy the balance of the disc, and to make its attitude less changeable. In other cases the growth of a large process from the edge of the disc on one side, as in *Steenstrupia*, Fig. 257—a process that is perhaps the morphological equivalent of one of the gemmæ just named—constitutes a similar modification, and a cause of further modification. The existence of this process makes the animal no longer divisible into any two quite similar halves, except those formed by a plane passing through the process; and unless the process is exactly of the same specific gravity as the disc, it must tend towards either the lowest or the highest point, and must so serve to increase the bilateralness, by keeping the two sides of the disc similarly conditioned while the top and bottom are differently conditioned. Fig. 258 represents the underside of another *Medusa*, in which a more decided bilateralness is produced by the presence of two such processes. Among the simple free-swimming *Actinozoa*, occur like deviations from radial symmetry, along with like motions through the water in bilateral attitudes. Of this a *Cydippe* is a familiar example. Though radial in some of its characters, as in the distribution of its meridional bands of locomotive paddles with their accompanying canals, this creature has a two-sided distribution of tentacles and various other parts, corresponding with its two-sided attitude in moving through the water. And in other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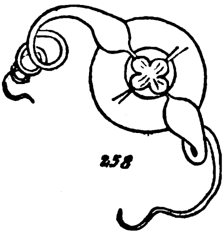
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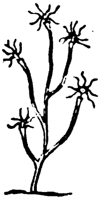
genera of this group, as in *Cestum*, *Eurhamphœa*, and *Callianira*, that almost equal distribution of parts which characterizes the *Beroe* is quite lost.

Here seems a fit place to meet the objection which some may feel to this and other such illustrations, that they amount very much to physical truisms. If the parts of a *Medusa* are disposed in radial symmetry around the axis of motion through the water, there will of course be no means of maintaining one part of its edge upwards more than another; and the equality of conditions may be ascribed to the radiateness, as much as the radiateness to the equality of conditions. Conversely, when the parts are not radially arranged round the axis of motion, they must gravitate towards some one attitude, implying a balance on the two sides of a vertical plane—a bilateralness; and the two-sided conditions so necessitated, may be as much ascribed to the bilateralness as the bilateralness to the two-sided conditions. Doubtless the form and the conditions are, in the way alleged, necessary correlates; and in so far as it asserts this, the objection harmonizes with the argument. To the difficulty which it at the same time raises by the implied question—Why make the form the result of the conditions, rather than the conditions the result of the form? the reply is this:—The radial type, both as being the least differentiated type and as being the most obviously related to lower types, must be taken as antecedent to the bilateral type. The individual variations which incidental circumstances produce in the radial type, will not cause divergence of a species from the radial type, unless such variations give advantages to the individuals displaying them; which there is no reason to suppose they will always do. Those occasional deviations from the radial type, which the law of the instability of the homogeneous warrants us in expecting to take place, will, however, in some cases be beneficial; and will then be likely to establish themselves. Such deviations must tend to destroy the original indefiniteness and variability of attitude—must cause gravitation towards an habitual attitude. And gravitation towards an habitual attitude having once commenced, will continually increase, where increase of it is not negatived by adverse agencies: each further degree of bilateralness rendering more decided the actions that conduce to bilateralness. If this reply be thought insufficient, it may be enforced by the further one, that as, among plants, the incident forces are the antecedents and the forms the consequents (changes of forces being in many cases visibly followed by changes of forms) we are warranted in concluding that the like order of cause and effect holds among animals.

§ 247. Keeping to the same type but passing to a higher degree of composition, we meet more complex and varied illustrations of the same general laws. In the compound *Cœlenterata*, presenting clusters of individuals that are severally homologous with the solitary individuals last dealt with, we have to note both the shapes of the individuals thus united, and the shapes of the aggregates made up of them.

Such of the fixed *Hydrozoa* and *Actinozoa* as form branched societies, continue radial; both because their varied attitudes do not expose them to appreciable differences in their relations to those surrounding actions which chiefly concern them (the actions of prey), and because such differences, even if they were appreciable, would be so averaged in their effects on the dissimilarly-placed members of each group as to be neutralized in the race. Among the tree-like coral-polypedoms, as well as in such ramified assemblages of simpler polypes as are shown in Figs. 149, 150, we have, indeed, cases in many respects parallel to the cases of scattered flowers (§ 233), which though placed laterally remain radial, because no differentiating agency can act uniformly on all of them. Meanwhile, in the groups which these united individuals compose, we see the shapes of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plants further simulated under a further parallelism of conditions. The attached ends differ from the free ends as they do in plants; and the regular or irregular branches obviously stand to environing actions in relations analogous to those in which the branches of plants stand.

The members of those compound *Cœlenterata* which move through the water by their own actions, in attitudes that are approximately constant, show us a more or less distinct two-sidedness. *Diphyes*, Fig. 259, furnishes an example. Each of the largely-developed and modified polypites forming its swimming sacs is bilateral, in correspondence with the bilateralness of its conditions; and in each of the appended polypites the insertion of the solitary tentacle produces a kindred divergence from the primitive radial type. The aggregate, too, which here very much subordinates its members, exhibits the same conformity of structure to circumstances. It admits of symmetrical bisection by a plane passing through its two contractile sacs, or nectocalyces, but not by any other plane; and the plane which thus symmetrically bisects it, is the vertical plane on the two sides of which its parts are similarly conditioned as it propels itself through the water.

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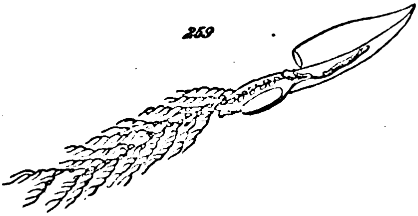
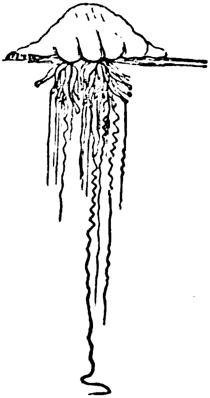


Another group of the oceanic *Hydrozoa*, the *Physophoridæ*, furnishes interesting evidence—not so much in respect of the forms of the united individuals, which we may pass over, as in respect of the forms of the aggregates. Some of these which are without swimming organs, have their parts suspended from air-vessels which habitually float on the surface of the water; and the distribution of their parts is asymmetrical. The *Physalia*, Fig. 152, is an example. Here the relations of the integrated group of individuals to the environment are indefinite; and there is hence no agency tending to change that comparatively irregular mode of growth that is probably derived from a primordial type of the branched *Hydrozoa*.



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So various are the modes of union among the compound *Cœlenterata*, that it is out of the question to deal with them all. Even did space permit, it would be impracticable for any one but a professed naturalist, to trace throughout this group the relations between shapes and conditions of existence. The above must be taken simply as a few of the most significant and easily-interpretable cases.

§ 248. In the sub-kingdom *Molluscoida*, we meet with examples not wholly unlike the foregoing. Among the types assembled under this title there are simple individuals or aggregates of the second order, and societies or tertiary aggregates produced by their union. The relations of forms to forces have to be traced in both.

Solitary Ascidians, fixed or floating, carry on an inactive and indefinite converse with the actions in the environment. Without power to move about vivaciously, and unable to catch any prey but that contained in the currents of water they absorb and expel, these creatures are not exposed to sets of forces that are equal on two or more sides; and their shapes consequently remain vague. Though there are in them traces of symmetrical arrangement, probably due to their derivation, yet they are substantially asymmetrical. Fig. 156 is an example. Among the composite Ascidians, floating and fixed, the shape of the aggregate, partly determined by the habitual mode of gemmation and partly by the surrounding conditions in each case, is in great measure indefinite. We can say no more about it than that it is not obviously at variance with the laws alleged.

Evidence of a more positive kind occurs among those compound *Molluscoida* which are most like the compound *Cœlenterata* in their modes of union—the *Polyzoa*. Many of these form groups that are more or less irregular—spreading as films over solid surfaces, combining into sea-weed-like fronds, budding out from creeping stolons, or growing up into tree-shaped societies; and besides aggregating irregularly they are irregularly placed on surfaces inclined in all directions. Merely noting that this asymmetrical distribution of the united individuals is explained by the absence of definiteness in the relations of the aggregate to incident forces, it concerns us chiefly to observe that the united individuals severally exemplify the same truth as do similarly-united individuals among the *Cœlenterata*. While their internal organs, though said to have a trace of bilateralness, cannot be said to display any definite symmetry; their external organs are completely radial. Averaging the members of each society, the ciliated tentacles they protrude are similarly related to prey on all sides; and therefore remain the same on all sides. This distribution of tentacles is not, however, without exception. Among the fresh-water *Polyzoa* there are some genera, as *Plumatella* and *Crystatella*, in which the arrangement of these parts is very decidedly bilateral. Some species of them show us such relations of the individuals to one another and to their surface of attachment, as give a clue to this modification; but in other species the meaning of this deviation from the radial type is not obvious.

§ 249. In that somewhat heterogeneous assemblage of animals now classed, perhaps provisionally, as *Annuloida*, we begin again with simple aggregates of the second order, and ascend to aggregates in which we have seen reason to suspect a higher degree of composition. Good examples of the connexions between forms and forces occur in this group.

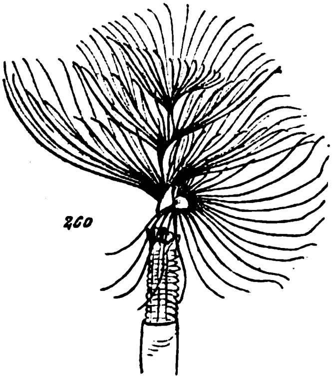
Among the lower annuloid types, the *Planaria* exemplifies the single bilateral symmetry which, even in very inferior forms, accompanies the habit of moving in one direction over a solid surface. Humbly organized as are these creatures and their allies the *Nemertidæ*, we see in them just as clearly as in the highest animals, that where the movements subject the body to different forces at its two ends, different forces on its under and upper surfaces, and like forces along its two sides, there arises a corresponding form, unlike at its extremities, unlike above and below, but having its two sides alike.

The *Echinodermata* furnish us with instructive illustrations —instructive because among types that are nearly allied, we meet with wide deviations of form answering to marked contrasts in the relations to the environment. The facts fall into four groups. The *Crinoidea*, once so abundant and now so rare, present a radial symmetry answering to an incidence of forces that is equal on every side. In the general attitudes of their parts towards surrounding actions, they are like uniaxial plants or like polypes; and show, as they do, marked differences between the attached ends and the free ends, along with even distributions of parts all round their axes. In the *Ophiuridea*, proved to be near akin to the Crinoids, and in the Star-fishes, we have radial symmetry co-existing with very different habits; but habits which nevertheless account for the maintenance of the form. Holding on to rocks and weeds by its simple or branched arms, or by the suckers borne on the under surface of its rays, one of these creatures moves about not always with one side foremost, but with any side foremost. Consequently, averaging its movements, its arms or rays are equally affected, and therefore remain the same on all sides. On watching the ways of the common Sea-urchin, we are similarly furnished with an explanation of its spherical, or rather its spheroidal, figure. Here the habit is not to move over any one approximately-flat surface; but the habit is to hold on by several surfaces on different sides at the same time. Frequenting crevices and the interstices among stones and weeds, the Sea-urchin protrudes the suckers arranged in meridional bands over its shell, laying hold of objects now on this side and now on that, now above and now below: the result being, that it does not move in all directions over one plane but in all directions through space. Hence the approach in general form towards spherical symmetry—an approach which is, however, restrained by the relations of the parts to the mouth and vent: the conditions not being exactly the same at the two poles as at other parts of the surface. Still more significant is that deviation from this shape which occurs among such of the *Echinidea* as have habitats of a different kind, and, consequently, different habits. The genera *Echinocyamus*, *Spatangus*, *Brissus*, and *Amphidotus*, diverge markedly towards a bilateral structure. These creatures are found not on rocky shores but on flat sea-bottoms, and some of them only on bottoms of sand or mud. Here, there is none of that distribution of surfaces on all sides which makes the spheroidal form congruous with the conditions. Having to move about over an approximately-horizontal plane, any deviation of structure which leads to one side being kept always foremost, will be an advantage: greater fitness to function becoming possible in proportion as function becomes fixed. Survival of the fittest will therefore tend to establish, under such conditions, a form that keeps the same part in advance—a form in which, consequently, the original radial symmetry diverges more and more towards bilateral symmetry. It may be well to add that the validity of these interpretations does not depend on the view taken of the alliances of the Echinoderms, and their primitive type of symmetry. If, as Professor Huxley contends, the Echinoderms, having bilateral larvæ, cannot be held akin to those lower types in which the radial structure is constant and complete; it does not follow that the above reasonings are erroneous. On the contrary the derivation of these radially-symmetrical forms from forms not radially-symmetrical, would show how entirely the structure of the organism is moulded by the distribution of forces to which its mode of life exposes it.

The remaining *Annuloida*, most of them parasitic, must be passed over. Living within the bodies of other creatures, they have their forms determined by conditions that are too obscure to be satisfactorily dealt with.

§ 250. Very definite and comparatively uniform, are the relations between shapes and circumstances among the *Annulosa*—including under that title the *Annelida* and the *Articulata*. The agreements and the disagreements are equally instructive.

At one time or other of its life, if not throughout its life, every annulose animal is locomotive; and its temporary or permanent locomotion, being carried on with one end habitually foremost and one surface habitually uppermost, it fulfils those conditions under which bilateral symmetry arises. Accordingly, bilateral symmetry is traceable throughout the whole of this sub-kingdom. Traceable, we must say, because, though it is extremely conspicuous in the immense majority of annulose types, it is to a considerable extent obscured where obscuration is to be expected. The embryos of the *Tubicolæ*, after swimming about awhile, settle down and build themselves tubes, from which they protrude their heads; and in them, or in some of them, the bilateral symmetry is disguised by the development of head-appendages in an all-sided manner. The tentacles of *Terebella* are distributed much in the same way as those of a polype. The breathing organs in *Sabella unispira*, Fig. 260, do not correspond on opposite sides of a median plane. Even here, however, the body retains its primitive bilateralness; and it is further to be remarked that this loss of bilateralness in the external appendages, does not occur where the relations to external conditions continue bilateral: witness the *Serpula*, Fig. 261, which has its respiratory tufts arranged in a two-sided way, under the two-sided conditions involved by the habitual position of its tube.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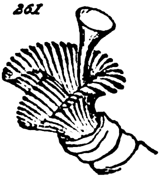
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The community of symmetry among the higher *Annulosa*, has an unobserved significance. That Flies, Beetles, Lobsters, Centipedes, Spiders, Mites, have in common the characters, that the end which moves in advance differs from the hinder end, that the upper surface differs from the under surface, and that the two sides are alike, is a truth received as a matter of course. After all that has been said above, however, it will be seen to have a meaning not to be overlooked; since it supplies a million-fold illustration of the laws that have been set forth. It is needless to give diagrams. Every reader can call to mind the unity indicated.

While, however, annulose animals repeat so uniformly these traits of structure, there are certain other traits in which they are variously contrasted; and their contrasts have to be here noted, as serving further to build up the general argument. In them we see the stages through which bilateral symmetry becomes gradually more marked, as the conditions it responds to become more decided. A common Earth-worm may be instanced as a member of this sub-kingdom that is among the least-conspicuously bilateral. Though internally its parts have a two-sided arrangement; and though the positions of its orifices give it an external two-sidedness, at the same time that they establish a difference between the two ends; yet its two-sidedness is not strongly marked. The form deviates but little from what we have distinguished as triple bilateral symmetry: if the creature is cut across the middle, the head and tail ends are very much alike; if cut in two along its axis by a horizontal plane, the under and upper halves are very much alike; and if cut in two along its axis by a vertical plane, the two sides are quite alike. Figs. 263 and 264 will make this clear. Such creatures as the *Julus* and the Centipede, may be taken as showing a transition to double bilateral symmetry. Besides being divisible into exactly similar halves by a vertical plane passing through the axis, one of these animals may be bisected transversely into parts that differ only slightly; but if cut in two by a horizontal plane passing through the axis, the under and upper halves are decidedly unlike. Figs. 265, 266, exhibit these traits. Among the isopodous crustaceans, the departure from these low types of symmetry is more marked. As

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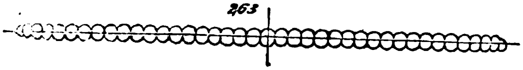

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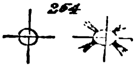

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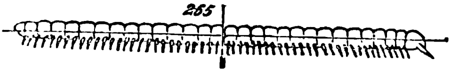

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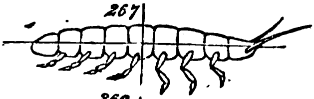

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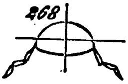

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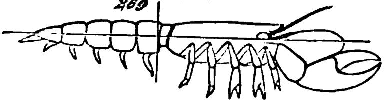

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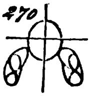
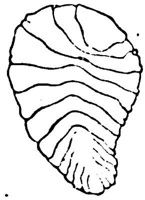


shown in Figs. 267 and 268, the contrast between the upper and under parts is greater, and the head and tail ends differ more obviously. In all the higher *Articulata*, the unlikeness between the front half and the hind half has become conspicuous: there is in them single bilateral symmetry of so pronounced a kind, that no other resemblance is suggested than that between the two sides. By Figs. 269 and 270, representing a decapodous crustacean divided longitudinally and transversely, this truth is made manifest. On calling to mind the habits of the creatures here drawn and described, it will be seen that they explain these forms. The incidence of forces is the same all around the Earth-worm as it burrows through the compact ground. The Centipede, creeping amid loose soil or *débris* or beneath stones, insinuates itself between solid surfaces—the interstices being mostly greater in one dimension than in others. And all the higher *Annulosa*, moving about as they do over exposed objects, have their dorsal and ventral parts as dissimilarly acted upon as are their two ends.

One other fact only respecting annulose animals needs to be noticed under this head—the fact, namely, that they become unsymmetrical where their parts are unsymmetrically related to the environment. The common Hermit-crab serves as an instance. Here, in addition to the unlikeness of the two sides implied by that curvature of the body which fits the creature to the shell it inhabits, there is an unlikeness due to the greater development of the limbs, and especially the claws, on the outer side. As in the embryo of the Hermit-crab the two sides are alike; and as the embryo may be taken to represent the type from which the Hermit-crab has been derived; we have in this case evidence that a symmetrically-bilateral form has been moulded into an unsymmetrically-bilateral form, by the action of unsymmetrically-bilateral conditions. A further illustration is supplied by *Bopyrus*, Fig. 271: a parasite the habits of which similarly account for its distorted shape.



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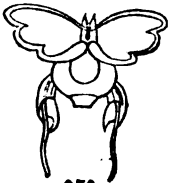
§ 251. Among the *Mollusca* we find more varied relations between shapes and circumstances. Some of them are highly instructive.

Mollusks of one order, the *Pteropoda*, swim in the sea much in the same way that butterflies fly in the air, and have shapes not altogether unlike those of butterflies. Fig. 272 represents one of these creatures. That its bilaterally-symmetrical shape harmonizes with its bilaterally-symmetrical conditions is sufficiently obvious.



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Among the *Lamellibranchiata*, we have diverse forms accompanying diverse modes of life. Such of them as frequently move about, like the fresh-water Mussel, have their two valves and the contained parts alike on the opposite sides of a vertical plane: they are bilaterally symmetrical in conformity with their mode of movement. The marine Mussel, too, though habitually fixed, and though not usually so fixed that its two valves are similarly conditioned, still retains that bilateral symmetry which is characteristic of the order; and it does this because in the species considered as a whole, the two valves are not dissimilarly conditioned. If the positions of the various individuals are averaged, it will be seen that the differentiating actions neutralize one another. In certain other fixed Lamellibranchs, however, there is a considerable deviation from bilateral symmetry; and it is a deviation of the kind to be anticipated under the circumstances. Where one valve is always downwards, or next to the surface of attachment, while the other valve is always upwards, or next to the environing water, we may expect to find the two valves become unlike. This we do find: witness the Oyster. In the Oyster, too, we see a further irregularity. There is a great indefiniteness of outline, both in the shell and in the animal — an indefiniteness made manifest by comparing different individuals. We have but to remember that growing clustered together, as Oysters do, they must interfere with one another in various ways and degrees, to see how the indeterminateness of form and the variety of form are accounted for.

Among the Gasteropods, modifications of a more definite kind occur. "In all Mollusks," says Professor Huxley, "the axis of the body is at first straight, and its parts are arranged symmetrically with regard to a longitudinal vertical plane, just as in a vertebrate or an articulate embryo." In some Gasteropods, as the *Chiton*, this bilateral symmetry is retained—the relations of the body to surrounding actions not being such as to disturb it. But in those more numerous types that have spiral shells, there is a marked deviation from bilateral symmetry, as might be expected. "This asymmetrical over-development never affects the head or foot of the mollusk:" only those parts which, by inclosure in a shell, are protected from environing actions, lose their bilateralness; while the external parts, subjected by the movements of the creatures to bilateral conditions, remain bilateral. Here, however, a difficulty meets us. Why is it that the naked Gasteropods, such as our common slugs, deviate from bilateral symmetry, though their modes of movement are those along with which complete bilateral symmetry usually occurs? The reply is, that their deviations from bilateral symmetry are probably inherited, and that they are maintained in such parts of their organization as are not exposed to bilaterally-symmetrical conditions. There is reason to believe that the naked Gasteropods are descended from Gasteropods that had shells: the evidence being that the naked Gasteropods have shells during the early stages of their development, and that some of them retain rudimentary shells throughout life. Now the shelled Gasteropods deviate from bilateral symmetry in the disposition of both the alimentary system and the reproductive system. The naked Gasteropods, in losing their shells, have lost that immense one-sided development of the alimentary system which fitted them to their shells, and have acquired that bilateral symmetry of external figure which fits them for their habits of locomotion; but the reproductive system remains one-sided, because, in respect to it, the relations to external conditions remain one-sided.

The Cephalopods, which are interpretable as higher developments on the Gasteropod type, show us bilaterally-symmetrical external forms along with habits of movement through the water in two-sided attitudes. At the same time, in the radial distribution of the arms, enabling one of these creatures to take an all-sided grasp of its prey, we see how readily upon one kind of symmetry there may be partially developed another kind of symmetry, where the relations to conditions favour it.

§ 252. The *Vertebrata* illustrate afresh the truths which we have already traced among the *Annulosa*. Flying through the air, swimming through the water, and running over the earth as vertebrate animals do, in common with annulose animals, they are, in common with annulose animals, different at their anterior and posterior ends, different at their dorsal and ventral surfaces, but alike along their two sides. This single bilateral symmetry remains constant under the extremest modifications of form. Among fish we see it alike in the horizontally-flattened Skate, in the vertically-flattened Bream, in the almost spherical *Diodon*, and in the greatly-elongated *Syngnathus*. Among reptiles the Turtle, the Snake, and the Crocodile all display it. And under the countless modifications of structure displayed by birds and mammals, it remains conspicuous.

A less obvious fact which it concerns us to note among the *Vertebrata*, parallel to one which we noted among the *Annulosa*, is that whereas the lower vertebrate forms deviate but little from triple bilateral symmetry, the deviation becomes great as we ascend. Figs. 273 and 274 show how, besides being divisible into similar halves by a vertical plane passing through its axis, a Fish is divisible into halves that are not very dissimilar by a horizontal plane passing through its axis, and also into other not very dissimilar halves by a plane cutting it transversely. If, as shown in Figs. 275 and 276, analogous sections be made of a superior Reptile, the divided parts differ more decidedly. When a Mammal and a Bird are treated in the same way, as shown in Figs. 277, 278, and Figs. 279, 280, the parts marked off by the dividing planes are unlike in far greater degrees. On considering the mechanical converse between organisms of these several types and their environments—on remembering that the fish habitually moves through a homogeneous medium of nearly the same specific gravity as itself, that the terrestrial reptile either crawls on the surface or raises itself very incompletely above it, that the more active mammal, having

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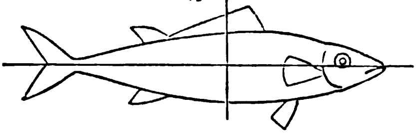

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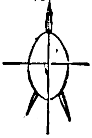

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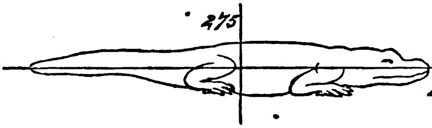

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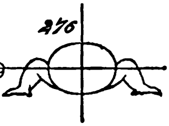

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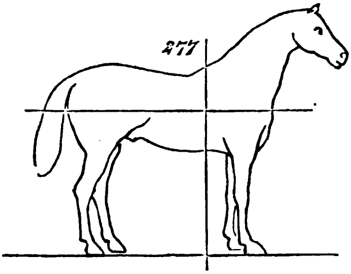

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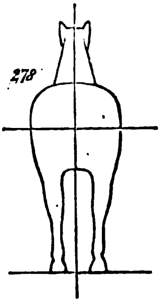

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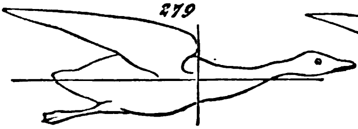

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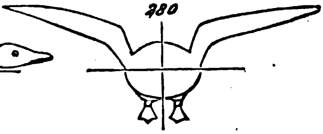


its supporting parts more fully developed, thereby has the under half of its body made more different from the upper half, and that the bird is subject by its mode of life to yet another set of actions and reactions; we shall see that these facts are quite congruous with the general doctrine, and furnish further support to it.

One other significant piece of evidence must be named. Among the *Annulosa* we found unsymmetrical bilateralness in creatures having habits exposing them to unlike conditions on their two sides; and among the *Vertebrata* we find parallel cases. They are presented by the *Pleuronectidæ*—the order of distorted flat fishes to which the Sole and the Flounder belong. On the hypothesis of evolution, we must conclude that fishes of this order have arisen from an ordinary bilaterally-symmetrical type of fish, which, feeding at the bottom of the sea, gained some advantage by placing itself with one of its sides downwards, instead of maintaining the vertical attitude. Besides the general reason there are specific reasons for concluding this. In the first place, the young Sole or Flounder is bilaterally symmetrical—has its eyes on opposite sides of its head, and swims in the usual way. In the second place, the metamorphosis which produces the unsymmetrical structure sometimes does not take place—there are abnormal Flounders that swim vertically, like other fishes. In the third place, the transition from the symmetrical structure to the unsymmetrical structure may be traced. Almost incredible though it seems, one of the eyes is transferred from the under-side of the head to the upper-side. Until lately it was supposed that the change by which the two eyes, originally placed on opposite sides, come to be placed on the same side, is effected by a distortion of the cranium; but it is now asserted that actual migration of an eye occurs. According to Prof. Steenstrup, the eye passes between the ununited bones of the skull; but according to Prof. Thomson, it passes under the skin. Be the course of the metamorphosis what it may, however, it furnishes several remarkable illustrations of the way in which forms become moulded into harmony with incident forces. For besides this divergence from bilateral symmetry involved by the presence of both eyes upon the upper side, there is a further divergence from bilateral symmetry involved by the differentiation of the two sides in respect to the contours of their surfaces and the sizes of their fins. And then, what is still more significant, there is a near approach to likeness between the halves that were originally unlike, but are, under the new circumstances, exposed to like conditions. The body is divisible into similarly-shaped parts by a plane cutting it along the side from head to tail: "the dorsal and ventral instead of the lateral halves become symmetrical in outline and are equipoised."

§ 253. Thus, little as there seems in common between the shapes of plants and the shapes of animals, we yet find, on analysis, that the same general truths are displayed by both. The one ultimate principle that in any organism equal amounts of growth take place in those directions in which the incident forces are equal, serves as a key to the phenomena of morphological differentiation. By it we are furnished with interpretations of those likenesses and unlikenesses of parts, which are exhibited in the several kinds of symmetry; and when we take into account inherited effects, wrought under ancestral conditions contrasted in various ways with present conditions, we are enabled to comprehend, in a general way, the actions by which animals have been moulded into the shapes they possess.

To fill up the outline of the argument, so as to make it correspond throughout with the argument respecting vegetal forms, it would be proper here to devote a chapter to the differentiations of those homologous segments out of which animals of certain types are composed. Though, among most animals of the third degree of composition, such as the rooted *Hydrozoa*, the *Polyzoa*, and the *Ascidioida*, the united individuals are not reduced to the condition of segments of a composite individual, and do not display any marked differentiations; yet there are some animals in which such subordinations, and consequent heterogeneities, occur. The oceanic *Hydrozoa* form one group; and we have seen reason to conclude that the *Annulosa* form another group. It is not worth while, however, to occupy space in detailing these unlikenesses of homologous segments, and seeking specific explanations of them. Among the oceanic *Hydrozoa* they are extremely varied; and the habits and derivations of these creatures are so little known, that there are no adequate data for interpreting the forms of the parts in terms of their relations to the environment. Conversely, among the *Annulosa* those differentiations of the homologous segments which accompany their progressing integration, have so much in common, and have general causes which are so obvious, that it is needless to deal with them at any length. They are all explicable as due to the exposure of different parts of the chain of segments to different sets of actions and reactions: the most general contrast being that between the anterior segments and the posterior segments, answering to the most general contrast of conditions to which annulose animals subject their segments; and the more special contrasts answering to the contrasts of conditions entailed by their more special habits.

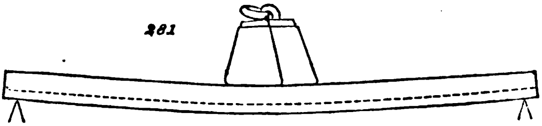
Were an exhaustive treatment of the subject practicable, there should here, also, come a chapter devoted to the internal structures of animals—meaning, more especially, the shapes and arrangements of the viscera. The relations between forms and forces among these inclosed parts, are, however, mostly too obscure to allow of interpretation. Protected as the viscera are in great measure from the incidence of external forces, we are not likely to find much correspondence between their distribution and the distribution of external forces. In this case the influences, partly mechanical, partly physiological, which the organs exercise on one another, become the chief causes of their changes of figure and arrangement; and these influences are complex and indefinite. One general fact may, indeed, be noted—the fact, namely, that the divergence towards asymmetry which generally characterizes the viscera, is marked among those of them which are most removed from mechanical converse with the environment, but not so marked among those of them which are less removed from such converse. Thus while, throughout the *Vertebrata,* the alimentary system, with the exception of its two extremities, is asymmetrically arranged, the respiratory system, which occupies one end of the body, generally deviates but little from bilateral symmetry, and the reproductive system, partly occupying the other end of the body, is in the main bilaterally symmetrical: such deviation from bilateral symmetry as occurs, being found in its most interiorly-placed parts, the ovaries. Just indicating these facts as having a certain significance, it will be best to leave this part of the subject as too involved for detailed treatment.

Internal structures of one class, however, not included among the viscera, admit of general interpretation—structures which, though internal, are brought into tolerably-direct relations with the environing forces, and are therefore subordinate in their forms to the distribution of those forces. These internal structures it will be desirable to deal with at some length; both because they furnish important illustrations enforcing the general argument, and because an interpretation of them which we have seen reason to reject, cannot be rejected without raising the demand for some other interpretation.

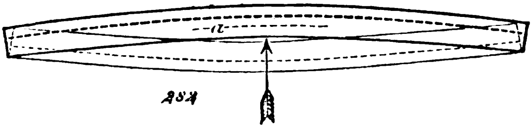
# CHAPTER XV.

## THE SHAPES OF VERTEBRATE SKELETONS.

§ 254. When an elongated mass of any substance is transversely strained, different parts of the mass are exposed to forces of opposite kinds. If, for example, a bar of metal or wood is supported at its two ends, as shown in Fig. 281, and has to bear a weight on its centre, its lower part is thrown into a state of tension, while its upper part is thrown into a state of compression. As will be manifest to any one who has observed what happens on breaking a stick across his knee, the greatest degree of tension falls on the fibres that form the convex surface, while the fibres forming the concave surface are subject to the greatest degree of compression. Between these extremes the fibres at different depths are subject to different forces. Progressing upwards from the under surface of the bar shown in Fig. 281, the tension of the fibres becomes less; and progressing downwards from the upper surface, the compression of the fibres becomes less; until, at a certain distance between the two surfaces, there is a place at which the fibres are neither extended nor compressed. This, shown by the dotted line in



the figure, is called in mechanical language the "neutral axis." It varies in position with the nature of the substance strained: being, in common pine-wood, at a distance of about five eighths of the depth from the upper surface or three eighths from the under surface. Clearly, if such a piece of wood instead of being subject to a downward force is secured at its ends and subject to an upward force, the distribution of the compressions and tensions will be reversed, and the neutral axis will be nearest to the upper surface. Fig. 282 represents these opposite attitudes of the bar and the changed position of its neutral axis: the arrow indicating the direction of the force producing the upward bend, and the faint dotted line *a*, showing the previous position of the neutral axis. Between the two neutral axes will be seen a central space; and it is obvious that when the bar has its strain from time to time reversed, the repeated changes of its molecular condition must affect the central space in a way different from that in which they affect the two outer spaces. Fig. 283 is a diagram conveying some idea of these contrasts in molecular condition. If A B C D be the middle part of a bar thus treated, while G H and K L are the alternating neutral axes; then the forces to which the bar is in each case subject, may be readily shown. Supposing the deflecting force to be acting in the direction of the arrow E, then the tensions to which the fibres between G and F are exposed, will be represented by a series of lines increasing in length as the distance from G increases; so that the triangle G F M, will express the amount and distribution of all the molecular tensions. But the molecular compressions throughout the space from G to E, must balance the molecular tensions; and hence, if the triangle G E N be made equal to the tri-



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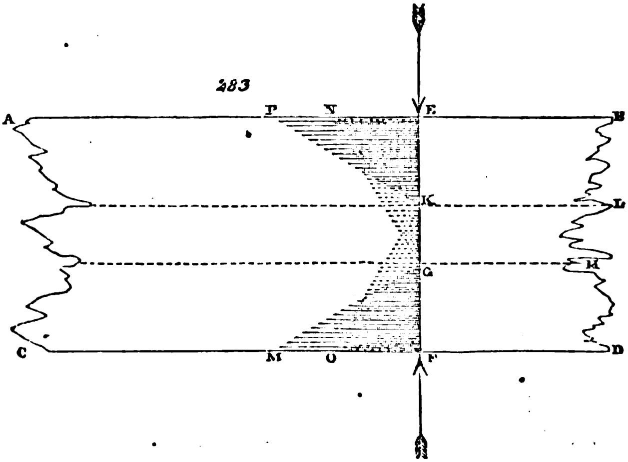
angle G F M, the parallel lines of which it is composed (here dotted for the sake of distinction) will express the amount and distribution of the compressions between E and G. Similarly, when the deflecting force is in the direction of the arrow F, the compressions and tensions will be quantitatively symbolized by the triangle K F O, and K E P. And thus the several spaces occupied by full lines and by dotted lines and by the two together, will represent the different actions to which different parts of the transverse section are subject by alternating transverse strains. Here then it is made manifest to the eye that the central space between G and K, is differently conditioned from the spaces above and below it; and that the difference of condition is sharply marked off. The fibres forming the outer surface C D, are subject to violent tensions and violent compressions. Progressing inwards the tensions and compressions decrease—the tensions the more rapidly. As we approach the point G, the tensions to which the fibres are alternately subject, bear smaller and smaller ratios to the compressions, and disappear at the point G. Thence to the centre occur compressions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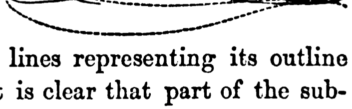
only, of alternating intensities, becoming at the centre small and equal; and from the centre we advance, through a reverse series of changes, to the other side.

Thus it is demonstrable that any substance in which the power of resisting compression is unequal to the power of resisting tension, cannot be subject to alternating transverse strains, without having a central portion differentiated in its conditions from the outer portions, and consequently differentiated in its structure. This conclusion may easily be verified by experiment. If something having a certain toughness but not difficult to break, as a thick piece of sheet lead, be bent from side to side till it is broken, the surface of fracture will exhibit an unlikeness of texture between the inner and outer parts.

§ 255. And now for the application of this seemingly-irrelevant truth. Though it has no obvious connection with the interpretation of vertebral structure, we shall soon see that it fundamentally concerns us.

The simplest type of vertebrate animal, the fish, has a mode of locomotion which involves alternating transverse strains. It is not, indeed, subjected to alternating transverse strains by some outer agency, as in the case we have been investigating: it subjects itself to them. But though the strains are here internally produced instead of externally produced, the case is not therefore removed into a wholly different category. For supposing Fig. 284 to represent the outline of a fish when bent on one side (the dotted lines representing its outline when the bend is reversed), it is clear that part of the substance forming the convex half must be in a state of tension. This state of tension implies the existence in the other half of some counter-balancing compression. And between the two there must be a neutral axis. The way in which this conclusion is reconcilable with the fact that there is tension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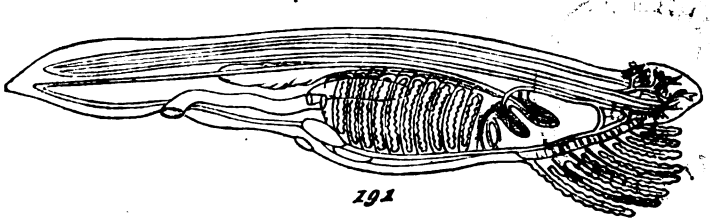
somewhere in the concave side of a fish, since the curve is caused by muscular contractions on the concave side, will be made clear by the rude illustration which a bow supplies. A bow may be bent by a thrust against its middle (the two ends being held back), or it may be bent by contracting a string that unites its ends; but the distributions of mechanical forces within the wood of the bow, though not quite alike in the two cases, will be very similar. Now while the muscular action on the concave side of a fish differs from that represented by the tightened string of a bow, the difference is not such as to destroy the applicability of the illustration: the parallel holds so far as this, that within that portion of the fish's body which is passively bent by the contracting muscles, there must be, as in a strung bow, a part in compression, a part in tension, and an intermediate part which is neutral.

Recognizing the fact that even in the developed fish with its complex locomotive apparatus, this law of the transverse strain holds in a qualified way, we shall understand how much more it must hold in any form that may be supposed to initiate the vertebrate type—a form devoid of that segmentation by which the vertebrate type is more or less characterized. We shall see that assuming a rudimentary animal still simpler than the *Amphioxus*, to have a feeble power of moving itself through the water by the undulations of its body, or some part of its body, there will necessarily come into play certain reactions that must affect the median portion of the undulating mass in a way unlike that in which they affect its lateral portions. And if there exists in this median portion a tissue that keeps its place with any constancy, we may expect that the differential conditions produced in it by the transverse strain, will initiate a differentiation. It is true that the distribution of the viscera in the *Amphioxus*, Fig. 191, and in the type from which we may suppose it to arise, is such as to interfere with this process. It is also true that the actions and reactions described would not of themselves give to the median portion



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a cylindrical shape, like that of the cartilaginous rod running along the back of the *Amphioxus.* But what we have here to note in the first place is, that these habitual alternate flexions have a tendency to mark off from the outer parts an unlike inner part, which may be seized hold of, maintained, and further modified, by natural selection, should any advantage thereby result. And we have to note in the second place, that an advantage *is* likely to result. The contractions cannot be effective in producing undulations, unless the general shape of the body is maintained. External muscular fibres unopposed by an internal resistent mass, would cause collapse of the body. To meet the requirements there must be a means of maintaining longitudinal rigidity without preventing bends from side to side; and such a means is presented by a structure initiated as described. In brief, whether we have or have not the actual cause, we have here at any rate "a true cause." Though there are difficulties in tracing out the process in a specific way, it may at least be said that the mechanical genesis of this rudimentary vertebrate axis is quite conceivable. And even the difficulties may, I think, be much more fully met than would at first sight seem possible.

What is to be said of the other leading trait which the simplest vertebrate animal has in common with all higher vertebrate animals—the segmentation of its lateral muscular masses? Is this, too, explicable on the mechanical hypothesis? Have we, in the perpetual transverse strains, a cause for the fact that while the rudimentary vertebrate axis is without any divisions, there are definite divisions of the substance forming the animal's sides? I think we have. A glance at the distribution of forces under the transverse strain, as represented in the foregoing diagrams, will show how much more severe is the strain on the outer parts than on the inner parts; and how, consequently, any modifications of structure eventually necessitated, will arise peripherally before they arise centrally. The perception of this may be enforced by a simple experiment. Take a stick of sealing-wax and warm it slowly and moderately before the fire, so as to give it a little flexibility. Then bend it gently until it is curved into a semi-circle. On the convex surface small cracks will be seen, and on the concave surface wrinkles; while between the two the substance remains undistorted. If the bend be reversed and re-reversed, time after time, these cracks and wrinkles will become fissures which gradually deepen. But now, if changes of this class, entailed by perpetual transverse strains, commence superficially, as they manifestly must; there arise the further questions—What will be the special modifications produced under these special conditions? and through what stages will these modifications progress? Every one has literally at hand an example of the way in which a flexible external layer that is now extended and now compressed, by the bending of the mass it covers, becomes creased; and a glance at the palms and the fingers will show that the creases are near one another where the skin is thin, and far apart where the skin is thick. Between this familiar case and the case of the rhinoceros-hide, in which there are but a few large folds, various gradations may be traced. Now the like must happen with the increasing layers of contractile fibres forming the sides of the muscular tunic in such a type as that supposed. The bendings will produce in them small wrinkles while they are thin, but more decided and comparatively distant fissures as they become thick. Fig 289, which is a horizontal longitudinal section, shows how these thickening layers will adjust themselves on the convex and the concave surfaces, supposing the fibres of which they are composed to be oblique, as their function requires; and it is not difficult to see that when once definite divisions have been established, they will advance inwards as the layers develop; and will so produce a series of muscular bundles. Here then we have something like the *myocommata* which are traceable in the *Amphioxus*, and are conspicuous in all superior fishes.

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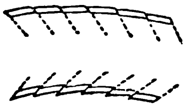

§ 256. These speculative conceptions I have ventured to present with the view of showing that the hypothesis of the mechanical genesis of vertebrate structure, is not wholly at fault when applied to the most rudimentary vertebrate animal. Lest it should be alleged that the question is begged if we set out with a type which, like the *Amphioxus*, already displays segmentation throughout its muscular system, it seemed needful to indicate conceivable modes in which there may have been mechanically produced those leading traits that distinguish the *Amphioxus*. It seemed needful to assign an origin for the notochord; and to this we see a clue in the differentiating effects of the transverse strain. It seemed needful to account for the existence of muscular divisions while yet there are no vertebral divisions; and for this, also, the transverse strain furnishes a feasible reason.

But now, having shown that the actions and reactions involved by its mode of locomotion, are possible causes of those rudimentary structures which the simplest vertebrate animal presents, let us return to the region of established fact, and consider whether such actions and reactions as we actually witness, are adequate causes of those observed differentiations and integrations which distinguish the more-developed vertebrate animals. Let us see whether the theory of mechanical genesis afford us a deductive interpretation of the inductive generalizations.

Before proceeding, we must note a process of functional adaptation which here co-operates with natural selection. I refer to the habitual formation of denser tissues at those parts of an organism which are exposed to the greatest strains—either compressions or tensions. Instances of hardening under compression are made familiar to us by the skin. We have the general contrast between the soft skin covering the body at large, and the indurated skin covering the inner surfaces of the hands and the soles of the feet. We have the fact that even within these areas the parts on which the pressure is habitually greatest, have the skin habitually thickest; and that in each person special points exposed to special pressures become specially dense—often as dense as horn. Further, we have the converse fact, that the skin of little-used hands becomes abnormally thin—even losing, in places, that ribbed structure which distinguishes skin subject to rough usage. Of increased density directly following increased tension, the skeletons, whether of men or animals, furnish abundant evidence. Anatomists easily discriminate between the bones of a strong man and those of a weak man, by the greater development of those ridges and crests to which the muscles are attached; and naturalists, on comparing the remains of domesticated animals with those of wild animals of the same species, find kindred differences. The first of these facts shows unmistakably the immediate effect of function on structure, and by obvious alliance with it the second may be held to do the same—both implying that the deposit of dense substance capable of great resistance, habitually takes place at points where the tension is excessive.

Taking into account, then, this adaptive process, continually aided by the survival of individuals in which it has taken place most rapidly, we may expect, on tracing up the evolution of the vertebrate axis, to find that as the muscular power becomes greater there arise larger and harder masses of tissue, serving the muscles as *points d'appui;* and that these arise first in those places where the strains are greatest. Now this is just what we *do* find. The myocommata are so placed that their actions are likely to affect first that upper coat of the notochord, where there are found "quadrate masses of somewhat denser tissue," which "seem faintly to represent neural spines," even in the *Amphioxus.* It is by the development of the neural spines, and after them of the hæmal spines, that the segments of the vertebral column are first marked out; and under the increasing strain of more-developed myocommata, it is just these peripheral appendages of the vertebral segments that must be most subject to the forces which cause the formation of denser tissue. It follows from the mechanical hypothesis that as the muscular segmentation must begin externally and progress inwards, so, too, must the vertebral segmentation. Besides thus finding reason for the fact that in fishes with wholly cartilaginous skeletons, the vertebral segments are indicated by these processes, while yet the notochord is unsegmented; we find a like reason for the fact that the transition from the less-dense cartilaginous skeleton to the more-dense osseous skeleton, pursues a parallel course. In the existing *Lepidosiren,* which by uniting certain piscine and amphibian characters betrays its close alliance with primitive types, the axial part of the vertebral column is unossified, while there is ossification of the peripheral parts. Similarly with numerous genera of fishes classed as palæozoic. The fossil remains of them show that while the neural and hæmal spines consisted of bone, the central parts of the vertebræ were not bony. It may in some cases be noted, too, both in extant and in fossil forms, that while the ossification is complete at the outer extremities of the spines it is incomplete at their inner extremities—thus similarly implying centripetal development.

§ 257. After these explanations the process of eventual segmentation in the spinal axis itself, will be readily understood. The original cartilaginous rod has to maintain longitudinal rigidity while permitting lateral flexion. As fast as it becomes definitely marked out, it will begin to concentrate within itself a great part of those pressures and tensions caused by transverse strains. As already said, it must be acted upon much in the same manner as a bow, though it is bent by forces acting in a more indirect way; and like a bow, it must, at each bend, have the substance of its convex side extended and the substance of its concave side compressed. So long as the vertebrate animal is small or inert, such a cartilaginous rod may have sufficient strength to withstand the muscular strains; but, other things equal, the evolution of an animal that is large, or active, or both, implies muscular strains that must tend to cause modification in such a cartilaginous rod. The results of greater bulk and of greater vivacity may be best dealt with separately. As the animal increases in size, the rod will grow both longer and thicker. On looking back at the diagrams of forces caused by transverse strains, it will be seen that as the rod grows thicker, its outer parts must be exposed to more severe tensions and pressures, if the degree of bend is the same. It is doubtless true that when the fish or reptile, advancing by lateral undulations, becomes longer, the curvature assumed by the body at each movement becomes less; and that from this cause the outer parts of the notochord are, other things equal, less strained—the two changes thus partially neutralizing one another. But other things are *not* equal. For while, supposing the shape of the body to remain constant, the force exerted in moving the body increases as the cubes of its dimensions, the sectional area of the notochord, on which fall the reactions of this exerted force, increases only as the squares of the dimensions: whence results an intenser stress upon its substance. Merely noting that the other varying factor—the resistance of the water—may here be left out of the account (since for similar masses moving with equal velocities the resistances increase but little faster than the squares of the dimensions, which is the rate at which the sectional areas of the notochords increase) we see that augmenting bulk, taken alone, involves but a moderate residuary increase of strain on each portion of the notochord; and this is probably the reason why it is possible for a large *sluggish* fish like the Sturgeon, to retain the notochordal structure. But now, passing to the effects of greater activity, a like dynamical inquiry at once shows us how rapidly the violence of the actions and reactions rises as the movements become more vivacious. In the first place, the resistance of a medium such as water increases as the square of the velocity of the body moving through it; so that to *maintain* double the speed, a fish has to expend four times the energy. But the fish has to do more than this—it has to *initiate* this speed, or to impress on its mass the force implied by this speed. Now the *vis viva* of a moving body varies as the square of the velocity; whence it follows that the energy required to generate that *vis viva* is measured by the square of the velocity it produces. Consequently, did the fish put itself in motion *instantaneously*, the expenditure of energy in generating its own *vis viva* and simultaneously overcoming the resistance of the water, would vary as the fourth power of the velocity. But the fish cannot put itself in motion instantaneously—it must do it by increments; and thus it results that the amounts of the forces expended to give itself different velocities must be represented by some series of numbers falling between the squares and the fourth powers of those velocities. Were the increments slowly accumulated, the ratio of increasing effort would but little exceed the ratio of the squares; but whoever observes the sudden, convulsive action with which an alarmed fish darts out of a shallow into deep water, will see that the velocity is very rapidly generated, and that therefore the ratio of increasing effort probably exceeds the ratio of the squares very considerably. At any rate it will be clear that the efforts made by fish in rushing upon prey or escaping enemies (and it is these extreme efforts which here concern us) must, as fish become more active, rapidly exalt the strains to be borne by their motor organs; and that of these strains, those which fall upon the notochord must be exalted in proportion to the rest. Thus the development of locomotive power, which survival of the fittest must tend in most cases to favour, involves such increase of stress on the primitive cartilaginous rod as will tend, other things equal, to cause its modification.

What must its modification be? Considering the complication of the influences at work, conspiring, as above indicated, in various ways and degrees, we cannot expect to do more than form an idea of its average character. The nature of the changes which the notochord is likely to undergo, where greater bulk is accompanied by higher activity, is rudely indicated by Figs. 291, 292, and 293. The successively thicker lines represent the successively greater strains to which the outer layers of tissue are exposed; and the widening inter-spaces represent the greater extensions which they have to bear when they become convex, or else the greater gaps that must be formed in them. Had these outer layers to undergo extension only, as on the convex side, continued natural selection might result in the formation of a tissue elastic enough to admit of the requisite stretching. But at each alternate bend, these outer layers, becoming concave, are subject to increased compression—a compression which they cannot withstand if they have become simply more extensible. To withstand this greater compression they must become harder as well as more extensible. How are these two requirements to be reconciled? If, as facts warrant us in supposing, a formation of denser substance occurs

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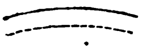

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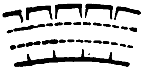

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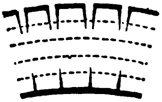

at those parts of the notochord where the strain is greatest; it is clear that this formation cannot so go on as to produce a continuous mass: the perpetual flexions must prevent this. If matter that will not yield at each bend, is deposited while the bendings are continually taking place, the bendings will maintain certain places of discontinuity in the deposit—places at which the whole of the stretching consequent on each bend will be concentrated. And thus the tendency will be to form segments of hard tissue capable of great resistance to compression, with intervals filled by elastic tissue capable of great resistance to extension—a vertebral column.

And now observe how the progress of ossification is just such as conforms to this view. That centripetal development of segments which holds of the vertebrate animal as a whole, as, if caused by transverse strains, it ought to do, and which holds of the vertebral column as a whole, as it ought to do, holds also of the central axis. On the mechanical hypothesis, the outer surface of the notochord should be the first part to undergo induration, and that division into segments that must accompany induration. And accordingly, in a vertebral column of which the axis is beginning to ossify, the centrums consist of bony rings inclosing a still-continuous rod of cartilage.

§ 258. Sundry other general facts which the comparative morphology of the *Vertebrata* discloses, supply further confirmation. Let us take first the structure of the skull.

On considering the arrangement of the muscular flakes, or myocommata, in any ordinary fish that comes to table—an arrangement already sketched out in the *Amphioxus*—it is not difficult to see that that portion of the body out of which the head of the vertebrate animal becomes developed, is a portion which cannot subject itself to bendings in the same degree as the rest of the body. The muscles developed there must be comparatively short, and much interfered with by the pre-existing orifices. Hence the cephalic part will not partake in any considerable degree of the lateral undulations; and there will not tend to arise in it any such distinct segmentation as arises elsewhere. We have here, then, an explanation of the fact, that from the beginning the development of the head follows a course unlike that of the spinal column; and of the fact that the segmentation, so far as it can be traced in the head, is most readily to be traced in the occipital region and becomes lost in the region of the face. Still more significantly, we have an explanation of the fact that the base of the skull, answering to the front end of the notochord, never betrays any sign of segmentation. This, which is absolutely at variance with the hypothesis of the transcendental anatomists, is in complete harmony with the foregoing hypothesis. For if, as we have seen, the segmentation consequent on mechanical actions and reactions must progress from without inwards, affecting last of all the axis; and if, as we have seen, the region of the head is so circumstanced that the causes of segmentation act but feebly even on its periphery; then, it is to be expected that its axis will not be segmented at all: that portion of the primitive notochord which is included in the head, having to undergo no lateral bendings, may ossify without division into segments.

Of other incidental evidences supplied by comparative morphology, let me next refer to the supernumerary bones, which the theory of Goethe and Oken as elaborated by Prof. Owen, has to get rid of by gratuitous suppositions. In many fishes, for example, there are what have been called interneural spines and inter-hæmal spines. These cannot by any ingenuity be affiliated upon the archetypal vertebra, and they are therefore arbitrarily rejected as bones belonging to the exo-skeleton; though in shape and texture they are similar to the spines between which they are placed. On the hypothesis of evolution, however, these additional bones are accounted for as arising under actions like those that gave origin to the bones adjacent to them. And similarly with such bones as those called sesamoid; together with others too numerous to name.

Again, in the course of evolution, both as displayed in the *Vertebrata* generally and in each vertebrate embryo, three skeletons succeed one another—the membranous, the cartilaginous, and the osseous. These substitutions take place variously and unsystematically. While one part of a skeleton retains the membranous character, another part of the same skeleton has become cartilaginous. At the same time that certain components have become partially or completely ossified, other components continue cartilaginous or membranous. Further, though there is a general succession of these stages, the succession is not regularly maintained; for in many cases bones are formed by the deposit of osseous matter in portions of the membranous skeleton, which thus do not pass through the cartilaginous stage. "Nor," says Prof. Huxley, "does any one of these states ever completely obliterate its predecessor; more or less cartilage and membrane entering into the composition of the most completely ossified skull, and more or less membrane being discoverable in the most completely chondrified skull." And then, too, the processes of chondrification and ossification often proceed with but little respect for the pre-existing divisions; but severally may result in the establishment of two parts where there was before one, or one where there were before two. Now wholly incongruous as these facts are with the hypothesis of an archetypal skeleton, they are quite congruous with the mechanical hypothesis. This shows us why, in the course of evolution, a feebly-resisting membranous structure came to be replaced by a more-resisting cartilaginous structure, and this, again, by a still-more-resisting osseous structure; and why, therefore, these successive stages succeed one another, as it seems so superfluously, in the vertebrate embryo. And it further shows us why there is irregularity in the succession; seeing that the varying mechanical actions to which the varying habits of the *Vertebrata* have exposed them, have involved variations in the process of solidification.

§ 259. Of course the foregoing synthesis is to be taken simply as an adumbration of the process by which the vertebrate structure may have arisen through the continued actions of known agencies. The motive for attempting it has been two-fold. Having, as before said, given reasons for concluding that the segments of a vertebrate animal are not homologous in the same sense as those of an annulose animal or a phænogamic axis, it seemed needful to do something towards showing how they are otherwise to be accounted for; and having here, for our general subject, the likenesses and differences among the parts of organisms, as determined by incident forces, it seemed out of the question to pass by the problem presented by the vertebrate skeleton.

Leaving out all that is hypothetical, the general argument may be briefly presented thus:—The evolution from the simplest known vertebrate animal, of a powerful and active vertebrate animal, implies the development of a stronger internal fulcrum. The internal fulcrum cannot be made stronger without becoming more dense. And it cannot become more dense while retaining its lateral flexibility, without becoming divided into segments. Further, in conformity with the general principles thus far traced, these segments must be alike in proportion as the forces to which they are exposed are alike, and unlike in proportion as these forces are unlike; and so there necessarily results that unity in variety by which the vertebral column is from the beginning characterized. Once more, we see that the explanation extends to those innumerable and more-marked divergences from homogeneity, which vertebræ undergo in the various higher animals. Thus, the production of vertebræ, the production of likenesses among vertebræ, and the production of unlikenesses among vertebræ, are interpretable as parts of one general process, and as harmonizing with one general principle.

Whether sufficient or insufficient, the explanation here given assigns causes of known kinds producing effects such as they are known to produce. It does not, as a solution of one mystery, offer another mystery of which no solution is to be asked. It does not allege a Platonic ἰδέα, or fictitious entity, which explains the vertebrate skeleton by absorbing into itself all the inexplicability. On the contrary, it assumes nothing beyond agencies by which structures in general are moulded—agencies by which these particular structures are, indeed, notoriously modifiable. An ascertained cause of certain traits in vertebræ and other bones, it extends to all other traits of vertebræ; and at the time assimilates the morphological phenomena they present to much wider classes of morphological phenomena.

# CHAPTER XVI.

## THE SHAPES OF ANIMAL CELLS.

§ 260. Among animals as among plants, the laws of morphological differentiation must be conformed to by the morphological units, as well as by the larger parts and the wholes formed of them. It remains here to point out that the conformity is traceable where the conditions are simple.

In the shapes assumed by those rapidly-multiplying cells out of which each animal is developed, there is a conspicuous subordination to the surrounding actions. Fig. 294 represents the cellular embryonic mass that arises by repeated spontaneous fissions. In it we see how the cells, originally spherical, are changed by pressure against one another and against the limiting membrane; and how their likenesses and unlikenesses are determined by the likenesses and unlikenesses of the forces to which they are exposed. This fact may be thought scarcely worth pointing out. But it is worth pointing out, because what is here so obvious a consequence of mechanical actions, is in other cases a consequence of actions composite in their kinds and involved in their distribution. Just as the equalities and inequalities of dimensions among aggregated cells, are here caused by the equalities and inequalities among their mutual pressures in different directions; so, though less manifestly, the equalities

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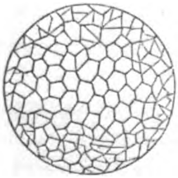
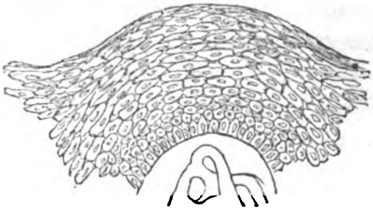


and inequalities of dimensions among other aggregated cells, are caused by the equalities and inequalities of the osmotic, chemical, thermal, and other forces besides the mechanical, to which their different positions subject them.

§ 261. This we shall readily see on observing the ordinary structures of limiting membranes internal and external. In Fig. 295, is shown a much-magnified section of a papilla from the gum. The cells of which it is composed originate in its deeper part; and are at first approximately spherical. Those of them which, as they develop, are thrust outwards by the new cells that continually take their places, have their shapes gradually changed. As they grow and successively advance to replace the superficial cells, when these exfoliate, they become exposed to forces that are more and more different in the direction of the surface from what they are in lateral directions; and their dimensions gradually assume corresponding differences.

295



Another species of limiting membrane, called cylinder-epithelium, is represented in Fig. 296. Though its mode of development is such as to render the shapes of its cells quite unlike those of pavement-epithelium, as the above-described kind is sometimes called, its cells equally exemplify the same general truth. For the chief contrast which each of them presents, is the contrast between its dimension at right angles to the surface of the membrane, and its dimension parallel to that surface.

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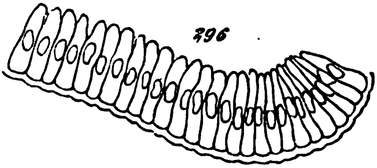

It is needless for our present purpose to examine further the evidence furnished by Histology; nor, indeed, would further examination of this evidence be likely to yield definite results. In the cases given above we have marked differences among the incident forces; and therefore have a chance of finding, as we do find, relations between these and differences of form. But the cells composing masses of tissue are severally subject to forces that are indeterminate; and therefore the interpretation of their shapes is impracticable. It must suffice that so far as the facts go they are congruous with the hypothesis.

# CHAPTER XVII.

## SUMMARY OF MORPHOLOGICAL DEVELOPMENT.

§ 262. THAT any formula should be capable of expressing a common character in the shapes of things so unlike as a tree and a cow, a flower and a centipede, is a remarkable fact; and is a fact which affords strong *primâ facie* evidence of truth. For in proportion to the diversity and multiplicity of the cases to which any statement applies, is the probability that it sets forth the essential relations. Those connexions which remain constant under all varieties of manifestation, are most likely to be the causal connexions.

Still higher will appear the likelihood of an alleged law of organic form possessing so great a comprehensiveness, when we remember that on the hypothesis of Evolution, there must exist between all organisms and their environments, certain congruities expressible in terms of their actions and reactions. The forces being, on this hypothesis, the causes of the forms, it is inferable, *à priori*, that the forms must admit of generalization in terms of the forces; and hence, such a generalization arrived at *à posteriori*, gains the further probability due to fulfilment of anticipation.

Nearer yet to certainty seems the conclusion thus reached, on finding that it does but assert in their special manifestations, the laws of Evolution in general—the laws of that universal re-distribution of matter and motion which hold throughout the totality of things, as well as in each of its parts.

It will be useful to glance back over the various minor inferences arrived at, and contemplate them in their ensemble from these higher points of view.

§ 263. That process of integration which every plant displays during its life, we found reason to think has gone on during the life of the vegetal kingdom as a whole. Protoplasm into cells, cells into folia, folia into axes, axes into branched combinations—such, in brief, are the stages passed through by every shrub; and such appear to have been the stages through which plants of successively-higher kinds have been evolved from lower kinds. Even among certain groups of plants now existing, we find aggregates of the first order passing through various gradations into aggregates of the second order—here forming small, incoherent, indefinite assemblages, and there forming large, definite, coherent fronds. Similar transitions are traceable through which these integrated aggregates of the second order pass into aggregates of the third order: in one species the unions of parent-fronds with the fronds that bud out from them, being temporary, and in another species such unions being longer continued; until, in species still higher, by a gemmation that is habitual and regular, there is produced a definitely-integrated aggregate of the third order—an axis bearing fronds or leaves. And even between this type and a type further compounded, a link occurs in the plants which cast off, in the shape of bulbils, some of the young axes they produce. As among plants, so among animals. A like spontaneous fission of cells ends here in separation, there in partial aggregation, while elsewhere, by closer combination of the multiplying units, there arises a coherent and tolerably definite individual of the second order. By the budding of individuals of the second order, there are in some cases produced other separate individuals like them; in some cases temporary aggregates of such like individuals; and in other cases permanent aggregates of them: certain of which become so definitely integrated that the individualities of their component members are almost lost in a tertiary individuality.

Along with this progressive integration there has gone on a progressive differentiation. Vegetal units of whatever order, originally homogeneous, have become heterogeneous while they have become united. Spherical cells aggregating into threads, into laminæ, into masses, and into special tissues, lose their sphericity; and instead of remaining all alike assume innumerable unlikenesses—from uniformity pass into multiformity. Fronds combining to form axes, severally acquire definite differences between their attached ends and their free ends; while they also diverge from one another in their shapes at different parts of the axes they compose. And axes, uniting into aggregates of a still higher order, become more or less contrasted in their sizes, curvatures, and arrangements of their appendages. Similarly among animals. Those components of them which, with a certain license, we class as morphological units, while losing their minor individualities in the major individualities formed of them, grow definitely unlike as they grow definitely combined. And where the aggregates so produced become, by coalescence, segments of aggregates of a still higher order, they, too, diverge from one another in their shapes.

The morphological differentiation which thus goes hand in hand with morphological integration, is clearly what the perpetually-complicating conditions would lead us to anticipate. Every addition of a new unit to an aggregate of such units, must affect the circumstances of the other units in all varieties of ways and degrees, according to their relative positions—must alter the distribution of mechanical strains throughout the mass, must modify the process of nutrition, must affect the relations of neighbouring parts to surrounding diffused actions; that is, must initiate a changed incidence of forces tending ever to produce changed structural arrangements.

§ 264. This broad statement of the correspondence between the general facts of Morphological Development and the principles of Evolution at large, may be reduced to statements of a much more specific kind. The phenomena of symmetry and unsymmetry and asymmetry, which we have traced out among organic forms, are demonstrably in harmony with those laws of the re-distribution of matter and motion to which Evolution conforms. Besides the myriad-fold illustrations of the instability of the homogeneous, that are afforded by these aggregates of units of each order, which, at first alike, lapse gradually into unlikeness; and besides the myriad-fold illustrations of the multiplication of effects, which these ever-complicating differentiations exhibit to us; we have also myriad-fold illustrations of the definite equalities and inequalities of structures, produced by definite equalities and inequalities of forces.

The proposition arrived at when dealing with the causes of Evolution, "that in the actions and reactions of force and matter, an unlikeness in either of the factors necessitates an unlikeness in the effects; and that in the absence of unlikeness in either of the factors the effects must be alike" (*First Principles*, § 129), is the general formula including all these particular likenesses and unlikenesses of parts which we have been tracing. For have we not everywhere seen that the strongest contrasts are between the parts that are most contrasted in their conditions; while the most similar parts are those most-similarly conditioned? In every plant the leading difference is between the attached end and the free end; in every branch it is the same; in every leaf it is the same. And in every plant the leading likenesses are those between the two sides of the branch, the two sides of the leaf, and the two sides of the flower, where these parts are two-sided in their conditions; or between all sides of the branch, all sides of the leaf, and all sides of the flower, where these parts are similarly conditioned on all sides. So, too, is it with animals that move about. The most marked contrasts they present are those between the part in advance and the part behind, and between the upper part and the under part; while there is complete correspondence between the two sides. Externally the likenesses and differences among limbs, and internally the likenesses and differences among vertebræ, are expressible in terms of this same law.

And here, indeed, we may see clearly that these truths are corollaries from that ultimate truth to which all phenomena of Evolution are referable. It is an inevitable deduction from the persistence of force, that organic forms which have been progressively evolved must present just those fundamental traits of form which we find them present. It cannot but be that during the intercourse between an organism and its environment, equal forces acting under equal conditions must produce equal effects; for to say otherwise, is, by implication, to say that some force can produce more or less than its equivalent effect, which is to deny the persistence of force. Hence those parts of an organism which are, by its habits of life, exposed to like amounts and like combinations of actions and reactions, must develop alike; while unlikenesses of development must as unavoidably follow unlikenesses among these agencies. And this being so, all the specialities of symmetry and unsymmetry and asymmetry which we have traced, are necessary consequences.

# PART V.

## PHYSIOLOGICAL DEVELOPMENT.

# CHAPTER I.

## THE PROBLEMS OF PHYSIOLOGY.

§ 265. THE questions to be treated under the above title are widely different from those which it ordinarily expresses. We have no alternative, however, but to use Physiology in a sense co-extensive with that in which we have used Morphology. We must here consider the facts of function in a manner parallel to that in which we have, in the foregoing Part, considered the facts of structure. As, hitherto, we have concerned ourselves with those most general phenomena of organic form which, holding irrespective of class and order and sub-kingdom, illustrate the processes of integration and differentiation characterizing Evolution in general; so, now, we have to concern ourselves with the evidences of those differentiations and integrations of organic functions which have simultaneously arisen, and which similarly transcend the limits of zoological and botanical divisions. How heterogeneities of action have progressed along with heterogeneities of structure—that is the inquiry before us; and obviously, in pursuing it, all the specialities with which Physiology usually deals can serve us only as materials.

Before entering on the study of Morphological Development, it was pointed out that while facts of structure may be empirically generalized apart from facts of function, they cannot be rationally interpreted apart; and throughout the foregoing pages this truth has been made abundantly manifest. Here we are obliged to recognize the inter-dependence still more distinctly; for the phenomena of function cannot even be conceived without direct and perpetual consciousness of the phenomena of structure. Though the subject-matter of Physiology is as broadly distinguished from the subject-matter of Morphology as motion is from matter; yet, just as the laws of motion cannot be known apart from some matter moved, so there can be no knowledge of function without a knowledge of some structure as performing function.

Much more than this is obvious. The study of functions, considered from our present point of view as arising by Evolution, must be carried on *mainly* by the study of the correlative structures. Doubtless, by experimenting on the organisms that are growing and moving around us, we may ascertain the connexions existing among certain of their actions, while we have little or no knowledge of the special parts concerned in those actions. In a living animal that can be conveniently kept under observation, we may learn the way in which conspicuous functions vary together—how the rate of a man's pulse increases with the amount of muscular exertion he is undergoing; or how a horse's rapidity of breathing is in part dependent on his speed. But though observations of this order are indispensable—though by accumulation and comparison of such observations we learn which parts perform which functions—though such observations, prosecuted so as to disclose the actions of all parts under all circumstances, constitute, when properly generalized and co-ordinated, what is commonly understood as Physiology; yet such observations help us but a little way towards learning how functions came to be established and specialized. We have next to no power of tracing up the genesis of a function considered purely as a function—no opportunity of observing the progressively-increasing quantities of a given action that have arisen in any order of organisms. In nearly all cases we are able only to establish the greater growth of the part which we have found performs the action, and to infer that greater action of the part has accompanied greater growth of it. The tracing out of Physiological Development, then, becomes substantially a tracing out of the development of the organs by which the functions are known to be discharged—the differentiation and integration of the functions being presumed to have progressed hand in hand with the differentiation and integration of the organs. Between the inquiry pursued in Part IV, and the inquiry to be pursued in this Part, the contrast is that, in the first place, facts of structure are now to be used to interpret facts of function, instead of conversely; and, in the second place, the facts of structure to be so used are not those of conspicuous shape so much as those of minute texture and chemical composition.

§ 266. The problems of Physiology, in the wide sense above described, are, like the problems of Morphology, to be considered as problems to which answers must be given in terms of incident forces. On the hypothesis of Evolution these specializations of tissues and accompanying concentrations of functions, must, like the specializations of shape in an organism and its component divisions, be due to the actions and reactions which its intercourse with the environment involves; and the task before us is to explain how they are wrought—how they are to be comprehended as results of such actions and reactions.

Or, to define these problems still more specifically:—Those extremely unstable substances which compose the protoplasm of which organisms are mainly built, have to be traced through the various modifications in their properties and powers, that are entailed on them by changes of relation to agencies of all kinds. Those organic colloids which pass from liquid to solid and from soluble to insoluble on the slightest molecular disturbance—those albumenoid matters which, as we see in clotted blood or the coagulable lymph that is poured out on abraded surfaces and causes adhesion between inflamed membranes, assume new forms with the greatest readiness, are to have their metamorphoses studied in connexion with the influences at work. Those compounds which, as we see in the quickly-acquired brownness of a bitten apple or in the dark stains produced by the milky juice of a Dandelion, immediately begin to alter when the surrounding actions alter, are to be everywhere considered as undergoing modifications by modified conditions. Organic bodies, consisting of substances that, as I here purposely remind the reader, are prone beyond all others to change when the incident forces are changed, we must contemplate as in all their parts differently changed in response to the different changes of the incident forces. And then we have to regard the concomitant differentiations of their reactions as being concomitant differentiations of their functions.

Here, as before, we must take into account two classes of factors. We have to bear in mind the inherited results of actions to which antecedent organisms were exposed, and to join with these the results of present actions. Each organism is to be considered as presenting a moving equilibrium of functions, and a correlative arrangement of structures, produced by the aggregate of actions and reactions that have taken place between all ancestral organisms and their environments. The tendency in each organism to repeat this adjusted arrangement of functions and structures, must be regarded as from time to time interfered with by actions to which its inherited equilibrium is not adjusted—actions to which, therefore, its equilibrium has to be re-adjusted. And in studying physiological development we have in all cases to contemplate the progressing compromise between the old and the new, ending in a restored balance or adaptation.

It is manifest that our data are so scanty that nothing more than very general and approximate interpretations of this kind are possible. If the hypothesis of Evolution furnishes us with a rude conception of the way in which the more conspicuous and important differentiations of functions have arisen, it is as much as can be expected.

§ 267. It will be best, for brevity and clearness, to deal with these physiological problems as we dealt with the morphological ones—to carry on the inductive statement and the deductive interpretation hand-in-hand: so disposing of each general truth before passing to the next. Treating separately vegetal organisms and animal organisms, we will in each kingdom consider:—first, the physiological differentiations and accompanying changes of structure that arise between outer tissues and inner tissues; next, those that arise between different parts of the outer tissues; and, finally, those that arise between different parts of the inner tissues. What little has to be said concerning physiological integration must come last. For though, in tracing up Morphological Evolution, we have to study those processes of integration by which organic aggregates are formed, before studying the differentiations that arise among their parts; we must, contrariwise, in tracing up Physiological Evolution, study the genesis of the different functions before we study the inter-dependence that eventually arises among them and constitutes physiological unity.

## CHAPTER II.

### DIFFERENTIATIONS BETWEEN THE OUTER AND INNER TISSUES OF PLANTS.

§ 268. The simplest plant presents a contrast between its peripheral substance and its central substance. In each protophyte, be it a spherical cell or a branched tube, or such a more-specialized form as a Desmid, a marked unlikeness exists between the limiting layer and that which it limits. These vegetal aggregates of the first order may differ widely from one another in the natures of their outer coats and in the natures of their contents. As in a *Palmella*, there may exist a clothing of jelly; or, as in Diatom, the walls may take the form of silicious valves variously sculptured. The contained matter may be here green, there red, and in other cases brown or black. But amid all these diversities there is this one uniformity—a strong distinction between the parts in contact with the environment and the parts not in contact with the environment.

When we remember that this trait is one which these simple living bodies have in common with bodies that are not living—when we remember that each inorganic mass eventually has its outer part more or less differentiated from its inner part, here by oxidation, there by drying, and elsewhere by the actions of light, of moisture, of frost; we can scarcely resist the conclusion that, in the one case as in the other, the contrast is due to the unlike actions to which the parts are subject. Given an originally-homogenous portion of protoplasm, and it follows from the general laws of Evolution (*First Principles*, §§ 109—115) first, that it must lose its homogeneity, and, second, that the leading dissimilarities must arise between the parts most-dissimilarly conditioned—that is, between the outside and the inside. The exterior must bear amounts and kinds of force unlike the amounts and kinds which the interior bears; and from the persistence of force it follows inevitably that unlike effects must be wrought on them—they must be differentiated.

What is the limit towards which the differentiation tends? We have seen that the re-distribution of matter and motion whence, under certain conditions, evolution results, can never cease until equilibrium is reached—proximately a moving equilibrium, and finally a complete equilibrium (*First Principles*, §§ 130—135). Hence, the differentiation must go on until it establishes such differences in the parts as shall balance the differences in the forces acting on them. When dealing with equilibration in general, we saw that this process is what is called adaptation (*First Principles*, § 133); and, more recently, we saw that by it the totality of functions of an organism is brought into correspondence with the totality of actions affecting it (§§ 159—163). Manifestly in this case, as in all others, either death or adjustment must eventually result. A force falling on one of these minute aggregates of protoplasm, must expend itself in working its equivalent of change. If this force is such that in expending itself it disturbs beyond rectification the balance of the organic processes, then the aggregate is disintegrated or decomposed. But if it does not overthrow that moving equilibrium constituting the life of the aggregate, then the aggregate continues in that modified form produced by the expenditure of the force. Thus, by direct equilibration, continually furthered by indirect equilibration, there must arise this distinction between the outer part adapted to meet outer forces, and the inner part adapted to meet inner forces. And their respective actions, as thus meeting outer and inner forces, must be what we call their respective functions.

§ 269. Aggregates of the second order exhibit parallel traits, admitting of parallel interpretations. Integrated masses of cells or units homologous with protophytes, habitually show us contrasts between the characters of the superficial tissues and the central tissues. Such among these aggregates of the second order as have their component units arranged into threads or laminæ, single or double, cannot, of course, furnish contrasts of this kind; for all their units are as much external as internal. We must turn to the more or less massive forms.

Of these, among *Fungi*, the common Puff-ball is a good example—good because it presents this fundamental differentiation but little complicated by others. In it we have a cortical layer of cellular tissue obviously unlike the mass of cellular tissue which it incloses. So far as the unlikeness between external and internal parts is concerned, we see here a relation analogous to that existing in the simple cell; and we see in it a similar meaning: there is a physiological differentiation corresponding to the difference in the incidence of forces.

Under various forms the *Algæ* show just the same relation. Where, as in *Codium Bursa*, we have ramified tubular cells aggregated into a hollow globular mass, the outer and inner surfaces are contrasted both in colour and structure; though the tubules composing the two surfaces are continuous with one another. In *Rivularia*, again, we see the like, both in the radial arrangement of the imbedded threads and in the difference of colour between the exterior of the imbedding jelly and its interior. The more-developed *Algæ* of all kinds repeat the antithesis. In branched stems, when they consist of more than single rows of cells, the outer cells become unlike the inner, as shown in Fig. 35. Such types as *Chrysymenia rosea* show us this unlikeness very conspicuously. And it holds even with ribbon-shaped fronds. Wherever one of these is composed of three, four, or more layers, as in *Laminaria* and *Punctaria*, the cells of the external layers are strongly distinguished from those of the internal layers, both by their comparative smallness and by their deep colour.

§ 270. The higher plants variously display the like fundamental distinction between outer and inner tissues. Each leaf, thin as it is, exemplifies this differentiation of the parts immediately in contact with the environment from the parts not in immediate contact with the environment. Its cuticular cells, forming a protecting envelope, diverge physically and chemically from the contained cells of parenchyma, which carry on the more active functions. And the contrast may be observed to establish itself in the course of development. At first the component cells of the leaf are all alike; and this unlikeness between the cells of the outer and inner layers, arises simultaneously with the rise of differences in their conditions—differences that have acted on all ancestral leaves as they act on the individual leaf.

An unlikeness more marked in kind but similar in meaning, exists between the bark of every branch and the tissues it clothes. The phænogamic axis, especially when exogenous, is commonly characterized by an outer layer differing from the inner layers in character and function, as it differs from them in position. Subject as this outer layer is to the unmitigated actions of forces around—to abrasions, to extremes of heat and cold, to evaporation and soaking with water—its units cannot cease changing until they are in equilibrium with these more violent actions, and have acquired molecular constitutions more stable than those of the interior cells. That is to say, the forces which differentiate the cortical part from the rest are the forces which it has to resist, and from which it passively protects the parts within. How clearly this heterogeneity of structure and function is consequent upon intercourse with the environment, every tree and shrub shows. The young shoots, alike of annuals and perennials, are quite green and soft at their extremities. Among plants of short lives, there is usually but a slight development of bark: such traces of it as the surface of the axis acquires being seen only at its lowermost or oldest portion. In long-lived plants, however, this formation of a tough opaque coating takes place more rapidly; and shows us distinctly the connexion between the degree of differentiation and the length of exposure. For, in a growing twig, we see that the bark, invisible at the bud, thickens by insensible gradations as we go downwards to the junction of the twig with the branch; and we come to still thicker parts of it as we descend along the branch towards the main stem. Moreover, on examining main stems we find that while in some trees the bark, cracked by expansion of the wood, drops off in flakes, leaving exposed patches of the inner tissue which presently become green and finally develop new cortical layers; in other trees the exfoliated flakes continue adherent, and in the course of years form a rugged fissured coat: so producing a still more marked contrast between outside and inside. Of course the establishment of this heterogeneity is furthered by natural selection, which, where a protective covering is needed, gives an advantage to those individuals in which it has become strongest. But that this divergence of structure commences as a direct adaptation, is clearly shown by other facts than the foregoing. There is the fact that many of the plants which in our gardens develop bark with considerable rapidity, do not develop it with the same rapidity in a greenhouse. And there is the fact that plants which, in some climates, have their stems covered only by thin semi-transparent layers, acquire thick opaque layers when taken to other climates.

Just noting, for the sake of completeness, that in the roots of the higher plants there arises a contrast between outer and inner parts, parallel to the one we have traced in their branches, let me draw attention to another differentiation of the same ultimate nature, which the higher plants exhibit to us—a differentiation which, familiar though it is, gains a new meaning by association with those named above, and makes their meaning still more manifest. I refer to the fact that when, by the budding of axes out of axes, there is produced one of those highly-compounded Phænogams which we call a tree, the central part of the aggregate becomes functionally and structurally unlike the peripheral part. On looking into a large tree, or even a small one that has thick foliage, like the Laurel, we see that the internal branches are almost or quite bare of leaves, while the leaf-clad branches form an external stratum; and all our experience unites in proving that this contrast arises by degrees, as fast as the growth of the tree entails a contrast between the conditions to which inner and outer branches are exposed. Now when, in these most-composite aggregates, we see a differentiation between peripheral and central parts demonstrably caused by a difference in the relations of these parts to environing forces, we get support for the conclusion otherwise reached, that there is a parallel cause for the parallel differentiations exhibited by all aggregates of lower orders—branches, leaves, cells.

§ 271. Before leaving this most general physiological differentiation, it may be well to say something respecting certain secondary unlikenesses that habitually arise between interior and exterior. For the contrast is not, as might be supposed from the foregoing descriptions, a simple contrast: it is a compound contrast. The outer structure itself is usually divisible into concentric structures. This is equally true of a protophyte and of a phænogamic axis. Between the centre of an independent vegetal cell and its surface, there are at least two layers; and the bark coating the substance of a shoot, besides being itself compound, includes another tissue lying between it and the wood. What is the physical interpretation of these facts?

When a mass of what we distinguish as inert matter is exposed to external agencies capable of working changes in it—when it is chemically acted upon, or when, being dry, it is allowed to soak, or when, being wet, it is allowed to dry—the changes set up progress in an equable way from the surface towards the centre. At any time during the process (supposing no other action supervenes) the modification wrought, first completed at the outside, either gradually diminishes as we approach the centre, or ceases suddenly at a certain distance from the centre. But now suppose that the mass, instead of being inert, is the seat of active changes—suppose that it is a portion of complex colloidal substance, permeable by light and by fluids capable of affecting its unstable molecules—suppose that its interior is a source of forces continually liberated and diffusing themselves outwards. Is it not likely that while at the centre the action of the internally-liberated forces will dominate, and while at the surface the action of the environing forces will dominate, there will be between the two a certain place at which their actions balance? And may we not expect that this will be the place where the most unstable matter exists—the place outside of which the matter becomes relatively stable in the face of external forces, and inside of which the matter becomes relatively stable in the face of internal forces?

Be this or be this not the explanation, the well-known fact is that the inner wall of each vegetal cell is a delicate membrane, the primordial utricle, composed of that nitrogenous substance specially characterized by instability; and that outside of this is the cellulose layer, and inside of it the granular colouring matter. And the similarly well-known fact is, that in each phænogamic axis the cambium layer, which shows its relative instability by the activity of the changes going on in it, lies between the bark and the mass of the axis; and is the place from which the differentiations producing these proceed in opposite directions.

But we are here chiefly concerned with the more general interpretation, which is independent of any such speculation as the foregoing. These contrasted tissues and the contrasted functions they severally perform are, beyond question, subordinated to the relations of outside and inside. And the evidence makes it tolerably clear that the unlike actions of forces involved by the relations of outside and inside, determine these contrasts—partly directly and partly indirectly.

# CHAPTER III.

## DIFFERENTIATIONS AMONG THE OUTER TISSUES OF PLANTS.

§ 272. The *Protococci* and such compound forms as the *Volvox globator*, which do not permanently expose any parts of their surfaces to actions unlike those which other parts are exposed to, have no parts of their surfaces unlike the rest in function and composition. This is what the hypothesis prepares us for. If physiological differentiations are determined by differences in the incidence of forces, then there will be no such differentiations where there are no such differences. Contrariwise, it is to be expected that the most conspicuous unlikeness of function and minute structure will arise between the most-dissimilarly circumstanced parts of the surface. We find that they do. The upper end and the lower end, or, more strictly speaking, the free end and the attached end, habitually present the strongest physiological contrasts.

Even aggregates of the first order illustrate this truth. Such so-called unicellular plants as those delineated in Figs 4, 5, and 6, show us, on comparing the contents of their fixed ends and their loose ends, that different processes are going on in them, and that different functions are being performed by their limiting membranes. *Caulerpa prolifera*, which "consists of a little creeping stem with roots below and leaves above," originating "in the growth of a body which may be regarded as an individual cell," supplies a still-better example. Among aggregates of the second order the like connexion is displayed in more various modes but with equal consistency. As, before, the Puff-ball served to exemplify the primary physiological differentiation of outer parts from inner parts; so, here, it supplies a simple illustration of the way in which the differentiated outer part is re-differentiated, in correspondence with the chief contrast in its relations to the environment. The only marked unlikeness which the cortical layer of the Puff-ball presents, is that between the portion next the ground and the opposite portion. The better-developed *Fungi* exhibit a more decided heterogeneity of parallel kind. Such incrusting *Algæ* as *Ralfsia deusta* furnish a kindred contrast; and in the higher *Algæ* it is uniformly repeated. Phænogams display this physiological differentiation very conspicuously. That earth and air are unlike portions of the environment, subjecting roots and leaves to unlike physical forces, which entail on them unlike reactions; and that the unlike functions and structures of their respective surfaces are fitted to these unlike physical forces; are familiar facts which it would be needless here to name, were it not that they must be counted as coming within a wider group of facts.

Is this unlikeness between the outer tissues of the attached ends and those of the free ends in plants, determined by their converse with the unlike parts of the environment? That they result from an equilibration partly arising in the individual and partly arising by the survival of individuals in which it has been carried furthest, is inferable *à priori;* and this *à priori* argument may be adequately enforced by arguments of the inductive order. A few typical ones must here suffice. The gemmules of the *Marchantia* are little disc-shaped masses of cells composed of two or more layers. Their sides being alike, there is nothing to determine which side falls lowermost when one of them is detached. Whichever side falls lowermost, however, presently begins to send out rootlets, while the uppermost side begins to assume those characters which distinguish the face of the frond. When this differentiation has commenced, the tendency to its complete establishment becomes more and more decided; as is proved by the fact that if the positions of the surfaces be altered, the gemmule bends itself so as to re-adjust them: the change towards equilibrium with environing forces having been once set up, there is acquired, as it were, an increasing momentum which resists any counter-change. But the evidence shows that at the outset, the relations to earth and air alone determine the differentiation of the under surface from the upper. The experiences of the gardener, multiplying his plants by cuttings and layers, constitute another class of evidences not to be omitted: they are commonplace but instructive examples of physiological differentiation. While circumstanced as it usually is, the cambium of each branch in a Phænogam continues to perform its ordinary function—transforming itself on its outer side into the cortical substances, and on its inner side into vascular and woody tissues. But change the conditions to those which the underground part of the plant is exposed to, and there begins another differentiation resulting in underground structures. Contact with water often suffices alone to produce this result, as in the branches of some trees when they droop into a pool, or as occasionally with a cutting placed in a bottle of water; and when the light is excluded by imbedding the end of the cutting, or the middle of the still-attached branch, in the earth, this production of tissues adapted to the function of absorbing moisture and mineral constituents proceeds still more readily. With such cases may be grouped those in which this development of underground organs by an above-ground tissue, is not exceptional but habitual. Creeping plants furnish good illustrations. From the shoots of the Ground-Ivy, rootlets are put out into the soil in a manner differing but little from that in which they are put out by an imbedded layer; save that the process follows naturally-induced conditions instead of following artificially-induced conditions. But in the common Ivy which, instead of running along the surface of the earth, runs up inclined or vertical surfaces, we see the process interestingly modified without being essentially changed. The rootlets, here differentiated by their conditions into organs of attachment much more than organs of absorption, still develop on that side of the shoot next the supporting surface, and do not develop where the shoot, growing away from the tree or wall, is surrounded equally on all sides by light and air—thus showing, undeniably, that the production of the rootlets is determined by the differential incidence of forces. That greenness which may be observed in these Ivy-branch rootlets while they are quite young, soft, and unshaded, introduces us to facts which are the converse of the foregoing facts; and prove that the parts ordinarily imbedded in the soil and adapted to its actions, acquire, often in a very marked degree, the superficial structures of the aërial parts, when they are exposed to light and air. This may be witnessed in Maize, which, when luxuriant, sends out from its nodes near the ground, clusters of roots that are thick, succulent, and of the same colour as the leaves. Examples more familiar to us in England, occur in every field of Turnips. On noting how green is the uncovered part of a Turnip-root, and how manifestly the area over which the greenness extends varies with the area exposed to light, as well as with the degree of the exposure, it will be seen that beyond question, root-tissue assumes to a considerable extent the appearance and function of leaf-tissue, when subject to the same agencies. Let us not forget, too, that where exposed roots do not approach in superficial character towards leaves, they approach in superficial character towards stems—becoming clothed with a thick, fissured bark, like that of the trunk and branches. But the most conclusive evidence is furnished by the actual substitutions of surface-structures and functions, that occur in aërial organs which have taken to growing permanently under ground, and in under-ground organs which have taken to growing permanently in the air. On the one hand, there is the *rhizoma*, exemplified by Ginger—a stem which, instead of shooting up vertically, runs horizontally below the surface of the soil, and assumes the character of a root, alike in colour, texture, and production of rootlets; and there is that kind of swollen under-ground axis, bearing axillary buds, which the Potato exemplifies—a structure which, though homologically an axis, simulates a tuberous root in surface-character, and when exposed to the air, manifests no greater readiness to develop chlorophyll than a tuberous root does. On the other hand, there are the aërial roots of certain Orchids, which, habitually green at their tips, continue green throughout their whole lengths when kept moist; which have become leaf-like not only by this development of chlorophyll, but also by the acquirement of stomata; and which do not bury themselves in the soil when they have the opportunity. Thus we have aërial organs so completely changed to fit under-ground actions, that they will not resume aërial functions; and under-ground organs so completely changed to fit aërial actions, that they will not resume under-ground functions.

That the physiological differentiation between the part of a plant's surface which is exposed to light and air and the part which is exposed to darkness and moisture and solid matter, is primarily due to the unlike actions of these unlike parts of the environment, is, then, clearly implied by observed facts—more clearly, indeed, than was to be expected. Considering how strong must be the inherited tendency of a plant to assume those special characters, physiological as well as morphological, which have resulted from an enormous accumulation of antecedent actions, it may be even thought surprising that this tendency can be counteracted to so great an extent by changed conditions. Such a degree of modifiability becomes comprehensible, only when we remember how little a plant's functions are integrated; and how much, therefore, the functions going on in each part may be altered without having to overcome the momentum of the functions throughout the whole plant. But this modifiability being as great as it is, we can have no difficulty in understanding how, by the cumulative aid of natural selection, this primary differentiation of the surface in plants has become what we see it.

§ 273. We will leave now these contrasts between the free surfaces of plants and their attached or imbedded surfaces, and turn our attention to the secondary contrasts existing between different parts of their free surfaces. Were a full statement of the evidence practicable, it would be proper here to dwell on that which is furnished by the inferior classes. It might be pointed out in detail that where, as among the *Algæ*, the free surfaces are not dissimilarly conditioned, there is no systematic differentiation of them—that the frond of an *Ulva*, the ribbon-shaped divisions of a *Laminaria*, and the dichotomous expansions of the *Fuci* that clothe the rocks between tide-marks, are alike on both sides; because, swayed about in all directions as they are by the waves and tides, their sides are equally affected. Conversely, from the *Fungi* might be drawn abundant proof that even among Thallogens, unlikenesses arise between different parts of the free surfaces when their circumstances are unlike—that in such laterally-growing kinds as are shown in Fig. 196 *b*, the honeycombed under surface and the smooth leathery upper surface, have their contrasts related to contrasted conditions; and that in the adjacently-figured Agarics, and other stalked genera, the pileus exhibits a parallel difference, explicable in a parallel way. But passing over Cryptogams, it must suffice if we examine more at length these traits as they are displayed by Phænogams. Let us first note the dissimilarities between the outer tissues of stems and leaves.

That these dissimilarities arose by degrees, as fast as the units of which the phænogamic axis is composed became integrated, is a conclusion in harmony with the truth that in every shoot of every plant, they are at first slight and become gradually marked. Already, in briefly tracing the contrasts between the outer and inner tissues of plants, some facts have been named showing, by implication, how the cessation of the leaf-function in axes is due to that change of conditions entailed by the discharge of other functions. Here we have to consider more closely facts of this class, together with others immediately to the point. On pulling off from a stem of grass the successive sheaths of its leaves, the more-inclosed parts of which are of a fainter green than the outer parts, it will be found that the tubular axis eventually reached is of a still fainter green; but when the axis eventually shoots up into a flowering stem, its exposed part acquires as bright a green as the leaves. In other Endogens, the leaf-sheaths of which are successively burst and exfoliated by the swelling axis, it may be observed that where the dead sheaths do not much obstruct the light and air, the surface of the axis underneath is full of chlorophyll. *Dendrobium* is an example. But when the dead sheaths accumulate into an opaque envelope, the chlorophyll disappears, and also, we may infer, the function its presence habitually implies. Carrying with us this evidence, we shall recognize a like relation in Exogens. While its outer layer remains tolerably transparent, an exogenous stem or branch continues to show, by the formation of chlorophyll, that it shares in the duties of the leaves; but in proportion as a bark which the light cannot penetrate is produced by the adherent flakes of dead skin, or by the actual deposit of a protective substance, the differentiation of duties becomes more decided. Cactuses and Euphorbias supply us with converse facts having the same implication. The swollen succulent axes so strangely combined in these plants, maintain for a long time the transparency of their outer layers; and doing this, they so efficiently perform the offices of leaves that leaves are not produced. In some cases, axes that are not succulent participate largely in the leaf-function, or entirely usurp it—still, however, by fulfilling the same essential conditions. Occasionally, as in *Statice brassicæplia,* stems become fringed; and the fringes they bear assume, along with the thinness of leaves, their darker green and general aspect. In the genus *Ruscus,* the flattened axis simulates so closely the leaf-structure, that were it not for the flower borne on its midrib, or edge, its axial nature would hardly be suspected. And let us not omit to note that where axes usurp the characters of leaves, in their attitudes as well as in their shapes and thickness, there exist contrasts between their under and upper surfaces, answering to the contrasts between the relations of these surfaces to the light. Of this *Ruscus androgynus* furnishes a striking example. In it the difference which the unaided eye perceives is much less conspicuous than that disclosed by the microscope; for I find that while the face of the pseudo-leaf has no stomata, the back is abundantly supplied with them. One more illustration must be added. Equally for the morphological and physiological truths which it enforces, the *Coccoloba platycladon* is one of the most instructive of plants. In it the simulation of forms and usurpation of functions, are carried out in a much more marvellous way than among the *Cactaceæ.* Imagine a growth resembling in outline a very long willow-leaf, but without a midrib, and having its two surfaces alike. Imagine that across this thin, green, semi-transparent structure, there are from ten to thirty divisions, which prove to be the successive nodes of an axis. Imagine that along the edges of this leaf-shaped aggregate of internodes, there arise axillary buds, some of which unfold into flowers, and others of which shoot up vertically into growths like the one which bears them. Imagine a whole plant thus seemingly composed of jointed willow-leaves growing from one another's edges, and some conception will be formed of the *Coccoloba*. The two facts which have meaning for us here are—first, that the performance of leaf-functions by these axes goes along with the assumption of a leaf-like translucency; and, second, that these flattened axes, retaining their upright attitudes, and therefore keeping their two faces similarly conditioned, have these two faces alike in colour and texture.

That physiological differentiation of the surface which arises in Phænogams between axial organs and foliar organs, is thus traceable with tolerable clearness to those differences between their conditions which integration has entailed—partly in the way above described, and partly in other ways still to be named. By its relative position, as being shaded by the leaves, the axis is less-favourably circumstanced for performing those assimilative actions effected by the aid of light. Further, that relatively-small ratio of surface to mass in the axis, which is necessitated by its functions as a support and a channel for circulation, prevents it from taking in, with the same facility as the leaves, those surrounding gases from which matter is to be assimilated. Both these special causes, however, in common with that previously assigned, fall within the general cause. And in the fact that where the differential conditions do not exist, the physiological differentiation does not arise, or is obliterated, we have clear proof that it is determined by unlikenesses in the relations of the parts to the environment.

§ 274. From this most general contrast between aërial surface-tissues—those of axes and those of folia—we pass now to the more special contrasts of like kind existing in folia themselves. Leaves present us with superficial differentiations of structure and function; and we have to consider the relations between these and the environing forces.

Over the whole surface of every phænogamic leaf, as over the fronds of the higher Acrogens, there extends a simple or compound cuticular layer, formed of cells that are closely united at their edges and devoid of that granular colouring matter contained in the layers of cells they inclose: the result being that the membrane formed of them is comparatively transparent. On the submerged leaves of aquatic Phænogams, this outer layer is thin, delicate, and permeable by water; but on leaves exposed to the air, and especially on their upper surfaces, it is comparatively strong, dense, often smooth, and impermeable by water: being thus fitted to prevent the rapid escape of the contained juices by evaporation. Similarly, while the leaves of terrestrial plants that live in temperate climates, usually have comparatively thin coats thus composed, in climates that are both hot and dry, leaves are commonly clothed with two, three, or more layers of such cells. Nor is this all. The outside of an aërial leaf differs from that of a submerged leaf by containing a deposit of waxy substance. Whether this be exuded by the exposed surfaces of the cells, as some contend, or whether it is deposited within the cells, as thought by others, matters not in so far as the general result is concerned. In either case a waterproof coating is formed at the outermost sides of these outermost cells; and in many cases produces that polish by which the upper surface of the leaf is more or less distinguished from the under surface. This external pellicle presents us with another contrast of allied meaning. On the upper surfaces of leaves subject to the direct action of the sun's rays, there are either few or none of those minute openings, or stomata, through which gases can enter or escape; but on the under surfaces these stomata are abundant—a distribution which, while permitting free absorption of the needful carbonic acid, puts a check on the exit of watery vapour. Two general exceptions to this arrangement may be noted. Leaves that float on the water have all their stomata on their upper sides, and leaves that are submerged have no stomata—modifications obviously appropriate to the conditions. What is to be said respecting the genesis of these differentiations? For the last there seems no direct cause: its cause must be indirect. The unlike actions to which the upper and under surfaces of leaves are subject, have no apparent tendency to produce unlikeness in the number of their breathing holes. Here the natural selection of spontaneous variations furnishes the only feasible explanation. For the first, however, there is a possible cause in the immediate actions of incident forces, which survival of the fittest continually furthers. The substance contained in the cells of leaves consists partly of wax and partly of chlorophyll. According to Mulder, "there is a genetic connexion between the production of wax and that of the green colouring matter in the leaves;" and he alleges, as the result of his own experiments and those of Berzelius, that chlorophyll "may be decomposed, both by oxidizing and de-oxidizing substances, so as to become colourless at last; and that wax seems to be producible from it by de-oxidizing actions." Now the superficial cells of leaves are more exposed to the de-oxidizing influence of light than the inner cells; those forming the upper surface are more exposed to it than those forming the under surface; and those which coat leaves in hot dry climates are more exposed to it than those by which leaves in temperate climates are coated. May it not be that the action of light, whence chlorophyll results as a transitional compound which afterwards passes into a colourless compound, is an action directly tending to form these bleached and transparent outer layers; and directly tending to produce a greater thickness of such layers in proportion as it is intense? There are difficulties in the way of this supposition; for I learn from Dr. Hooker that some of the *Balanophoræ*, which grow in the shade, are very full of wax. As these are parasites, however, and absorb the prepared juices of other plants, the comparison is interfered with. But whatever be its origin, we have to note that this waxy substance suspended in the fluid which these bleached outer cells contain, must be deposited as fast as the fluid escapes. Where will it be deposited? The fluid exhaling through the walls of the cells next the air, will be likely to leave behind the suspended substance attached to these walls. On remembering the pellicle that is apt to form on thick solutions or emulsions as they dry, and how this pellicle as it grows retards the further drying, it will be perceived that the deposit of waxy substance next to the outer surfaces of the cuticular cells in leaves, is probably initiated by the evaporation which it eventually checks. We have here, indeed, a very simple case of equilibration. Where the loss of water is too great, this waxy pellicle left behind by the escaping water will protect most those individuals of the species in which it is thickest or densest; and by inheritence and continual survival of the fittest, there will be established in the species that thickness of the layer which brings the evaporation to a balance with the supply of water.

Another superficial differentiation, still more familiar, has to be noted. Every child soon learns to distinguish by its colour the upper side of a leaf from its under side, if the leaf is one that has grown in such way as to establish the relations of upper and under. The upper surfaces of leaves are habitually of a deeper green than the under. Microscopic examination shows that this deeper green results from the closer clustering of those parenchyma-cells full of chlorophyll that are in some way concerned with the assimilative actions; while beneath them are more numerous intercellular passages communicating with those openings or stomata through which is absorbed the needful air. Now when it is remembered that the formation of chlorophyll is clearly traceable to the action of light—when it is remembered that leaves are pale where they are much shaded and colourless when developed in the dark, as in the heart of a Cabbage—when it is remembered that succulent axes and petioles, like those of Sea-kale and Celery, remain white while the light is kept from them and become green when exposed; it cannot be questioned that this greater production of chlorophyll next to the upper surface of a leaf, is directly consequent on the greater amount of light received. Here, as in so many other cases, we must regard the differentiation as in part due to direct equilibration and in part to indirect equilibration. Familiar facts compel us to conclude that from the beginning, each individual foliar organ has undergone a certain immediate adaptation of its surfaces to the incidence of light; that when there arose a mode of growth which exposed the leaves of successive generations in similar ways, this immediately-produced adaptation, ever tending to be transmitted, was furthered by the survival of individuals inheriting it in the greatest degree; and that so there was gradually established that difference between the two surfaces which each leaf displays before it unfolds to the light, but which becomes more marked when it has unfolded.*

From the ordinary cases let us now pass to the exceptional cases. We will look first at those in which the two faces of the leaves differ but little, or not at all—their circumstances being similar or equal. Leaves that grow in approximately-upright attitudes, and attitudes which do not maintain the relative positions of the two surfaces with constancy, may be expected to display an unusual likeness between the two surfaces; and among them we see it. The Grasses may be named as a group exemplifying this relation; and if, instead of comparing them as a group with other groups, we compare

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* The current doctrine that chlorophyll is *the* special substance concerned in vegetal assimilation, either as an agent or as an incidental product, must be taken with considerable qualification. Besides the fact that among the *Algæ* there are many red and black kinds which thrive; and besides the fact that among the lower Acrogens there are species which are purple or chocolate-coloured; there is the fact that Phænogams are not all green. We have the Copper-Beech, we have the black-purple *Coleus Verschaffeltii*, and we have the red variety of Cabbage, which seems to flourish as well as the other varieties. Chlorophyll, then, must be regarded simply as the most general of the colouring matters found in those parts of plants in which assimilation is being effected by the agency of light.

those dwarf kinds of them which spread out their leaves horizontally, with the large aspiring kinds, such as *Arundo*, we trace a like antithesis: in the one the contrast of upper and under is very obvious, while in the other it is scarcely to be detected. Leaves of various other Endogens that grow in a similar way, similarly show us a near approach to uniformity of the two surfaces; as instance the genus *Clivia*, and the thinner-leaved kinds of *Yucca*. Where the contrast of upper and under is greatly diminished by the assumption of a rounded or cylindrical form instead of a flattened form, the same thing happens. The genus *Kleinia* furnishes illustrations. It may be remarked, too, that even within the limits of this genus there are instructive variations; for while in *Kleinia ficoides* the leaves, shaped like pea-pods, are broadest in a vertical direction, and have their lateral surfaces alike in conditions and structure, in other species the leaves, broader horizontally than vertically, exhibit unlikeness between the upper and under sides. Equally to the point is the evidence furnished by vertically-growing leaves that are cylindrical, as those of *Sanseviera cylindrica*, or as those of the Rush-tribe: the similarly-placed surface has all around a similar character. Of kindred meaning, and still more conclusive, are the cases in which the under side of the leaf, being more exposed to light than the upper side, usurps the character and function of the upper side. If a common Flag be pulled to pieces, it will be seen that what answers to the face in other leaves, forms merely the inside of the sheath including the younger leaves, and is obliterated higher up. The two surfaces of the blade answer to the two under halves of a leaf that has been, as it were, folded together lengthways, with the two halves of its upper surface in contact. And here, in default of an upper surface, the under surface acquires its character and discharges its function. A like substitution occurs in *Witsenia corymbosa;* and there are some of the Orchids, as *Lockhartia*, which display it in a very obvious way.

When joined with the foregoing evidence, the evidence which another kind of substitution supplies is of great weight. I refer to that which occurs in the Australian Acacias, already instanced as throwing light on morphological changes. In these plants the leaves properly so called are undeveloped, and the footstalks, flattened out into foliaceous shapes, acquire veins and midribs, and so far simulate leaves as ordinarily to be taken for them—a fact in itself of much physiological significance. But that which it concerns us especially to note, is the absence of distinction between the two faces of these phyllodes, as they are named, and the cause of its absence. These transformed petioles do not flatten themselves out horizontally, so as to acquire under and upper sides, as most true leaves do; but they flatten themselves out vertically: the result being that their two sides are similarly circumstanced with respect to light and other agencies; and there is consequently nothing to cause their differentiation. And then we find an analogous case where differential conditions arise, and where some differentiation results. In *Oxalis bupleurifolia*, Fig. 66, there is a similar flattening out of the petiole into a pseudo-leaf; but in it the flattening takes place in the same plane as the leaf, so as to produce an under and an upper surface; and here the two surfaces of the pseudo-leaf are slightly unlike—in contour if in nothing else.

§ 275. We come now to such physiological differentiations among the outer tissues of plants, as are displayed in the contrasts between foliar organs on the same axis, or on different axes—contrasts between the seed-leaves and the leaves subsequently formed, between submerged and aërial leaves in certain aquatic plants, between leaves and bracts, and between bracts and sepals. To deal even briefly with these implies information which even a professed botanist would have to increase by special inquiries, before attempting interpretations. Here it must suffice to say something respecting those marked unlikenesses that exist between the tissues of the more characteristic parts of flowers, and the tissues of the homologous foliar organs.

It was pointed out in § 196, that the terminal parts of a phænogamic axis have sundry characters in common with such fronds as those out of which we concluded that the phæno-gamic axis has arisen by integration—common characters of a kind to be expected. In their simple cellular composition, comparative want of chlorophyll, and deficiency of vascular structures, the undeveloped ends of leaf-shoots and the developed ends of flower-shoots, approach to the fronds of the simpler Acrogens. We also noted between them another resemblance. It is said of the *Jungermanniaceæ*, that "though under certain circumstances of a pure green, they are inclined to be shaded with red, purple, chocolate, or other tints;" and answering to this we have the facts that such colours commonly occur in the terminal folia of a phænogamic axis when arrest of its development leads to the formation of a flower, and that very frequently they are visible at the ends of leaf-axes. In the unfolding parts of shoots, more or less of red, or copper-colour, or chocolate-colour, may generally be seen: often indeed it characterizes the leaves for some time after they are unfolded. Occasionally the traces of it are permanent; and, as in the scarlet terminal leaves of *Poinsettia pulcherrima*, we see that it may become, and continue, extremely conspicuous. The question, then, now to be asked, is—has this colouring by which the immature part of the phænogamic axis is characterized, anything to do with the colouring of flowers? Has this difference between undeveloped folia and folia that are further developed, been increased by natural selection where an advantage accrued from it, until it has ended in the strong contrast we now see? I think we may not irrationally infer that this has been the case.

Facts, very numerous and varied, united to warrant us in concluding that gamogenesis commences where the forces that conduce to growth are nearly equilibrated by the forces that resist growth (§ 78); and the induction that in plants, fertilized germs are produced at places where there is an approach towards this balance, we found to be in harmony with the deduction that an advantage to the species must be gained by sending off migrating progeny from points where nutrition is failing. Other things equal, failure of nutrition may be expected in parts that have the most remote or most indirect access to the materials furnished by the roots—materials that have to be carried great distances by a very imperfect apparatus. The ends of lateral axes are therefore the probable points of fructification, in aggregates of the third order that have taken to growing vertically. But if these points at which nutrition is failing, are also the points at which the colours inherited from lower types are likely to recur in more marked degrees than elsewhere; then we may infer that the organs of fructification will not unfrequently co-exist with such colours at the ends of such axes. How may the resulting contrast between the older fronds and the fronds next the germ-producing organs be increased? If uninterfered with it would be likely to diminish. These traits inherited from remote ancestry, might be expected slowly to fade away. How, then, is the intensification of them to be explained?

If a contrast of the kind described favours the propagation of a race in which it exists, it will be maintained and increased; and if we take into account an agency of which Mr. Darwin has shown the great importance—the agency of insects—we shall have little difficulty in understanding how such a contrast may facilitate propagation. We cannot, of course, here assume the agency of insects so specialized in their habits as Bees and Butterflies; for their specialized habits imply the pre-existence of the contrast to be explained. But there is an insect-agency of a more general kind which may be fairly counted upon as coming into action. Various small Flies and Beetles wander over the surfaces of plants in search of food. It is a legitimate assumption that they will frequent most those parts in which they find most food, or food most to their liking—especially if at the same time they gain the advantage of concealment. Now the ends of axes, formed of young, soft, and closely-packed folia, are the parts which more than any others offer these several advantages. They afford shelter from enemies; they frequently contain exuded juices and when they do not, their tissues are so tender as to be easily pierced in search of the sap. If, then, from the first, as at present, these ends of axes have been favourite haunts of small insects; and if, where the closely-clustered folia contained the generative organs, the insects frequenting them occasionally carried adherent fructifying cells from one plant to another, and so aided fertilization; it would follow that anything which made such terminal clusters more attractive to such insects, or more conspicuous to them, or both, would further the multiplication of the race, and would so be continually increased by the extra multiplication of individuals in which it was greatest. Here we find the clue. This contrast of colour between the folia next to the fructifying parts and all other folia, must constantly have facilitated insect-agency; supposing the insects to have had the power of distinguishing between colours. That Bees and Butterflies have this power is manifest: they may be watched flying from flower to flower, disregarding all other parts of the plants. And if the less-specialized insects possessed some degree of such discrimination, then the initial contrasts of colour above described would be maintained and increased. Let such a connexion be once established, and it must tend to become more decided. Insects most able to discern the parts of plants which afford what they seek, will be those most likely to survive and leave offspring. Plants presenting most of the desired food, and showing most clearly where it lies, will have their fertilization and multiplication furthered in the greatest degree. And so the mutual adaptation will become ever closer; while it is rendered at the same time more varied by the special requirements of the insects and of the plants in each locality, under each change of conditions. Of course, the genesis of the sweet secretions and the odours of flowers, has a parallel interpretation. The simultaneous production of honey, or some kindred substance, is implied above; since, unless a bait co-existed with the colour, the colour would not attract insects, and would not be maintained and intensified by natural selection. Gums, and resins, and balsams, are familiar products of plants; apparently, in many cases, excreted as useless matters from various parts of their surfaces. These substances, admitting of wide variations in quality, as they do, afford opportunities for the action of natural selection wherever any of them attractive to insects, happen to be produced near the organs of fructification. And this action of natural selection once set up, may lead to the establishment of a local excretion, to the production of an excretion more and more attractive, and to the disposal of the organ containing it in such a way as most to facilitate the carrying away of pollen. Similarly and simultaneously with odours. Odours, like colours, draw insects to flowers. After observing how Bees come swarming into a house where honey is largely exposed, or how Wasps find their way into a shop containing much ripe fruit, it cannot be questioned that insects are to a considerable extent guided by scent. Being thus sensitive to the aromatic substances which flowers exhale, they may, when the flowers are in large masses, be attracted by them from distances at which the flowers themselves are invisible. And manifestly, the flowers which so attract them from the greatest distances, increasing thereby their chances of efficient fertilization, will be most likely to perpetuate themselves. That is to say, survival of the fittest must tend to produce perfumes that are both more powerful and more attractive.

These physiological differentiations, then, which mark off the foliar organs of flowers from other foliar organs, are the consequences of indirect equilibration. They are not due to the immediate actions of unlike incident forces on the parts of the individual plant; but they are due to the actions of such unlike incident forces on the aggregate of individuals, generation after generation.*

§ 276. The unity of interpretation which we here find for phenomena of such various orders, could hardly be found were the phenomena otherwise caused. That the stronger and the feebler contrasts among the different parts of the outer tissues in plants, should so constantly occur along with stronger and feebler contrasts among the incident forces, is in itself weighty evidence that unlike outer actions have caused unlike inner actions, and correspondingly-unlike structures; either by changing the functional equilibrium in the individual, or by changing it in the race, or by both.

Even in the absence of more direct proof, there would be great significance in the marked differences that habitually exist between the exposed and imbedded parts of plants, between the stems and the leaves, and between the upper and under surfaces of the leaves. The significance of these differences is increased when we discover that they vary in degree

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* This seems as fit a place as any for noting the fact, that the greater part of what we call beauty in the organic world, is in some way dependent on the sexual relation. It is not only so with the colours and odours of flowers. It is so, too, with the brilliant plumage of birds, and with the songs of birds, both of which, in Mr. Darwin's view, are due to sexual selection; and it is probable that the colours of the more conspicuous insects are in part similarly determined. The remarkable circumstance is, that these characteristics, which have originated by furthering the production of the best offspring, while they are naturally those which render the organisms possessing them attractive to one another, directly or indirectly, should also be those which are so generally attractive to us—those without which the fields and woods would lose half their charm. It is interesting, too, to observe how the conception of human beauty is in a considerable degree thus originated. And the trite observation that the element of beauty which grows out of the sexual relation is so predominant in æsthetic products—in music, in the drama, in fiction, in poetry—gains a new meaning when we see how deep down in organic nature this connexion extends.

as the differences in the conditions vary in degree. Still greater becomes the force of the evidence on finding that these strongly-contrasted parts may, when placed in one another's conditions, and kept in them from generation to generation, permanently assume one another's functions, and, in a great degree, one another's structures. Even more conclusive yet is the argument rendered, by the discovery that, where these substitutions of function and structure take place, the superinduced modifications differ in different circumstances; just as the original modifications do. The fact that a flattened stem simulating a vertically-growing leaf has its two surfaces alike, while when it simulates a horizontally-growing leaf its upper and under surfaces differ, is a fact which, standing alone, might prove little, but proves much when joined with all the other evidence. And its profound meaning becomes the more obvious on discovering that the same thing happens with petioles when they usurp leaf-functions.

Finally, when we remember how rapidly analogous modifications of function and structure arise in the superficial tissues of individual plants, the general inference can scarcely be resisted. When we meet with so striking a case as that of the *Begonia*-leaf, a fragment of which stuck in the ground produces roots from its under surface and leaves from its upper surface—when we see that though, in this case, the typical structure of the plant presently begins to control the organizing process, yet the initial differentiations are set up by the differential actions of the environment; the presumption becomes extremely strong that the heterogeneities of surface which we have considered, result, as alleged, directly or indirectly from heterogeneities in the incident forces.

# CHAPTER IV.

## DIFFERENTIATIONS AMONG THE INNER TISSUES OF PLANTS.*

§ 277. In passing from plants formed of threads or thin laminæ, to plants having some massiveness, we find that after the external and internal parts have become distinguished from one another, there arise dictinctions among the internal parts themselves, as well as among the external parts themselves: the primarily-differentiated parts are both re-differentiated.

From types of very low organisation illustrations of this may be drawn. In the thinner kinds of *Laminaria* there exists but the single contrast between the outer layer of cells and an inner layer; but in larger species of the same genus, as *L. digitata,* there are three unlike layers on each side of a central layer differing from them—augmentation of bulk is accompanied by multiplication of concentric internal structures, having their unlikenesses obviously related to unlikenesses in their conditions. In *Furcellaria* and various *Algæ* of similarly swollen forms, the like relation may be traced.

Just indicating the generality of this contrast, but not

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* Students of vegetal physiology, familiar with the controversies respecting sundry points dealt with in this chapter, will probably be surprised to find taken for granted in it, propositions which they have habitually regarded as open to doubt. Hence it seems needful to say that the conclusions here set forth, have resulted from investigations undertaken for the purpose of forming opinions on several unsettled questions which I had to treat, but which I could find in books no adequate data for treating. The details of these investigations, and the entire argument of which this chapter is partly an abstract, will be found in Appendix C.

attempting to seek in these lower types for any more specific interpretation of it, let us pass to the higher types. The argument will be amply enforced by the evidence obtained from them. We will look first at the conditions which they have to fulfil; and then at the way in which the functions and structures adapting them to these conditions arise.

§ 278. A terrestrial plant that grows vertically needs no marked modification of its internal tissues, so long as the height it reaches is very small. As we before saw, the spiral or cylindrical rolling up of a simple cellular frond, or the more bulky growth of a simple cellular axis, may give the requisite strength; and the requisite circulation may be carried on through the unchanged cellular tissue. But in proportion as the height to be attained and the mass to be supported increase, the supporting part must acquire greater bulk or greater density, or both; and some modification that shall facilitate the transfer of nutritive liquids must take place. Hence, in the inner tissues of plants we may expect to find that structural changes answering to these requirements become marked, as the growth of the aërial part becomes great. Facts correspond with these expectations.

Among the humbler Acrogens, which creep over, or raise themselves but little above, the surfaces they flourish upon, there is scarcely any internal differentiation: the vascular and woody structures, if not in all cases absolutely unrepresented, are rarely and very feebly indicated. But among the higher Acrogens—the Ferns and Lycopodiums—which raise their fronds to considerable heights, there are vascular bundles and hard tissues like wood; and by the Tree-Ferns massive axes are developed. That the relation which thus shows itself among Cryptogams is habitual among Phænogams, scarcely needs saying.

Phænogams, however, are not universally thus characterized in a decided way. Besides the comparative want of woody substance in flowering plants of humble growth, and besides the paucity of vessels in ordinary water-plants, there are cases of much more marked divergence from this typical internal structure. These exceptional cases occur under exceptional conditions, and are highly instructive. They are of two kinds. One group of them is furnished by certain plants that are parasitic on the exposed roots of trees—parasitic not partially, as the Mistletoe, but to the extent of subsisting wholly on the sap they absorb. Fungus-like in colour and texture, and having scales for leaves, these *Balanóphoræ* and *Rafflesiaceæ* are recognizable as Phænogams by scarcely any other traits than their fructifications. Along with their abortive leaves and absence of chlorophyll, there is a great degradation of those internal tissues by which Phænogams are commonly distinguished. Though Dr. Hooker has shown that they are not, as some botanists thought, devoid of spiral vessels; yet, as shown by the mistake previously made in classifying them, their appliances for circulation are rudimentary. And this trait goes along with a greatly-simplified distribution of nutriment. In the absence of leaves there can be but little down-current of nutriment, such as leaves usually supply to roots: there cannot be much beyond an upward current of the absorbed juices. The other cases occur where circulation is arrested or checked in a different way; namely, in plants that are wholly submerged. These are the *Podostemones,* which are aquatic even to the extent of flowering under water. Clothing as they do the submerged rocks in tropical rivers, their roots, like those of the *Algæ*, serve only for attachment; their foliar expansions, frond-like in shape, are everywhere bathed by the water; and their organs of fructification never exposed to the air, but perhaps aided in their functions by water-insects instead of air-insects, are the only marked signs of kinship to other Phænogams. Observe then the connexion of facts. One of these *Podostemones* needs no internal stiffening substance, for it exists in a medium of its own specific gravity; and having no unlikeness between the materials assimilated at its fixed and its free ends, it has no need for a circulation—nor, indeed, in the absence of evaporation from any part of its surface, could any active circulation take place. Here, accordingly, the ordinary internal structures are undeveloped: though spiral vessels are not entirely absent, yet they are so rare as to do no more than verify the inference of phænogamic relationship drawn from the flowers.

The method of agreement, the method of difference, and the method of concomitant variations, thus unite in proving a direct relation between the demand for support and circulation, and the existence of these vascular woody bundles which the higher plants habitually possess. The question which we have to consider is—Under what influences are these structures, answering to these requirements, developed? How are these internal differentiations caused? The inquiry may be conveniently divided. Though the supporting tissues and the tissues concerned in the circulation of liquids are closely connected, and indeed entangled, with one another, we may fitly deal with them apart. Let us take first the supporting tissue.

§ 279. Many common-place facts indicate that the mechanical strains to which upright-growing plants are exposed, themselves cause increase of the dense deposits by which such plants are enabled to resist such strains. There is the fact that the massiveness of a tree-trunk varies according to the stress habitually put upon it. If the contrast between the slender stem of a tree growing in a wood and the bulky stem of a kindred tree growing in the fields, be ascribed to difference of nutrition rather than difference of exposure to winds; there is still the fact that a tree trained against a wall has a less bulky stem than a tree of the same kind growing unsupported; and that between the long weak branches of the one and the stiff ones of the other there are decided contrasts. If it be objected that a tree so trained and branches so borne have relatively less foliage, and that therefore these unlikenesses also are due to unlikenesses of general nutrition, which may in part be true; there are still such cases as those of garden plants, which when held up by tying them to sticks have weaker stems than when they are unpropped, and sink down if their props are taken away. Again, there is the evidence supplied by roots. Though the contrast between the feeble roots of a sheltered tree and the strong roots of an exposed tree, may, like the contrast of their stems, be mainly due to difference of nutrition, and therefore supplies but doubtful evidence, we get tolerably clear evidence where trees growing on inclined rocky surfaces, send into crevices that afford little moisture or nutriment, roots which nevertheless become thick where they are so directed as to bear great strains. Suspicion thus raised is strengthened into conviction by special evidences occurring in the places where they are to be expected. The Cactuses, with their succulent growths that pass into woody growths slowly and irregularly, give us the opportunity of tracing the conditions under which the wood is formed. Good examples occur in the genus *Cereus*, and especially in forms like *C. crenulatus*. Here, from a massive vertically-growing rod of fleshy tissue, two inches or more in diameter, there grow at intervals lateral rods similarly bulky, which, quickly curving themselves, take vertical directions. One of these heavy branches puts great strains on its own substance and that of the stem at their point of junction; and here both of them become brown and hard, while they continue green and succulent all around. Such differentiations may be traced internally before they are visible on the surface. If a joint of an *Opuntia* be sliced through longitudinally, the greater resistance to the knife all around the narrow neck, indicates there a larger deposit of lignin than elsewhere; and a section of the tissue placed under the microscope, exhibits at the narrowest part a concentration of the woody and vascular bundles. Clear evidence of another kind has been noted by Mr. Darwin, in the organs of attachment of climbing plants. Speaking of *Solanum jasminoides* he says:—"When the flexible petiole of half- or a quarter-grown leaf has clasped any object, in three or four days it increases much in thickness, and after several weeks becomes wonderfully hard and rigid; so that I could hardly remove one from its support. On comparing a thin transverse slice of this petiole with one from the next or older leaf beneath, which had not clasped anything, its diameter was found to be fully doubled, and its structure greatly changed. * * * This clasped petiole had actually become thicker than the stem close beneath; and this was chiefly due to the greater thickness of the ring of wood, which presented, both in transverse and longitudinal sections, a closely similar structure in the petiole and axis. The assumption by a petiole of this structure is a singular morphological fact; but it is a still more singular physiological fact that so great a change should have been induced by the mere act of clasping a support."

If there is a direct relation between mechanical stress and the formation of wood, it ought to explain for us the internal distribution of the wood. Let us see whether it does this.

When seeking in mechanical actions and reactions the cause of that indurated structure which forms the vertebrate axis (§§ 254-7), it was pointed out that in a transversely-strained mass, the greatest pressures and tensions are thrown on the molecules of the concave and convex surfaces. Hence, supposing the transversely-strained mass to be a cylinder, bent backwards and forwards not in one plane but now in this plane and now in that, its peripheral layers will be those on which the greatest stress falls. An ordinary exogenous axis is such a cylinder so strained. The maintenance of its attitude either as a lateral shoot or a vertical shoot, implies subjection to the bendings caused by its own weight and by the ever-varying wind. These bendings imply tensions and pressures falling most severely first on one side of its outer layers and then on another. And if the dense substance able to resist these tensions and pressures is deposited most where they are greatest, we ought to find it taking the shape of a cylindrical casing. This is just what we do find. On cutting across a shoot in course of formation, we see its central space either unoccupied or occupied only by soft tissue. That the layer of hard tissue surrounding this is not the outermost layer, is true: there lies beyond it the cambium layer, from which it is formed. But outside of the cambium there is another layer of dense tissue, the liber, having frequently a tenacity greater even than that of the wood—a layer which, while it protects the cambium and offers additional resistance to the transverse strain, admits of being fissured as fast as the cylinder of wood thickens. That is to say, the deposit of resisting substance is as completely peripheral as the exogenous mode of growth permits. So, too, in general arrangement is it with the endogenous stem. Different as is here the mode of growth, and different as is the internal structure, there yet holds the same general distribution of tissues, answering to the same mechanical conditions. The vascular woody bundles, more abundant towards the outside of the stem than near the centre, produce a harder casing surrounding a softer core. In the supporting structures of leaves we find significant deviations from this arrangement. While axes are on the average exposed to equal strains on all sides, most leaves, spreading out their surfaces horizontally, have their petioles subject to strains that are not alike in all directions; and in them the hard tissue is differently arranged. Its transverse section is not ring-shaped but crescent-shaped: the two horns being directed towards the upper surface of the petiole. That this arrangement is one which answers to the mechanical conditions, is not easy to demonstrate: we must satisfy ourselves by noting that here, where the distribution of forces is different, the distribution of resisting tissue is different. And then, showing conclusively the connexion between these differences, we have the fact that in petioles growing vertically and supporting peltate leaves—petioles which are therefore subject to equal transverse strains on all sides—the vascular bundles are arranged cylindrically, as in axes.

Such, then, are some of the reasons for concluding that the development of the supporting tissue in plants, is caused by the incident forces which this tissue has to resist. The individuals in which this direct balancing of inner and outer actions progresses most favourably, are those which, other things equal, are most likely to prosper; and by habitual survival of the fittest, there is established a systematic and constant distribution of a deposit adapted to the circumstances of each type.

§ 280. The function of circulation may now be dealt with. We have to consider here by what structures this is discharged; and what connexion exists between the demand for them and the genesis of them.

The contrast between the rates at which a dye passes through simple cellular tissue and cellular tissue of which the units have been elongated, indicates one of the structural changes required to facilitate circulation. If placed with its cut surface in a coloured liquid, the parenchyma of a potato or the medullary mass of a cabbage-stalk, will absorb the liquid with extreme slowness; but if the stalk of a fungus be similarly placed, the liquid runs up it, and especially up its loose central substance, very quickly. On comparing the tissues which thus behave so differently, we find that whereas in the one case the component cells, packed close together, have deviated from their primitive sphericity only as much as mutual pressure necessitates, in the other case, they are drawn out into long tubules with narrow spaces among them—the greatest dimensions of the tubules and the spaces being in the direction which the dye takes so rapidly. That which we should infer, then, from the laws of capillary action, is experimentally shown: liquid moving through tissues follows the lines in which the elements of the tissues are most elongated. It does this for two reasons. That narrowing of the cells and intercellular spaces which accompanies their elongation, facilitates capillarity; and at the same time fewer of the septa formed by the joined ends of the cells have to be passed through in a given distance. Hence the general fact that the establishment of a rudimentary vascular system, is the formation of bundles of cells lengthened in the direction which the liquid is to take. This we see very obviously among the lower Acrogens. In one of the lichen-like Liverworts, the veins which, branching through its frond, serve as communications with its scattered rootlets, are formed of cells longer than those composing the general tissue of the frond: the lengths of these cells corresponding in their directions with the lengths of the veins. So, too, is it with the midribs of such fronds as assume more definite shapes; and so, too, is it with the creeping stems which unite many such fronds. That is to say, the current which sets towards the growing part from the part which supplies the materials for growth, sets through a portion of the tissues composed of units that are longer in the line of the current than at right angles to that line. The like is true of Phænogams. Omitting all other characteristics of those parts of them through which chiefly the currents of sap flow, we find the uniform fact to be that they consist of cells and intercellular spaces distinguished from others by their lengths. It is thus with veins, and midribs, and petioles; and if we wish proof that it is thus with stems, we have but to observe the course taken by a coloured solution into which a stem is inserted.

What is the original cause of this differentiation? Is it possible that this modification of cell-structure which favours the transfer of liquid towards each place of demand, is itself caused by the current which the demand sets up? Does the stream make its own channel? There are various reasons for thinking that it does. In the first place, the simplest and earliest channels, such as we see in the Liverworts, do not develop in any systematic way, but branch out irregularly, following everywhere the irregular lobes of the frond as these spread; and on examining under a magnifier the places at which the veins are lost in the cellular tissue, it will be seen that the cells are there slightly longer than those around: suggesting that the lengthening of them which produces an extension of the veins, takes place as fast as the growth of the tissue beyond causes a current to pass through them. In the second place, a disappearance of the granular contents of these cells accompanies their union into a vein—a result which the transmission of a current may not improbably bring about. But be the special causes of this differentiation what they may, the evidence favours very much the conclusion that the general cause is the setting up of a current towards a place where the sap is being consumed. In the histological development of the higher plants we find confirmation The more finished distributing canals in Phænogams are formed of cells previously lengthened. At parts of which the typical structure is fixed, and the development direct, this fact is not easy to trace; the cells rapidly take their fibrous structures in anticipation of their pre-determined functions. But in places where new vessels are required in adaptation to a modifying growth, we may clearly trace this succession. The swelling root of a turnip, continually having its vascular system further developed, and the component vessels lengthened as well as multiplied, gives us an opportunity of watching the process. In it we see that the reticulated cells which unite to form ducts, arise in the midst of bundles of cells that have previously become elongated, and that they arise by transformation of such elongated cells; and we also see that these bundles of elongated cells have an arrangement quite suggestive of their formation by passing currents.

Are there grounds for thinking that these further transformations by which strings of elongated cells pass into vessels lined with spiral, annular, reticulated, or other frameworks, are also in any way determined by the currents of sap carried? There are some such grounds.

As just indicated, the only places where we may look for evidence with any rational hope of finding it, are places where some local requirement for vessels has arisen in consequence of some local development which the type does not involve. In these cases we find such evidence. Good illustrations occur in those genera of the *Cactaceæ*, which simulate leaves, like *Epiphyllum* and *Phyllocactus*. A branch of one of these is outlined in Fig. 256. As before explained, this is a flattened axis; and the notches along its edges are the seats of the axillary buds. Most of these axillary buds are arrested; but occasionally one of them grows. Now if, taking an *Epiphyllum*-shoot which bears a lateral shoot, we compare the parts of it that are near the abortive axillary buds with the part that is near the developed axillary bud, we find a conspicuous difference. In the neighbourhood of an abortive axillary bud there is no external sign of any internal differentiation; and on holding up the branch against the light, the uniform translucency shows that there is no greater amount of dense tissue near it than in other parts of the succulent mass. But where an axillary bud has developed, a prominent rounded ridge joins the midrib of the lateral branch with the midrib of the parent branch. In the midst of this rounded ridge an opaque core may be seen. And on cutting through it, this opaque core proves full of vascular bundles imbedded in woody deposits. Clearly, these clusters of vessels imply transformations of the tissues, caused by the passage of increased currents of sap. The vessels were not there when the axillary bud was formed; they would not have developed had the axillary bud proved abortive; but they arise as fast as growth of the axillary bud draws the sap along the lines in which they lie. Verification is obtained by examining the internal structures. If longitudinal sections be made through a growing bud of *Opuntia* or *Cereus*, it will be found that the vessels in course of formation converge towards the point of growth, as they would do if the sap-currents determined their formation; that they are most developed near their place of convergence, which they also would be if so produced; and that their terminations in the tissue of the parent shoot are partially-formed lines of irregular fibrous cells, like those out of which the vessels of a leaf or bud are developed.

Concluding, then, that sap-vessels arise along the lines of least resistance, through which currents are drawn or forced, the question to be asked is—What physical process produces them? Their component cells, united end to end more or less irregularly in ways determined by their original positions, form a channel much more permeable, both longitudinally and laterally, than the tissue around. How is this greater permeability caused? The idea, first propounded I believe by Wolff, that the adjoined ends of the cells are perforated or destroyed by the passing current, is one for which much is to be said. Whether these septa are dissolved by the liquids they transmit, or whether they are burst by those sudden gushes which, as we shall hereafter see, must frequently take place along these canals, needs not be discussed: it is sufficient for us that the septa do, in many cases, disappear, leaving internal ridges showing their positions; and, in other cases, become extremely porous. Though it is manifest that this is not the process of vascular development in tissues that unfold after pre-determined types, since, in these, the dehiscences or perforations of septa occur before such direct actions can have come into play; yet it is still possible that the disappearances of septa which now arise by repetition of the type were established in the type by such direct actions. Be this as it may, however, a simultaneous change undergone by these longitudinally-united cells must be otherwise caused. Frame-works are formed in them—frame-works which, closely fitting their inner surfaces, may consist either of successive rings, or continuous spiral threads, or networks, or structures between spirals and networks, or networks with openings so far diminished that the cells containing them are distinguished as fenestrated. Their differences omitted, however, these structures have the common character that, while supporting the coats of the vessels and serving to restore their diameters after they have been compressed, they also give special facilities for the passage of liquids, both through the sides of the transformed cells and through their united ends, where these are not destroyed. For one of these internal frame-works is not, as usually stated, produced by the deposition of substance on the cell-membrane, in the shape which the frame-work eventually assumes. Were it so, this frame-work would have a thickness additional to that of the cell-wall as previously existing, which it has not. On comparing one of these cells longitudinally cut through, with an adjacent cell of the kind to which it was originally similar, we see that over every opening in the frame-work, the wall of the cell is far thinner than the walls of the adjacent cells: the cell-membrane at each of these openings being quite bare, instead of being, as in adjacent cells, covered by a layer of deposit. Hence this transformation of cells into sap-channels, is in part the arrangement or re-arrangement of their substance in such ways as greatly to diminish the resistance to the passage of liquid, both longitudinally and laterally.

To attempt any physical interpretation of this change is scarcely safe: the conditions are so complex. There are many reasons for suspecting, however, that it arises from a vacuolation of the substance deposited on the cell wall. If rapidly deposited, as it is likely to be along lines where sap is freely supplied, this may, in passing from the state of a soluble colloid to that of an insoluble colloid, so contract as to leave uncovered spaces on the cell-membrane; and this change, originally consequent on a physico-chemical action, may be so maintained and utilized by natural selection, as to result in structures of a definite kind, regularly formed in growing parts in anticipation of functions to be afterwards discharged. But, without alleging any special cause for this metamorphosis, there is good evidence that it is in some way consequent upon the carrying of sap. If we examine tissues such as that in the interior of a growing turnip that has not yet become stringy, we may, in the first place, find bundles of elongated cells not having yet developed in them those fenestrated or reticulated structures by which the ducts are eventually characterized. Along the centres of adjacent bundles we may find incomplete lines of such cells—some that are partially or wholly transformed, with some between them that are not transformed. In other bundles, completed chains of such transformed cells are visible. And then, in still older bundles, there are several complete chains running side by side. All which facts imply a metamorphosis of the elongated cells, caused by the continued action of the currents carried.

§ 281. Here, however, presents itself a further problem. Taking it as manifest that there is a typical distribution of supporting tissue adapted to meet the mechanical strains a plant is exposed to by its typical mode of growth, and also that there goes on special adaptation of the supporting tissue to the special strains the individual plant has to bear; and taking it as tolerably evident that the sap channels are originally determined by the passage of currents along lines of least resistance; there still remains the ultimate question—Through what physical actions are established these general and special adjustments of supporting tissue to the strains borne, and these distributions of nutritive liquid required to make possible such adjustments? Clearly, if the external actions produce internal reactions; and if this play of actions and reactions results in a balancing of the strains by the resistances; we may rationally suspect that the incident forces are directly conducive to the structural changes by which they are met. Let us consider how they must work.

When any part of a plant is bent by the wind, the tissues on its convex surface are subject to longitudinal tension, and these extended outer layers compress the layers beneath them. Such of the vessels or canals in these subjacent layers as contain sap, must have some of this sap expelled. Part of it will be squeezed through the more or less porous walls of the canals into the surrounding tissue, thus supplying it with assimilable materials; while part of it, and probably the larger part, will be thrust along the canals longitudinally upwards and downwards. When the branch or twig or leaf-stalk recoils, these vessels, relieved from pressure, expand to their original diameters. As they expand, the sap rushes back into them from above and below. In whichever of these directions least has been expelled by the compression, from that direction most must return during the dilation; seeing that the force which more efficiently resisted the thrusting back of the sap is the same force which urges it into the expanded vessels again, when they are relieved from pressure. At the next bend of the part a further portion of sap will be squeezed out, and a further portion thrust forwards along the vessels. This rude pumping process thus serves for propelling the sap to heights which it could not reach by capillary action, at the same time that it incidentally serves to feed the parts in which it takes place. It strengthens them, too, just in proportion to the stress to be borne; since the more severe and the more repeated the strains, the greater must be the exudation of sap from the vessels or ducts into the surrounding tissue, and the greater the thickening of this tissue by secondary deposits. By this same action the movement of the sap is determined either upwards or downwards, according to the conditions. While the leaves are active and evaporation is going on from them, these oscillations of the branches and petioles urge forward the sap into them; because so long as the vessels of the leaves are being emptied, the sap in the compressed vessels of the oscillating parts will meet with less resistance in the direction of the leaves than in the opposite direction. But when evaporation ceases at night, this will no longer be the case. The sap drawn to the oscillating parts, to supply the place of the exuded sap, must come from the directions of least resistance. A slight breeze will bring it back from the leaves into the gently-swaying twigs, a stronger breeze into the bending branches, a gale into the strained stem and roots—roots in which longitudinal tension produces, in another way, the same effects that transverse tension does in the branches.

Two possible misinterpretations must be guarded against. It must not be supposed that this force-pump action causes movement of the sap towards one point rather than another: it is simply an aid to its movement. From the stock of sap distributed through the plant, more or less is everywhere being abstracted—here by evaporation; here by the unfolding of the parts into their typical shapes; here by both. The result is a tension on the contained liquid columns, that is greatest now in this direction and now in that. This tension it is which must be regarded as the force that determines the current upwards or downwards; and all which the mechanical actions do is to facilitate the transfer to the places of greatest demand. Hence it happens that in a plant prevented from oscillating, but having a typical tendency to assume a certain height and bulk, the demands set up by its unfolding parts will still cause currents; and there will still be alternate ascents and descents, according as the varying conditions change the direction of greatest demand—the only difference being, that in the absence of oscillations the the growth will be less vigorous. Similarly, it must not be supposed that mechanical actions are here alleged to be the sole causes of wood-formation in the individual plant. The tendency of the individual plant to form wood at places where wood has been habitually formed by ancestral plants, is manifestly a cause, and, indeed, the chief cause. In this, as in all other cases, inherited structures repeat themselves irrespective of the circumstances of the individual: absence of the appropriate conditions resulting simply in imperfect repetition of the structures. Hence the fact that in trained trees and hothouse shrubs, dense substance is still largely deposited; though not so largely as where the normal mechanical strains have acted. Hence, too, the fact, that in such plants as the Elephants-foot or the *Welwitschia mirabilis*, which for untold generations can have undergone no oscillations, there is an extensive formation of wood (though not to any considerable height above the ground), in repetition of an ancestral type: natural selection having here maintained the habit as securing some other advantage than that of support.

Still, it must be borne in mind that though intermittent mechanical strains cannot be assigned as the direct causes of these internal differentiations in plants that are artificially sheltered or supported, they are assignable as the indirect causes; since the inherited structures, repeated apart from such strains, are themselves interpretable as accumulated results of such strains acting on successive generations of ancestral plants. This will become clear on combining the several threads of the argument and bringing it to a close, which we may now do.

§ 282. To put the co-operative actions in their actual order, would require us to consider them as working on individuals small modifications that become conspicuous and definite only by inheritance and gradual increase; but it will aid our comprehension without leading us into error, if we suppose the whole process resumed in a single continuously-existing plant.

As the plant erects the integrated series of fronds whose united parts form its rudimentary axis, the increasing area of frond-surface exposed to the sun's rays entails an increasing draught upon the liquids contained in the rudimentary axis. The currents of sap so produced, once established along certain lines of cells that offer least resistance, render them by their continuous passage more and more permeable. This establishment of channels is aided by the wind. Each bend produced by it while yet the tissue is undifferentiated, squeezes towards the place of growth and evaporation the liquids that are passing by osmose from cell to cell; and when the lines of movement become defined, each bend helps, by forcing the liquid along these lines, to remove obstructions and make continuous canals. As fast as this transfer of sap is facilitated, so fast is the plant enabled further to raise itself, and add to its assimilating surfaces; and so fast do the transverse strains, becoming greater, give more efficient aid. The channels thus formed can be neither in the centre of the rudimentary axis nor at its surface; for at neither of these places can the transverse strains produce any considerable compressions. They must arise along a tract between the outside of the axis and its core—a tract along which there occur the severest squeezes between the extended outer layers and the internal mass. Just that distribution which we find, is the distribution which these mechanical actions tend to establish.

As the plant gains in height, and as the mass of its foliage accumulates, the strains thrown upon its axis, and especially the lower part of its axis, rapidly increase. Supposing the forms to remain similar, the strains must increase in the ratio of the cubes of the dimensions; or even in a somewhat higher ratio. One consequence must be, that the compressions to which the vessels at the lower part of the stem are subject, become greater as fast as the height to which the sap has to be raised becomes greater; and another consequence must be, that the local exudation of sap produced by the pressure is proportionately augmented. Hence the materials for nutrition of the surrounding tissues being there supplied more abundantly, we may expect thickening of the surrounding tissues to show itself there first: in other words, wood will be formed round the vessels of the lower part of the stem. The resulting greater ability of this lower part of the stem to bear strains, renders possible an increase of height; and while after an increase of height the lowest part becomes still further strained, and still further thickens, the part above it, exposed to like actions, undergoes a like thickening. This induration, while it spreads upwards, also spreads outwards. As fast as the rude cylinder of dense matter formed in this way, begins to inclose the original vessels, it begins to play the part of a resistant mass, between which and the outer layers the greatest compression occurs at each bend. While, therefore, the original vessels become useless, the peripheral cells of the developing wood become those which have their liquid contents squeezed out longitudinally and laterally with the greatest force; and, consequently, amid them are formed new sap-channels, from which there is the most active local exudation, producing the greatest deposit of dense matter.

Thus fusing together, as it were, the individualities of successive generations of plants, and letting that facilitation of the process which natural selection has all along given, be represented by the most favourable working together of these mechanical processes, we are enabled to interpret the leading internal differentiations of plants as consequent on a direct equilibration between inner and outer forces. Here, indeed, we see illustrated in a way more than usually easy to follow, the eventual balancing of outer actions by inner reactions. The relation between the demand for liquid and the formation of channels that supply liquid, as well as that between the incidence of strains and the deposit of substance that resists strains, are among the clearest special examples of the general truth that the moving equilibrium of an organism, if not overthrown by an incident force, must eventually be adjusted to it.

The processes here traced out are, of course, not to be taken as the only differentiating processes to which the inner tissues of plants have been subject. Besides the chief changes we have considered. various less conspicuous changes have taken place. These must be passed over as arising in ways too involved to admit of specific interpretations; even supposing them to have been produced by causes of the kind assigned. But the probability, or rather indeed the certainty, is, that some of them have not been so produced. Here, as in nearly all other cases, indiect requilibration has worked in aid of direct equilibration; and in many cases indirect equilibration has been the sole agency. Besides ascribing to natural selection the rise of various internal modifications of other classes than those above treated, we must ascribe some even of these to natural selection. It is so with the dense deposits which form thorns and the shells of nuts: these cannot have resulted from any inner reactions immediately called forth by outer actions; but must have resulted mediately through the effects of such outer actions on the species. Let it be understood, therefore, that the differentiations to which the foregoing interpretation applies, are only those most conspicuous ones which are directly related to the most conspicuous incident forces. They must be taken as instances on the strength of which we may conclude that other internal differentiations have had a natural genesis, though in ways that we cannot trace.

# CHAPTER V.

## PHYSIOLOGICAL INTEGRATION IN PLANTS.

§ 283. A good deal has been implied on this topic in the preceding chapters. Here, however, we must for a brief space turn our attention immediately to it.

Plants do not display integration in such distinct and multiplied ways as do animals. But its advance may be traced both directly and indirectly—directly in the increasing co-ordination of actions, and indirectly in the effect of this upon the powers and habits.

Let us group the facts under these heads: ascending in both cases from the lower to the higher types.

§ 284. The inferior *Algæ*, along with little unlikeness of parts, show us little mutual dependence of parts. Having surfaces similarly circumstanced everywhere, much physiological division of labour cannot arise; and therefore there cannot be much physiological unity. Among the superior *Algæ*, however, the differentiation between the attached part and the free part is accompanied by some integration. There is evidently a certain transfer of materials, which is doubtless facilitated by the elongated forms of the cells in the stem, and probably leads to the formation of dense tissue at the places of greatest strain, in a way akin to that recently explained in other cases. And where there is this co-ordination of actions, the parts are so far mutually dependent that each dies if detached from the other. That though the organization is so low neither part can reproduce the other and survive by so doing, is probably due to the circumstance that neither part contains any considerable stock of untransformed protoplasm, out of which new tissues may be produced.

Fungi and Lichens present no very significant advances of integration. We will therefore pass at once to the Acrogens. In those of them which, either as single fronds or strings of fronds, spread over surfaces, and which, rooting themselves as they spread, do not need that each part should receive aid from remote parts, there is no developed vascular system serving to facilitate transfer of nutriment: the parts being little differentiated there is but little integration. But along with assumption of the upright attitude and the accompanying specializations, producing vessels for distributing sap and hard tissue for giving mechanical support, there arises a decided physiological division of labour; rendering the aërial part dependent on the imbedded part and the imbedded part dependent on the aërial part. Here, indeed, as elsewhere, these concomitant changes are but two aspects of the same change. Always the gain of power to discharge a special function involves a loss of power to perform other functions; and always, therefore, increased mutual dependence constituting physiological integration, must keep pace with that increased fitting of particular parts to particular duties which constitutes physiological differentiation.

Making a great advance among the Acrogens, this physiological integration reaches its climax among Endogens and Exogens. In them we see interdependence throughout masses that are immense. Along with specialized appliances for support and transfer, we find an exchange of aid at great distances. We see roots giving the vast aërial growth a hold tenacious enough to withstand violent winds, and supplying water enough even during periods of drought; we see a stem and branches of corresponding strength for upholding the assimilating organs under ordinary and extraordinary strains; and in these assimilating organs we see elaborate appliances for yielding to the stem and roots the materials enabling them to fulfil their offices. As a consequence of which greater integration accompanying the greater differentiation, there is ability to maintain life over an immense period under marked vicissitudes.

Even more conspicuously exemplified in Phænogams, is that physiological integration which holds together the functions not of the individual only but of the species as a whole. The organs of reproduction, both in their relations to other parts of the individual bearing them and in their relations to corresponding parts of other individuals, show us a kind of integration conducing to the better preservation of the race; as those already specified conduce to the better preservation of the individual. In the first place, this greater co-ordination of functions just described, itself enables Phænogams to bequeath to the germs they cast off, stores of nutriment, protective envelopes, and more or less of organization: so giving them greater chances of rooting themselves. In the second place, certain differentiations among the parts of fructification, the meaning of which Mr. Darwin has so admirably explained, give to the individuals of the species a kind of integration that makes possible a mutual aid in the production of vigorous offspring. And it is interesting to observe how, in that dimorphism by which in some cases this mutual aid is made more efficient, the greater degree of integration is dependent on the greater degree of differentiation—not simply differentiation of the fructifying organs from other parts of the plant bearing them, but differentiation of these fructifying organs from the homologous organs of neighbouring individuals of the same race. Another form of this co-ordination of functions that conduces to the maintenance of the species, may be here named—partly for its intrinsic interest. I refer to the strange processes of multiplication that occur in the genus *Bryophyllum*. It is well known that the succulent leaves of *B. calycinum*, borne on foot-stalks so brittle that they are easily snapped by the wind, send forth from their edges when they fall to the ground, buds that root themselves and grow into independent plants. The correlation here obviously furthering the preservation of the race, is more definitely established in another species of the genus—*B. proliferum.* This plant, shooting up to a considerable height, and having a stem containing but little woody fibre, habitually breaks near the bottom while still in flower; and is thus generally prevented from ripening its seeds. The multiplication is, however, secured in another way. Before the stem is broken young plants have budded out from the pedicels of the flowers, and have grown to considerable lengths; and on the fall of the parent they forthwith commence their separate lives. Here natural selection has established a remarkable kind of co-ordination between a special habit of growth and decay, and a special habit of proliferation.

§ 285. The advance of physiological integration among plants as we ascend to the higher types, is implied by their greater constancy of structure, as well as by the stricter limitation of their habitats and modes of life. "Complexity of structure is generally accompanied with a greater tendency to permanence in form," says Dr. Hooker; or, conversely, "the least complex are also the most variable." This is the second aspect under which we have to contemplate the facts.

The differences between the simpler *Algæ* and *Fungi*, and between them and the Lichens, are so feebly marked that botanists have been unable to frame satisfactory definitions of these classes. "Linnæus, for instance, and Jussieu, considered Lichens as forming a part of *Algæ*, in which they are followed by Fries." Mr. Berkeley, however, quoting the admission of Fries "that there is no certain distinction between Lichens and *Fungi*, except the presence in the former of green globules, resembling grains of chlorophyll," himself prefers to unite *Fungi* and Lichens under the general head of *Mycetales*. This structural indefiniteness is accompanied by functional indefiniteness. Though, considered collectively, these Thallogens form "three very natural groups, according as they inhabit the water, the earth, or the air;" yet if, instead of their higher members we look at their lower members, we find these distinctions of habitat very undecided. *Algæ*, which are mostly aquatic, include many small forms that frequent the damp places preferred by Lichens and *Fungi*. Among Lichens, as among *Fungi*, there are kinds that lead submerged lives like the *Algæ*. While terrestrial Lichens and *Fungi* compete for the same places, as well as simulate one another's modes of growth. Besides this indistinctness of the classes, there is great variability in the shapes and modes of life of their species—a variability so great that what were at first taken to be different species, or different genera, or even different orders, have proved to be merely varieties of one species. So inconstant in structure are the *Algæ* that Schleiden quotes with approval the opinion of Kutzing, that "there are no species but merely forms of *Algæ*." In all which groups of facts we see that these lowest types of plants, little differentiated, are also but little integrated.

Acrogens present a parallel relation between the small specialization of functions which constitutes physiological differentiation, and the small combination of functions which constitutes physiological integration. "Mosses," says Mr. Berkeley, "are no less variable than other cryptogams, and are therefore frequently very difficult to distinguish. Not only will the same species exhibit great diversity in the size, mode of branching, form and nervation of the leaves, but the characters of even the peristome itself are not constant." And concerning the classification of the remaining group, *Filicales*, he says:—"Not only is there great difficulty in arranging ferns satisfactorily, but it is even more difficult to determine the limits of species."

After this vagueness of separation as well as inconstancy of structure and habit among the lower plants, the stability of structure and habit and divisibility of groups among the higher plants, appear relatively marked. Though Phænogams are much more variable than most botanists have until recently allowed, yet the definitions of species and genera may be made with far greater precision and are far less capable of change than among Cryptogams. And this comparative fixity of type, implying, as it does, a closer combination of the component functions, we see to be the accompaniment of the greater differentiation of those functions and of the structures performing them. That these characters are correlatives is further shown by the fact that the higher plants are more restricted in their habitats than the lower plants, both in space and time. "The much narrower delimitation in area of animals than plants," says Dr. Hooker, "and greater restriction of Faunas than Floras, should lead us to anticipate that plant types are, geologically speaking, more ancient and permanent than the higher animal types are, and so I believe them to be, and I would extend the doctrine even to plants of highly complex structure." "Those classes and orders which are the least complex in organization are the most widely distributed."

§ 286. Thus that which the general doctrine of evolution leads us to anticipate, we find implied by the facts. The physiological division of labour among parts, can go on only in proportion to the mutual dependence of parts; and the mutual dependence of parts can progress only as fast as there arise structures by which the parts are efficiently combined, and the mutual utilization of their actions made easy.

To say definitely by what process is brought about this co-ordination of functions which accompanies their specialization, is hardly practicable. Direct and indirect equilibration doubtless co-operate in establishing it. We may see, for example, that every increase of fitness for function produced in the aërial part of a plant by light, as well as every increase of fitness for function produced in its imbedded part by the direct action of the moist earth, must conduce to an increased current of the liquid evaporated from the one and supplied by the other—must serve, therefore, to aid the formation of sap-channels in the ways already described; that is—must serve to develop the structures through which mutual aid of the parts is given: the additional differentiation tends immediately to bring about the additional integration. Contrariwise, it is obvious that an interdependence such as we see between the secretion of honey and the fertilization of germs, or between the deposit of albumen in the cotyledons of an embryo-plant and the subsequent striking root, is a kind of integration in the actions of the individual or of the species, which no differentiation has a direct tendency to initiate. Hence we must regard the total results as due to a plexus of influences acting simultaneously on the individual and on the species: some chiefly affecting the one and some chiefly affecting the other.

## CHAPTER VI.

### DIFFERENTIATIONS BETWEEN THE OUTER AND INNER TISSUES OF ANIMALS.

§ 287. What was said respecting the primary physiological differentiation in plants, applies with little beyond change of terms to animals. Among *Protozoa*, as among *Protophyta*, the first definite contrast of parts that arises is that between outside and inside. The speck of jelly or sarcode which appears to constitute the simplest animal, proves, on closer examination, to be a mass of substance containing a nucleus—a periplast in the midst of which there is a minute endoplast, consisting of a spherical membrane and its contents.

This parallel, only just traceable among these Rhizopods, which are perpetually changing the distribution of their outer substance, becomes at once marked in those higher *Protozoa* which have fixed shapes, and maintain constant relations between their surfaces and their environments. Indeed the Rhizopods themselves, on passing into a state of quiescence in which the relations of outer and inner parts are fixed, become encysted: there is formed a hardened outer coat different from the matter which it contains. And what is here a temporary character answering to a temporary definiteness of conditions, is in the *Infusoria* a constant character, answering definite conditions that are constant. Each of these minute creatures, though not coated by a distinct membrane, has the outer layer of its sarcode indurated: the indurated substance being not separable from the substance inclosed, but passing into it insensibly.

§ 288. The early establishment of this primary contrast of tissues answering to this primary contrast of conditions, is no less conspicuous in aggregates of the second order. The feebly-integrated units of a Sponge, with individualities so little merged in that of the whole they form that most of them still retain their separate activities, nevertheless show us, in the unlikeness that arises between the outermost layer and the contained mass, the effect of converse with unlike conditions. This outermost layer is composed of units somewhat flattened and united into a continuous membrane—a kind of rudimentary skin.

Secondary aggregates in which the lives of the units are more subordinate to the life of the whole, carry this distinction further. The leading physiological trait of every cœlenterate animal is the divisibility of its substance into endoderm and ectoderm—the part next the food and the part next the environment. Fig. 147, rudely representing a portion of the body-wall of a *Hydra* seen in section, gives some idea of this fundamental differentiation. The creature consists of a simple sac, the cavity of which is in direct communication with the surrounding water; and hence there is but little unlikeness between the outer and inner layers: indeed they are said to be capable of exchanging their functions. The essential contrast is that between the parts in contact with foreign substances and the parts sheltered from them—between the developed surfaces of the endoderm and ectoderm, and that intermediate stratum of nucleated sarcode from which the two grow in opposite directions.

Between this case and the case of the Sponge, we may readily trace the connexion. Suppose a mass of *Amœba*-form units, the outermost of which are united into a layer analogous to that by which a living Sponge is covered, to be represented by a lump of plastic clay; and for convenience of identification, suppose the surface of the clay to be coated by an extensible film, say of caoutchouc. Let this clay, so coated, be moulded into the shape of a cup; the cup be gradually deepened until it becomes jar-shaped; and finally, by narrowing its neck, vase-shaped. And conceive the stretched film to continue everywhere covering the surface during these changes of form. What will finally be the relations of the parts to one another? The caoutchouc will line the inside of the vase as well as coat its outside. The vase will consist of a stratum of the clay included between the two India-rubber surfaces. We shall have a distribution of layers answering completely to the distribution of tissues in the *Hydra*. Now if we imagine that this artificial layer which has covered the clay during its changes of form, is produced by transformation of the clay, we shall see that when the mass is changed into the vase-shape, the surfaces that have become outer and inner will develop in opposite directions from the substance lying between them; just as do the *Hydra's* ectoderm and endoderm. And if, once more, we conceive these outer and inner surfaces so resulting, to be affected by conditions somewhat unlike—the one by matters placed in the jar, and the other by the medium surrounding the jar—we shall have, in the slight difference produced between them, a difference corresponding to that between the surfaces of the *Hydra's* stomach and skin.

Besides being able thus to understand how an aggregate of *Amœba*-form units, originally coated by a single layer, may pass into an aggregate composed of a double layer; we may also understand under what influences the transition takes place. If the habit which some of the primary aggregates have, of wrapping themselves round masses of nutriment, is followed by a secondary aggregate, there will naturally arise just that re-differentiation which the *Hydra* shows us.

§ 289. These duplicated surfaces which we see in every simple cœlenterate animal, are re-duplicated in all animals of higher classes—the more developed *Cœlenterata* themselves showing us the transition. "Compared with the Hydroid Polypes," says Prof. Huxley, "the higher forms are double animals, and a section of their bodies is, morphologically speaking, like a section of two *Hydræ*, one contained within the other." The relations of the parts may be illustrated thus:—Cut off the finger of a leather glove that has a lining; and let the leather and the lining represent the ectoderm and endoderm of a *Hydra*. Thrust the point of the glove-finger back into the cavity, until the introverted portion comes out beyond the open end. Cut off the projecting apex of the introverted portion level with the edges of the open end; and then unite the edges of the introverted portion and the outer portion. The arrangement of structures will then typify that which is common to all animals except the *Protozoa* and the lower *Cœlenterata:* the introverted part representing the alimentary canal; the outer part representing the body-wall; and the closed cavity between the two representing the peri-visceral sac. This, however, is not the whole parallelism. If in the glove-finger, representing in its original form the *Hydra*, we suppose the leather standing for the ectoderm to be growing outwards, and the lining standing for the endoderm to be growing inwards, then if in the part that is introverted the same relations of growth are maintained, it is manifest that of its two layers the one which was outermost and is now innermost, will grow towards the open cavity which stands for the alimentary canal, while the other layer will grow towards the closed cavity standing for the peri-visceral sac. And these are the directions of growth actually found in the parts thus symbolized.

This simile must not have more meaning given to it than is intended. Though there is reason for suspecting that a re-duplication has taken place in the course of evolution, and that the peri-visceral sac which distinguishes all the higher classes of animals from the lower, has been formed by it; yet the method of re-duplication cannot have been anything like that described; and has probably been so different a one as to negative the implied homologies of the layers. The illustration is here used merely to convey, in a way easy to follow, an idea of the relations between outer and inner tissues, as they exist in the more complex animals. The two facts which we have to note are these:—First, that, as Prof. Huxley points out in his essay on "Tegumentary Organs," the course of differentiation in the body-wall of the *Hydra*, is paralleled by the course of differentiation in the skin of every more complex animal up to the highest mammal. Between the epidermis and the derma there is a layer of indifferent tissue corresponding to the layer that lies between the endoderm and ectoderm of the *Hydra*; and from this layer, as from its homologue, the differentiations proceed in opposite directions. Though the resulting two layers, exposed to more unlike conditions than those of the *Hydra*, are more unlike one another, yet we see in them essentially the same course of metamorphosis and the same subordination of it to the relations of outside and inside. In the second place, we have to note that the wall of the alimentary canal, though it is in one sense internal by contrast with the skin as external, and is correspondingly differentiated from the skin, is in another sense like the skin, in having one surface in contact with foreign substances (presented as food) and the other surface in contact with the living substance of the body; and that consequently it undergoes, like the skin, a differentiation into two layers, one growing towards the relatively external or food-containing cavity, and the other towards the rigorously internal cavity—the closed peri-visceral sac.

§ 290. Whether direct equilibration or indirect equilibration has had the greater share in producing this universally-present contrast between the inner and outer tissues of animals, must be left undecided. The two causes have all along co-operated—modification of the individual accumulated by inheritance predominating in some cases, and in other cases modification of the race by survival of the incidentally fittest. On the one hand, the action of the medium on the organism cannot fail to change its surface more than its centre, and so differentiate the two; while on the other hand, the surfaces of organisms inhabiting the same medium display extreme unlikenesses which cannot be due to the immediate actions of their medium. Let us dwell a moment on the antithesis.

We have abundant evidence that animal protoplasm is rapidly modified by light, heat, air, water, and the salts contained in water—coagulated, turned from soluble into insoluble, partially changed into isomeric compounds, or otherwise chemically altered. Immediate metamorphoses of this kind are often obviously produced in ova by changes of their media. At the outset, therefore, before yet there existed any such differentiation as that which now usually arises by inheritance, these environing agencies must have tended to originate a protective envelope. For a modification produced by them on the superficial part of the protoplasm, must either have been a decomposition or else the formation of a compound that remained stable under their subsequent action. There would be generated an outer layer of substance that was so molecularly immobile as to be incapable of further metamorphoses, while it would shield the contained protoplasm from that too great action of external forces which, by rapidly changing the unstable equilibrium of its molecules into a relatively stable equilibrium, would arrest development. Evidently organic evolution, whether individual or general, must always and everywhere have been subordinate to these physical necessities. Though natural selection, beginning with minute portions of protoplasm, must all along have tended to establish a molecular composition apt to undergo this differentiation of surface from centre to the most favourable extent; yet it must all along have done so while controlled by this process of direct equilibration.

Contrariwise, the many and great unlikenesses among the dermal structures of creatures inhabiting the same element, cannot be ascribed to any such cause. The contrasts between naked and shelled Gastropods, between marine Worms and Crustaceans, between soft-skinned Fish and Fish in armour like the *Pterichthys*, must have been produced entirely by natural selection. Environing forces are, as before, the ultimate causes; but the forces are now not so much those exercised by the medium as those exercised by the other inhabitants of the medium; and they do not act by modifying the surface of the individual, but by killing off individuals whose surfaces are least fitted to the requirements: thus slowly affecting the species. The dermal skeleton bristling with spines, which protects the *Diodon* or the *Cyclicthys* from enemies it could not escape, still comes within the general formula of an outer tissue differentiated from inner tissues by the outer actions to which the creature is exposed—the differentiation having gone on until there is equilibrium between the destructive forces to be met and the protective forces which meet them.

If we venture to apportion the respective shares which mediate and immediate actions have had in differentiating outer from inner tissues, we shall probably not be far wrong in ascribing that part of the process which is alike in all animals, mainly to the direct actions of their media; while we ascribe the multitudinous unlikenesses of the process in various animals, partly to the indirect actions of the media, and partly to the indirect actions of other animals by which the media are inhabited. That is to say, while assigning the specialities of the differentiations to the specialities of converse with the agencies in the environment, most of them organic, we may assign to the constant and universal converse with its inorganic agencies, that universal characteristic of tegumentary structures—their development into a double layer separated by undifferentiated substance, from which the outermost grows outwardly and the innermost grows inwardly.

Here let me add a piece of evidence which strengthens very greatly the general argument, at the same time that it justifies this apportionment. When ulceration has gone deep enough to destroy the tegumentary structures, these are never reproduced. The puckered surface formed where an ulcer heals, consists of modified connective tissue, which, as the healing goes on, spreads inwards from the edges of the ulcer —some of it, perhaps, growing from the portions of connective tissue that dip down between the muscular bundles. This connective tissue, mark, out of which is thus constituted the make-shift skin, is normally covered by both the epidermis and that stratum of indifferent tissue from which the growth proceeds in opposite directions—is the inner layer that grows inwardly. What has happened to it? It has now become the outermost layer. And how does it comport itself under its new conditions? It produces a layer that plays the part of epidermis and grows outwardly. For since the surface, subject to friction and exfoliation, has to be continually renewed, there must be a continual reproduction of a superficial layer from a layer beneath. That is to say, the contact of this deep-seated tissue with outer agencies, produces in it some approach towards that composition which we find universally characterizes outer-tissue—a protomorphic layer, which differentiates in opposite directions. But while we see under this exposure to the conditions common to all integument, a tendency to assume the structure common to all integument, we see no tendency to assume any of the specialities of tegumentary structure; no rudiments of glands or hair sacs make their appearance.

This apportionment we shall see the more reason to accept as approximately expressing the truth, on remembering that the mode of differentiation of outer from inner tissues which is common to all animals is common to all plants; and on observing, further, that the more special interpretation suggested as not improbable in the case of plants, is not improbable in the case of animals. For as it was argued that in plants the forces evolved from within the organism, and the forces falling on it from without, must have some place between centre and surface at which they balance; and that at this place will lie the unstable protoplasm that develops outwardly into a substance which is stable in face of outer forces, and inwardly into a substance which is stable in face of inner forces; so in animals, we may regard this universally-present layer whence epidermis grows outwardly and connective tissue inwardly, as similarly the place of equilibrium between these antagonist forces. And for this *à priori* interpretation we may indeed, among animals, find *à posteriori* warrant. We have but to increase the mechanical action or chemical irritation at some part of an animal's surface, to make this plane of indifferent tissue retreat inwardly; for to say that the epidermis becomes thicker, is, in mechanical terms, to say that the place of equilibrium between outer and inner forces is further from the surface.

# CHAPTER VII.

## DIFFERENTIATIONS AMONG THE OUTER TISSUES OF ANIMALS.

§ 291. The outer tissues of animals, originally homogeneous over their whole surfaces, pass into a heterogeneity which fits their respective parts to their respective conditions. So numerous and varied are the implied differentiations, that it is impracticable here to deal with them all even in outline. To trace them up through classes of animals of increasing degrees of aggregation, would carry us into undue detail.

Did space permit, it would be possible to point out among the *Protozoa*, various cases analogous to that of the *Arcella;* which may be described as like a microscopic Limpet, having a sarcode body of which the upper surface has become horny, while the lower surface with its protruding pseudopodia, retains the primitive jelly-like character. That differentiations of this kind have been gradually established among these minute creatures through the unlike relations of their parts to the environment, is an inference supported by cases like that of *Pamphagus*—an intermediate form which is like the *Amœba* in having no carapace, but "agrees with *Arcella* and *Difflugia* in having the pseudopodia protrusible from one extremity only of the body."

Many parallel specializations of surface among aggregates of the second order might be instanced from the *Cœlenterata*. In the *Hydra*, the ectoderm presents over its whole area no conspicuous unlikenesses; but there usually exist in the hydroid polypes of superior types, decided contrasts between the higher and lower parts. While the higher parts retain their original characters, the lower parts excrete hard outer layers yielding support and protection. Various stages of the differentiation might be followed. "In *Hydractinia*," says Prof. Green, this horny layer "becomes elevated at intervals to form numerous rough processes or spines, while over the general surface of the ectoderm its presence is almost imperceptible." In other types, as in *Cordylophora*, it spreads part way up the animal's sides, ending indefinitely. In *Bimeria* it "extends itself so as to enclose the entire body of each polypite, leaving bare only the mouth and tips of the tentacles." While in *Campanularia* it has become a partially-detached outer cell, into which the creature can retract its exposed parts.

But it is as needless as it would be wearisome to trace through the several sub-kingdoms the rise of these multiform contrasts, with the view of seeking interpretations of them. It will suffice if we take a few groups of the illustrations furnished by the higher animals.

§ 292. We may begin with those modifications of surface which subserve respiration. Though we ordinarily think of respiration as the quite special function of a quite special organ, yet originally it is not so. Little-developed animals part with their carbonic acid and absorb oxygen, through the general surface of the body. Even in the lower types of the higher classes, the general surface of the body aids largely in aërating the blood; and the parts that discharge the greater part of this function are substantially nothing more than slightly altered and extended portions of the skin.

Such differentiations, marked in various degrees, are to be seen among *Mollusca*. In the *Pteropoda* the only modification which appears to facilitate respiration, is the minute vascularity of one part of the skin. In other types the specialized parts facilitating the exchange of gases, are those simple but numerous expansions of surface constituting the papillæ;

which, in the *Eolis* and kinds allied to it, are distributed in rows or clusters all along the back. Instead of these, the *Doris* has appendages developed into elaborately-branched forms—small trees of blood-vessels covered by slightly-changed dermal tissues. And these arborescent branchiæ are gathered together into a single cluster. Thus there is evidence that large external respiratory organs have arisen by degrees from simple skin: as, indeed, they do arise during the development of each individual having them. Just as gradually as in the embryo the simple bud on the integument, with its contained vascular loop, passes by secondary buddings into a tree-like growth penetrated everywhere by dividing and sub-dividing blood-vessels; so gradually has there probably proceeded the differentiation which has turned part of the outer surface into an organ for excreting carbonic acid and absorbing oxygen.

Certain inferior vertebrate animals present us with a like metamorphosis of tissues. These are the *Amphibia*. The branchiæ here developed from the skin are covered with cellular epidermis, not much thinner than that covering the rest of the body. Like it they have their surfaces speckled with pigment-cells; and are not even conspicuous by their extra vascularity—where they are temporary at least. They facilitate the exchange of gases in scarcely any other way than by affording a larger area of contact with the water, and interposing a rather thinner layer of tissue between the water and the blood-vessels. Those very simple branchiæ of the larval *Amphibia* that have them but for a short time, graduate into the more complex ones of those that have them for a long time or permanently; showing, as before, the small stages by which this heterogeneity of surface accompanying heterogeneity of function may arise.

In what way are such differentiations established? Partly, no doubt, by natural selection; but also to some degree, I think, by the inheritance of direct adaptations. That a portion of the integument at which aëration is favoured by local conditions, should thereby be led to grow into a larger surface of aëration, appears improbable: survival of those individuals which happen to have this portion of the integument somewhat more developed, seems here the only likely cause. Nevertheless there is reason for suspecting that respiratory activity itself aids in the development of a respiratory appendage. The reason is this. Exchange of liquids through membrane depends on some difference, physical or chemical, between the liquids: if they are in all respects alike, and under equal pressures, no exchange will take place; while, conversely, if they are much unlike there will be a rapid exchange. Now through the walls of capillaries, or through the sides of lacunæ not yet developed into capillaries, there continually goes on an oozing both ways—from the blood into the tissues and from the tissues into the blood. By this double movement nutrition and depuration are alike made possible; and it is obvious both that in the absence of difference it would not occur, and that nothing would be gained if it did occur. Among other differences continually arising between the intra-vascular liquid and the extra-vascular liquid, is that due to their unlike charges of oxygen and carbonic acid. This difference, like other differences, will cause exchange—the rapidity of the exchange doubtless being greater where the difference is greater. Hence if any part of an aquatic animal's skin is nearest to the place where the blood has become most highly carbonized, or if it is so bathed with moving water that the plasma beneath its surface is more oxygenated than elsewhere, or both; then, other things equal, this part of the skin will be the seat of an osmotic movement greater than goes on in the rest of the skin. But the exchange of oxygen for carbonic acid, proceeding faster here than elsewhere, will have for its accompaniment a more rapid exudation of nutritive matters. The liquid passing out of the blood-vessels to be replaced by the liquid passing into them, is a liquid containing the substances that build up the surrounding tissues. Hence these tissues may be expected to grow: the area supplied by the increased currents of blood set up by this exchange, will become protuberant—will bud out; and the bud so formed will give origin to secondary buds at those parts of its surface which, as before, are most favourably circumstanced for carrying on the aëration. Of course this process will be checked where, though otherwise advantageously placed, the growing branchiæ would be specially liable to damage, or would be great hindrances to the creature's movements. But bearing in mind that functionally-produced adaptation will here, as in other cases, be both aided and controlled by natural selection, we may ascribe to it an important share, if not a leading share, in the differentiation.

§ 293. Among the conspicuous modifications by which the originally-uniform outer layer is rendered multiform, are the protective structures. Let us look first at the few cases in which the formation of these is ascribable mainly to direct equilibration.

Already reference has been more than once made to those thickenings that occur where the skin is exposed to unusual pressure and friction. Are these adaptations inheritable? and may they, by accumulation through many generations, produce permanent dermal structures fitted to permanent or frequently-recurring stress? Taking, for instance, the callosities on the knuckles of the *Gorilla,* which are adapted to its habit of partially supporting itself on its closed hands when moving along the ground—shall we suppose that these defensive thickenings are produced afresh in each individual by the direct actions; or that they are inherited modifications caused by such direct actions; or that they are wholly due to the natural selection of spontaneous variations? The last supposition does not seem a probable one; since it implies that those slight extra thicknesses of skin on the knuckles, with which we must suppose the selection to have commenced, were so advantageous as to cause survivals of the individuals having them. That survivals so caused, if they ever occurred at all, should have occurred with the frequency requisite to establish and increase the variation, is hardly supposable. And if we reject, as also unlikely, the reproduction of these callosities *de novo* in each individual, there remains only the inference that they have arisen by the transmission and accumulation of functional adaptations. Another case which seems interpretable only in an analogous way, is that of the spurs that are developed on the wings of certain birds—on those of the Chaja screamer for example. These are weapons of offence and defence. It is a familiar fact that many birds strike with their wings, often giving severe blows; and in the birds named, the blows are made more formidable by the horny, dagger-shaped growths standing out from those points on the wings which deliver them. Are these spurs directly or indirectly adaptive? To conclude that natural selection of spontaneous variations has caused them, is to conclude that, without any local stimulus, thickenings of the skin occurred symmetrically on the two wings at the places required; that such thickenings, so localized, happened to arise in birds given to using their wings in fight; and that on their first appearance the thickenings were decided enough to give appreciable advantages to the individuals distinguished by them—advantages in bearing the reactions of the blows if not in inflicting the blows. But to conclude this is, I think, to conclude against probability. Contrariwise, if we assume that the thickening of the epidermis produced by habitual rough usage is inheritable, the development of these structures presents no difficulty. The points of impact would become indurated in wings used for striking with unusual frequency. The callosities of surface thus generated, rendering the parts less sensitive, would enable the bird in which they arose to give, without injury to itself, more violent blows and a greater number of them—so, in some cases, helping it to conquer and survive. Among its descendants, inheriting the modification and the accompanying habit, the thickening would be further increased in the same way—survival of the fittest tending ever to accelerate the process. Presently the horny nodes so formed, hitherto defensive only in their effects, would, by their prominence, become offensive—would make the blows given more hurtful. And now natural selection, aiding more actively, would mould the nodes into spurs: the individuals in which the nodes were most pointed would be apt to survive and propagate; and the pointedness generation after generation thus increased, would end in the well-adapted shape we see.

But if in these cases the differentiations which fit particular parts of the outer tissues to bear rough usage, are caused mainly by the direct balancing of external actions by internal reactions, then we may suspect that the like is true of other modifications that occur where special strains and abrasions have to be met. Possibly it is true of sundry parts that are formed of hardened epidermis, such as the nails, claws, hoofs, and hollow horns of Mammals; "all of which," says Prof. Huxley, "are constructed on essentially the same plan, being diverticula of the whole integument, the outer layer of whose ecderon has undergone horny metamorphosis." Leaving open, however, the question what tegumentary structures are due to direct equilibration, furthered and controlled by indirect equilibration, it is tolerably clear that direct equilibration has been one of the factors.

How has it produced its effects? that is to say—by what physical processes do pressure and friction bring about dermal hardenings? To this inquiry there is an answer similar to that which was given to the inquiry respecting the formation of wood. (§ 280-2.) As in plants we saw that intermittent compressions of sap-canals increase the exudation of sap, and thus cause increased deposits of its contained substances in the surrounding tissues; so in animals, we have good reason for concluding that intermittent compressions of the capillaries increase the exudation of serum, and by thus supplying extra nutriment to the structures adjacent, lead, other things equal, to thickening or induration. The data for the conclusion are these:—Through the walls of the capillaries the liquid plasma of the blood continually oozes. The oozing is partly osmotic and partly mechanical—partly due, that is, to the exchange of the unlike liquids that lie inside and outside the capillaries, and partly to the greater pressure put upon the liquid inside. That this last is one of the causes is proved by the phenomena of dropsy—a disease in which the exudation is unduly rapid. Dropsy in the legs gets worse during the day, when by sitting and standing the weight of the blood to be borne by the vessels of the legs is increased; and gets better during the night, when by the recumbent attitude these vessels are relieved from this weight. Contrariwise, that œdematous swelling under the eyes which is common in the aged and debilitated, increases during the night and decreases during the day—gravitation serving, when the body is upright, to diminish the pressure of the blood at this part, and not having this effect when the body is horizontal. But if the plasma is to some extent forced through the walls of the capillaries by pressure, then not only will the action of the heart, aided at some parts by gravity, further the exudation, but the exudation will be furthered by external pressures from time to time falling on the capillaries. If the capillaries of the skin be squeezed by the thrust of some object against the surface, part of their contained blood will be driven back into the arteries, more will be driven forwards into the veins, and some will be made to exude. Immediately they are relieved from the pressure they will be refilled from the arteries, again to yield an extra portion of their contents to the tissues around when again squeezed. Thus recurrent thrusts or impacts, acting on the body from without, aid in the nutrition of the parts on which they fall: producing, in some cases, a node upon the subjacent bone, as on the instep where a boot has pinched; producing, in other cases, growth of the connective tissue, as in a bunion;

and producing, more frequently, thickening of the epidermis.* It is no doubt true that the sensation which pressure causes, propagated to the spinal chord, and reflected thence through the vaso-motor nerve going to the spot, aids the process by exciting a wave of contraction along the minute arteries, thereby helping them to refill the capillaries the instant the pressure is taken off; and doubtless, as alleged, the excessive exudation that forms a blister when the intermittent compressions are violent and long-continued, is attributable to this reflex nervous action. But it is clear that the nervous action is secondary, and cannot of itself produce the effect; for in the absence of *intermittent* pressure no exudation takes place, however acute and persistent the sensation may be. Continued pressure produces absorption instead of exudation.

In animals therefore, as in plants, the external mechanical actions to be resisted, are themselves directly instrumental in working in the tissues they fall upon, the changes which fit those tissues to meet them. And it needs but to contemplate the process of thickening described, to see that it will go on until the shield produced suffices to protect the capillaries from excessive pressures—will go on, that is, until there is equilibrium between the outer and inner forces.

§ 294. Dermal structures of another class are developed mainly, if not wholly, by the actions of external causes on species rather than on individuals. These are the

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* An inquiry into the causes of these differences of result, brings further evidence to light. The condition under which only the hypertrophy can arise, is that the pressure intermits sufficiently to allow the capillaries to refill frequently. The epidermis thickens where the pressures are habitually taken off so completely, that the capillaries next the surface can refill, as in the hands. If we consider what happens where the instep is pressed by a tight boot, we shall see that the variations of pressure which occur in walking, do not suffice to relieve the quite superficial vessels and allow them to refill; but in consequence of the slight mobility and elasticity of the tissues, the vessels at some distance beneath the surface are able to refill, and hence the thickening occurs round them.

various kinds of clothing—hairs, feathers, quills, scales, scutes.

Readers who are unfamiliar with the extreme modifiability of organic structures, will be startled by the proposition that all of these—certainly all of them but the last, respecting which there may be doubts—are homologous parts. Inspection of a few cases makes this seemingly-incredible proposition not simply credible but obviously true. A retrograde metamorphosis from feathers to appendages that are almost scale-like, is well seen in the coat of the Penguin. Carry the eye along the surface of one of these birds, and there is manifest a transition from the bird-like covering to the fish-like covering—a transition so gradual that no place can be found where an appreciable break occurs. Less striking perhaps, but scarcely less significant, are the modifications through which we pass from feathers to hairs, on the surfaces of the Ostrich and the Cassowary. The skin of the Porcupine shows us hairs and quills united by a series of intermediate structures, differing from one another inappreciably. Even more remarkable is the extension of this alliance to certain other dermal structures. "It may be taken as certain, I think," says Prof. Huxley, "that the scales, plates, and spines of all fishes are homologous organs; nor as less so that the tegumentary spines of the Plagiostomes are homologous with their teeth, and thence with the teeth of all vertebrata. Again, it appears to me indubitable that the teeth and the hairs are homologous organs."

The ultimate justification for classing these unlike parts as divergent modifications of the same thing, is the unity in their modes of development. Besides a linking together of them by intermediate structures, as above indicated, there is a linking together by their common origin. To quote again from Prof. Huxley's essay on "Tegumentary Organs":—"The *Hairs* and *Spines* of mammals, the *Feathers* of birds, and the *Integumentary Glands*, agree in one essential point, that their development is preceded by that of an involution of the ecderon, within which they are formed, and by which the former are, at first, entirely enclosed." And though the scales of fishes and the dermal plates of reptiles present difficulties, yet Prof. Huxley concludes that the course of their development is at first essentially the same. Some idea of it, and of the relations it proves among these structures, may be given thus:—Suppose a small pit to be formed on the previously flat skin; and suppose that the growth and casting off of horny cells which goes on over the skin in general, continues to go on at the usual rate over the depressed surface of this pit. Clearly the quantity of horny matter produced within this hollow, will be greater than that produced on a level portion of the skin subtending an equal area of the animal's outside. Suppose such a pit to be deepened until it becomes a small sac. If the exfoliation goes on as before, the result will be that the horny matter; expelled, as it must be, through the mouth of the sac, which now bears a small proportion to the internal surface of the sac, will be large in quantity compared with that exfoliated from a portion of the skin equal in area to the mouth of the sac: there will be a conspicuous thrusting forth of horny matter. Suppose once more that the sac, instead of remaining simple, has its bottom pushed up into its interior, like the bottom of a beer-bottle—the introversion being carried so far that the introverted part reaches nearly to the external opening, and leaves scarcely any space between the introverted part and the walls of the sac. It is easy to see that the exfoliation continuing from the surface of the introverted part as well as from the inside of the sac generally, the horny matter cast off will form a double layer; and will come out of the sac in the shape of a tube having within its lower end the introverted part, as the core on which it is moulded, and from the apex of which is cast off the substance filling, less densely, its interior. The structure resulting will be what we know as a hair. Manifestly by progressive enlargement of the sac, and further complication of that introverted part on which the excreted substance is moulded, the protruding growth may be rendered larger and more involved, as we see it in quills and feathers. So that insensible steps, thus indicated in principle, carry us from the exfoliation of epidermis by a flat surface, to the exfoliation of it by a hollow simple sac, an introverted sac, and a sac further complicated; each of which produces its modified kind of tegumentary appendage.

§ 295. Among many other differentiations of the outer tissues, the most worthy to be noticed in the space that remains, are those by which organs of sense are formed. We will begin with the simplest and most closely allied to the foregoing.

Every hair that is not too long or flexible to convey to its rooted end a strain put upon its free end, is a rudimentary tactual organ; as may be readily proved by touching one of those growing on the back of the hand. If, then, a creature has certain hairs so placed that they are habitually touched by the objects with which it deals, or amid which it moves, an advantage is likely to accrue if these hairs are modified in a way that enables them the better to transmit the impressions derived. Such modified hairs we have in the *vibrissæ*, or, as they are commonly called, the "whiskers" possessed by Cats and feline animals generally, as well as by Seals and many Rodents. These hairs are long enough to reach objects at considerable distances; they are so stiff that forces applied to their free ends, cause movements of their imbedded ends; and the sacs containing their imbedded ends being well covered with nerve-fibres, these developed hairs serve as instruments of exploration. By constant use of them the animal learns to judge of the relative positions of objects past which, or towards which, it is moving. When stealthily approaching prey or stealthily escaping enemies, such aids to perception are obviously important: indeed their importance has been proved by the diminished power of self-guidance in the dark, that results from cutting them off. These, then, are dermal appendages originally serving the purpose of clothing, but afterwards differentiated into sense-organs.

That eyes are essentially dermal structures seems scarcely conceivable. Yet an examination of their rudimentary types, and of their genesis in creatures that have them well developed, shows us that they really arise by successive modifications of the double layer composing the integument. They make their first appearance among the simpler animals as specks of pigment, covered by portions of epidermis slightly convex and a little more transparent than that around it. Here their fundamental community of structure with the skin is easy to trace; and the formation of them by differentiation of it presents no difficulty. Not so far in advance of these as much to obscure the relationship, are the eyes which the Crustaceans possess. In every fishmonger's shop we may see that the eyes of a Lobster are carried on pedicles; and when the Lobster casts its shell, the outer coat of each eye, being continuous with the epidermis of its pedicle, is thrown off along with the rest of the exoskeleton. This pedicle, which gives the name of "stalk-eyed" *Crustacea* to a large group, is, strange as it may seem, a transformed limb. Otherwise shown by the homologies of the parts, this truth is made manifest by those transitional cases in which the original form of the limb is retained, and the transparent portion which serves as a visual organ is merely a prominent patch on its under surface, somewhat like a blister, spreading a little up the sides of the limb—an arrangement almost thrusting upon us the suspicion that an eye is a modified portion of the skin. That which the outer appearance suggests is proved by the structure within. Beneath the transparent epidermic layer, there exists a group of eyes of the kind which we see in an insect; and these, according to a high authority, are inclosed in the dermal system. Describing the arrangement of the parts, M. Milne Edwards writes:—"But the most remarkable circumstance is, that the large cavity within which the whole of these parallel columns, every one of which is itself a perfect eye, are contained, is closed posteriorly by a membrane, which appears to be neither more nor less than the middle tegumentary membrane, pierced for the passage of the optic nerve; so that the ocular chamber at large results from the separation at a point of the two external layers of the general envelope." Thus too is it, in the main, even with the highly-developed eyes of the *Vertebrata.* "The three pairs of sensory organs appertaining to the higher senses," says Prof. Huxley—"the nasal sacs, the eyes, and the ears—arise as simple cœcal involutions of the external integument of the head of the embryo. That such is the case, so far as the olfactory sacs are concerned, is obvious, and it is not difficult to observe that the lens and the anterior chamber of the eye are produced in a perfectly similar manner. It is not so easy to see that the the labyrinth of the ear arises in this way, as the sac resulting from the involution of the integument is small, and remains open but a very short time. But I have so frequently verified Huschke's and Remak's statement that it does so arise, that I entertain no doubt whatever of the fact. The outer ends of the olfactory sacs remain open, but those of the ocular and auditory sacs rapidly close up, and shut off their contents from all direct communication with the exterior." So that, marvellous as the fact appears, all that part of the eye which lies between its outer surface and the back of the crystalline lens, is formed in the same way as an ordinary hair-sac, and is composed of homologous parts. The interior coat is the epidermic layer, originally continuous with the surface of the skin; and only made discontinuous with it by closure of the sac at the point which is afterwards the centre of the cornea. This cornea, or front wall of the chamber thus shut off, is consequently composed of a doubled epidermic layer and an intermediate layer of the derma included in the fold of the integument. The crystalline lens, lying at the far side of this chamber, is simply a thickening of the epidermic layer lining that part of the chamber—is developed from it in the same way that the substance of a hair is developed from the papilla at the bottom of its sac. The iris originates as an annular thrusting-in of the walls of this chamber in front of the crystalline lens; and between the two layers of the epidermic lining, thus folded, comes a portion of the derma in which muscular fibres eventually arise. Though the foundation of the part behind the crystalline lens is laid by a hollow *diverticulum* from the brain, which grows outwards to meet the inward-growing tegumentary sac, yet here, too, structures belonging to the tegumentary system eventually predominate. For into this *cul-de-sac* proceeding from the nervous centre, there takes place a lateral growth of dermal tissue, which, introverting the wall of the sac, and presently filling the whole cavity of it, is at last shut off by the closure of the now doubled walls of the sac; and out of this intruding mass of dermal tissue the vitreous humour is formed. That is to say, the eye considered as an optical apparatus is wholly produced by metamorphoses of the skin: the only parts of it not thus produced, being the membranes lying between the sclerotic and the vitreous humour, including those retinal structures formed in them. All is tegumentary save that which has to appreciate the impressions which the modified integument concentrates upon it.

Thus, as Prof. Huxley has somewhere pointed out, there is a substantial parallelism between all the sensory organs in their modes of development: as there is, too, between their modes of action. A *vibrissa* may be taken as their common type. Increased impressibility by an external stimulus, requires an increased peripheral expansion of the nervous system on which the stimulus may fall; and this is secured by an introvertion of the integument, forming a sac on the walls of which a nerve may ramify. That the more extended sensory area thus constituted may be acted upon, there requires some apparatus conveying to it from without the appropriate stimulus; and in the case of the *vibrissa*, this apparatus is the epidermic growth which, under the form of a hair, protrudes from the sac. And that the greatest sensitiveness may be obtained, the external action must be exaggerated or multiplied by the apparatus which conveys it to the recipient nerve; as in the case of the *vibrissa*, it is by the development of a hair into an elastic lever, that transforms the slight force acting through considerable space on its exposed end, into a greater force acting through a smaller space at its rooted end. Similarly with the organs of the higher senses. In a rudimentary eye, we have but a slight peripheral expansion of a nerve to take cognizance of the impression; and to concentrate the impression upon it, there is nothing beyond a thickening of the epidermis into a lens-shape. But the developed eye shows us a termination of the nerve greatly expanded and divided to receive the external stimulus. It shows us an introverted portion of the integument containing the apparatus by which the external stimulus is conveyed to the recipient nerve. The structure developed in this sac not only conveys the stimulus, but also, like its homologue, concentrates it; and in the one case as in the other, the structure which does this is an epidermic growth from the bottom of the sac. Even with the ear it is the same. Again we have an introverted portion of the integument, on the walls of which the nerve is distributed. The otolithes contained in the sac thus formed, are bodies which are set in motion by the vibrations of the surrounding medium, and convey these vibrations in an exaggerated form to the nerves. And though it is not alleged that these otolithes are developed from the epidermic lining of the chamber, yet as, if not so developed, they are concretions from the contents of an epidermic sac, they must still be regarded as epidermic products.

Whether these differentiations are due wholly to indirect equilibration, or whether direct equilibration has had a share in working them, are questions that must be left open. Possibly a short hair so placed on a mammal's face as to be habitually touched, may, by conveying excitations to the nerves and vessels at its root, cause extra growth of the bulb and its appendages, and so the development of a *vibrissa* may be furthered. Possibly too, the light itself, to which the tissues of some inferior animals are everywhere sensitive, may aid in setting up certain of the modifications by which the nervous parts of visual organs are formed—producing, as it must, the most powerful effects at those points on the surface which the movements of the animal expose to the greatest and most frequent contrasts of light and shade; and propagating from those points currents of molecular change through the organism. But it seems clear that the complexities of the sensory organs are not thus explicable. They must have arisen by the natural selection of favourable variations.

§ 296. A group of facts, serving to elucidate those put together in the several foregoing sections, has to be added. I have reserved this group to the last, partly because it is transitional—links the differentiations of the literally outer tissues with those of the truly inner tissues. Though physically internal, the mucous coat of the alimentary canal has a *quasi*-externality from a physiological point of view. As was pointed out in the last chapter, the skin and the assimilating surface have this in common, that they come in direct contact with matters not belonging to the organism; and we saw that along with this community of relation to alien substances, there is a certain community of structure and development. The like holds with the linings of all internal cavities and canals that have external openings.

The transition from the literally outer tissues to those tissues that are intermediate between them and the truly inner tissues, is visible at all the orifices of the body; where skin and mucous membrane are continuous, and the one passes insensibly into the other. This visible continuity is not simply associated with a great degree of morphological continuity, but also with a great degree of physiological continuity. That is to say, these literally outer and *quasi*-outer layers are capable of rapidly assuming one another's structures and functions when subject to one another's conditions. Mucous surfaces, normally kept covered, become skin-like if exposed to the air; but resume more or less fully their normal characters when restored to their normal positions. These are truths familiar to pathologists. They continually meet with proofs that permanent eversion of the mucous membrane, even where it is by prolapse of a part deeply seated within the body, is followed by an adaptation eventually almost complete: originally moist, tender to the touch, and irritated by the air, the surface gradually becomes covered with a thick, dry cuticle; and is then scarcely more sensitive than ordinary integument.

Whether this equilibration between new outer forces and reactive inner forces, which is thus directly produced in individuals, is similarly produced in races, must remain as a question not to be answered in a positive way. On the one hand, we have the fact that among the higher animals there are cases of *quasi*-outer tissues which are in one species habitually ensheathed, while in another species they are not ensheathed; and that these two tissues, though unquestionably homologous, differ as much as skin and mucous membrane differ. On the other hand, there are certain analogous changes of surface, as on the abdomen of the Hermit-Crab, which give warrant to the supposition that survival of the fittest is the chief agent in establishing such differentiations; since the abdomen of a Hermit-Crab, bathed by water within the shell it occupies, is not exposed to physical conditions that directly tend to differentiate its surface from the surface of the thorax. But though in cases like this last, we must assign the result to the natural selection of variations arising incidentally; we may I think legitimately assign the result to the immediate action of changed conditions where, as in cases like the first, we see these producing in the individual, effects of the kinds observed in the race.

However this may be, the force of the general argument remains the same. In these exchanges of structure and function between the outer and *quasi*-outer tissues, we get undeniable proof that they are easily differentiable. And seeing this, we are enabled the more clearly to see how there have, in course of time, arisen those extreme and multitudinous differentiations of the outer tissues that have been glanced at.

## CHAPTER VIII.

### DIFFERENTIATIONS AMONG THE INNER TISSUES OF ANIMALS.

§ 297. The change from the outside of the lips to their inside, introduces us to a new series of interesting and instructive facts, joining on to those with which the last chapter closed. They concern the differentiations of those coats of the alimentary canal, which, as we have seen, are physiologically outer, though physically inner.

These coats are greatly modified at different parts; and their modifications vary greatly in different animals. In the lower types, where they compose a simple tube, running from end to end of the body, they are almost uniform in their histological characters; but on ascending from these types, we find them presenting an increasing variety of minute structures between their two ends. The argument will be adequately enforced if we limit ourselves to the leading modifications they display in some of the higher animals.

The successive parts of the alimentary canal are so placed with respect to its contents, that the physical and chemical changes undergone by its contents while passing from one end to the other, inevitably tend to transform its originally homogeneous surface into a heterogeneous surface. Clearly, the effect produced on the food at any part of the canal by trituration, by adding a secretion, or by absorbing its nutritive matters, implies the delivery of the food into the next part of the canal in a state more or less unlike its previous states—implies that the surface with which it now comes in contact is differently affected by it from the preceding surfaces—implies, that is, a differentiating action. To use concrete language;—food that is broken down in the mouth acts on the œsophagus and stomach in a way unlike that which it would have done had it been swallowed whole; the masticated food, to which certain solvents or ferments are added, becomes to the intestine a different substance from that which it must have otherwise been; and the altered food, resolved by these additions into its proximate principles, cannot have those proximate principles absorbed in the next part of the intestine, without the remoter parts being affected as they would not have been in the absence of absorption. It is true that in developed alimentary canals, such as the reasoning here tacitly assumes, these marked successive differentiations of the food are themselves the results of pre-established differentiations in the successive parts of the canal. But it is also true that actions and reactions like those here so definitely marked, must go on indefinitely in an undeveloped alimentary canal. If the food is changed at all in the course of its transit, which it must be if the creature is to live by it, then it cannot but act dissimilarly on the successive tracts of the alimentary canal, and cannot but be dissimilarly reacted on by them. Inevitably, therefore, the uniformity of the surface must lapse into greater or less multiformity: the differentiation of each part tending ever to initiate differentiations of other parts.

Not, indeed, that the implied process of direct equilibration can be regarded as the sole process. Indirect equilibration aids; and, doubtless, there are some of the modifications which only indirect equilibration can accomplish. But we have here one unquestionable cause—a cause that is known to work in individuals, changes of the kind alleged. Where, for instance, cancerous disease of the œsophagus so narrows the passage into the stomach as to prevent easy descent of the food, the œsophagus above the obstruction becomes enlarged into a kind of pouch; and the inner surface of this pouch begins to secrete juices that produce in the food a kind of rude digestion. Again, stricture of the intestine, when it arises gradually, is followed by hypertrophy of the muscular coat of the intestine above the constricted part: the ordinary peristaltic movements being insufficient to force the food forwards, and the lodged food serving as a constant stimulus to contraction, the muscular fibres, habitually more exercised, become more bulky. The deduction from general principles being thus inductively enforced, we cannot, I think, resist the conclusion that the direct actions and reactions between the food and the alimentary canal have been largely instrumental in establishing the contrasts among its parts. And we shall hold this view with the more confidence on observing how satisfactorily, in pursuance of it, we are enabled to explain one of the most striking of these differentiations, which we will take as a type of the class.

The gizzard of a bird is an expanded portion of the alimentary canal, specially fitted to give the food that trituration which the toothless mouth of the bird cannot give. Besides having a greatly-developed muscular coat, this grinding-chamber is lined with a thick, hard cuticle, capable of bearing the friction of the pebbles swallowed to serve as grind-stones. This differentiation of the mucous coat into a ridged and tubercled layer of horny matter—a differentiation which, in the analogous organs of certain *Mollusca*, is carried to the extent of producing from this membrane bony plates, and even teeth—varies in birds of different kinds, according to their food. It is moderate in birds that feed on flesh and fish, and extreme in granivorous birds and others that live on hard substances. How does this immense modification of the alimentary canal originate? In the stomach of a mammal, the macerating and solvent actions are united with that triturating action which finishes what the teeth have mainly done; but in the bird, unable to masticate, these internal functions are specialized, and while the crop is the maccrating chamber, the gizzard becomes a chamber adapted to triturate more effectually. This adaptation requires simply an exaggeration of certain structures and actions which characterize stomachs in general, and, in a less degree, alimentary canals throughout their whole lengths. The massive muscles of the gizzard are simply extreme developments of the muscular tunic, which is already considerably developed over the stomach, and incloses also the œsophagus and the intestine. The indurated lining of the gizzard, thickened into horny buttons at the places of severest pressure, is nothing more than a greatly strengthened and modified epithelium. And the grinding action of the gizzard is but a specialized form of that rhythmical contraction by which an ordinary stomach kneads the contained food, and which in the œsophagus effects the act of swallowing, while in the intestine it becomes the peristaltic motion. Allied as the gizzard thus clearly is in structure and action to the stomach and alimentary canal in general; and capable of being gradually differentiated from a stomach where a growing habit of swallowing food unmasticated entails more trituration to be performed before the food passes the pylorus; the question is—Does this change of structure arise by direct adaptation? There is warrant for the belief that it does. Besides such collateral evidence as that mucous membrane becomes horny on the toothless gums of old people, when subject to continual rough usage, and that the muscular coat of the intestine thickens where unusual activity is demanded of it, we have the direct evidence of experiment. Hunter habituated a sea-gull to feed upon grain, and found that the lining of its gizzard became hardened, while the gizzard-muscles doubled in thickness. A like change in the diet of a kite was followed by like results. Clearly, if differentiations so produced in the individuals of a race under changed habits, are in any degree inheritable, a structure like a gizzard will originate through the direct actions and reactions between the food and the alimentary canal.

Another case—a very interesting one, somewhat allied to this—is presented by the ruminating animals. Here several dilatations of the alimentary canal precede the true stomach; and in these, large quantities of unmasticated food are stored, to be afterwards returned to the mouth and masticated at leisure. What conditions have made this specialization advantageous? and by what process has it been established? To both these questions the facts indicate answers which are not unsatisfactory. Creatures that obtain their food very irregularly—now having more than they can consume, and now being for long periods without any—must, in the first place, be apt, when very hungry, to eat to the extreme limits of their capacities; and must, in the second place, profit by peculiarities which enable them to compensate themselves for long fasts, past and future. A perch which, when its stomach is full of young frogs, goes on filling its œsophagus also; or a trout which, rising to the fisherman's fly, proves when taken off the hook to be full of worms and insect-larvæ up to the very mouth, gains by its ability to take in such unusual supplies of food when it meets with them—obviously thrives better than it would do could it never eat more than a stomachful. That this ability to feed greatly in excess of immediate requirement, is one that varies in individuals of the same race, we see in the marked contrast between our own powers in this respect, and the powers of uncivilized men; whose fasting and gorging are to us so astonishing. Carrying with us these considerations, we shall not be surprised at finding dilatations of the œsophagus in vultures and eagles, which get their prey at long intervals in large masses; and we may naturally look for them too in birds like pigeons, which, coming in flocks upon occasional supplies of grain, individually profit by devouring the greatest quantity in a given time. Now where the trituration of the food is, as in these cases, carried on in a lower part of the alimentary canal, nothing further is required than the storing-chamber; but for a mammal, having its grinding apparatus in its mouth, to gain by the habit of hurriedly swallowing unmasticated food, it must also have the habit of regurgitating the food for subsequent mastication. This correlation of habits with their answering structures, may, as we shall see, arise in a very simple way. The starting point of the explanation is a familiar fact—the fact that indigestion, often resulting from excess of food, is apt to cause that reversed peristaltic action known as vomiting. From this we pass to the fact, also within the experience of most persons, that during slight indigestion the stomach sometimes quietly regurgitates a small part of its contents as far as the back of the mouth—giving an unpleasant acquaintance with the taste of the gastric juices. Exceptional facts of the same class help the argument a step further. "There are certain individuals who are capable of returning, at will, a greater or smaller portion of the contents of the digesting stomach into the cavity of the mouth. * * * In some of these cases, the expulsion of the food has required a violent effort. In the majority, it has been easily evoked or suppressed. While in others, it has been almost uncontrollable; or its non-occurrence at the habitual time has been followed by a painful feeling of fulness, or by the act of vomiting." Here then we have a certain physiological action, occasionally happening in most persons and in some developed into a habit more or less pronounced: indigestion being the habitual antecedent. Suppose then that gregarious animals, living on innutritive food such as grass, are subject to a like physiological action, and are capable of like variations in the degree of it. What will naturally happen? They wander in herds, now over places where food is scarce and now coming to places where it is abundant. Some masticate their food completely before swallowing it; while some masticate it incompletely. If an oasis, presently bared by their grazing, has not supplied the whole herd a full meal, then the individuals which masticate completely will have had less than those which masticate incompletely—will not have had enough. Those which masticate incompletely and distend their stomachs with food difficult to digest, will be liable to these regurgitations; but if they re-masticate what is thus returned to the mouth (and we know that animals often eat again what they have vomited), then the extra quantity of food taken, eventually made digestible, will yield them more nourishment than is obtained by those which masticate completely at first. The habit initiated in this natural way, and aiding survival when food is scarce, will be apt to cause modifications of the alimentary canal. We know that dilatations of canals readily arise under habitual distensions. We know that canals habitually distended become gradually more tolerant of the contained masses that at first irritated them. And we know that there commonly take place adaptive modifications of their surfaces. Hence if a habit of this kind and the structural changes resulting from it, are in any degree inheritable, it is clear that, increasing in successive generations, both immediately by the cumulative effect of repetitions and mediately by survival of the individuals in which they are most decided, they may go on until they end in the peculiarities which Ruminants display.

§ 298. There are structures belonging to the same group which cannot, however, be accounted for in this way. They are the organs that secrete special products facilitating digestion—the liver, pancreas, and various smaller glands. All these appendages of the alimentary canal, large and independent as some of them seem, really arise by differentiations from its coats. The primordial liver, as we see it in a simple animal such as the *Planaria*, consists of nothing more than bile-cells scattered along a tract of the intestinal surface. Accumulation of these bile-cells is accompanied by increased growth of the surface which bears them—a growth which at first takes the form of a *cul-de-sac*, having an outside that projects from the intestine into the peri-visceral cavity.

As the mass of bile-cells becomes greater, there arise secondary lateral cavities opening into the primary one, and through it into the intestine; until eventually these cavities with their coatings of bile-cells, become ramifying ducts distributed through the solid mass we know as a liver. How is this differentiation caused?

Before attempting any answer to this question, it is requisite to inquire the nature of bile. Is that which the liver throws into the intestines a waste product of the organic actions? or is it a secretion aiding digestion? or is it mixture of these? Modern investigations imply that it is most likely the last. The liver is found to have a compound function. Bernard has proved to the satisfaction of physiologists, that there goes on in it a formation of glycogen—a substance that is transformed into sugar before it leaves the liver and is afterwards carried away by the blood to eventually disappear in the lungs. It is also shown, experimentally, that there are generated in the liver certain biliary acids; and by the aid either of these or of some other compounds, it is clear that bile renders certain materials more absorbable: its effect on fat is demonstrable out of the body; and the greatly diminished absorption of fat from the food when the discharge of bile into the intestine is prevented, is probably one of the causes of that pining away that results. But while recognizing the fact that the bile consists in part of a solvent, or solvents, aiding digestion, there is abundant evidence that one element of it is an effete product; and probably this is the primary element. The yellow-green substance called biliverdine, which gives its colour to bile, is found in the blood before it reaches the liver; which is not the case with the glycogen or the biliary acids. "As soon as the biliary secretion is in abeyance," says Dr. Harley, the most recent authority on the subject, "biliverdine accumulates in the blood (until the serum is as it were completely saturated with the pigment), from which it exudes and stains the tissues, and produces the colour we term jaundice;"

* * * "the urine assumes a saffron tint in consequence of the elimination of the colouring matter by the kidneys;" and afterwards "the sweat, the milk, the tears, the sputa" become yellow. We have clear proof, then, that biliverdine is an excrementitious matter, which, if not got rid of through the liver, makes its way out, to some extent, through other organs, producing in them more or less derangement—itching of the skin, and sometimes, in the kidneys, a secondary disease. That of the bile discharged into the intestine, only some components are re-absorbed, is demonstrated by the fact that when injected into the blood, bile destroys life in less than twenty-four hours; and that biliverdine is not among the re-absorbed components, is shown both by the persistence of the colour which it gives to the substances in the intestine, and by the absence of that jaundice which, if re-absorbed, it would produce. Hence we are warranted in classing biliverdine as a waste product. And considering that the bile-cells, where they first make their appearance among animals, are distinguished by the colour ascribable to this substance, we may fairly infer that the excretion of biliverdine is the original function of the liver.

One further preliminary is requisite. We must for a moment return to those physico-chemical data, set down in the first chapter of this work (§§ 7—8.) We there saw that the complex and large-atomed colloids which mainly compose living organic matter, have extremely little molecular mobility; and, consequently, extremely little power of diffusing themselves. Whereas we saw not only that those absorbed matters, gaseous and liquid, which further the decomposition of living organic matter, have very high diffusibilities; but also that the products of the decomposition are much more diffusible than the components of living organic matter. And we saw that, as a consequence of this, the tissues give ready entrance to the substances that decompose them, and ready exit to the substances into which they are decomposed. Hence it follows that, primarily, the escape of effete matters from the organism, is a physical action parallel to that which goes on among mixed colloids and crystalloids that are dead or even inorganic. Excretion is simply a specialized form of this spontaneous action; and what we have to inquire is,—how the specialization arises.

Two causes conspire to establish it. The first is that these products of decomposition are diffusible in widely different degrees. While the carbonic acid and water permeate the tissues with ease in all directions, and escape more or less from all the exposed surfaces, urea, and other waste substances incapable of being vaporized, cannot escape thus readily. The second is that the different parts of the organism, being subject to different physical conditions, are from the outset sure severally to favour the exit of these various products of decomposition in various degrees. How these causes must have co-operated in localizing the excretions, we shall see on remembering how they now co-operate in localizing the separation of morbid materials. The characteristic substances of gout and rheumatism have their habitual places of deposit. Tuberculous matter, though it may be present in various organs, gravitates towards some much more than towards others. Certain products of disease are habitually got rid of by the skin, instead of collecting internally. Mostly, these have special parts of the skin which they affect rather than the rest; and there are those which, by breaking out symmetrically on the two sides of the body, show how definitely the places of their excretion are determined by certain favouring conditions, which corresponding parts may be presumed to furnish in equal degrees. Further, it is to be observed of these morbid substances circulating in the blood, that having once commenced segregating at particular places, they tend to continue segregating at those places. Assuming, then, as we may fairly do, that this localization of excretion, which we see continually commencing afresh with morbid matters, has always gone on with the matters produced by the waste of the tissues, let us take a further step, and ask how localizations become fixed. Other things equal, that which from its physical conditions is a place of least resistance to the exit of an effete product, will tend to become established as the place of excretion; since the rapid exit of an effete product will profit the organism. Other things equal, a place at which the excreted matter produces least detrimental effect will become the established place. If at any point the excreted matter produces a beneficial effect, then, other things equal, natural selection will determine it to this point. And if facility of escape anywhere goes along with utilization of the escaping substance, then, other things equal, the excretion will be there localized by survival of the fittest.

Such being the conditions of the problem, let us ask what will happen with the lining membrane of the alimentary canal. This, physiologically considered, is an external surface; and matters thrown off from it make their way out of the body. It is also a surface along which is moving the food to be digested. Now, among the various waste products continually escaping from the living tissues, some of the more complex ones, not very stable in composition, are likely, if added to the food, to set up changes in it. Such changes may either aid or hinder the preparation of the food for absorption. If an effete matter, making its exit through the wall of the intestine, hinders the digestive process, the enfeeblement and disappearance of individuals in which this happens, will prevent the intestine from becoming the established place for its exit. While if it aids the digestive process, the intestine will, for converse reasons, become more and more the place to which its exit is limited. Equally manifest is it that if there is one part of this alimentary canal at which, more than at any other part, the favourable effect results, this will become the place of excretion. If from this general statement we pass to the special case before us, we find our data to be these:—The substance to be excreted, biliverdine, a waste product of the organic actions, is, as jaundice shows us, capable of escaping out of the body through all its surfaces, even in so differentiated a type as the highest mammal; and in the undifferentiated types we may infer that the facility of escape is nearly the same through all the surfaces. For the gradual localization of its escape at a particular part of the intestinal surface, it is requisite only that either some disadvantage consequent on its escape elsewhere should be avoided, or some advantage due to its effect on digestion should be gained; and this advantage may be either direct or indirect. It is not necessary that the biliverdine should itself act on the food: it is enough if it aids in the elaboration of other matters, either nutritive or solvent. If its presence causes or furthers the formation of glycogen from other components of the blood; or if it sets up the complex reactions which generate the biliary acids; these effects will suffice to establish, as the place of its excretion, the place where these products are useful. And once this place of excretion having been established, the development of a liver is simply a question of time and natural selection.

Whether in this case, as well as in the cases of the exclusively secreting glands formed along the alimentary canal (to which a modification of the foregoing argument is applicable), any tendency to localization results from the immediate action of the local conditions, is an interesting question. It is possible that the contrasts between the intra-vascular and extra-vascular liquids at these places may be a factor in the differentiation, as in a case already dealt with. (§ 292.) But this possibility must be left undiscussed.

§ 299. A differentiation of another order occurring in the alimentary canal, is that by which a part of it is developed into a lateral chamber or chambers, through which carbonic acid exhales and oxygen is absorbed. Comparative anatomy and embryology unite in showing that a lung is formed, just as a liver or other appendage of the alimentary canal is formed, by the growth of a hollow bud into the peri-visceral cavity, or space between the alimentary canal and the wall of the body. The interior of this bud is simply a *cul-de-sac* of the alimentary canal, with the mucous lining of which its own mucous lining is continuous. And the development of this *cul-de-sac* into an air-chamber, simple or compound, is merely a great extension of area in the internal surface of the *cul-de-sac*, along with that specialization which fits it for excreting and absorbing substances different from those which other parts of the mucous surface excrete and absorb. These lateral air-chambers, universal among the higher *Vertebrata* and very general among the lower, and everywhere attached to the alimentary canal between the mouth and the stomach, have not in all cases the respiratory function. In most fishes that have them they are what we know as swim-bladders. In some fishes the cavities of these swim-bladders are completely shut off from the alimentary canal: nevertheless showing, by the communications which they have with it during the embryonic stages, that they are originally *diverticula* from it. In other fishes there is a permanent *ductus pneumaticus*, uniting the cavity of the swim-bladder with that of the gullet—the function, however, being still not respiratory in an appreciable degree, if at all. But in certain still extant representatives of the sauroid fishes, as the *Lepidosteus*, the air-bladder is "divided into two sacs that possess a cellular structure," and "the trachea which proceeds from it opens high-up in the throat, and is surrounded with a glottis." In the *Amphibia* the corresponding organs are chambers over the surfaces of which there are saccular depressions, indicating a transition towards the air-cells characterizing lungs; and accompanying this advance we see, as in the common *Triton*, the habit of coming up to the surface and taking down a fresh supply of air in place of that discharged.

How are the internal air-chambers, respiratory or non-respiratory, developed? Upwards from the amphibian stage, in which they are partially refilled at long intervals, there is no difficulty in understanding how, by infinitesimal steps, they pass into complex and ever-moving lungs. But how is the differentiation that produces them initiated? How comes a portion of the internal surface to be specialized for converse with a medium to which it is not naturally exposed? The problem appears a difficult one; but there is a not unsatisfactory solution of it.

When many gold-fish are kept in a small aquarium, as with thoughtless cruelty they frequently are, they swim close to the surface, so as to breathe that water which is from instant to instant absorbing fresh oxygen. In doing this they often put their mouths partly above the surface, so that in closing them they take in bubbles of air; and sometimes they may be seen to continue doing this—the relief due to the slight extra aëration of blood so secured, being the stimulus to continue. Air thus taken in may be detained. If a fish that has taken in a bubble turns its head downwards, the bubble will ascend to the back of its mouth, and there lodge; and coming within reach of the contractions of the œsophagus, it may be swallowed. If, then, among fish thus naturally led upon occasion to take in air-bubbles, there are any having slight differences in the alimentary canal that facilitate lodgment of the air, or slight nervous differences such as in human beings cause an accidental action to become "a trick," it must happen that if an advantage accrues from the habitual detention of air-bubbles, those individuals most apt to detain them, will, other things equal, be more likely than the rest to survive; and by the survival of descendants inheriting their peculiarities in the greatest degrees, and increasing them, an established structure and an established habit may arise. And that they do in some way arise we have proof: the common Loach is well known to swallow air, which it afterwards discharges loaded with carbonic acid.

From air thus swallowed the advantages that may be derived are of two kinds. In the first place, the fish is made specifically lighter, and the muscular effort needed to keep it from sinking is diminished—or, indeed, if the bubble is of the right size, is altogether saved. The contrast between the movements of a Goby, which, after swimming up towards the surface falls rapidly to the bottom on ceasing its exertions, and the movements of a Trout, which remains suspended just balancing itself by slight undulations of its fins, shows how great an economy results from an internal float, to fishes which seek their food in mid-water or at the surface. Hence the habit of swallowing air having been initiated in the way described, we see why natural selection will, in certain fishes, aid modifications of the alimentary canal favouring its lodgment—modifications constituting air-sacs. In the second place, while from air thus lodged in air-sacs thus developed, the advantage will be that of flotation only if the air is infrequently changed or never changed; the advantage will be that of supplementary respiration if the air-sacs are from time to time partially emptied and refilled. The requirements of the animal will determine which of the two functions predominates. Let us glance at the different sets of conditions under which these divergent modifications may be expected to arise.

The respiratory development is not likely to take place in fishes that inhabit seas or rivers in which the supply of aërated water never fails: there is no obvious reason why the established branchial respiration should be replaced by a pulmonic respiration. Indeed, if a fish's branchial respiration is adequate to its needs, a loss would result from the effort of coming to the surface for air; especially during those first stages of pulmonic development when the extra aëration achieved was but small. Hence in fishes so circumstanced, the air-chambers arising in the way described would naturally become specialized mainly or wholly into floats. Their contained air being infrequently changed, no advantage would arise from the development of vascular plexuses over their surfaces; nothing would be gained by keeping open the communication between them and the alimentary canal; and there might thus eventually result closed chambers the gaseous contents of which, instead of being obtained from without, were secreted from their walls, as gases often are from mucous membranes. Contrariwise, aquatic vertebrata in which the swallowing of air-bubbles, becoming habitual, had led to the formation of sacs that lodged the bubbles; and which continued to inhabit waters not always supplying them with sufficient oxygen; might be expected to have the sacs further developed, and the practice of changing the contained air made regular, if either of two advantages resulted—either the advantage of being able to live in old habitats that had become untenable without this modification, or the advantage of being able to occupy new habitats. Now it is just where these advantages are gained that we see the pulmonic respiration coming in aid of the branchial respiration, and in various degrees replacing it. Shallow waters are liable to three changes which conspire to make this supplementary respiration beneficial. The summer's sun heats them, and raising the temperatures of the animals they contain, accelerates the circulation in these animals, exalts their functional activities, increases the production of carbonic acid, and thus makes aëration of the blood more needful than usual. Meanwhile the heated water, instead of yielding to the highly carbonized blood brought to the branchiæ the usual quantity of oxygen, yields less than usual; for as the heat of the water increases, the quantity of air it contains diminishes. And this greater demand for oxygen joined with smaller supply, pushed to an extreme where the water is nearly all evaporated, is at last still more intensely felt in consequence of the excess of carbonic acid discharged by the numerous creatures congregated in the muddy puddles that remain. Here, then, it is, that the habit of taking in air-bubbles is likely to become established, and the organs for utilizing them developed; and here it is, accordingly, that we find all stages of the transition to aërial respiration. The Loach before-mentioned, which swallows air, frequents small waters liable to be considerably warmed; and the *Cuchia*, an anomalous eel-shaped fish, which has vascular air-sacs opening out at the back of the mouth, "is generally found lurking in holes and crevices, on the muddy banks of marshes or slow-moving rivers." Still more significant is the fact that the *Lepidosiren*, or "mud-fish" as it is called from its habits, is the only true fish that has lungs. But it is among the *Amphibia* that we see most conspicuously this relation between the development of air-breathing organs, and the peculiarities of the habitats. Pools, more or less dissipated annually, and so rendered uninhabitable by most fishes, are very generally peopled by these transitional types. Just as we see, too, that in various climates and in various kinds of shallow waters, the supplementary aërial respiration is needful in different degrees; so do we find among the *Amphibia* many stages in the substitution of the one respiration for the other. The facts, then, are such as give to the hypothesis a *vraisemblance* greater than could have been expected.

The relative effects of direct and indirect equilibration in establishing this further heterogeneity, must, as in many other cases, remain undecided. The habit of taking in bubbles is scarcely interpretable as a result of spontaneous variation: we must regard it as arising accidentally during the effort to obtain the most aërated water; as being persevered in because of the relief obtained; and as growing by repetition into a tendency bequeathed to offspring, and by them, or some of them, increased and transmitted. The formation of the first slight modifications of the alimentary canal favouring the lodgment of bubbles, is not to be thus explained. Some favourable variation in the shape of the passage must here have been the initial step. But the gradual increase of this structural modification by the survival of individuals in which it is carried furthest, will, I think, be all along aided by immediate adaptation. The part of the alimentary canal previously kept from the air, but now habitually in contact with the air, must be in some degree modified by the action of the air; and the directly-produced modification, increasing in the individual and in successive individuals, cannot cease until there is a complete balance between the actions of the changed agency and the changed tissue. It is indeed probable that the growth as well as the differentiation of the pulmonic surface, when once commenced, will be furthered by the direct process. The reasoning before used in the case of branchiæ (§ 292) applies in the case of lungs. If exchange between the plasma in the blood-vessels and the plasma in the tissues surrounding them, goes on with a rapidity that becomes greater where the difference between them becomes greater; if, consequently, at some place where the carbonized plasma inside the blood-vessels is brought close to an unusually decarbonized or much oxygenated plasma outside of the blood-vessels, the exchange of these liquids becomes unusually active; if, as a result, the circulation in the part is augmented; then it is to be inferred that the extra nutrition will cause extra growth. The surface of the rudimentary lung will increase in area so long as the capillary osmose is much greater than in other parts of the body; and it will continue to be greater until, by the extension of the aërating surface, the respiratory exchange has been rendered so efficient as to bring down the contrast between the intra-vascular and extra-vascular liquids to a level with the contrasts between the intra-vascular and extra-vascular liquids in other organs. That is to say, the growth which this direct action produces, will go on until the functional efficiency of the lungs is in equilibrium with the functional efficiencies of other parts throughout the organism.

§ 300. We come now to differentiations among the truly inner tissues—the tissues which have direct converse neither with the environment nor with the foreign substances taken into the organism from the environment. These, speaking broadly, are the tissues which lie between the double layer forming the integument with its appendages, and the double layer forming the alimentary canal with its *diverticula.* We will take first the differentiation which produces the vascular system.

Certain forces producing and aiding distribution of liquids in animals, come into play before any vascular system exists; and continue to further circulation after the development of a vascular system. The first of these is osmotic exchange, acting locally and having an indirect general action; the second is osmotic distension, acting generally and having an indirect local action; the third is local variation of pressure which movement of the body throws on the tissues and their contained liquids. A few words are needed in elucidation of each. If in any creature, however simple, different changes are going on in parts that are differently conditioned —if, as in a *Hydra*, one surface is exposed to the surrounding medium while the other surface is exposed to dissolved food; then between the unlike liquids which the dissimilarly-placed parts contain, osmotic currents must arise; and a movement of liquid through the intermediate tissue must go on as long as an unlikeness between the liquids is kept up. This primary cause of re-distribution remains one of the causes of re-distribution in every more-developed organism: the passage of matters into and out of the capillaries is everywhere thus set up. And obviously in producing these local currents, osmose must also indirectly produce general currents, or aid them if otherwise produced. Osmose, however, still further aids circulation by the liquid pressure which it establishes throughout the organism. More marked than the contrasts between the liquids in some parts and those in other parts, is the contrast between the whole mass of liquid in the animal and the liquid bathing its surfaces—either the water in which it is immersed, or the water taken into its alimentary canal. Its blood and all its juices being denser than water, the result is an osmotic absorption tending ever to distend all its permeable parts—its tissues, and its vessels when it has them. But these vessels and tissues are elastic; and if distended must everywhere compress their contents—must tend, therefore, to squeeze out their contents where there is least resistance. Consequently, if at any place there is an abstraction of nutritive liquid, either for growth or function, more nutritive liquid will be forced towards that place. This cause of currents, which cannot fail to work throughout the distended tissues even of animals that are without blood-vessels, comes more actively into play where the body is everywhere traversed by these branching tubes with elastic walls. When we learn that the pressure of blood within the arteries and veins of a mammal varies from some 3 lbs. to ¼ of a lb. per square inch, we see, on averaging this pressure, that the coats of the vascular system exert considerable force on the blood. This average pressure cannot be due to the heart's action; since if, in the absence of the heart's action, the whole mass of the blood in the vascular system were not above atmospheric pressure, the heart's action could not produce a pressure above that of the atmosphere in one part of the vascular system without lowering the pressure below that of the atmosphere in another part of the vascular system. Hence it follows that irrespective of the heart's action, the distended walls of the vascular system must so compress the blood, as to cause a flow of it towards places where its escape is least resisted—towards places, that is, where it is most rapidly abstracted by function or growth. This is a cause of distribution which is at work before any central organ of circulation exists. Though in the rudimentary vascular systems of the simpler animals, the osmotic distension is probably nothing like so great, there must be some of it; and in the absence of a pumping organ, this force is probably an important aid to that movement of the blood which the functions set up. How the third cause—the changes of internal pressure which an animal's movements produce—furthers circulation, will be sufficiently manifest. That parts which are bent or strained necessarily have their contained vessels squeezed, has been before shown (§ 281); and whether the bend or strain is caused, as in a plant, by an external force, or, as usually in an animal, by an internal force, there must be a thrusting of the liquids towards places of least resistance—that is, towards places of greatest consumption. This which in animals without hearts is a main agent of circulation, continues to further it very considerably even among the highest animals. There is experimental proof of the fact. The pressure in the jugular vein of a horse, which is about ⅜ of a pound per square inch while the muscles are at rest, rises to 2½ lbs. per square inch when the muscles are contracted to raise the head. Such, then, are the several forces we have to take into account in studying the genesis of the vascular system. Let us now pass to the facts to be interpreted.

Even in such simple types as the *Hydrozoa*, cavities in the sarcode faintly indicate a structure that facilitates the transfer of nutritive matters. These vacuoles, possibly caused by the contraction of colloid substance in passing from the soluble to the insoluble state, become reservoirs filled with the plasma that slowly oozes through the sarcode; and every movement of the animal, accompanied as it must be by changed pressures and tensions on these reservoirs, tends here to fill them and there to squeeze out their contents in that or the other direction—possibly aiding to produce, by union of several vacuoles, those lacunæ or irregular canals which the sarcode in some cases presents.

Irregular canals of this kind, not lined with any membranes but being simply cavities running through the flesh, mainly constitute the vascular system in *Molluscoida* and many *Mollusca*. In the simplest of these types the nutritive liquid, absorbed into the cavity of the peri-visceral sac, is thrust hither and thither through this sac with every change in the creature's attitude, and simultaneously fills some of the sinuses which open out of this sac and run through the substance of the body. This distribution of the plasma, which muscular movement and osmotic distension here combine to aid, is, in somewhat more developed types, further aided by a rudimentary heart: in the peri-visceral sac is seated an open-mouthed tube, along which a wave of contraction proceeds, first for a while in one direction and then again in the opposite direction. The higher orders of *Mollusca* have this simple contractile tube developed into a branched system of vessels or arteries, which run into the substance of the body and end in lacunæ or simple fissures. This ending in lacunæ takes place at various distances from the vascular centre. In some genera the arterial structure is carried to the periphery of the blood-system, while in others it stops short midway. Throughout most orders of the *Mollusca* the back current of blood continues to be carried by channels of the original kind: there are no true veins, but the blood having been delivered into the tissues, finds its way back to the peri-visceral cavity through inosculating sinuses. Among the Cephalopods, however, the afferent blood-canals, as well as the efferent ones, acquire distinct walls; but even here the shutting off of the vascular system from the general cavity of the body is not complete; since there are still certain veins which empty themselves into the peri-visceral sac. Putting together these facts we may see pretty clearly the stages of vascular development. From the original reservoir of nutritive liquid between the alimentary canal and the wall of the body, a portion is partially shut off; and by the vermicular contraction of the open tube thus formed, there is produced a more rapid transfer of the nutritive liquid from one part of the peri-visceral sac to another, than was originally produced by the motions of the animal. Clearly, the extension of this contractile tube and the development from it of branches running hither and thither into the tissues, must, by defining the channels of the blood throughout a part of its course, render its distribution more regular and active. As fast as this centrifugal growth of definite channels advances, so fast are the efferent currents of blood, prevented from escaping laterally, obliged to move from the centre towards the circumference; and so fast also does the less-developed set of channels become, of necessity, occupied by afferent currents. When, by a parallel increase of definiteness, the lacunæ and irregular sinuses through which the afferent currents pass, become transformed into veins, the accompanying disappearance of all stagnant or slow-moving collections of blood, implies a further improvement in the circulation.

By what agency is effected this differentiation of a definite vascular system from the indefinite peri-visceral sac? No sufficient reply is obvious. The genesis of the primordial heart is not comprehensible as a result of direct equilibration; and we cannot readily see our way to it as a result of indirect equilibration; for it is difficult to imagine what favourable variation natural selection could have seized hold of to produce such a structure. A contractile tube that aided the distribution of nutritive liquid, being once established, survival of the fittest would suffice for its gradual extension and its successive modifications. But what were the early stages of the contractile tube, while it was yet not sufficiently formed to help circulation, and while it must nevertheless have had some advantage without which no selective process could go on? This part of the question we must leave as at present insoluble. To another part of the question, however, an answer may be ventured. If we ask the origin of those ramifying channels which, first appearing as simple channels, eventually become vessels having definite walls, a reply admitting of considerable justification, is, that the currents of nutritive liquid forced and drawn hither and thither through the tissues themselves initiate these channels. We know that streams running over and through solid and quasi-solid inorganic matter, tend to excavate definite courses. We saw reason for concluding that the development of sap-channels in plants conforms to this general principle. May we not then suspect that the nutritive liquid contained in the tissue of a simple animal, made to ooze now in this direction and now in that by osmotic distension and by the changes of pressure which the animal's movements cause, comes to have certain lines along which it is thrust backwards and forwards more than along other lines; and must by repeated passings make these more and more permeable, until they become lacunæ? Such actions will inevitably go on;. and such actions appear competent to produce some, at least, of the observed effects. The leading facts which indicate that this is a part cause of vascular development, are these.

Growths normally recurring in certain places at certain intervals, are accompanied by local formations of blood-vessels. The periodic maturation of ova among the *Mammalia*, supplies an instance. Through the stroma of an ovarium are distributed innumerable minute vesicles, which, in their early stages, are microscopic. Of these, severally contained in their minute ovi-sacs, any one may develop: the determining cause being probably some slight excess of nutrition. When the development is becoming rapid, the capillaries of the neighbouring stroma increase and form a plexus on the walls of the ovi-sac. Now since there is no typical distribution of the developing ova; and since the increase of an ovum to a certain size precedes the increase of vascularity round it; we can scarcely help concluding that the setting up of currents towards the point of growth determines the formation of the blood-vessels. It may be that having once commenced, this local vascular structure completes itself in a typical manner; but it seems clear that this greater development of blood-vessels around the growing ovum is initiated by the draught towards it. Abnormal growths show still better this relation of cause and effect. The false membranes sometimes found in the bronchial tubes in croup, may perhaps fairly be held abnormal in but a partial sense: it may be said that their vascular systems are formed after the type of the membranes to which they are akin. But this can scarcely be said of the morbid growths classed as malignant. The blood-vessels in an encephaloid cancer, are led to enlarge and ramify, often to an immense extent, by the unfolding of the morbid mass to which they carry blood. Alien as is the structure as a whole to the type of the organism; and alien in great measure as is its tissue to the tissue on which it is seated; it nevertheless happens that the growth of the alien tissue and accompanying abstraction of materials from the blood-vessels, determine a corresponding growth of these blood-vessels. Unless, then, we say that there is a providentially-created type of vascular structure for each kind of morbid growth (and even this would not much help us, since the vascular structure has no constancy within the limits of each kind), we are compelled to admit that in some way or other the currents of blood are here directly instrumental in forming their own channels. One more piece of evidence, before cited as exemplifying adaptation (§ 67), may be called to mind. When any main channel for blood, leading to or from a certain part of the body, has been rendered impervious, others among the channels leading to or from this same part, enlarge to the extent requisite for fulfilling the extra function that falls upon them: the enlargement being caused, as we must infer, by the increase of the currents carried.

Here then are facts warranting inductively the deduction above drawn. It is true that we are left in the dark respecting the complexities of the process. How the channels for blood come to have limiting membranes, and many of them muscular coats, the hypothesis does not help us to say. But the evidence assigned goes far to warrant the belief that vascular development is initiated by direct equilibration; though indirect equilibration may have had the larger share in establishing the structures which distinguish finished vascular systems.

§ 301. Of the inner tissues which remain let us next take bone. In what manner is differentiated this dense substance serving in most cases for internal support?

Already when considering the vertebrate skeleton under its morphological aspect (§ 256) it was pointed out that the formation of dense tissues, internal as well as external, is, in some cases at least, brought about by the mechanical forces to be resisted. Through what process it is brought about we could not then stay to inquire: this question being not morphological but physiological. Answers to some kindred questions have since been attempted. Certain actions to which the internal dense tissues of plants may be ascribed, have been indicated; and more recently, analogous actions have been assigned as causes of some external dense tissues of animals. We have now to ask whether actions of the same nature have produced these internal dense tissues of animals.

The problem is an involved one. Bones have more than one stage: they are membranous or cartilaginous before they become osseous; and their successive component substances so far differ that the effects of mechanical actions upon them differ. And having to deal with transitional states in which bone is formed of mixed tissues, having unlike physical properties and unlike minute structures, the effects of strains become too complicated to follow with precision. Anything in the way of interpretation must therefore be regarded as tentative. If analysis and comparison show that the phenomena are not inconsistent with the hypothesis of mechanical genesis, it is as much as can be expected. Let us first observe more nearly the mechanical conditions to which bones are subject.

The endo-skeleton of a mammal with the muscles and ligaments holding it together, may be rudely compared to a structure built up of struts and ties; of which, speaking generally, the struts bear the pressures and the ties bear the tensions. The framework of an ordinary iron roof will give an idea of the functions of these two elements, and of the mechanical characters required by them. Such a framework consists partly of pieces that have each to bear a thrust in the direction of its length, and partly of pieces that have each to bear a pull in the direction of its length; and these struts and ties are differently formed to adapt them to these different strains. Further, it should be remarked that though the rigidity of the framework depends on the ties which are flexible, as much as on the struts which are stiff, yet the ties help to give the rigidity simply by so holding the struts in position that they cannot escape from the thrusts which fall on them. Now the like relation holds with a difference among the bones and muscles—the difference being, that here the ties admit of being lengthened or shortened and the struts of being moved about upon their joints. The mechanical relations are not altered by this however. The actions are of essentially the same kind in an animal that is standing, or keeping itself in a strained attitude, as in one that is changing its attitude—the same in so far that we have in each a set of flexible parts that are pulling and a set of rigid parts that are resisting. It needs but to remember the sudden collapse and fall that take place when the muscles are paralyzed, or to remember the inability of a bare skeleton to support itself, to see that the struts without the ties cannot suffice. And we have but to think of the formless mass into which a man would sink when deprived of his bones, to see that the ties without the struts cannot suffice. To trace the way in which a particular bone has its particular thrust thrown upon it, may not always be practicable. Though it is easy to perceive how a flexor or extensor of the arm causes by its tension a reactive pressure along the line of the humerus, and is enabled to produce its effect only by the rigidity of the humerus; yet it is not so easy to perceive how such bones as those of a horse's haunch are similarly acted upon. Still, as the weight of the hind quarters has to be transferred from the pelvis to the feet, and must be so transferred through the bones, it is manifest that though these bones form a very crooked line, the weight must produce a pressure along the axis of each: the muscles and ligaments concerned serving here, as in other cases, so to hold the bones that they bear the pressure instead of being displaced by it. Not forgetting that many processes of the bones have to bear tensions, we may then say that generally, though by no means universally, bones are internal dense masses that have to bear pressures—pressures which in the cylindrical bones become longitudinal thrusts. Leaving out exceptional cases, let us consider bones as masses thus circumstanced.

When giving reasons for the belief that the vertebrate skeleton is mechanically originated, one of the facts put in evidence was, that in the vertebrate series the transition from the cartilaginous to the osseous spine begins peripherally (§ 257): each vertebra being at first a ring of bone surrounding a mass of cartilage. And it was pointed out that this peripheral ossification is ossification at the region of greatest pressures. Now it is not vertebræ only that follow this course of development. In a cylindrical bone, though it is differently circumstanced, the places of commencing ossification are still the places on which the severest stress falls. Let us consider how such a bone that has to bear a longitudinal pressure is mechanically affected. If the end of a walking-cane be thrust with force against the ground, the cane bends; and partially resuming its straightness when relieved, again bends, usually towards the same side, when the thrust is renewed. A bend so caused acts on the fibres of the cane in nearly the same way as does a bend caused by supporting the cane horizontally at its two ends and suspending a weight from its middle. In either case the fibres on the convex side are extended and the fibres on the concave side compressed. Kindred actions occur in a rod that is so thick as not to yield visibly under the force applied. In the absence of complete homogeneity of its substance, complete symmetry in its form, and an application of a force exactly along its axis, there must be some lateral deflection; and therefore some distribution of tensions and pressures of the kind indicated. And then, as the fact which here specially concerns us, we have to note that the strongest tensions and pressures are borne by the outer layers of fibres. Now the shaft of a long bone, subject to mechanical actions of this kind, similarly has its outer layer most strained. In this layer, therefore, on the mechanical hypothesis, ossification should commence, and here it does commence—commences, too, midway between the ends where the bends produce on the superficial parts their most intense effects. But we have not in this place simply to observe that ossification commences at the places of greatest stress, but to ask what causes it to do this. Can we trace the physical actions which set up this deposit of dense tissue? It is, I think, possible to indicate a "true cause" that is at work; though whether it is a sufficient cause may be questioned. We concluded that in certain other cases, the formation of dense tissue indirectly results from the alternate squeezing and relaxation of the vessels running through the part; and the inquiry now to be made is, whether, in developing bone, the same actions go on in such ways as to produce the observed effects. At the outset we are met by what seems a fatal difficulty—cartilage is a non-vascular tissue: this substance of which unossified bones consist is not permeated by minute canals carrying nutritive liquid, and cannot, therefore, be a seat of actions such as those assigned. This apparent difficulty, however, furnishes a confirmation. For cartilage that is wholly without blood-vessels does not ossify: ossification takes place only at those parts of it into which the capillaries penetrate. Hence, we get additional reason for suspecting that bone-formation is due to the alleged cause; since it occurs where mechanical strains can produce the actions described, but does not occur where mechanical strains cannot produce them. Let us consider more closely what the factors are, and how they will coöperate under the particular conditions. It seems possible that these canals that exist in the superficial layer of a cartilaginous bone before it begins to ossify, are themselves produced by the mechanical actions. For every time a mass of cartilage is strained and its superficial layers more especially subject to tensions and pressures, the nutritive liquid diffused through the substance of the cartilage, compressed as it must be, will tend to ooze from the surface of the cartilage, and to return again when the stress is taken off. Such alternate movements of the nutritive liquid, perpetually repeated, will be apt to form channels. These, at first quite superficial and inappreciable, will become more appreciable; since, when they are once commenced, any further additions of substance to the surface will be prevented from closing their openings by the alternate rushes of liquid; and so a vascular layer of appreciable thickness may gradually be formed. But without doing more than hint this, it will suffice for the argument if we commence with the external vascular layer as already existing, and consider what will take place in it. Cartilage is elastic—is somewhat extensible, and spreads out laterally under pressure, but resumes its form when relieved. How, then, will the capillaries traversing such a substance be affected at the places where it is strained by a bend? Those on the convex side will be laterally squeezed, in the same way that we saw the sap-vessels on the convex side of a bent branch are squeezed; and as exudation of the sap into the adjacent prosenchyma will be caused in the one case, so, in the other, there will be caused exudation of serum into the adjacent cartilage: extra nutrition and increase of strength resulting in both cases. The parallel ceases here, however. In the shoot of a plant, bent in various directions by the wind, the side which was lately compressed, is now extended; and hence that squeezing of the sap-vessels which results from extension, suffices to feed and harden the tissue on all sides of the shoot. But it is not so with a bone. Having yielded on one side under longitudinal pressure, and resumed as nearly as may be its previous shape when the pressure is taken off, the bone yields again towards the same side when again longitudinally pressed. Hence the substance of its concave side, never rendered convex by a bend in the opposite direction, would not receive any extra nutrition did no other action come into play. But if we consider how intermittent pressures must act on cartilage, we shall see that there will result extra nutrition of the concave side also. Squeeze between two pieces of glass a thin bit of caoutchouc that has a hole through it. While the caoutchouc spreads out away from the centre, it also spreads inwards, so as partially to close the hole. Everywhere its molecules move away in directions of least resistance; and for those near the hole, the direction of least resistance is towards the hole. Let this hole stand for the transverse section of one of the capillaries passing through cartilage, and it will be manifest that on the side of the unossified bone made concave in the way described, the compressed cartilage will squeeze the capillaries traversing it; and in the absence of perfect homogeneity in the cartilage, the squeeze will cause extra exudation from the capillaries into the cartilage. Thus every additional strain will give to the cartilage it falls upon, an additional supply of the materials for growth. So that presently the side which, by yielding more than any other, proves itself to be the weakest, will cease to be the weakest. What further will happen? Some other side will yield a little—the bends will take place in some other plane; and the portions of cartilage on which repeated tensions and pressures now fall will be strengthened. Thus the rate of nutrition, greatest at the place where the bending is greatest, and changing as the incidence of forces changes, will bring about at every point a balance between the resistances and the strains. Thus, too, there will be determined that peripheral induration which we see in bones so circumstanced. As in a shoot we saw that the woody deposit takes place towards the outside of the cylinder, where, according to the hypothesis, it ought to take place; so, here, we see that the excess of exudation and hardening, occurring where the strains are most intense, will form a cylinder having a dense outside and a porous or hollow inside. These processes will be essentially the same in bones subject to more complex mechanical actions; such as sundry of the flat bones and others that serve as internal fulcra. Be the strains transverse or longitudinal, be they torsion strains or mixed strains, the outer parts of the bone will be more affected by them than its inner parts. They will therefore tend everywhere to produce resisting masses having outer parts more dense than their inner parts. And by causing most growth where they are most intense, will call out reactive forces adequate to balance them—forms and thicknesses of bone offering resistances equal to the strains, however numerous and varied. There are doubtless obstacles in the way of this interpretation. It may be said that the forces acting on the outer layers in the manner described, would compress the capillaries too little to produce the alleged effects; and if evenly distributed along the whole lengths of the layers, they would probably be so. But it needs only to bend a flexible mass and observe the tendency to form creases on the concave surface, to feel assured that along the surface of an ossifying bone, the yielding of the tissue when bent will not be uniform. In the absence of complete homogeneity, the interstitial yielding will take place at some points more than others, and at one point above all others. At these weakest points, and especially at one, the action on the capillaries will be concentrated. When, at the weakest point—the centre of commencing ossification—an extra amount of deposit has been caused, it will cease to be the weakest; and adjacent points, now the weakest, will become the places of yielding and induration. And in proportion as the layer becomes filled with unyielding matter, the remaining compressible parts of it, and their contained capillaries, will be more severely compressed. It may be further objected that the hypothesis is incompatible with the persistence of cartilage for so long a time between the epiphyses of bones and the bony masses which they terminate. But there is the reply that the places occupied by this cartilage, being places at which the bone lengthens, the non-ossification is in part apparent only—it is rather that new cartilage is formed as fast as the pre-existing cartilage ossifies; and there is the further reply that the slowness of the ultimate ossification of this part, is due to its non-vascularity, and to mechanical conditions that are unfavourable to its acquirement of vascularity. Once more, the demurrer that in the epiphyses ossification does not begin at the surface but within the mass of the cartilage, is met by an explanation parallel to that before given (§ 293, note) of the deep-seated induration produced by an external pressure which, during long intervals, does not intermit completely; as in a bunion, a node on the instep, and what is called "housemaid's knee."

Of course it is not meant that this osseous development by direct equilibration, takes place in the individual. Though it is a corollary from the argument that in each individual the process must be furthered and modified by the particular actions to which the particular bones are exposed; yet the leading traits of structure assumed by the bones are assumed in conformity with the inherited type. This, however, is no difficulty. The type itself is to be regarded as the accumulated result of such modifications, transmitted and increased from generation to generation. The actions above described as taking place in the bone of an individual, must be understood as producing their total effect little by little in the corresponding bones of a long series of individuals. Even if but a small modification can be so wrought in the individual, yet if such modification, or a part of it, is inheritable, we may readily understand how, in the course of geologic epochs, the observed structures may arise by the assigned way.

Here may fitly come in a strong confirmation. If we find cases where individual bones, subject in exceptional degrees to the actions described, present in exceptional amounts the modifications attributed to them, we are greatly helped in understanding how there may be produced in the race that aggregate of modifications which the hypothesis implies.

Such cases occur in ricketty children. I am indebted to Mr. Busk for pointing out these abnormal formations of dense tissue, that are not apparently explicable as results of mechanical actions and re-actions. It was only on tracing out the processes here at work, that there suggested itself the specific interpretation of the normal process, as above set forth. When, from constitutional defect, bones do not ossify with due rapidity, and are meanwhile subject to the ordinary strains, they become distorted. Remembering how a mass which has been made to yield in any direction by a force it cannot withstand, is some little time before it recovers completely its previous form, and usually, indeed, undergoes what is called a "permanent set;" it is inferable that when a bone is repeatedly bent at the same time that the liquid contained in its capillaries is poor in the materials for forming dense tissue, there will not take place a proportionate strengthening of the parts most strained; and these parts will give way. This happens in rickets. But this having happened, there goes on what, in teleological language, we call a remedial process. Supposing the bone to be one commonly affected—a femur; and supposing a permanent bend to have been caused in it by the weight of the body; the subsequent result is an unusual deposition of cartilaginous and osseous matter on the concave side of the bone. If the bone is represented by a strung bow, then the deposit occurs at the part represented by the space between the bow and the string. And thus occurring where its resistance is most effective, it increases until the approximately-straight piece of bone formed within the arc, has become strong enough to bear the pressure without appreciably yielding. Now this direct adaptation, seeming so like a special provision, and furnishing so remarkable an instance of what, in medical but unscientific language, is called the *vis medicatrix naturæ*, is simply a result of the above-described mechanical actions and re-actions, going on under the exceptional conditions. Each time such a bent bone is subject to a force which again bends it, the severest compression falls on the substance of its concave side. Each time, then, the capillaries running through this part of its substance are violently squeezed—far more squeezed than they or any other of the capillaries would have been, had the bone remained straight. Hence, on every repetition of the strain, these capillaries near the concave surface have their contents forced out in more than normal abundance. The materials for the formation of tissue are supplied in quantity greater than can be assimilated by the tissue already formed; and from the excess of exuded plasma, new tissue arises. A layer of organizable material accumulates between the concave surface and the periosteum; in this, according to the ordinary course of tissue-growth, new capillaries appear; and the added layer presently assumes the histological character of the layer from which it has grown. What next happens? This added layer, further from the neutral axis than that which has thrown it out, is now the most severely compressed, and its capillaries are the most severely squeezed. The place of greatest exudation and most rapid deposit of matter, is therefore transferred to this new layer; and at the same time that active nutrition increases its density, the excess of organizable material forms another layer external to it: the successive layers so added, encroaching on the space between the concave surface of the bone and the chord of its arc. What limits the encroachment on this space?—what stops the process of filling it up? The answer to this question will be manifest on observing that there comes into play a cause which gradually diminishes the forces falling on each new layer. For the transverse sectional area is step by step increased; and an increase of the area over which the weight borne is distributed, implies a relatively smaller pressure upon each part of it. Further, as the transverse dimensions of the bone increase, the materials composing its convex and concave layers, becoming further from the neutral axis, become better placed for resisting the strains to be borne.

So that both by the increased quantity of dense matter and by its mechanically more-advantageous position, the bendings of the bone are progressively decreased. But as they are decreased, each new layer formed on the concave surface, has its substance and its capillaries less compressed; and the resulting growth and induration are rendered less rapid. Evidently, then, the additions, slowly diminishing, will eventually cease; and this will happen when the bone no longer bends. That is to say, the thickening of the bone will reach its limit when there is equilibrium between the incident forces and the forces which resist them. Here, indeed, we may trace with great clearness the process of direct equilibration—may see how an unusual force, falling on the moving equilibrium of an organism and not overthrowing it, goes on working modifications until the re-action balances the action.

That, however, which now chiefly concerns us, is to note how this marked adaptation supports the general argument. Unquestionably bone is in this case formed under the influence of mechanical stress, and formed just where it most effectually meets the stress. This result, not otherwise explained, is explained by the hypothesis above set forth. And when we see that this special deposit of bone is accounted for by actions like those to which bone-formation in general is ascribed, the probability that these are the actions at work becomes very great.

Of course it is not alleged that osseous structures arise in this way alone. The bones of the skull and various dermal bones cannot be thus interpreted. Here the natural selection of favourable variations appears the only assignable cause—the equilibration is indirect. We know that ossific deposits now and then occur in tissues where they are not usually found; and such deposits, originally abnormal, if they occurred in places where advantages arose from them, might readily be established and increased by survival of the fittest. Especially might we expect this to happen when a constitutional tendency to form bone had been established by actions of the kind described; for it is a familiar fact that differentiated types of tissue, having once become elements of an organism, are apt occasionally to arise in unusual places; and there to repeat all their peculiar histological characters. And this may possibly be the reason why the bones of the skull, though not exposed to forces such as those which produce, in other bones, dense outer layers including less dense interiors, nevertheless repeat this general trait of bony structure. While, however, it is beyond doubt that some bones are not due to the direct influence of mechanical stress, we may, I think, conclude that mechanical stress initiates bone-formation.

§ 302. What is the origin of nerve? In what way do its properties stand related to the properties of that protoplasm whence the tissues in general arise? and in what way is it differentiated from protoplasm simultaneously with the other tissues? These are profoundly interesting questions; but questions to which positive answers cannot be expected. All that can be done is to indicate answers which seem feasible.

That the property specially displayed by nerve, is a property which protoplasm possesses in a lower degree, is manifest. The sarcode of a Rhizopod and the substance of an unimpregnated ovum, exhibit movements that imply a propagation of stimulus from one part of the mass to another; and through the nerveless body of a polype, we see slowly travelling and spreading a contraction set up by touching a tentacle—a contraction which implies the passage from part to part of some stimulus causing the contraction. We have not far to seek for a probable origin of this phenomenon. There is good reason for ascribing it to the extreme instability of the organic colloids of which protoplasm consists. These, in common with colloids in general, assume different isomeric forms with great facility; and they display not simply isomerism but polymerism. Further, this readiness to undergo molecular re-arrangement, habitually shows itself in colloids by the rapid propagation of the re-arrangement from part to part. As Prof. Graham has shown, matter in this state often "pectizes" almost instantaneously—a touch will transform an entire mass. That is to say, the change of molecular state once set up at one end, spreads to the other end—there is a progress of a stimulus to change; and this is what we see in a nerve. So much being understood, let us re-state the case more completely.

Molecular change, implying as it does motion of molecules, communicates motion to adjacent molecules; be they of the same kind or of a different kind. If the adjacent molecules, either of the same kind or of a different kind, be stable in composition, a temporary increase of oscillation in them as wholes, or in their parts, may be the only result; but if they are unstable there are apt to arise changes of arrangement among them, or among their parts, of more or less permanent kinds. Especially is this so with the complex molecules which form colloidal matter, and with the organic colloids above all. Hence it is to be inferred that a molecular disturbance in any part of a living animal, set up by either an external or internal agency, will almost certainly disturb and change some of the surrounding colloids not originally implicated—will diffuse a wave of change towards other parts of the organism: a wave which will, in the absence of perfect homogeneity, travel further in some directions than in others. Let us ask next what will determine the differences of distance travelled in different directions. Obviously any molecular agitation spreading from a centre, will go furthest along routes that offer least resistance. What routes will these be? Those along which there lie most molecules that are easily changed by the diffused molecular motion, and which yet do not take up much molecular motion in assuming their new states. Molecules which are tolerably stable will not readily propagate the agitation; for they will absorb it in the increase of their own oscillations, instead of passing it on. Molecules which are unstable but which, in assuming isomeric forms, absorb motion, will not readily propagate it; since it will disappear in working the changes in them. But unstable molecules which, in being isomerically transformed, do not absorb motion, and still more those which, in being so transformed, give out motion, will readily propagate any molecular agitation; since they will pass on the impulse either undiminished, or increased, to adjacent molecules. If then we assume, as we are not only warranted in doing but are obliged to do, that protoplasm contains two or more colloids, either mingled or feebly combined (since it cannot consist of simple albumen or fibrin or casein, or any allied proximate principle); it may be concluded that any molecular agitation set up by what we call a stimulus, will diffuse itself further along some lines than along others, if the components of the protoplasm are not quite homogeneously dispersed, and if some of them are isomerically transformed more easily, or with less expenditure of motion, than others; and it will especially travel along spaces occupied chiefly by those molecules which give out molecular motion during their metamorphoses, if there should be any such. But now let us ask what structural effects will be wrought along a tract traversed by this wave of molecular disturbance. As is shown by those transformations that so rapidly propagate themselves through colloids, molecules that have undergone a certain change of form, are apt to communicate a like change of form to adjacent molecules of the same kind—the impact of each overthrow is passed on and produces another overthrow. Probably the proneness towards isochronism of molecular movements necessitates this. If any molecule has had its components re-arranged, and their oscillations consequently altered, there result movements not concordant with the movements in adjacent untransformed molecules, but which, impressing themselves on the parts of such untransformed molecules, tend to generate in them concordant movements—tend, that is, to produce the re-arrangements involved by these concordant movements. Is this action limited to strictly isomeric substances? or may it extend to substances that are closely allied? If along with the molecules of a compound colloid there are mingled those of some kindred colloid; or if with the molecules of this compound colloid there are mingled the components out of which other such molecules may be formed; then there arises the question—does the same influence which tends to propagate the isomeric transformations, tend also to form new molecules of the same kind out of the adjacent components? There is reason to suspect that it does. Already when treating of the nutrition of parts (§ 64), it was pointed out that we are obliged to recognize a power possessed by each tissue to build up, out of the materials brought to it, molecules of the same type as those of which it is formed. This building up of like molecules seems explicable as caused by the tendency of the new components which the blood supplies, to acquire movements isochronous with those of the like components in the tissue; which they can do only by uniting into like compound molecules. Necessarily they must gravitate towards a state of equilibrium; such state of equilibrium—moving equilibrium of course—must be one in which they oscillate in the same times with neighbouring molecules; and so to oscillate they must fall into groups identical with the groups around them. If this be a general principle of tissue-growth and repair, we may conclude that it will apply in the case before us. A wave of molecular disturbance passing along a tract of mingled colloids closely allied in composition, and isomerically transforming the molecules of one of them, will be apt at the same time to form some new molecules of the same type, at any place where there exist the proximate components, either uncombined or feebly combined in some not very different way. And this will be most likely to occur where the molecules of the colloid that are undergoing the isomeric change, predominate, but have scattered through them the other molecules out of which they may be formed, either by composition or modification. That is to say, a wave of molecular disturbance diffused from a centre, and travelling furthest along a line where lie most molecules that can be isomerically transformed with facility, will be likely at the same time to further differentiate this line, and make it more characterized than before by the easy-transformability of its molecules. One additional step, and the interpretation is reached. Analogy shows it to be not improbable that these organic colloids, isomerically transformed by slight molecular impact or increase of molecular motion, will some of them resume their previous molecular structures after the disturbance has passed. We know that what are stable molecular arrangements under one degree of molecular agitation, are not stable under another degree; and there is evidence that re-arrangements of an inconspicuous kind are occasionally brought about by very slight changes of molecular agitation. Water supplies a case. Prof. Graham infers that water undergoes a molecular re-arrangement at about 32°—that ice has a colloid form as well as a crystalloid form, dependent on temperature. Send through it an extra wave of the molecular agitation we call heat, and its molecules aggregate in one way. Let the wave die away, and its molecules resume their previous mode of aggregation. And obviously such transformations may be repeated backwards and forwards within narrow limits of temperature. Now among the extremely unstable organic colloids, such a phenomenon is far more likely to happen. Suppose, then, that the nerve-colloid is one of which the molecules are changed in form by a passing wave of extra agitation, but resume their previous form when the wave has passed: the previous form being the most stable under the conditions which then recur. What follows? It follows that these molecules will be ready again to undergo isomeric transformation when there again occurs the stimulus; will, as before, propagate the transformation most along the tract where they are most abundant; will, as before, simultaneously tend to form new molecules of their own type; will, as before, make the line along which they lie one of easier transfer for the molecular agitation. Every repetition will help to increase, to integrate, to define more completely, the course of the escaping molecular motion—extending its remoter part while it makes its nearer part more permeable—will help, that is, to form a line of discharge, a line for conducting impressions, a nerve.

Such seems to me a not unfair series of deductions from the known habitudes of colloids in general and the organic colloids in particular. And I think that the implied nature and properties of nerve, correspond better with the observed phenomena than do the nature and properties implied by other hypotheses. Of course the speculation as it here stands is but tentative, and leaves much unexplained. It gives no obvious reply to the questions—what causes the formation of nerves along some lines rather than others? what determines their appropriate connexions?—questions, however, to which, when we come to deal with physiological integration, we may find not unsatisfactory answers. Moreover it says nothing about the genesis of ganglia. A ganglion, it is clear, must consist of a colloidal matter equally unstable, or still more unstable, which, when disturbed, falls into some different molecular arrangement, perhaps chemically simpler, and gives out in so doing a large amount of molecular motion—serves as a reservoir of molecular motion which may be suddenly discharged along an efferent nerve or nerves, when excitement of an afferent nerve has disengaged it. How such a structure as this results, the hypothesis does not show. But admitting these shortcomings it may still be held that we are, in the way pointed out, enabled to form an idea of the actions by which nervous tissue is differentiated.

§ 303. A speculation akin to, and continuous with, the last, is suggested by an inquiry into the origin of muscular tissue.

Contractility as well as irritability is a property of protoplasm or sarcode; and, as before suggested (§ 22), is not improbably due to isomeric change in one of its component colloids. It is a feasible supposition that of the several isomeric changes simultaneously set up among these component colloids, some may be accompanied by decided change of bulk and some not. Clearly the isomeric change undergone by the colloid which we suppose to form nerve, must be one not accompanied by appreciable change of bulk; since change of bulk implies "internal work," as physicists term it, and therefore expenditure of force. Conversely, the colloid out of which muscle originates, may be one that readily passes into an isomeric state in which it occupies less space: the molecular disturbance causing this contraction being communicated to it from adjacent portions of nerve-substance that are molecularly disturbed; or being otherwise communicated to it by direct mechanical or chemical stimuli; as happens where nerves do not exist, or where their influence has been cut off. This interpretation seems, indeed, to be directly at variance with the fact that muscle does not diminish in bulk during contraction but merely changes its shape. That which we see take place with the muscle as a whole, is said also to take place with each fibre—while it shortens it also broadens. There is, however, a possible solution of this difficulty. A contracting colloid yields up its water; and the contracted colloid *plus* the free water, may have the same bulk as before though the colloid has less. If it be replied that in this case the water should become visible between the substance of the fibre and its sarcolemma or sheath, it may be rejoined that this is not necessary—it may be deposited interstitially. Possibly the striated structure is one that facilitates its exudation and subsequent re-absorption; and to this may be due the superiority of striated muscle in rapidity of contraction. Granting the speculative character of this interpretation, let us see how far it agrees with the facts. If the actions are as here supposed, the contracted or more integrated state of the muscular colloid will be that which it tends continually to assume—that into which it has an increasing aptitude to pass when artificial paralysis has been produced, as shown by Dr. Norris—that into which it lapses completely in *rigor mortis.* The sensible motion generated by the contraction can arise only from the transformation of insensible motion. This insensible motion suddenly yielded up by a contracting mass, implies the fall of its component molecules into more stable arrangements. And there can be no such fall unless the previous arrangement is unstable. From this point of view, too, it is possible to see how the hydro-carbons and oxy-hydro-carbons consumed in muscular action, may produce their effects. It was said, when exposing The Data of Biology, that non-nitrogenous substance might evolve heat only when transformed in the circulating fluids, "but partly heat, and partly another force, when transformed in some active tissue that has absorbed it: just as coal, though producing little else but heat as ordinarily burnt, has its heat partially transformed into mechanical motion if burnt in a steam-engine furnace" (§ 18); and recent inquiries make it clear that some such relation exists.* Here a feasible *modus operandi* becomes manifest. For these non-nitrogenous elements of food when consumed in the tissues, give out large amounts of molecular motion. They do this in presence of the muscular colloids that have lost molecular motion during their fall in the stable or contracted state. And from the molecular motion they give out, may be restored the molecular motion lost by the contracted colloids: these contracted colloids may so have their molecules raised to that unstable state from which, again falling, they can again generate mechanical motion.

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* See account of experiments made by Profs. Fick and Wislicenus, translated by Prof. Wanklyn in the *Phil. Mag.* for May or June, 1866. See also an article by Prof. Frankland in the September number of the same journal.

This conception of the nature and mode of action of muscle, while it is suggested by known properties of colloidal matter and conforms to the recent conclusions of organic chemistry and molecular physics, establishes a comprehensible relation between the vital actions of the lower and the higher animals. If we contemplate the movements of cilia, of a Rhizopod's pseudo-podia, of a Polype's body, or of the long pendant tentacles of a *Medusa*, we shall see great congruity between them and this hypothesis. Bearing in mind that the contractile substance of developed muscle is affected not by nervous influence only, but, where nervous influence is destroyed, is made to contract by mechanical disturbance and chemical action, we may infer that it does not differ intrinsically from the primordial contractile substance, which, in the lowest animals, changes its bulk under other stimuli than the nervous. We shall see significance in the fact ascertained by Dr. Ransom, that various agents which excite and arrest nervo-muscular movements in developed animals, excite and arrest the protoplasmic movements in ova. We shall understand how tissues not yet differentiated into muscle and nerve, have this joint irritability and contractility; how muscle and nerve may arise by the segregation of their mingled colloids, the one of which, not appreciably altering its bulk during isomeric change, readily propagates molecular disturbance, while the other, contracting when isomerically changed, less readily passes on the molecular disturbance; and how by this differentiation and integration of the conducting and the contracting colloids, the one ramifying through the other, it becomes possible for a whole mass to contract suddenly, instead of contracting gradually, as it does when undifferentiated.

The question remaining to be asked is—What causes the specialization of contractile substance?—What causes the growth of colloid masses which monopolize this contractility, and leave kindred colloids to monopolize other properties? Has natural selection gradually localized and increased the primordial muscular substance? or has the frequent recurrence of irritations and consequent contractions at particular parts done it? We have, I think, reason to conclude that direct equilibration rather than indirect equilibration has been chiefly operative. The reasoning that was used in the case of nerve applies equally in the case of muscle. A portion of undifferentiated tissue containing a predominance of the colloid that contracts in changing, will, during each change, tend to form new molecules of its own type from the other colloids diffused through it: the tendency of these entangled colloids to fall into unity with those around them, will be aided by every shock of isomeric transformation. Hence, repeated contractions will further the growth of the contracting mass, and advance its differentiation and integration. If, too, we remember that the muscular colloid is made to contract by mechanical disturbance, and that among mechanical disturbances one which will most readily affect it simultaneously throughout its mass is caused by stretching, we shall be considerably helped towards understanding how the contractile tissues are developed. If extension of a muscular colloid previously at rest, produces in it that molecular disturbance that leads to isomeric change and decrease of bulk, then there is no difficulty in explaining the movements of cilia. The formation of a contractile layer in the vascular system becomes comprehensible: each dilatation of a blood-vessel caused by a gush of blood, will be followed by a constriction; the heart will pulsate violently in proportion as it is violently distended; arteries will develop in power as the stress upon them becomes greater. And we shall similarly have an explanation of the increased muscularity of the alimentary canal that is brought about by increased distension of it.

That the production of contractile tissue in certain localities, is due to the more frequent excitement in those localities of the contractility possessed by undifferentiated tissue in general, is a view harmonizing with facts which the differentiated contractile tissues exhibit. These are the relations between muscular exercise, muscular power, and muscular structure; and it is the more needful for us here to notice them because of certain anomalies they present, which, at first sight, seem inconsistent with the belief that the functionally-determined modifications of muscle are inheritable.

Muscles disagree greatly in their tints—all gradations between white and deep red being observable. Contrasts are visible between the muscles of different animals, between the muscles of the same animal at different ages, and between different muscles of the same animal at the same age. We will glance at the facts under these heads: noting under each of them the connexion which here chiefly concerns us—that between the activity of muscle and its depth of colour. The cold-blooded *Vertebrata* are, taken as a group, distinguished from the warm-blooded by the whiteness of their flesh; and they are also distinguished by their comparative inertness. Though a fish or a reptile can exert considerable force for a short time, it is not capable of prolonged exertion. Birds and mammals show greater endurance along with darker-coloured muscles. If among birds themselves or mammals themselves we make comparisons, we meet with kindred contrasts—especially between wild and domestic creatures of allied kinds. Barn-door fowls are lighter-fleshed than most untamed gallinaceous birds; and among these last the pheasant, moving about but little, is lighter-fleshed than the partridge and the grouse which are more nomadic. The muscles of the sheep are not on the average so dark as those of the deer; and it is said that the flesh of the wild-boar is darker than that of the pig. Perhaps, however, the contrast between the hare and the rabbit affords, among familiar animals, the best example of the alleged relation: the dark-fleshed hare having no retreat and making wide excursions, while the white-fleshed rabbit, passing a great part of its time in its burrow, rarely wanders far from home. The parallel contrast between young and old animals has a parallel meaning. Veal is much whiter than beef, and lamb is of lighter colour than mutton. Though at first sight these facts may not seem to furnish confirmatory evidence, since lambs in their play appear to expend more muscular force than their sedate dams; yet the meaning of the contrast is really as alleged. For in consequence of the law that the strains which animals have to overcome, increase as the cubes of the dimensions, while their powers of overcoming them increase only as the squares (§ 46), the movements of an adult animal cost very much more in muscular effort than do those of a young animal: the result being that the sheep and the cow exercise their muscles more vigorously in their quiet movements, than the lamb and the calf in their lively movements. It may be added as significant, that the domestic animal in which no very marked darkening of the flesh takes place along with increasing age, namely the pig, is one which, ordinarily kept in a sty, leads so quiescent a life that the assigned cause of darkening does not come into action. But perhaps the most conclusive evidences are the contrasts that exist between the active and inactive muscles of the same animal. Between the leg-muscles of fowls and their pectoral muscles, the difference of colour is familiar; and we know that fowls exercise their leg-muscles much more than the muscles which move their wings. Similarly in the turkey, in the guinea fowl, in the pheasant. And then, adding much to the force of this evidence, we see that in partridges and grouse, which belong to the same order as our domestic fowls, but use their wings as habitually as their legs, little or no difference is visible between the colours of these two groups of muscles. Special contrasts like these do not, however, exhaust the proofs; for there is a still more significent general contrast. The muscle of the heart, which is the most active of all muscles, is the darkest of all muscles.

The connection of phenomena thus shown in so many ways, implies that the bulk of a muscle is by no means the sole measure of the quantity of force it can evolve. It would seem that, other things equal, the depth of colour varies with the constancy of action; while, other things equal, the bulk varies with the amount of force that has to be put forth upon occasion. These of course are approximate relations. More correctly we may say that the actions of pale muscles are either relatively feeble though frequent (as in the massive flanks of a fish), or relatively infrequent though strong (as in the pectoral muscles of a common fowl); while the actions of dark muscles are both frequent and strong. Some such differentiation may be anticipated by inference from the respective physiological requirements. A muscle which has upon occasion to evolve considerable force, but which has thereafter a long period of rest during which repair may restore it to efficiency, requires neither a large reserve of the contractile substance that is in some way deteriorated by action, nor highly-developed appliances for bringing it nutritive materials and removing effete products. Where, contrariwise, an exerted muscle that has undergone much molecular change in evolving mechanical force, has soon again to evolve much mechanical force, and so on continually; it is clear that either the quantity of contractile substance present must be great, or the apparatus for nutrition and depuration must be very efficient, or both. Hence we may look for marked unlikenesses of minute structure between muscles that are markedly contrasted in activity. And we may suspect that these conspicuous contrasts of colour between active and inactive muscles, are due to these implied differences of minute structure—partly differences between the numbers of blood-vessels and partly differences between the quantities of sarcous matter.

Here, then, we have a key to the apparent anomaly above hinted at—the maintenance of bulk by certain muscles which have been rendered comparatively inactive by changed habits of life. That the pectoral muscles of those domestic birds which fly but little, have not dwindled to any great extent, has been thought a fact at variance with the conclusion that functionally-produced adaptations are inheritable. It has been argued that if parts which are exercised increase, not only in the individual but in the race, while parts which become less active decrease; then a notable difference of size should exist between the muscles used for flight in birds that fly much, and those in birds of an allied kind that fly little. But, as we here see, this is not the true implication. The change in such cases must be chiefly in vascularity and abundance of contractile substance; and cannot be, to any great extent, in bulk. For a bird to fly at all, its pectoral muscles, bones of attachment, and all accompanying appliances, must be kept up to a certain level of power. If the parts dwindle much, the creature will be unable to lift itself from the ground. Bearing in mind that the force which a bird expends to sustain itself in the air during each successive instant of a short flight, is, other things equal, the same as it expends in each successive instant of a long flight, we shall see that the muscles employed in the two cases must have something like equal intensities of contractile power; and that the structural differences between them must have relation mainly to the lengths of time during which they can continue to repeat contractions of like intensity. That is to say, while the power of flight is retained at all, the muscles and bones cannot greatly dwindle; but the dwindling, in birds whose flights are short or infrequent or both, will be in the reserve stock of the substance that is incapacitated by action, or in the appliances that keep the apparatus in repair, or in both. Only where, as in the struthious birds, the habit of flight is lost, can we expect atrophy of all the parts concerned in flight; and here we find it.

Are such differentiations among the muscles functionally produced? or are they produced by the natural selection of variations distinguished as spontaneous? We have, I think, good grounds for concluding that they are functionally produced. We know that in individual men and animals, the power of sustained action in muscles is rapidly adaptable to the amount of sustained action required. We know that being "out of condition," is usually less shown by the inability to put out a violent effort than by the inability to continue making violent efforts; and we know that the result of training for prize-fights and races, is more shown in the prolongation of energy than in the intensification of energy. At the same time, experience has taught us that the structural change which accompanies this functional change, is not so much a change in the bulk of the muscles as a change in their internal state: instead of being soft and flabby they become hard. We have inductive proof, then, that exercise of a muscle causes some interstitial growth along with the power of more sustained action; and there can be no doubt that the one is a condition to the other. What is this interstitial growth? There is reason to suspect that it is in part an increased deposit of the sarcous substance and in part a development of blood-vessels. Microscopic observation tends to confirm the conclusions before drawn, that repetition of contractions furthers the formation of the matter which contracts, and that greater draughts of blood determine greater vascularity. And if the contrasts of molecular structure and the contrasts of vascularity, directly caused in muscles by contrasts in their activities, are to any degree inheritable; there results an explanation of those constitutional differences in the colours and textures of muscles, which accompany constitutional differences in their degrees of activity.

It may be added that if we are warranted in so ascribing the differentiations of muscles from one another to direct equilibration, then we have the more reason for thinking that the differentiation of muscles in general from other structures is also due to direct equilibration. That unlikenesses between parts of the contractile tissues having unlike functions, are caused by the unlikenesses of their functions, renders it the more probable that the unlikenesses between contractile tissue and other tissues, have been caused by analogous unlikenesses.

§ 304. These interpretations, which have already occupied too large a space, must here be closed. Of course out of phenomena so multitudinous and varied, it has been impracticable to deal with any but the most important; and it has been practicable to deal with these only in a general way. Much, however, as remains to be explained, I think the possibility of tracing, in so many cases, the actions to which these internal differentiations may rationally be ascribed, makes it likely that the remaining internal differentiations are due to kindred actions. We find evidence that in more cases than seemed probable, these actions produce their effects directly on the individual; and that the unlikenesses are produced by accumulation of such effects from generation to generation. While for the remaining unlikenesses, we have, as an adequate cause, the indirect effects wrought by the survival, generation after generation, of the individuals in which favourable variations have occurred—variations such as those of which human anatomy furnishes endless instances. Thus accounting for so much, we may not unreasonably presume that these co-operative processes of direct and indirect equilibration will account for what remains.

Though not strictly included under the title of the chapter, there is a subject on which a few words may here be added, because of the elucidations yielded to it by some parts of the chapter. I refer to the repair and growth of the differentiated tissues. When treating inductively of that restoration which takes place in worn organs, it was admitted that little in the way of deductive interpretation is apparent—nothing beyond the harmony between the facts and the general principle of segregation (§ 64). And it was further admitted that it is not obvious why, within certain limits, an organ grows in proportion as it is exercised. Certain of the foregoing considerations, however, help us towards a partial rationale of these phenomena. When treating of the development of respiratory surfaces, external or internal, at places where the greatest contrast exists between the oxygenated plasma outside the vessels and the carbonized blood inside them, reference was made to the truth that the exchange of liquids must, other things equal, be rapid in proportion as the contrast between them is great. Now this truth holds generally. In every tissue the rate of osmotic exchange must vary as this contrast varies; and where the contrast is produced by composition or decomposition going forward in the tissue, the amount of exchange must be proportionate to the amount of composition or decomposition. If the blood is circulating through an inactive organ, there is nothing to disturb, in any great degree, the proximate equilibrium between the plasma within the blood-vessels and the plasma without them. But if the tissue is functionally excited—if it is made to yield up and expend part of the force latent in its molecules or the molecules of the oxy-hydro-carbons permeating it, its contained liquid necessarily becomes charged with molecules of another order—simpler molecules; and the greater the amount of function the more different is it made from the liquid contained in the blood-vessels. Hence the osmotic exchange must be most rapid where the metamorphosis of substance is most rapid—the materials for consumption and for re-integration of tissue, must be supplied in proportion to the demand. This, however, is not the sole process by which waste and repair are equilibrated. There is the osmotic distension above pointed out as one of the causes of circulation—a force tending ever to thrust most blood to the places where there is the greatest escape for it; that is—the greatest consumption of it. For since in an active tissue, the plasma passing out of its capillaries into its substance is continually yielding up its complex molecules, either to be assimilated or to be decomposed; and since the products of decomposition, whether of the nitrogenous tissue or of its contained hydro-carbons, are simpler than the substances from which they arise, and therefore have greater molecular mobility; it follows that the liquid contained in an active tissue has a greater average molecular mobility than the liquids elsewhere; and therefore makes its way through the channels of excretion faster than elsewhere: the two chief products, carbonic acid and water, escaping with especial facility. Hence the place becomes a place of least resistance, through which the distended walls of the elastic vascular system tend continually to force out an extra quantity of plasma. The argument carried a step further, yields us an idea of the way in which not only repair but also growth of the exercised tissue may be caused—at least, where this tissue is one which evolves force. Assuming it to be established that the force generated by muscle does not result from the consumption of its nitrogenous substance, but from the consumption of its contained hydro-carbons and oxy-hydro-carbons; and inferring that a large amount of muscular action may be performed without a corresponding loss of nitrogenous substance; we get a clue to the process of increase in a specially-exercised muscle. For if osmotic exchange and osmotic distension conspire to produce a more rapid passage of plasma out of the capillaries into this active tissue than into inactive tissues; and if, of the substances in this larger supply of plasma, only the non-nitrogenous are consumed; then there must be an accumulation of the nitrogenous substances. If the waste of the albuminous components of the tissue has not kept pace with the consumption of its carbonaceous contents; then there will exist in the liquid permeating it more albuminous substance than is needed for its repair—there will be material for its growth. The growth thus resulting, however, will be limited both by the capacity of the channels of supply and by the competing absorption of other active tissues. So long as one muscle, or set of muscles, is specially exercised, while the rest discharge but small amounts of duty—so long, that is, as the quantity of tissue-forming matters taken from the alimentary canal into the blood, is not largely draughted off elsewhere, this local growth may go on. But if many other sets of muscles are similarly active, the abstraction of tissue-forming matters at various places, will so far diminish their abundance in the blood, as to reduce the supply available at any one place for growth: eventually leaving sufficient for repair only.

Though we lack data for thus interpreting specifically the repair and growth of other active tissues, yet we may see, in a general way, that a parallel interpretation holds. For if any tissue that consumes, transforms, excretes, or secretes matters that pass into it from the blood, is not formed of the same constituents as these matters it transforms or excretes; or if it does not undergo waste proportionate to the quantity of matter it transforms or excretes; then it seems fairly inferable that along with any unusual quantity of such matters to be transformed or excreted, the plasma passing into it must bring a surplus of the materials for its own repair and growth.

## CHAPTER IX.

### PHYSIOLOGICAL INTEGRATION IN ANIMALS.

§ 305. Physiological differentiation and physiological integration, are correlatives that vary together. We have but to recollect the familiar parallel between the division of labour in a society and the physiological division of labour, to see that as fast as the kinds of work performed by the component parts of an organism become more numerous, and as fast as each part becomes more restricted to its own work, so fast must the parts have their actions combined in such ways that no one can go on without the rest and the rest cannot go on without each one.

Here our inquiry must be, how the relationship of these two processes is established—what causes the integration to advance *pari passu* with the differentiation. Though it is manifest, *à priori*, that the mutual dependence of functions must be proportionate to the specialization of functions; yet it remains to find the mode in which the increasing co-ordination is determined.

Already, among the Inductions of Biology, this relation between differentiation and integration has been specified and illustrated (§ 59). Before dealing with it deductively, a few further examples, grouped so as to exhibit its several aspects, will be advantageous.

§ 306. If the lowly-organized *Planaria* has its body broken up and its gullet detached, this will, for a while, continue to perform its function when called upon, just as though it were in its place: a fragment of the creature's own body placed in the gullet, will be propelled through it, or swallowed by it. But, as the seeming strangeness of this fact implies, we find no such independent actions of analogous parts in the higher animals. A piece cut out of the disc of a *Medusa*, continues with great persistence repeating those rhythmical contractions which we see in the disc as a whole; and thus proves to us that the contractile function in each portion of the disc, is in great measure independent. But it is not so with the locomotive organs of more differentiated types. When separated from the rest, these lose their powers of movement. The only member of a vertebrate animal which continues to act after detachment, is the heart; and the heart has a motor apparatus complete within itself.

Where there is this small dependence of each part upon the whole, there is but small dependence of the whole upon each part. The longer time which it takes for the arrest of a function to produce death in a less differentiated animal than in a more differentiated animal, may be illustrated by the case of respiration. Suffocation in a man speedily causes resistance to the passage of the blood through the capillaries, followed by congestion and stoppage of the heart: great disturbance throughout the system results in a few seconds; and in a minute or two all the functions cease. But in a frog, with its undeveloped respiratory organ, and a skin through which a considerable aëration of the blood is carried on, breathing may be suspended for a long time without injury. Doubtless this difference is proximately due to the greater functional activity in the one case than in the other, and the more pressing need for discharging the produced carbonic acid; but the greater functional activity being itself made possible by the higher specialization of functions, this remains the primary cause of the greater dependence of the other functions on respiration, where the respiratory apparatus has become highly specialized. Here, indeed, we see the relation under another aspect. This more rapid rhythm of the functions which increased heterogeneity of structure makes possible, is itself a means of integrating the functions. Watch, when it is running down, a complicated machine of which the parts are not accurately adjusted, or are so worn as to be somewhat loose. There will be observed certain irregularities of movement just before it comes to rest—certain of the parts which stop first, are again made to move a little by the continued movement of the rest, and then become themselves, in turn, the causes of renewed motion in other parts which have ceased to move. That is to say, while the connected rhythmical changes of the machine are quick, their actions and reactions on one another are regular—all the motions are well integrated; but as the velocity diminishes, irregularities arise —the motions become somewhat disintegrated. Similarly with organic functions: increase of their rapidity involves increase of a joint momentum which controls each and co-ordinates all. Thus, if we compare a Snake with a Mammal, we see that its functions are not tied together so closely. The Mammal, and especially the superior Mammal, requires food with considerable regularity; keeps up a respiration that varies within but moderate limits; and has periods of activity and rest that alternate evenly and frequently. But the Snake, taking food at long intervals, may have these intervals greatly extended without fatal results; its dormant and its active states recur less uniformly; and its rate of respiration varies within much wider limits—now being scarcely perceptible, and now, as you may prove by exciting it, becoming conspicuous. So that here, where the rhythms are very slow, they are individually less regular, and are united into a less regular compound rhythm—are less integrated.

Perhaps the clearest general idea of the co-ordination of functions that accompanies their specialization, is obtained by observing the slowness with which a little-differentiated animal responds to a stimulus applied to one of its parts, and the rapidity with which such a local stimulus is responded to by a more-differentiated animal. A Polype and a Polyzoon, two creatures somewhat similar in their outward appearances but very unlike in their internal structures, will serve for the comparison. A tentacle of a Polype, when touched, slowly contracts; and if the touch has been rude, the contraction presently extends to the other tentacles and eventually to the entire body: the stimulus to movement is gradually diffused throughout the organism. But if you touch a tentacle of a Polyzoon, or slightly disturb the water near it, the whole cluster of tentacles is instantly withdrawn, along with the protruded part of the creature's body, into its sheath. Whence arises this contrast? The one creature has no specialized contractile organs, or fibres for conveying impressions. The other has definite muscles and nerves. The parts of the little-differentiated Polype have their functions so feebly co-ordinated, that one may be strongly affected for a long time before any effect is felt by another at a distance from it; but in the more-differentiated Polyzoon, various remote parts instantly have changes propagated to them from the affected part, and by their united actions thus set up, the whole organism adjusts itself so as to avoid the danger.

These few added illustrations will make the nature of this general relation sufficiently clear. Let us now pass to the interpretation of it.

§ 307. If a *Hydra* is cut in two, the nutritive liquids diffused through its substance cannot escape rapidly, since there are no open channels for them; and hence the condition of the parts at a distance from the cut is but little affected. But where, as in the more-differentiated animals, the nutritive liquid is contained in vessels that have continuous communications, cutting the body in two, or cutting off any considerable portion of it, is followed by escape of the liquid from these vessels to a large extent; and this affects the nutrition and efficiency of organs remote from the place of injury. Then where, as in further-developed creatures, there exists an apparatus for propelling the blood through these ramifying channels, injury of a single one will cause a loss of blood that quickly prostrates the entire organism. Hence the rise of a completely-differentiated vascular system, is the rise of a system which integrates all members of the body, by making each dependent on the integrity of the vascular system, and therefore on the integrity of each member through which it ramifies. In another mode, too, the establishment of a distributing apparatus produces a physiological union that is great in proportion as this distributing apparatus is efficient. As fast as it assumes a function unlike the rest, each part of an animal modifies the blood in a way more or less unlike the rest, both by the materials it abstracts and by the products it adds; and hence the more differentiated the vascular system becomes, the more does it integrate all parts by making each of them feel the qualitative modification of the blood which every other has produced. This is simply and conspicuously exemplified by the lungs. In the absence of a vascular system, or in the absence of one that is well marked off from the imbedding tissues, the nutritive plasma or the crude blood, gets what small aëration it can, only by coming near the creature's outer surface, or those inner surfaces that are bathed by water; and it is probably more by osmotic exchange than in any other way, that the oxygenated plasma slowly permeates the tissues. But where there have been formed definite channels branching throughout the body; and particularly where there exist specialized organs for pumping the blood through these channels; it manifestly becomes possible for the aëration to be carried on in one part peculiarly modified to further it, while all other parts have the aërated blood brought to them. And how greatly the differentiation of the vascular system thus becomes a means of integrating the various organs, is shown by the fatal result that follows when the current of aërated blood is interrupted.

Here, indeed, it becomes obvious both that certain physiological differentiations make possible certain physiological integrations; and that, conversely, these integrations make possible other differentiations. Besides the waste products that escape through the lungs, there are waste products that escape through the skin, the kidneys, the liver. The blood has separated from it in each of these structures, the particular product which this structure has become adapted to separate; leaving the other products to be separated by the other adapted structures. How have these special adaptations been made possible? By union of the organs as recipients of one circulating mass of blood. While there is no efficient apparatus for transfer of materials through the body, the waste products of each part have to make their escape locally; and the local channels of escape must be competent to take off indifferently all the waste products. But it becomes practicable and advantageous for the differently-localized excreting structures, to become fitted to separate different waste products, as soon as the common circulation through them grows so efficient that the product left unexcreted by one is quickly carried to another better fitted to excrete it. So that the integration of them through a common vascular system, is the condition under which only they can become differentiated. How the specialization of each is rendered possible only by its connexion with others that have become similarly specialized, we indirectly see in such a fact as that in chronic jaundice secondary disease of the kidneys is apt to arise in consequence of the biliverdine accumulated in the system being partly excreted through them: the implication being that a structure peculiarly fitted to excrete urea can exist only when it is functionally united with another structure peculiarly fitted to excrete biliverdine. Perhaps the clearest idea of the way in which differentiation leads to integration, and how, again, increased integration makes possible still further differentiation, will be obtained by contemplating the analogous dependence in the social organism. While it has no roads, a country cannot have its industries much specialized: each locality must produce, as best it can, the various commodities it consumes, so long as it has no facilities for barter with other localities. But the localities being unlike in their natural fitnesses for the various industries, there tends ever to arise some exchange of the commodities they can respectively produce with least labour. This exchange leads to the formation of channels of communication. The currents of commodities once set up, make their foot-paths and horse-tracks more permeable; and as fast as the resistance to exchange becomes less, the currents of commodities become greater. Each locality takes more of the products of adjacent ones, and each locality devotes itself more to the particular industry for which it is naturally best fitted: the functional integration makes possible a further functional differentiation. This further functional differentiation reacts. The greater demand for the special product of each locality, excites improvements in production—leads to the use of methods which both cheapen and perfect the commodity. Hence results a still more active exchange; a still clearer opening of the channels of communication; a still closer mutual dependence. Yet another influence comes into play. As fast as the intercourse, at first only between neighbouring localities, makes for itself better roads—as fast as rivers are bridged and marshes made easily passable, the resistance to distribution becomes so far diminished, that the things grown or made in each district can be profitably carried to a greater distance; and as the economical integration is thus extended over a wider area, the economical differentiation is again increased; since each district, having a larger market for its commodity, is led to devote itself more exclusively to producing this commodity. These actions and reactions continue until the various localities, becoming greatly developed and highly specialized in their industries, are at the same time functionally integrated by a network of roads, and finally railways, along which rapidly circulate the currents severally sent out and received by the localities. And it will be manifest that in individual organisms a like correlative progress must have been caused in an analogous way.

§ 308. Another and higher form of physiological integration in animals, is that which the nervous system effects. Each part as it becomes specialized, begins to act upon the rest not only indirectly through the matters it takes from and adds to the blood, but also directly through the molecular disturbances it sets up and diffuses. Whether nerves themselves are differentiated by the molecular disturbances thus propagated in certain directions, or whether they are otherwise differentiated, it must equally happen that as fast as they become channels along which molecular disturbances travel, the parts they connect become physiologically integrated, in so far that a change in one initiates a change in the other. We may dimly perceive that if portions of what was originally a uniform mass having a common function, undertake sub-divisions of the function, the molecular changes going on in them will be in some way complementary to one another: that peculiar form of molecular motion which the one has lost in becoming specialized, the other has gained in becoming specialized. And if the molecular motion that was common to the two portions while they were undifferentiated, becomes divided into two complementary kinds of molecular motion; then between these portions there will be a contrast of molecular motions such that whatever is *plus* in the one will be *minus* in the other; and hence there will be a special tendency towards a restoration of the molecular equilibrium between the two: the molecular motion continually propagated away from either will have its line of least resistance in the direction of the other. If, as argued in the last chapter, repeated restorations of molecular equilibrium, always following the line of least resistance, tend ever to make it a line of diminished resistance; then, in proportion as any parts become more physiologically integrated by the establishment of this channel for the easy transmission of molecular motion between them, they may become more physiologically differentiated. The contrast between their molecular motions leads to the line of discharge; the line of discharge, once formed, permits a greater contrast of their molecular motions to arise; thereupon the quantities of molecular motion transferred to restore equilibrium, being increased, the channel of transfer is made more permeable; and its further permeability, so caused, renders possible a still more marked unlikeness of action between the parts. Thus the differentiation and the integration progress hand in hand as before. How the same principle holds throughout the higher stages of nervous development, can be seen only still more vaguely. Nevertheless, it is comprehensible that as functions become further divided, there will arise the need for sub-connexions along which there may take place secondary equilibrations subordinate to the main ones. It is manifest, too, that whereas the differentiation of functions proceeds, not necessarily by division into two, but often by division into several, and usually in such ways as not to leave any two functions that are just complementary to one another, the restorations of equilibrium cannot be so simple as above supposed. And especially when we bear in mind that many differentiated functions, as those of the senses, cannot be held complementary to any other functions in particular; it becomes manifest that the equilibrations that have to be made in an organism of much heterogeneity, are extremely complex, and do not take place between each organ and some other, but between each organ and all the others. The peculiarity of the molecular motion propagated from each organ, has to be neutralized by some counter-peculiarity in the average of the molecular motions with which it is brought into relation. All the variously-modified molecular motions from the various parts, must have their pluses and minuses mutually cancelled: if not locally, then at some centre to which each unbalanced motion travels until it meets with some opposite unbalanced motion to destroy it. Still, involved as these actions must become, it is possible to see how the general principle illustrated by the simple case above supposed, will continue to hold. For always the molecular motion proceeding from any one differentiated part, will travel most readily towards that place where a molecular motion most complementary to it in kind exists—no matter whether this complementary molecular motion be that proceeding from any one other organ, or the *resultant* of the molecular motions proceeding from many other organs. So that the tendency will be for each channel of communication or nerve, to unite itself with some centre or ganglion, where it comes into relation with other nerves. And if there be any parts of its peculiar molecular motion uncancelled by the molecular motions it meets at this centre; or if, as will probably happen, the average molecular motion which it there unites to produce, differs from the average molecular motion elsewhere; then, as before, there will arise a discharge along another channel or nerve to another centre or ganglion, where the residuary difference may be cancelled by the differences it meets; or from whence it may be still further propagated till it is so cancelled. Thus there will be a tendency to a general nervous integration keeping pace with the differentiation.

Of course this must be taken as nothing more than the indication of initial tendencies—not as an hypothesis sufficient to account for all the facts. It leaves out of sight the origin and functions of ganglia, considered as something more than nerve-junctions. Were there only these lines of easy transmission of molecular disturbance, a change set up in one organ could never do more than produce its equivalent of change in some other or others; and there could be none of that large amount of motion initiated by a small sensation, which we habitually see. The facts show, unmistakably, that the slight disturbance communicated to a ganglion, causes an overthrow of that highly-unstable nervous matter contained in it, and a discharge from it of the greatly-increased quantity of molecular motion so generated. This, however, is beyond our immediate topic. All we have here to note is the interdependence and unification of functions that naturally follow the differentiation of them.

§ 309. Something might be added. concerning the further class of integrations by which organisms are constituted mechanically-coherent wholes. Carrying further certain of the arguments contained in the last chapter, it might be not unreasonably inferred that the binding together of parts by bones, muscles, and ligaments, is a secondary result of those same actions by which bones, muscles, and ligaments are specialized. But adequate treatment of this division of the subject is at present scarcely possible.

What little of fact and inference has been above set down, will, however, serve to make comprehensible the general truths respecting which, in their main outlines, there can be no question. Beginning with the feebly-differentiated sponge, of which the integration is also so feeble that cutting off a piece interferes in no appreciable degree with the activity and growth of the rest, it is undeniable that the advance is through stages in which the multiplication of unlike parts having unlike actions, is accompanied by an increasing interdependence of the parts and their actions; until we come to structures like our own, in which a slight change initiated in one part will instantly and powerfully affect all other parts—will convulse an immense number of muscles, send a wave of contraction through all the blood-vessels, awaken a crowd of ideas with an accompanying gush of emotions, affect the action of the lungs, of the stomach, and of all the secreting organs. And while it is a manifest necessity that along with this subdivision of functions which the higher organisms show us, there must be this close co-ordination of them, the foregoing paragraphs suggest how this necessary correlation is brought about. For a great part of the physiological union that accompanies the physiological specialization, there appears to be a sufficient cause in the process of direct equilibration; and indirect equilibration may be fairly presumed a sufficient cause for that which remains.

# CHAPTER X.

## SUMMARY OF PHYSIOLOGICAL DEVELOPMENT.

§ 310. Intercourse between each part and the particular conditions to which it is exposed, either habitually in the individual or occasionally in the race, thus appears to be the origin of physiological development; as we found it to be the origin of morphological development. The unlikenesses of form that arise among members of an aggregate that were originally alike, we traced to unlikenesses in the incident forces. And in the foregoing chapters we have traced to unlikenesses in the incident forces, those unlikenesses of minute structure and chemical composition that simultaneously arise among the parts.

In summing up the special truths illustrative of this general truth, it will be proper here to contemplate more especially their dependence on first principles. Dealing with biological phenomena as phenomena of evolution, we have to interpret not only the increasing morphological heterogeneity of organisms, but also their increasing physiological heterogeneity, in terms of the re-distribution of matter and motion. While we make our rapid re-survey of the facts, let us then more particularly observe how they are subordinate to the universal course of this re-distribution.

§ 311. The instability of the homogeneous, or, strictly speaking, the inevitable lapse of the more homogeneous into the less homogeneous, which we before saw endlessly exemplified by the morphological differentiations of the parts of organisms, we have here seen afresh exemplified in ways also countless, by the physiological differentiations of their parts. And in the one case as in the other, this change from uniformity into multiformity in organic aggregates, is caused, as it is in all inorganic aggregates, by the necessary exposure of their component parts to actions unlike in kind or quantity or both. General proof of this is furnished by the order in which the differences appear. If parts are rendered physiologically heterogeneous by the heterogeneity of the incident forces; then the earliest contrasts should be between parts that are the most strongly contrasted in their relations to incident forces; the next earliest contrasts should occur where there are the next strongest contrasts in these relations; and so on. It turns out that they do this.

Everywhere the differentiation of outside from inside comes first. In the simplest plants the unlikeness of the cell-wall to the cell-contents is the conspicuous trait of structure. The contrasts seen in the simplest animals are of the same kind: the film that covers a Rhizopod and the more indurated coat of an *Infusorium*, are more unlike the contained sarcode than the other parts of this are from one another; and the tendency during the life of the animal is for the unlikeness to become greater. What is true of *Protophyta* and *Protozoa*, is true of the germs of all organisms up to the highest: the differentiation of outer from inner is the first step. When the endochrome of an *Alga*-cell has broken up into the clusters of granules which are eventually to become spores, each of these quickly acquires a membranous coating; constituting an unlikeness between surface and centre. Similarly with the ovule of every higher plant: the mass of cells forming it, early exhibits an outside layer of cells distinguished from the cells within. With animal germs it is the same. Be it in a ciliated gemmule, be it in the pseud-ova of *Aphides* and of the *Cecidomyia*, or be it in true ova, the primary differentiation conforms to the relations of exterior and interior. If we turn to adult organisms, vegetal or animal, we see that whether they do or do not display other contrasts of parts, they always display this contrast. Though otherwise almost homogeneous, such *Fungi* as the Puff-ball, or, among *Algæ*, all which have a thallus of any thickness, present marked differences between those of their cells which are in immediate contact with the environment and those which are not. Such differences they present in common with every higher plant; which, here in the shape of bark and there in the shape of cuticle, has an envelope inclosing it even up to its petals: the only parts not so inclosed, being those short-lived terminations of the fructifying organs, from which the disintegrated tissue is being cast off to form the germs of new individuals. In like manner among animals, there is always either a true skin or an outer coat analogous to one. Wherever aggregates of the first order have united into aggregates of the second and third orders—wherever they have become the morphological units of such higher aggregates—the outermost of them have grown unlike those lying within. Even the Sponge is not without a layer that may by analogy be called dermal.

This lapse of the relatively homogeneous into the relatively heterogeneous, first showing itself, as on the hypothesis of evolution it must do, by the rise of an unlikeness between outside and inside, goes on next to show itself, as we infer that it must do, by the establishment of secondary contrasts among the outer parts answering to secondary contrasts among the forces falling on them. So long as the whole surface of a plant remains similarly related to the environment, as in a *Protococcus* or a *Volvox*, it remains uniform; but when there come to be an attached surface and a free surface, these, being subject to unlike actions, are rendered unlike. This is visible even in a unicellular *Alga* when it becomes fixed; it is shown in the distinction between the under and upper parts of ordinary *Fungi;* and we see it in the universal difference between the imbedded ends and the exposed ends of the higher plants. And then among the less marked contrasts of surface answering to the less marked contrasts in the incident forces, come those between the upper and under sides of leaves; which, as we have seen, vary in degree as the contrasts of forces vary in degree, and disappear where these contrasts disappear. Equally clear proof is furnished by animals, that the original uniformity of surface lapses into multiformity, in proportion as the actions of the environment upon the surface become multiform. In a Worm, burrowing through damp soil that acts equally on all its sides, or in a *Tænia,* uniformly bathed by the contents of the intestine it inhabits, the parts of the integument do not appreciably differ from one another; but in creatures not surrounded by the same agencies, as those that crawl and those that have their bodies partially inclosed, there are unlikenesses of integument corresponding to unlikenesses of the conditions. A Snail's foot has an under surface not uniform with the exposed surface of its body, and this again is not uniform with the protected surface. Among articulate animals there is usually a distinction between the ventral and the dorsal aspects; and in those of the *Articulata* which subject their anterior and posterior ends to different environing agencies, as do the Ant-lion and the Hermit-crab, these become superficially differentiated. Analogous general contrasts occur among the *Vertebrata.* Fish, though their outsides are uniformly bathed by water, have their backs more exposed to light than their bellies; and the two are commonly distinct in colour. Where it is not the back and belly that are thus dissimilarly conditioned, but the sides, as in the *Pleuronectidæ,* then it is the sides that become contrasted; and there may be significance in the fact, that those abnormal individuals of this order which revert to the ancestral undistorted type, and swim vertically, have the two sides alike. In such higher vertebrates as Reptiles, we see repeated this differentiation of the upper and under surfaces: especially in those of them which, like Snakes, expose these surfaces to the most diverse actions. Even in Birds and Mammals which usually, by raising the under surface considerably above the ground, greatly diminish the contrast between its conditions and the conditions to which the upper surface is subject, there still remains some unlikeness of clothing answering to the remaining unlikeness between the conditions. Thus, without by any means saying that all such differentiations are directly caused by differences in the actions of incident forces, which, as before shown (§ 294), they cannot be, it is clear that many of them are so caused. It is clear that parts of the surface exposed to very unlike environing agencies, become very unlike; and this is all that needs be shown.

Complex as are the transformations of the inner parts of organisms from the relatively homogeneous into the relatively heterogeneous, we still see among them a conformity to the same general order. In both plants and animals the earlier internal differentiations answer to the stronger contrasts of conditions. Plants, absorbing all their nutriment through their outer surfaces, are internally modified mainly by the transfer of materials and by mechanical stress. Such of them as do not raise their fronds above the surface, have their inner tissues subject to no marked contrasts save those caused by currents of sap; and the lines of lengthened and otherwise changed cells that are formed where these currents run, and are most conspicuous where these currents must obviously be the strongest, are the only decided differentiations of the interior. But where, as in the higher Cryptogams and in Phænogams, the leaves are upheld, and the supporting stem is transversely bent by the wind, the inner tissues, subject to different amounts of mechanical strain, differentiate accordingly: the deposit of dense substance commences in that region where the sap-containing cells and canals suffer the greatest intermittent compressions. Animals, or at least such of them as take food into their interiors, are subject to forces of another class tending to destroy their original homogeneity. Food is a foreign substance which acts on the interior as an environing object which touches it acts on the exterior—is literally a portion of the environment, which, when swallowed, becomes a cause of internal differentiations as the rest of the environment continues a cause of external differentiations. How essentially parallel are the two sets of actions and reactions, we have seen implied by the primordial identity of the endoderm and ectoderm in simple animals, and of the skin and mucous membrane in complex animals (§§ 288, 289). Here we have further to observe that as food is the original source of internal differentiations, these may be expected to show themselves first where the influence of the food is greatest; and to appear later in proportion as the parts are more removed from the influence of the food. They do this. In animals of low type, the coats of the alimentary cavity or canal, are more differentiated than the tissue that lies between the alimentary canal and the wall of the body. This tissue in the higher *Cœlenterata*, is a feebly-organized parenchyma traversed by lacunæ—either simple channels, or canals lined with simple ciliated cells; and in the lower *Mollusca* the structures bounding the perivisceral cavity and its ramifying sinuses, are similarly imperfect. Further, it is observable that the differentiation of this perivisceral sac and its sinuses into a vascular system, proceeds centrifugally from the region where the absorbed nutriment enters the mass of circulating liquid, and where this liquid is qualitatively more unlike the tissues than it is at the remoter parts of the body.

Physiological development, then, is initiated by that instability of the homogeneous which we have seen to be everywhere a cause of evolution (*First Principles*, §§ 109—115). That the passage from comparative uniformity of composition and minute structure to comparative multiformity, is set up in organic aggregates, as in all other aggregates, by the necessary unlikenesses of the actions to which the parts are subject, is shown by the universal rise of the primary differentiation between the parts that are universally most contrasted in their circumstances, and by the rise of secondary differentiations obviously related in their order to secondary contrasts of conditions.

§ 312. How physiological development has all along been aided by the multiplication of effects—how each differentiation has ever tended to become the parent of new differentiations, we have had, incidentally, various illustrations. Let us here review the working of this cause.

Among plants we see it in the production of progressively-multiplying heterogeneities of tissue by progressive increase of bulk. The integration of fronds into axes and of axes into groups of axes, sets up unlikenesses of action among the integrated units, followed by unlikenesses of minute structure. Each gust transversely strains the various parts of the stem in various degrees, and longitudinally strains in various degrees the roots; and while there is inequality of stress at every place in stem and branch, so, at every place in stem and branch, the outer layers and the successively inner layers are severally extended and compressed to unequal amounts, and have unequal modifications wrought in them. Let the tree add to its periphery another generation of the units composing it, and immediately the mechanical strains on the supporting parts are all changed in different degrees, initiating new differences internally. Externally, too, new differences are initiated. Shaded by the leaf-bearing outer stratum of shoots, the inner structures cease to bear leaves, or to put out shoots that bear leaves; and instead of that green covering which they originally had, become covered with bark of increasing thickness. Manifestly, then, the larger integration of units that are originally simple and uniform, entails physiological changes of various orders, varying in their degrees at all parts of the aggregate. Each branch which, favourably circumstanced, flourishes more than its neighbours, becomes a cause of physiological differentiations, not only in its neighbours from which it abstracts sap and presently turns from leaf-bearers into fruit-bearers, but also in the remoter parts.

That among animals physiological development is furthered by the multiplication of effects, we have lately seen proved by the many changes in other organs, which the growth or modification of each excreting and secreting organ initiates. By the abstracted as well as by the added materials, it alters the quality of the blood passing through all members of the body; or by the liquid it pours into the alimentary canal, it acts on the food, and through it on the blood, and through it on the system as a whole: an additional differentiation in one part thus setting up additional differentiations in many other parts; from each of which, again, secondary differentiating forces reverberate through the organism. Or, to take an influence of another order, we have seen how the modified mechanical action of any member not only modifies that member, but becomes, by its reactions, a cause of secondary modifications—how, for example, the burrowing habits of the common Mole, leading to an almost exclusive use of the fore limbs, have entailed a dwindling of the hind limbs, and a concomitant dwindling of the pelvis, which, becoming too small for the passage of the young, has initiated still more anomalous modifications.

So that throughout physiological development, as in evolution at large, the multiplication of effects has been a factor constantly at work, and working more actively as the development has advanced. The secondary changes wrought by each primary change, have necessarily become more numerous in proportion as organisms have become more complex. And every increased multiplication of effects, further differentiating the organism and, by consequence, further integrating it, has prepared the way for still higher differentiations and integrations similarly caused.

§ 313. The general truth next to be resumed, is that these processes have for their limit a state of equilibrium—proximately a moving equilibrium and ultimately a complete equilibrium. The changes we have contemplated are but the concomitants of a progressing equilibration. In every aggregate which we call living, as well as in all other aggregates, the instability of the homogeneous is but another name for the absence of balance between the incident forces and the forces which the aggregate opposes to them; and the passage into heterogeneity is the passage towards a state of balance. And to say that in every aggregate, organic or other, there goes on a multiplication of effects, is but to say that one part which has a fresh force impressed on it, must go on changing and communicating secondary changes, until the whole of the impressed force has been used up in generating equivalent reactive forces.

The principle that whatever new action an organism is subject to, must either overthrow the moving equilibrium of its functions and cause the sudden equilibration called death, or else must progressively alter the organic rhythms, until, by the establishment of a new reaction balancing the new action, a new moving equilibrium is produced, applies as much to each member of an organism as to the organism in its totality. Any force falling on any part not adapted to bear it, must either cause local destruction of tissue, or must, without destroying the tissue, continue to change it until it can change it no further; that is—until the modified reaction of the part has become equal to the modified action. Whatever the nature of the force, this must happen. If it is a mechanical force, then the immediate effect is some distortion of the part—a distortion having for its limit that attitude in which the resistance of the structures to further change of position, balances the force tending to produce the further change; and the ultimate effect, supposing the force to be continuous or recurrent, is such a permanent alteration of form, or alteration of structure, or both, as establishes a permanent balance. If the force is physico-chemical, or chemical, the general result is still the same: the component molecules of the tissue must have their molecular arrangements changed, and the change in their molecular arrangements must go on until their molecular motions are so re-adjusted as to equilibrate the molecular motions of the new physico-chemical or chemical agent. In other words, the organic matter composing the part, if it continues to be organic matter at all, must assume that molecular composition which enables it to bear, or as we say adapts it to, the incident forces.

Nor is it less certain that throughout the organism as a whole, equilibration is alike the proximate limit of the changes wrought by each action, as well as the ultimate limit of the changes wrought by any recurrent actions or continuous action. The ordinary movements every instant going on, are movements towards a new state of equilibrium. Raising a limb causes a simultaneous shifting of the centre of gravity, and such altered tensions and pressures throughout the body as re-adjust the disturbed balance. Passage of liquid into or out of a tissue, implies some excess of force in one direction there at work; and ceases only when the force so diminishes or the counter-forces so increase that the excess disappears. A nervous discharge is reflected and re-reflected from part to part, until it has all been used up in the re-arrangements produced—equilibrated by the reactions called out. And what is thus obviously true of every normal change, is equally true of every abnormal change—every disturbance of the established rhythm of the functions. If such disturbance is a single one, the perturbations set up by it, reverberating throughout the system, leave its moving equilibrium slightly altered. If the disturbance is repeated or persistent, its successive effects accumulate until they have produced a new moving equilibrium adjusted to the new force.

Each re-balancing of actions, having for its necessary concomitant a modification of tissues, it is an obvious corollary that organisms subjected to successive changes of conditions, must undergo successive differentiations and re-differentiations. Direct equilibration in organisms, with all its accompanying structural alterations, is as certain as is that universal progress towards equilibrium of which it forms part. And just as certain is that indirect equilibration in organisms to which the remaining large class of differentiations is due. The development of favourable variations by the killing of individuals in which they do not occur or are least marked, is, as before, a balancing between certain local structures and the forces they are exposed to; and is no less inevitable than the other.

§ 314. In all which universal laws, we find ourselves again brought down to the persistence of force, as the deepest knowable cause of those modifications which constitute physiological development; as it is the deepest knowable cause of all other evolution. Here, as elsewhere, the perpetual lapse from less to greater heterogeneity, the perpetual begetting of secondary modifications by each primary modification, and the perpetual approach to a temporary balance on the way towards a final balance, are necessary implications of the ultimate fact that force cannot disappear, but can only change its form.

It is an unquestionable deduction from the persistence of force, that in every individual organism each new incident force must work its equivalent of change; and that where it is a constant or recurrent force, the limit of the change it works must be an adaptation of structure such as opposes to the new outer force an equal inner force. The only thing open to question is, whether such re-adjustment is inheritable; and further consideration will, I think, show, that to say it is not inheritable is indirectly to say that force does not persist. If all parts of an organism have their functions co-ordinated into a moving equilibrium, such that every part perpetually influences all other parts, and cannot be changed without initiating changes in all other parts—if the limit of change is the establishment of a complete harmony among the movements, molecular and other, of all parts; then among other parts that are modified, molecularly or otherwise, must be those which cast off the germs of new organisms. The molecules of their produced germs must tend ever to conform the motions of their components, and therefore the arrangements of their components, to the molecular forces of the organism as a whole; and if this aggregate of molecular forces is modified in its distribution by a local change of structure, the molecules of the germs must be gradually changed in the motions and arrangements of their components, until they are re-adjusted to the aggregate of molecular forces. For to hold that the moving equilibrium of an organism may be altered without altering the movements going on in a particular part of it, is to hold that these movements will not be affected by the altered distribution of forces; and to hold this is to deny the persistence of force.

# PART VI.

# LAWS OF MULTIPLICATION.

# CHAPTER I.

## THE FACTORS.*

§ 315. If organisms have been evolved, their respective powers of multiplication must have been determined by natural causes. Grant that the countless specialities of structure and function in plants and animals, have arisen from the actions and reactions between them and their environments, continued from generation to generation; and it follows that from these actions and reactions have also arisen those countless degrees of fertility which we see among them. As in all other respects an adaptation of each species to its conditions of existence is directly or indirectly brought about; so must there be directly or indirectly brought about an adaptation of its reproductive activity to its conditions of existence.

We may expect to find, too, that permanent and temporary differences of fertility have the same general interpretation. If the small variations of structure and function that arise within the limits of each species, are due to actions like those

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* An outline of the doctrine set forth in the following chapters, was originally published in the *Westminster Review* for April, 1852, under the title of, *A Theory of Population deduced from the General Law of Animal Fertility;* and was shortly afterwards republished with a prefatory note, to the effect that it must be accepted as a sketch which I hoped at some future time to elaborate. In now revising and completing it, I have omitted a non-essential part of the argument, while I have expanded the remainder by adding to the number of facts put in evidence, by meeting objections which want of space before obliged me to pass over, and by drawing various secondary conclusions.

which, by their long-accumulating effects, have produced the immense contrasts between the various types; we may conclude that, similarly, the actions to which changes in the rate of multiplication of each species are due, also produce, in great periods of time, the enormous differences between the rates of multiplication of different species.

Before inquiring in what ways the rapidities of increase are adjusted to the requirements, both temporary and permanent, it will be needful to look at the factors. Let us set down first those which belong to the environment, and then those which belong to the organism.

§ 316. Every living aggregate being one of which the inner actions are adjusted to balance outer actions, it follows that the maintenance of its moving equilibrium depends on its exposure to the right amounts of these actions. Its moving equilibrium may be overturned if one of these actions is either too great or too small in amount; and it may be so overturned either by excess or defect of some inorganic agency in its environment, or by excess or defect of some organic agency.

Thus a plant, constitutionally fitted to a certain warmth and humidity, is killed by extremes of temperature, as well as by extremes of drought and moisture. It may dwindle away from want of soil, or die from the presence of too great or too small a quantity of some mineral substance which the soil supplies to it. In like manner, every animal can maintain the balance of its functions so long only as the environment adds to or deducts from its heat at rates not exceeding definite limits. Water, too, must be accessible in amount sufficient to compensate its loss: if the parched air is rapidly abstracting its liquid which there is no pool or river to restore, its functions cease; and if it is an aquatic creature, drought may kill it either by drying up its medium or by giving it a medium inadequately aërated. Thus each organism, adjusted to a certain average in the actions of its inorganic environment, or rather, we should say, adjusted to certain moderate deviations from this average, is destroyed by extreme deviations. So, too, is it with the environing organic agencies. Among plants, only the parasitic kinds depend for their individual preservation on the presence of certain other organisms (though the presence of certain other organisms is needful to most plants for the preservation of the race by aiding fertilization). Here, for the continuance of individual life, particular organisms must be absent or not very numerous—beasts that browse, caterpillars that devour leaves, aphides that suck juices. Among animals, however, the maintenance of the functional balance is both positively and negatively dependent on the amounts of surrounding organic agents. There must be an accessible sufficiency of the plants or animals serving for food; and of organisms that are predatory or parasitic or otherwise detrimental, the number must not pass a certain limit.

This dependence of the moving equilibrium in every individual organism on an adjustment of its forces to the forces of the environment, and the overthrow of this equilibrium by failure of the adjustment, is comprehensive of all cases. At first sight it does not seem to include what we call natural death; but only death by violence, or starvation, or cold, or drought. But in reality natural death, no less than every other kind of death, is caused by the failure to meet some outer action by a proportionate inner action. The apparent difference is due to the fact that in old age, when the quantity of force evolved in the organism gradually diminishes, the momentum of the functions becomes step by step less, and the variations of the external forces relatively greater; until there finally comes an occasion when some quite moderate deviation from the average to which the feeble moving equilibrium is adjusted, produces in it a fatal perturbation.

§ 317. The individuals of every species being thus dependent on certain environing actions; and severally having their moving equilibria sooner or later overthrown by one or other of these environing actions; we have next to consider in what ways the environing actions are so met as to prevent extinction of the species. There are two essentially different ways. There may be in each individual a small or great ability to adjust itself to variations of the agencies around it and to a small or great number of such varying agencies —there may be little or much power of preserving the balance of the functions. And there may be much or little power of producing new individuals to replace those whose moving equilibria have been overthrown. A few facts must be set down to enforce these abstract statements.

There are both active and passive adaptations by which organisms are enabled to survive adverse influences. Plants show us but few active adaptations: that of the Pitcher-plant and those of the reproductive parts of some flowers (which do not, however, conduce to self-preservation) are exceptional instances. But plants have various passive adaptations; as thorns, stinging hairs, poisonous and acrid juices, repugnant odours, and the woolliness or toughness that makes their leaves uneatable. Animals exhibit far more numerous adjustments, both passive and active. In some cases they survive desiccation, they hybernate, they acquire thicker clothing, and so are fitted to bear unfavourable inorganic actions; and they are in many cases fitted passively to meet the adverse actions of other organisms, by bearing spines or armour or shells, by simulating neighbouring objects in colour or form or both, by emitting disagreeable odours, or by having disgusting tastes. In still more numerous ways they actively contend with unfavourable conditions. Against the seasons they guard by storing up food, by secreting themselves in crevices, or by forming burrows and nests. They save themselves from enemies by developed powers of locomotion, taking the shape of swiftness or agility or aptitude for changing their media; by their strength either alone or aided by weapons; lastly by their intelligence, without which, indeed, their other superiorities would avail them little. And then these various active powers serving for defence, become, in other cases, the powers that enable animals to aggress, and to preserve their lives by the success of their aggressions.

The second process by which extinction is prevented—the formation of new individuals to replace the individuals destroyed—is carried on, as described in the chapter on "Genesis," by two methods, the sexual and the asexual. Plants multiply by spontaneous fission, by gemmation, by proliferation, and by the evolution of young ones from detached cells and scales and leaves; and they also multiply by the casting off of spores and sporangia and seeds. In like manner among animals, there are varied kinds of agamogenesis, from spontaneous fission up to parthenogenesis, all of them conducing to rapid increase of numbers; and we have the more familiar process of gamogenesis, also carried on in a great variety of ways. This formation of new individuals to replace the old, is, however, inadequately conceived if we contemplate only the number born or detached on each occasion. There are four factors, all variable, on which the rate of multiplication depends. The first is the age at which reproduction commences; the second is the frequency with which broods are produced; the third is the number contained in each brood; and the fourth is the length of time during which the bringing forth of broods continues. There must be taken into account a further element —the amount of aid given by the parent to each germ in the shape of stored-up nutriment, continuous feeding, warmth, protection, &c.: on which amount of aid, varying between immensely wide limits, depends the number of the new individuals that survive long enough to replace the old, and perform the same reproductive process.

Thus, regarding every living organism as having a moving equilibrium dependent on environing forces, but ever liable to be overthrown by irregularities in those forces, and always so overthrown sooner or later; we see that each kind of organism can be maintained only by generation of new individuals with a certain rapidity, and by helping them more or less fully to establish their moving equilibria.

§ 318. Such are the factors with which we are here concerned. I have presented them in abstract shapes, for the purpose of showing how they are expressible in general terms of force—how they stand related to the ultimate laws of redistribution of matter and motion.

For the purposes of the argument now to follow, we may, however, conveniently deal with these factors under a more familiar guise. Ignoring their other aspects, we may class the actions which affect each race of organisms as forming two conflicting sets. On the one hand, by what we call natural death, by enemies, by lack of food, by atmospheric changes, &c., the race is constantly being destroyed. On the other hand, partly by the endurance, the strength, the swiftness, and the sagacity of its members, and partly by their fertility, it is constantly being maintained. These conflicting sets of actions may be generalized as—the forces destructive of race and the forces preservative of race. So generalizing them, let us ask what are the necessary implications.

## CHAPTER II.

### *À PRIORI* PRINCIPLE.

§ 319. The number of a species must at any time be either decreasing or stationary or increasing. If, generation after generation, its members die faster than others are born, the species must dwindle and finally disappear. If its rate of multiplication is equal to its rate of mortality, there can be no numerical change in it. And if the deductions by death are fewer than the additions by birth, the species must become more abundant. These we may safely set down as necessities. The forces destructive of race must be either greater than the forces preservative of race, or equal to them, or less than them; and there cannot but result these effects on number.

We are here concerned only with races that continue to exist; and may therefore leave out of consideration those cases in which the destructive forces, remaining permanently in excess of the preservative forces, cause extinction. Practically, too, we may exclude the stationary condition of a species; for the chances are infinity to one against the maintenance of a permanent equality between the births and the deaths. Hence, our inquiry resolves itself into this:—In races that continue to exist, what laws of numerical variation result from these variable conflicting forces, that are respectively destructive of race and preservative of race?

§ 320. Clearly if the forces destructive of race, when once in excess, had nothing to prevent them from remaining in excess, the race would disappear; and clearly if the forces preservative of race, when once in excess, had nothing to prevent them from remaining in excess, the race would go on increasing to infinity. In the absence of any compensating actions, the only possible avoidance of these opposite extremes would be an unstable equilibrium between the conflicting forces, resulting in a perfectly constant number of the species: a state which we know does not exist, and against the existence of which the probabilities are, as already said, infinite. It follows, then, that as in every continuously-existing species, neither of the two conflicting sets of forces remains permanently in excess; there must be some way of stopping that excess of the one or the other which is ever occurring.

How is this done? Should any one allege, in conformity with the old method of interpretation, that there is in each case a providential interposition to rectify the disturbed balance, he commits himself to the supposition that of the millions of species inhabiting the Earth, each one is yearly regulated in its degree of fertility by a miracle; since in no two years do the forces which foster, or the forces which check, each species, remain the same; and therefore, in no two years is there required the same fertility to balance the mortality. Few if any will say that God continually alters the reproductive activity of every parasitic fungus and every Tape-worm or Trichina, so as to prevent its extinction or undue multiplication; which they must say if they adopt the hypothesis of a supernatural adjustment. And in the absence of this hypothesis there remains only one other. The alternative possibility is, that the balance of the preservative and destructive forces is self-sustaining—is of the kind distinguished as a stable equilibrium: an equilibrium such that any excess of one of the forces at work, itself generates, by the deviation it produces, certain counter-forces that eventually out-balance it, and initiate an opposite deviation. Let us consider how, in the case before us, such a stable equilibrium must be constituted.

§ 321. When a season favourable to it, or a diminution of creatures detrimental to it, causes any species to become more numerous than usual; an immediate increase of certain destructive influences takes place. If it is a plant, the supposed greater abundance itself implies occupation of the available places for growth—an occupation which, leaving fewer such places as the multiplication goes on, itself becomes a check on further multiplication—itself causes a greater mortality of seeds that fail to root themselves. And afterwards, in addition to this passive resistance to continued increase, there comes an active resistance: the creatures that thrive at the expense of the species—the larvæ, the birds, the herbivores—increase too. If it be an animal that has grown more numerous, then, unless by some exceptional coincidence a simultaneous and proportionate addition to the animals or plants serving for food has occurred, there must result a relative scarcity of food. Enemies, too, be they beasts of prey or be they parasites, must quickly begin to multiply. Hence, each kind of organism, previously existing in something like its normal number, cannot have its number raised without a rise of the destructive forces, negative and positive, quickly commencing. Both negative and positive destructive forces must augment until this increase of the species is arrested. The competition for places on which to grow, if the species be vegetal, or for food if it be animal, must become more intense as the over-peopling of the habitat progresses; until there is reached the limit at which the mortality equals the reproduction. And as, at the same time, enemies will multiply with a rapidity which soon brings them abreast of the augmented supply of prey, the positive restraint they exert will help to bring about an earlier arrest of the expansion than pressure of population alone would cause. One more inference may be drawn. Had the species to meet no repressing influence save that negative one of relatively-diminished space or relatively-diminished food-supply, the cause leading to its increase might carry it up to the limit set by this, and there leave it: its enlarged number might be permanent. But the positive repressing influence that has been called into existence, will prevent this. For the increase of enemies, commencing, as it must, after the increase of the species, and advancing in geometrical progression until it is itself checked in like manner, will end in an excess of enemies. Whereupon must result a mortality of the species greater than its multiplication—a decrease which will continue until its habitat is underpeopled, its unduly-numerous enemies decimated by starvation, and the destroying agencies so reduced to a minimum. Whence will follow another increase.

Thus, as before indicated (*First Prin.* § § 96, 133), there is here, as wherever antagonistic forces are in action, an alternate predominance of each, causing a rhythmical movement —a rhythmical movement which constitutes a moving equilibrium in those cases where the forces are not dissipated with appreciable rapidity, or are re-supplied as fast as they are dissipated. While, therefore, on the one hand, we see that the continued existence of a species necessarily implies some action by which the destructive and preservative forces are self-adjusted; we see, on the other hand, that such an action is an inevitable consequence of the universal process of equilibration.

§ 322. Is this the sole equilibration that must exist? Clearly not. The temporary compensating adjustments of multiplication to mortality in each species, are but introductory to the permanent compensating adjustments of multiplication to mortality among species in general. The above reasoning would hold just as it now does, were all species equally prolific and all equally short-lived. It yields no answer to the inquiries—why do their fertilities differ so enormously, or why do their mortalities differ so enormously? and how is the general fertility adapted to the general mortality in each? The balancing process we have contemplated, can go on only within moderate limits—must fail entirely in the absence of a due proportion between the ordinary birth-rate and the ordinary death-rate. If the reproduction of mice proceeded as slowly as the reproduction of men, mice would be extinct before a new generation could arise: even did their natural lives extend to fifteen or sixteen years, it would still be extremely improbable that any would for so long survive all the dangers they are exposed to. Conversely, did oxen propagate as fast as infusoria, the race would die of starvation in a week. Hence, the minor adjustment of varying multiplication to varying mortality in each species, implies some major adjustment of average multiplication to average mortality. What must this adjustment be?

We have already seen that the forces preservative of race are two—ability in each member of the race to preserve itself, and ability to produce other members—power to maintain individual life, and power to generate the species. These must vary inversely. When, from lowness of organization, the ability to contend with external dangers is small, there must be great fertility to compensate for the consequent mortality; otherwise the race must die out. When, on the contrary, high endowments give much capacity of self-preservation, a correspondingly-low degree of fertility is requisite. Given the dangers to be met as a constant quantity; then, as the ability of any species to meet them must be a constant quantity too, and as this is made up of the two factors—power to maintain individual life and power to multiply—these cannot do other than vary inversely: one must decrease as the other increases.

It needs but to conceive the results of nonconformity to this law, to see that every species must either conform to it or cease to exist. Suppose, first, a species whose individuals having but small self-preservative powers are rapidly destroyed, to be at the same time without reproductive powers proportionately great. The defect of fertility, if extreme, will result in the death of one generation before another has grown up. If less extreme, it will entail a scarcity such that in the next generation sexual congress will be too infrequent to maintain even the small number that remains; and the race will dwindle with increasing rapidity. If still less extreme, the consequent degree of rareness, while not so great as to prevent an adequate number of procreative unions, will be so great as to render special food very abundant and special enemies very few—will thus diminish the destructive forces so much that the self-preservative forces will become *relatively* great: so great, relatively, that when combined with the small ability to propagate the species, they will suffice to balance the small destructive forces. Suppose, next, a species whose individuals have great powers of self-preservation, while they have powers of multiplication much beyond what is needful. The excess of fertility, if extreme, will cause sudden extinction of the species by starvation. If less extreme, it must produce a permanent increase in the number of the species; and this, followed by intenser competition for food and augmented number of enemies, will involve such an increase of the dangers to individual life, that the great self-preserving powers of the individuals will not be more than sufficient to cope with them. That is to say, if the fertility is relatively too great, then the ability to maintain individual life inevitably becomes smaller, *relatively* to the requirements; and the inverse proportion is thus established.

So that when, from comparing the different states of the same species, we go on to compare the states of different species, we see that there is an analogous adjustment—analogous in the sense that great mortality is associated with great multiplication, and small mortality with small multiplication. And we see that the unlikeness of the cases consists merely in this, that what is a temporary relation in the one is a permanent relation in the other.

§ 323. For the moment it does not concern us to inquire what is the origin of this permanent relation. That which we have now to note, is simply that in some way or other there must be established an inverse proportion between the power to sustain individual life and the power to produce new individuals. Here it is enough for us to recognize this as a necessary truth. Whether or not the permanent relation is self-adjusting in long periods of time, as the temporary relation is self-adjusting in short periods of time, is a separate question. The purpose of this chapter is fulfilled by showing that such a permanent relation must exist.

But having recognized the *à priori* principle that in races which continuously survive, the forces destructive of race must be equilibrated by the forces preservative of race; and that supposing these are constant, there must be an inverse proportion between self-preservation and race-preservation; we may go on to inquire how this relation, necessary in theory, arises in fact. Leaving out the untenable hypothesis of a supernatural pre-adjustment, we have to ask in what way an adjustment comes about as a result of Evolution. Is it due to the survival of varieties in which the proportion of fertility to mortality happens to be the best? Or is the fertility adapted to the mortality in a more direct way? To these questions let us now address ourselves.

# CHAPTER III.

## OBVERSE *A PRIORI* PRINCIPLE.

§ 324. When dealing with its phenomena inductively, we saw that however it may be carried on, Genesis "is a process of negative or positive disintegration; and is thus essentially opposed to that process of integration, which is one element of individual evolution." (§ 76.) Each new individual, whether separated as a germ or in some more-developed form, is a deduction from the mass of a pre-existing individual or of two pre-existing individuals. Whatever nutritive matter is stored up along with the germ, if it be deposited in the shape of an egg, is so much nutritive matter lost to the parent. No drop of blood can be absorbed by the fœtus, and no draught of milk sucked by the young when born, without taking from the mother tissue-forming and force-evolving materials to an equivalent amount. And all subsequent supplies given to progeny, if they are nurtured, involve, to a parent or parents, so much waste in exertion that does not bring its return in assimilated food.

Conversely, the continued aggregation of materials into one organism, renders impossible the formation of other organisms out of those materials. As much assimilated food as is united into a single whole, is so much assimilated food withheld from a plurality of wholes that might else have been produced. Given the absorbed nutriment as a constant quantity, and the longer the building of it up into a concrete shape goes on, the longer must be postponed any building of it up into discrete shapes. And similarly, the larger the proportion of matter consumed in the functional actions of parents, the smaller must be the proportion of matter that can remain to establish and support the functional actions of offspring.

Though the necessity of these universal relations is tolerably obvious as thus generally stated, it will be useful to dwell for a brief space on their leading aspects.

§ 325. That disintegration which constitutes genesis, may be such as to disperse entirely the aggregate which integration has previously produced—the parent may dissolve wholly into progeny. This dissolution of each aggregate into two or many aggregates, may occur at very short intervals, in which case the bulk attained can be but extremely small; or it may occur at longer intervals, in which case a larger bulk may be attained.

Instead of quickly losing its own individuality in the individualities of its offspring, each member of the race may, after growing for a time, have portions of its substance begin to develop into the parental shape and presently detach themselves; and the parent, maintaining its own identity, may continue indefinitely so to produce young ones. But clearly, the earlier it commences doing this, and the more rapidly it does it, the sooner must the increase of its own bulk be stopped.

Or again, growth and development continuing for a long period without any deduction of materials, an individual of considerable size and organization may result; and then the abstraction of substance for the formation of new individuals, or rather the eggs of them, may be so great that as soon as the eggs are laid the parent dies of exhaustion—dies, that is, from an excessive loss of the nutritive matters needed for its own activities.

Once more, the deduction of materials for the propagation of the species may be postponed long enough to allow of great bulk and complex structure being attained. The procreative subtraction then setting in, while it checks and presently stops growth, may be so moderate as to leave vital capital sufficient to carry on the activities of the parent; may go on as long as parental vigour suffices to furnish, without fatal result, the materials needed to produce young ones; and may cease when such a surplus cannot be supplied, leaving the parental life to continue.

§ 326. The opposite side of this antagonism has also several aspects. Progress of organic evolution may be shown in increased bulk, in increased structure, in increased amount or variety of action, or in combinations of these; and under any of its forms this carrying higher of each individuality, implies a correlative retardation in the establishment of new individualities.

Other things equal, every addition to the bulk of an organism is an augmentation of its life. Besides being an advance in integration, it implies a greater total of activities gone through in the assimilation of materials; and it implies, thereafter, a greater total of the vital changes taking place from moment to moment in all parts of the enlarged mass. Moreover, while increased size is thus, in so far, the expression of increased life, it is also, where the organism is active, the expression of increased ability to maintain life—increased strength. Aggregation of substance is almost the only mode in which self-preserving power is shown among the lowest types; and even among the highest, sustaining the body in its integrity is that in which self-preservation fundamentally consists—is the end which the widest intelligence is indirectly made to subserve. While, on the one hand, the increase of tissue constituting growth is conservative both in essence and in result; on the other hand, decrease of tissue, either from injury, disease, or old age, is in both essence and result the reverse. And if so, every addition to individual life thus implied, necessarily delays or diminishes the casting off of matter to form new individuals.

Other things equal, too, a greater degree of organization involves a smaller degree of that disorganization shown by the separation of reproductive gemmæ and germs. Detachment of a living portion or portions from what was previously a living whole, is a ceasing of co-ordination; and is therefore essentially at variance with that establishment of greater co-ordination which is achieved by structural development. In the extreme cases where a living mass is continually dividing and subdividing, it is manifest that there cannot arise much physiological division of labour; since progress towards mutual dependence of parts is prevented by the parts becoming independent. Contrariwise, it is equally clear that in proportion as the physiological division of labour is carried far, the separative process must be localized in some comparatively small portion of the organism, where it may go on without affecting the general structure—must become relatively subordinate. The advance that is shown by greater heterogeneity, must be a hindrance to multiplication in another way. For organization entails cost. That transfer and transformation of materials implied by differentiation, can be effected only by expenditure of force; and this supposes consumption of digested and absorbed food, which might otherwise have gone to make new organisms, or the germs of them. Hence, that individual evolution which consists in progressive differentiation, as well as that which consists in progressive integration, necessarily diminishes that species of dissolution, general or local, which propagation of the race exhibits.

In active organisms we have yet a further opposition between self-maintenance and maintenance of the race. All motion, sensible and insensible, generated by an animal for the preservation of its life, is motion liberated from decomposed nutriment—nutriment which, if not thus decomposed, would have been available for reproduction; or rather—might have been replaced by nutriment fitted for reproductive purposes, absorbed from other kinds of food. Hence, in proportion as the activities increase—in proportion as, by its more varied, complex, rapid, and vigorous actions, an animal gains power to support itself and to cope with surrounding dangers, it must lose power to propagate.

§ 327. How may this antagonism be best expressed in a brief way? If self-preservation displayed itself in the highest organisms, as it does in the lowest, in little else but continuous growth; and if race-preservation consisted always, as it does often, of nothing beyond detachment of portions from the parental mass; then the antagonism would be, throughout, the obviously-necessary one of integration and disintegration. Maintenance of the individual and propagation of the species, being respectively aggregative and separative, it would be as self-evident that they vary inversely, as it is self-evident that addition and subtraction undo one another. But though the simplest types show us the opposition of self-maintenance and race-maintenance almost wholly under this form; and though higher types, up to the most complex, exhibit it to a great extent under this form; yet, as we have just seen, this is not its only form. The total material monopolized by the individual and withheld from the race, must be stated as the quantity united to form its fabric, *plus* the quantity expended in differentiating its fabric, *plus* the quantity expended in its self-conserving actions. Similarly, the total material devoted to the race at the expense of the individual, includes that which is directly subtracted from the parent in the shape of egg or fœtus, *plus* that which is directly subtracted in the shape of milk, *plus* that which is indirectly subtracted in the shape of matter consumed in the exertions of fostering the young. Hence this inverse variation is not expressible in simple terms of aggregation and separation. As we advance to more highly-evolved organisms, the total cost of an individual becomes very much greater than is implied by the amount of tissue composing it. So, too, the total cost of producing each new individual becomes very much greater than that of its mere substance. And it is between these two total costs that the antagonism exists.

We may, indeed, reduce the antagonism to a form comprehensive of all cases, if we consider it as existing between the sums of the forces, latent and active, used for the two purposes. The molecules which make up a plant or animal, have been formed by the absorption of forces directly or indirectly derived from the sun; and hence the quantity of matter raised to the form called organic, which a plant or animal presents, is equivalent to a certain amount of force. Another amount of force is expressed by the totality of its differentiations. A further amount of force is that dissipated in its actions. And in these three amounts added together, we have the whole expense of the individual life. So, too, the whole expense of establishing each new individual includes—first the forces latent in the substance composing it when born or hatched; second the forces latent in the prepared nutriment afterwards supplied; and third the forces expended in feeding and protecting it. These two sets of forces being taken from a common fund, it is manifest that either set can increase only by decrease of the other. If, of the force which the parent obtains from the environment, much is consumed in its own life, little remains to be consumed in producing other lives; and, conversely, if there is a great consumption in producing other lives, it can only be where comparatively little is reserved for parental life.

Hence, then, Individuation and Genesis are necessarily antagonistic. Grouping under the word Individuation all processes by which individual life is completed and maintained; and enlarging the meaning of the word Genesis so as to include all processes aiding the formation and perfecting of new individuals; we see that the two are fundamentally opposed. Assuming other things to remain the same—assuming that environing conditions as to climate, food, enemies, &c., continue constant; then, inevitably, every higher degree of individual evolution is followed by a lower degree of race-multiplication, and *vice versâ*. Progress in bulk, complexity, or activity, involves retrogress in fertility; and progress in fertility involves retrogress in bulk, complexity, or activity.

This statement needs a slight qualification. For reasons to be hereafter assigned, the relation described is never completely maintained; and in the small departure from it, we shall find an admirable self-acting tendency to further the supremacy of the most-developed types. Here, however, this hint must suffice: explanation would carry us too far out of our line of argument. For the present it will not lead us astray if we regard this inverse variation of Individuation and Genesis as exact.

§ 328. Thus, then, the condition which each race must fulfil if it is to survive, is a condition which, in the nature of things, it ever tends to fulfil. In the last chapter we saw that a species cannot be maintained unless the power to preserve individual life and the power to propagate other individuals vary inversely. And here we have seen that, irrespective of an end to be subserved, these powers cannot do other than vary inversely. On the one hand, given a certain totality of destroying forces with which the species has to contend; and in proportion as its members have severally but small ability to resist these forces, it is requisite that they should have great ability to form new individuals, and *vice versâ*. On the other hand, given the quantity of force, absorbed as food or otherwise, which the species can use to counterbalance these destroying forces; and in proportion as much of it is expended in preserving the individual, little of it can be reserved for producing new individuals and *vice versâ*. There is thus complete accordance between the requirements considered under each aspect. The two necessities correspond.

We might rest on these deductions and their several corollaries. Without going further we might with safety assert the general truths that, other things equal, advancing evolution must be accompanied by declining fertility; and that, in the highest types, fertility must still further decrease if evolution still further increases. We might be sure that if, other things equal, the relations between an organism and its environment become so changed as permanently to diminish the difficulties of self-preservation, there will be a permanent increase in the rate of multiplication; and, conversely, that a decrease of fertility will result where altered circumstances make self-preservation more laborious.

But we need not content ourselves with these *à priori* inferences. If they are true, there must be an agreement between them and the observed facts. Let us see how far such an agreement is traceable.

# CHAPTER IV.

## DIFFICULTIES OF INDUCTIVE VERIFICATION.

§ 329. Were all species subject to the same kinds and amounts of destructive forces, it would be easy, by comparing different species, to test the inverse variation of Individuation and Genesis. Or if either the power of self-preservation or the power of multiplication were constant, there would be little difficulty in seeing how the other changed as the destroying forces changed. But comparisons are nearly always partially vitiated by some want of parity. Each factor, besides being variable as a whole, is compounded of factors that are severally variable. Not simply is the sum of the forces destructive of race different in every case; and not simply are both sets of forces preservative of race unlike in their totalities in every case; but each is made up of actions that bear such changing proportions to one another as to prevent any positive estimation of its amount.

Before dealing with the facts as well as we can, it will be best to glance at the chief difficulties; so that we may see the kind of verification which is alone possible.

§ 330. Either absolutely, or relatively to any species, every environment differs more or less from every other. There are the unlikenesses of media—air, water, earth, organic matter; severally involving special resistances to movement, and special losses of heat. There are the contrasts of climate: here great expenditure for the maintenance of temperature is needed, and there very little; in one zone an organism is supplied with abundant light all the year round, and in another only for a few months; this region yields an almost unfailing supply of water, while that entails the exertion of travelling many miles every night for a draught.

Permanent differences in the natures and distributions of aliment greatly interfere with the comparisons. The Swallow goes through more exertion than the Sparrow in securing a given weight of food; but then their foods are dissimilar in nutritive qualities. There is a want of parallelism between the circumstances of those herbivores that live where the plains are annually covered for a time with rich herbage, but afterwards become parched up, and of those inhabiting more temperate regions. Insects whose larvæ feed on an abundant plant, as those of the genus *Vanessa* on the Nettle, have practically an environment very unlike that of insects such as *Deilephila Euphorbiæ*, whose larvæ feed on a comparatively rare plant—the Sea-Spurge.

Again, comparisons between creatures otherwise akin in their constitutions and circumstances, are hindered by inequalities in their relations to enemies. Two animals, of which one is predatory and has no foes but parasites, while the other is much pursued, cannot properly be contrasted with a view to determining the influence of size or complexity.

Without multiplying instances, it will be clear enough then that the aggregate of destructive actions, positive and negative, which each species has to contend with, is so undefinable in the amounts and kinds of its components, that nothing beyond a vague idea of its relative total can be formed.

§ 331. Besides these immense variations in the outer actions to be counter-balanced, there are immense variations in the inner actions required to counter-balance them. Even if species were similarly conditioned, self-preservation would require of them extremely unlike expenditures of force.

The cost of locomotion increases in a greater ratio than the size. In virtue of the law that the weights of animals increase as the cubes of their dimensions, while their strengths increase only as the squares of their dimensions (§ 46), a given speed requires a large animal to consume more substance in proportion to its weight, than it requires a small animal to consume; and this law holding of all the mechanical actions, there results, other things equal, a difficulty of self-maintenance that augments in a more rapid ratio than the bulk. Nor must we overlook the further complication, that among aquatic creatures the variation of resistance of the medium partially neutralizes this effect.

Again, the heat-consumption is a changing element in the total expense of self-preservation. Creatures that have temperatures scarcely above that of the air or water, may, other things equal, accumulate more surplus nutriment than creatures that have to keep their bodies warm spite of the continual loss by radiation and conduction. This difference of cost is modified by the presence or absence of natural clothing; and it is also modified by unlikenesses of size. Here the bulky animals have the advantage: small masses cooling more rapidly than large ones.

Dissimilarities of attack and defence are also causes of variation in the outlay for self-maintenance. A creature that has to hunt, as compared with another that gets a sufficiency of prey by lying in wait, or a creature that escapes by speed as compared with another that escapes by concealment, obviously leads a life that is physiologically more costly. Animals that protect themselves passively, as the Hedge-hog by its spines or as the Skunk and the Musk-rat by their intolerable odours, are relatively economical; and have the more vital capital for other purposes.

Amplification is needless. These instances will show that anything beyond very general conceptions of the individual expenditures in different cases, cannot be reached.

§ 332. Still more entangled are we among qualifying considerations when we contrast species in their powers of multiplication. The total cost of Genesis admits of even less definite estimation than does the total cost of Individuation. I do not refer merely to the truth that the degree of fertility depends on four factors—the age of commencing reproduction, the number in each brood, the frequency of the broods, and the time during which broods continue to be repeated. There are many further obstacles in the way of comparisons.

Were all multiplication carried on sexually, the problem would be less involved; but there are many kinds of asexual multiplication alternating with the sexual. This asexual multiplication is in some cases perpetual instead of occasional; and often has more forms than one in the same species. The result is that we have to compare what is here a periodic process with what is elsewhere a cyclical process partly continuous and partly periodic—the calculation of fertility in this last case being next to impossible.

We have to avoid being misled by the assumption that the cost of Genesis is measured by the number of young produced, instead of being measured, as it is, by the weight of nutriment abstracted to form the young, *plus* the weight consumed in caring for them. This total weight may be very diversely apportioned. In contrast to the Cod with its million of small ova spawned without protection, we may put the *Hippocampus* or the Pipe-fish, with its few relatively-large ova carried about by the male in a caudal pouch, or seated in hemispherical pits in its skin; or we may put the still more remarkable genus *Arius*, and especially *Arius Boakeii*—a fish some six or seven inches long, which produces ten or a dozen eggs as large as marbles, that are carried by the male in his mouth till they are hatched. Here though the degrees of fertility, if measured by the numbers of fertilized germs deposited, are extremely unlike, they are less unlike if measured by the numbers of young that are hatched and survive long enough to take care of themselves; nor will the tax on the parent-Cod seem so immensely different from that on the parent-*Arius*, if the masses of the ova, instead of their numbers, are compared. Again, while sometimes the parental loss is little else but the matter deducted to form eggs, &c.; at other times it takes the shape of a small direct deduction joined with a large indirect outlay. The Mason-wasp furnishes a typical instance. In journeyings hither and thither to fetch bit by bit the materials for building a cell; in putting together these materials, as well as in secreting glutinous matter to act as cement; and then, afterwards, in the labour of seeking for, and carrying, the small caterpillars with which it fills up the cell to serve its larva with food when it emerges from the egg; the Mason-wasp probably expends more substance than is contained in the egg itself. And this supplementary expenditure is manifestly so great, that but few eggs can be housed and provisioned.

Estimates of the cost of Genesis are further complicated by variations in the ratio borne by the two sexes. Among Fishes the mass of milt approaches in size the mass of spawn; but among higher *Vertebrata* the substance lost by the one sex in the shape of sperm-cells is small compared with that lost by the other sex in the shape of albumen stored-up in the eggs, or blood supplied to the fœtus, or milk given to the young. Then there come the differences of indirect tax on males and females. While, frequently, the fostering of the young devolves entirely on the female, occasionally, the male undertakes it wholly or in part. After building a nest, the male Stickleback guards the eggs till they are hatched; as does also the great *Silurus glanis* for some forty days, during which he takes no food. And then, among most birds, we have the male occupied in feeding the female during incubation, and the young afterwards. Evidently all these differences affect the proportion between the total cost of reproduction and the total cost of individuation.

Whether the species is monogamous or polygamous, and whether there are marked differences of size or of structure between males and females, are also questions not to be overlooked. If there are many females to one male, the total quantity of assimilated matter devoted by each generation to the production of a new generation, is greater than if there is a male to each female. Similarly, where the requirements are such that small males will suffice, the larger quantity of food left for the females, makes possible a greater surplus available for reproduction. And where, as in some of the *Cirrhipedia,* or such a parasite as *Sphærularia Bombi,* the female is a thousand or many thousand times the size of the male, the reproductive capacity is almost doubled: the effect on the rate of multiplication being something like that which would result if any ordinary race could have all its males replaced by fertile females. Conversely, where the habits of the race render it needless that both sexes should have developed powers of locomotion—where, as in the Glow-worm and sundry *Lepidoptera,* the female is wingless while the male has wings—the cost of Individuation not being so great for the species as a whole, there arises a greater reserve for Genesis: the matter which would otherwise have gone to the production of wings and the using of them, may go to the production of ova.

Other complications, as those which we see in Bees and Ants, might be dwelt on; but the foregoing will amply serve the intended purpose.

§ 333. To ascertain by comparison of cases whether Individuation and Genesis vary inversely, is thus an undertaking so beset with difficulties, that we might despair of any satisfactory results, were not the relation too marked a one to be hidden even by all these complexities. Species are so extremely contrasted in their degrees of evolution, and so extremely contrasted in their rates of multiplication, that the law of relation between these characters becomes unmistakable when the evidence is looked at in its *ensemble*. This we shall soon find on ranging in order a number of typical cases.

In doing this it will be convenient to neglect, temporarily, all unlikenesses among the circumstances in which organisms are placed. At the outset, we will turn our attention wholly to the antagonism displayed between the integrative process which results in individual evolution and the disintegrative process which results in multiplication of individuals; and this we will consider first as we see it under the several forms of agamogenesis, and then as we see it under the several forms of gamogenesis. We will next look at the antagonism between propagation and that evolution which is shown by increased complexity. And then we will consider the remaining phase of the antagonism, as it exists between the degree of fertility and the degree of evolution expressed by activity.

Afterwards, passing to the varying relations between organisms and their environments, we will note how relative increase in the supply of food, or relative decrease in the quantity of force expended by the individual, entails relative increase in the quantity of force devoted to multiplication, and *vice versâ*.

Certain minor qualifications, together with sundry important corollaries, may then be entered upon.

## CHAPTER V.

### ANTAGONISM BETWEEN GROWTH AND ASEXUAL GENESIS.

§ 334. When illustrating, in Part IV., the morphological composition of plants and animals, there were set down in groups, numerous facts which we have here to look at from another point of view. Then we saw how, by union of small simple aggregates, there are produced large compound aggregates. Now we have to observe the reactive effect of this process on the relative numbers of the aggregates. Our present subject is the antagonism of Individuation and Genesis as seen under its simplest form, in the self-evident truth that the same quantity of matter may be divided into many small wholes or few large wholes; but that number negatives largeness and largeness negatives number.

In setting down some examples, we may conveniently adopt the same arrangement as before. We will look at the facts as they are presented by vegetal aggregates of the first order, of the second order, and of the third order; and then as they are presented by animal aggregates of the same three orders.

§ 335. The ordinary unicellular plants are at once microscopic and enormously prolific. The often cited *Protococcus nivalis*, which shows its immense powers of multiplication by reddening wide tracts of snow in a single night, does this by developing in its cavity a brood of young cells, which, being presently set free by the bursting of the parent-cell, severally grow and quickly repeat the process. The like occurs among sundry of those kindred forms of minute *Algæ* which, by their enormous numbers, sometimes suddenly change pools to an opaque green. So, too, the *Desmidiaceæ* often multiply so greatly as to colour the water; and among the *Diatomaceæ* the rate of genesis by self-division, "is something really extraordinary. So soon as a frustule is divided into two, each of the latter at once proceeds with the act of self-division; so that, to use Professor Smith's approximative calculation of the possible rapidity of multiplication, supposing the process to occupy, in any single instance, twenty-four hours, 'we should have, as the progeny of a single frustule, the amazing number of one thousand millions in a single month.'" In these cases the multiplication is so carried on that the parent is lost in the offspring—the old individuality disappears either in the swarms of zoospores it dissolves into, or in the two or four new individualities simultaneously produced by fission. Vegetal aggregates of the first order, have, however, a form of agamogenesis in which the parent individuality is not lost: the young cells arise from the old cells by external gemmation. This process, too, repeated as it is at short intervals, results in immense fertility. The Yeast-fungus, which in a few hours thus propagates itself throughout a large mass of wort, offers a familiar example.

In certain compound forms that must be classed as plants of the second order of aggregation, though very minute ones, self-division similarly increases the numbers at high rates. The *Sarcina ventriculi,* a parasitic plant that infests the stomach and swarms afresh as fast as previous swarms are vomited, shows us a spontaneous fission of clusters of cells. An allied mode of increase occurs in *Gonium pectorale:* each cell of the cluster resolving itself into a secondary cluster, and the secondary clusters then separating. "Supposing, which is very probable, that a young *Gonium* after twenty-four hours is capable of development by fission, it follows that under favourable conditions a single colony may on the second day develop 16, on the third 256, on the fourth 4,096, and at the end of a week 268,435,456 other organisms like itself." In the *Volvocinæ* this continual dissolution of a primary compound individual into secondary compound individuals, is carried on endogenously—the parent bursting to liberate the young; and the numbers arising by this method, also are sometimes so great as to tint large bodies of water. More fully established and organized aggregates of the second order, such as the higher Thallogens and the lower Acrogens, do not sacrifice their individualities by fission; but nevertheless, by the kindred process of gemmation, are continually hindered in the increase of their individualities. The gemmæ called tetraspores are cast off in great numbers by the marine *Algæ*. Among those simple *Jungermanniaceæ* which consist of single fronds, the young ones that bud out grow for a time in connexion with their parents, send rootlets from their under sides into the soil, and presently separate themselves—a habit which augments the number of individuals in proportion as it checks their growths.

Plants of the third order of composition, arising by arrest of this separation, exhibit a further corresponding decrease in the abundance of the aggregates formed. Acrogens of inferior types, in which the axes produced by integration of fronds are but small and feeble, are characterized by the habit of throwing off bulbils—bud-shaped axes which, falling and taking root, add to the number of distinct individuals. This agamic multiplication, very general among the Mosses and their kindred, and not uncommon under a modified form in such higher types as the Ferns, many of which produce young ones from the surfaces of their fronds, becomes very unusual among Phænogams. The detachment of bulbils, though not unknown among them, is exceptional. And while it is true that some flowering plants, as the Strawberry, multiply by a process allied to gemmation, yet this is anything but characteristic of the class. A leading trait of these highest groups, to which the largest members of the vegetal kingdom belong, is that agamogenesis has so far ceased that it does not originate independent plants. Though the axes which, budding one out of another, compose a tree, are the equivalents of asexually-produced individuals; yet the asexual production of them stops short of separation. These vast integrations arise where spontaneous disintegration, and the multiplication effected by it, have come to an end.

Thus, not forgetting that certain Phænogams, as *Begonia phyllomaniaca,* revert to quite primitive modes of increase, we may hold it as beyond question that while among the most minute plants asexual multiplication is universal, and produces enormous numbers in short periods, it becomes step by step more restricted in range and frequency as we advance to large and compound plants; and disappears so generally from the largest, that its occurrence is regarded as anomalous.

§ 336. Parallel examples showing the inverse variation of growth and asexual genesis among animals, make clear the purely quantitative nature of this relation under its original form. Of the *Amœba* it is said that " when a large variable process has been shot out far from the chief mass and become enlarged at the extremity, the expanded end retains its position, whilst the portion connecting it with the body becomes finer and finer by being withdrawn into the parent mass, until it at last breaks across, leaving a detached piece, which immediately on its own account shoots out processes, and manifests an independent existence. This phenomenon is therefore one of simple detachment, and cannot rightly be called a process of fission." But it shows us, nevertheless, how the primordial form of multiplication is nothing more than a separation, instead of a continued union, of the growing mass. Among the *Protozoa,* as among the *Protophyta,* there occurs that process by which the individuality of the parent is wholly lost in producing offspring

—the breaking up of the parental mass into a number of germs. An example is supplied by one of the lowest of the class—the *Gregarina.* This creature, which is nothing more than a minute spheroidal nucleated mass of protoplasm, having a structureless outer layer denser than the rest, but being without mouth or any organ, resolves itself into a multitude of still more minute masses, which when set free by bursting of the envelope, shortly become *Amœba*-form, and severally assuming the structure of the parent, go through the same course. Some of the *Infusoria,* as for instance those of the genus *Kolpoda,* similarly become encysted and subsequently break up into young ones. The more familiar mode of increase among these animal-aggregates of the first order, by fission, though it sacrifices the parent individuality by merging it in the individualities of the two produced, sacrifices it less completely than does the dissolution into a great number of germs. Occurring, however, as this fission does, very frequently, and being completed, in some cases that have been observed, in the course of half-an-hour, it results in immensely-rapid multiplication. If all its offspring survive, and continue dividing themselves, a single *Paramecium* is said to be capable of thus originating 268 millions in the course of a month. Nor is this the greatest known rate of increase. Another animalcule, visible only under a high magnifying power, "is calculated to generate 170 billions in four days." And these enormous powers of propagation are accompanied by a minuteness so extreme, that of some species one drop of water would contain as many individuals as there are human beings on the Earth! Making allowance for exaggeration in these estimates, it is beyond question that among these smallest of animals the rate of asexual multiplication is by far the greatest; and this suffices for the purposes of the argument.*

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* That these estimated rates are not greater than is probable, may be inferred from such observations as that of Mr. Brightwell on the buds of *Zoothamnium.* "At nine in the morning, one of these buds, or ova, was

Of animal aggregates belonging to the second order, that multiply asexually with rapidity, the familiar Polypes furnish conspicuous examples. By gemmation in most cases, in other cases by fission, and in some cases by both, the agamogenesis is carried on among these tribes. As shown in Fig. 148, the budding of young ones from the parent *Hydra* is carried on so actively, that before the oldest of them is cast off half-a-dozen or more others have reached various stages of growth; and even while still attached, the first-formed of the group have commenced budding out from their sides a second generation of young ones. In the *Hydra tuba* this gemmiparous multiplication is from time to time interrupted by a transverse splitting-up of the body into segments, which successively separate and swim away: the result of the two processes being, that in the course of a season there are produced from a single germ, great numbers of young *Medusæ*, which are the adult or sexual forms of the species. Respecting Cœlenterate animals of this degree of composition, it may be added that when we ascend to the larger kinds we find asexual genesis far less active. Though comparisons are interfered with by differences of structure and mode of life, yet the contrasts are too striking to have their meanings much obscured. If, for instance, we take a solitary *Actinozoon* and a solitary *Hydrozoon*, we see that the relatively-great bulk of the first, goes along with a relatively-slow agamogenesis. The common Sea-anemones are but occasionally observed to undergo self-division: their numbers are not rapidly increased by this process. A higher class of secondary aggregates exemplifies the same

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observed fixed to the glass by a sheathed pedicle; a ciliary motion became perceptible at the top of the bulb; and at ten it had divided longitudinally into two buds, each supported by a short stalk. The ciliary motion continued in the centre of each of these two buds, which by degrees expanded longitudinally, and at twelve had become four buds. By four in the afternoon, these four buds had divided in like manner and increased to nine, with an elongated footstalk, and interior contractile muscle."

general truth with a difference. In the smaller members the agamogenesis is incomplete, and in the larger it disappears. Each sub-section of the *Molluscoida* shows us this. The gemmation of the minute *Polyzoa,* though it does not end in the separation of the young individuals, habitually goes to the extent of producing families of partially-independent individuals; but their near allies the *Brachiopoda,* which immensely exceed them in size, are solitary and not gemmiparous. So, too, is it with the *Ascidioida.* And then among the true *Mollusca,* including all the largest forms belonging to this sub-kingdom, no such thing is known as fission or gemmation.

Take next the *Annulosa,* including under this title the *Annuloida.* When treating of morphological composition, reasons were given for the belief that the annulose animal is an aggregate of the third order, the segments of which, produced one from another by gemmation, originally became separate, as they still become in the cestoid *Entozoa;* but that by progressive integration, or arrested disintegration, there resulted a type in which many such segments were permanently united (§§ 205-7). Part of the evidence there assigned, is evidence to be here repeated in illustration of the direct antagonism of Growth and Asexual-Genesis. We saw how, among the lower Annelids, the string of segments produced by gemmation presently divides transversely into two strings; and how, in some cases, this resolution of the elongating string of segments into groups that are to form separate individuals, goes on so actively that as many as six groups are found in different stages of progress to ultimate independence—a fact implying a high rate of fissiparous multiplication. Then we saw that, in the superior annulose types, distinguished in the mass by including the larger species, fission does not occur. The higher Annelids do not propagate in this way; there is no known case of new individuals being so formed among the *Myriapoda;* nor do the Crustaceans afford us a single instance of this primordial mode of increase. It is, indeed, true that while articulate animals never multiply asexually after this simplest method, and while they are characterized in the mass by the cessation of agamogenesis of every kind, there nevertheless occur in a few of their small species, those higher forms of agamogenesis known as parthenogenesis, pseudo-parthenogenesis and internal metagenesis; and that by these some of them multiply very rapidly. Hereafter we shall find, in the interpretation of these anomalies. further support for the general doctrine.

To the above evidence has to be added that which the *Vertebrata* present. This may be very briefly summed up. On the one hand, this class, whether looked at in the aggregate or in its particular species, immensely exceeds all other classes in the sizes of its individuals; and on the other hand, agamogenesis under any form is absolutely unknown in it.

§ 337. Such are a few leading facts serving to show how deduction is inductively verified, in so far as the antagonism between Growth and Asexual Genesis is concerned. In whatever way we explain this opposition of the integrative and disintegrative processes, the facts and their implications remain the same. Indeed we need not commit ourselves to any hypothesis respecting the physical causation: it suffices to recognize the results under their most general aspects. We cannot help admitting there are at work these two antagonist tendencies to aggregation and separation; and we cannot help admitting that the proportion between the aggregative and separative tendencies, must in each case determine the relation between the increase in bulk of the individual and the increase of the race in number.

The antithesis is as manifest *à posteriori* as it is necessary *à priori*. While the minutest organisms multiply asexually in their millions; while the small compound types next above them thus multiply in their thousands; while larger and more compound types thus multiply in their hundreds and their tens; the largest types do not thus multiply at all. Conversely, those which do not multiply asexually at all, are a billion or a million times the size of those which thus multiply with greatest rapidity; and are a thousand times, or a hundred times, or ten times the size of those which thus multiply with less and less rapidity. Without saying that this inverse proportion is regular, which, as we shall hereafter see, it cannot be, we may unhesitatingly assert its average truth. That the smallest organisms habitually reproduce asexually with immense rapidity; that the largest organisms never reproduce at all in this manner; and that between these extremes there is a general decrease of asexual reproduction along with an increase of bulk; are propositions that admit of no dispute.

# CHAPTER VI.

## ANTAGONISM BETWEEN GROWTH AND SEXUAL GENESIS.

§ 338. In so far as it is a process of separation, sexual genesis is like asexual genesis; and is therefore, equally with asexual genesis, opposed to that aggregation which results in growth. Whether a deduction is made from one parent or from two, whether it is made from any part of the body indifferently or from a specialized part, or whether it is made directly or indirectly, it remains in any case a deduction; and in proportion as it is great, or frequent, or both, it must restrain the increase of the individual.

Here we have to group together the leading illustrations of this truth. We will take them in the same order as before.

§ 339. The lowest vegetal forms, or rather, we may say, those forms which we cannot class as either distinctly vegetal or distinctly animal, show us a process of sexual multiplication that differs much less from the asexual process than in the higher forms. The common character which distinguishes sexual from asexual genesis, is that the mass of protoplasm whence a new generation is to arise, has been produced by the union of two portions of matter that were before more widely separated. I use this general expression, because among the simplest *Algæ*, this is not invariably matter supplied by different individuals: certain *Diatomaceæ* exhibit within a single cell, the formation of a sporangium by a drawing together of the opposite halves of the endochrome into a ball. Mostly, however, sporangia are products of conjugation. The endochromes of two cells unite to form the germ-mass; and these conjugating cells may be either entirely independent, as in many *Desmidiaceæ* and in the *Palmellæ;* or they may be two of the adjacent cells forming a thread, as in some *Conjugateæ;* or they may be cells belonging to adjacent threads, as in *Zygnema.* But whether it is originated by a single parent-cell, or by two parent-cells, the sporangium, after remaining quiescent until there recur the fit conditions for growth, breaks up into a multitude of spores, each of which produces an individual that multiplies asexually; and the fact here to be noted is, that as the entire contents of the parent-cells unite to form the sporangium, their individualities are lost in the germs of a new generation. In these minute simple types, sexual propagation just as completely sacrifices the life of the parent or parents, as does that form of asexual propagation in which the endochrome resolves itself directly into zoospores. And in the one case as in the other, this sacrifice is the concomitant of a prodigious fertility. Slightly in advance of this, but still showing us an almost equal loss of parental life in the lives of offspring, is the process seen in such unicellular *Algæ* as *Hydrogastrum,* and in minute *Fungi* of the same degree of composition. These exhibit a relatively-enormous development of the spore-producing part, and an almost entire absorption of the parental substance into it. As evidence of the resulting powers of multiplication, we have but to remember that the spread of mould over stale food, the rapid destruction of crops by mildew, and other kindred occurrences, are made possible by the incalculably numerous spores thus generated and universally dispersed.

Plants a degree higher in composition, supply a parallel series of illustrations. We have among the larger *Fungi,* in which the reproductive apparatus is relatively so enormous as to constitute the ostensible plant, a similar subordination of the individual to the race, and a similarly-immense fertility.

Thus, as quoted by Dr. Carpenter, Fries says—"in a single individual of *Reticularia maxima*, I have counted (calculated?) 10,000,000 sporules." It needs but to note the clouds of particles, so minute as to look like smoke, which ripe puff-balls give off when they are burst, and then to remember that each particle is a potential fungus, to be impressed with the almost inconceivable powers of propagation which these plants possess. The Lichens, too, furnish examples. Though they are nothing like so prolific as the *Fungi* (the difference yielding, as we shall hereafter see, further support to the general argument), yet there is a great production of germs, and a proportionate sacrifice of the parental individuality. Considerable areas of the frond here and there develop into *apotheccia* and *spermagonia*, which resolve themselves into sperm-cells and germ-cells. Some contrasts presented by the higher *Algæ* may also be named as exemplifying the inverse proportion between the size of the individual and the extent of the generative structures. While in the smaller kinds relatively large portions of the fronds are transformed into reproductive elements, in the larger kinds these portions are relatively small: instance the *Macrocystis pyrifera*, a gigantic sea-weed, which sometimes attains a length of 1,500 feet, of which Dr. Carpenter remarks—"This development of the nutritive surface takes place at the expense of the fructifying apparatus, which is here quite subordinate."

When we turn to vegetal aggregates of the third order of composition, facts having the same meaning are conspicuous. On the average these higher plants are far larger than plants of a lower degree of composition; and on the average their rates of sexual reproduction are far less. Similarly if, among Acrogens, Endogens, and Exogens, we compare the smaller types with the larger, we find them proportionately more prolific. This is not manifest if we simply calculate the number of seeds ripened by an individual in a single season; but it becomes manifest if we take into account the further factor which here complicates the result—the age at which sexual genesis commences. The smaller Phænogams are mostly either annuals, or perennials that die down annually; and seeding as they do annually before their deaths, or the deaths of their reproductive parts, it results that in the course of a year, each gives origin to a multitude of potential plants, of which every one may the next year, if preserved, give origin to an equal multitude. Supposing but a hundred offspring to be produced the first year, ten thousand may be produced in the second year, a million in the third, a hundred millions in the fourth. Meanwhile, what has been the possible multiplication of a large Phænogam? While its small congener has been seeding and dying, and leaving multitudinous progeny to seed and die, it has simply been growing; and may so continue to grow for ten or a dozen years without bearing fruit. Before a Cocoa-nut tree has ripened its first cluster of nuts, the descendants of a wheat plant, supposing them all to survive and multiply, will have become numerous enough to occupy the whole surface of the Earth. So that though, when it begins to bear, a tree may annually shed as many seeds as a herb, yet in consequence of this delay in bearing, its fertility is incomparably less; and its relatively-small fertility becomes still further reduced where, as in *Lodoicea Sechellarum*, the seeds take two years from the date of fertilization to the date of germination.

§ 340. Some observers state that in certain *Protozoa* there occurs a process of conjugation akin to that which the *Protophyta* exhibit—a coalescence of the substance of two individuals to form a germ-mass. This has been alleged more especially of *Actinophrys*. The statement is questionable; but if proved true, then of the minute forms that appear to be more animal than vegetal in their characters, some have a mode of sexual multiplication by which the parents are sacrificed bodily in the production of a new generation. A modified mode, apparently not fatal to the parents, has been observed in certain of the more developed *Infusoria.* Our knowledge of these microscopic types is, however, so rudimentary that evidence derived from them must be taken with a qualification.

Among small animal aggregates of the second order, the first to be considered are of course the *Cœlenterata.* A *Hydra* occasionally devotes a large part of its substance to sexual genesis. In the walls of its body groups of ova, or spermatozoa, or both, take their rise; and develop into masses greatly distorting the creature's form, and leaving it greatly diminished when they escape. Here, however, gamogenesis is obviously supplementary to agamogenesis—the immensely rapid multiplication by budding continues as long as food is abundant and warmth sufficient, and is replaced by gamogenesis only at the close of the season. A better example of the relation between small size and active gamogenesis is supplied by the *Planaria,* which does not multiply asexually with so much rapidity. The generative system is here enormous. Ova are developed all through the body, occupying everywhere the interspaces of the assimilative system; so that the animal may be said to consist of a part that absorbs nutriment and a part that transforms that nutriment into sperm-cells and germ-cells. Even saying nothing of the probably-early maturity of these animals, and therefore frequent repetition of sexual multiplication, it is clear that their fertility must be very great.

The *Annulosa,* including among them the inferior kindred types, have habits and conditions of life so various that only the broadest contrasts can be instanced in support of the proposition before us. Of the microscopic forms belonging to this sub-kingdom, the *Rotifera* may be named as having, along with small bulk, a great rate of sexual increase. *Hydatina senta* "is capable of a four-fold propagation every twenty-four or thirty-hours, bringing forth in this time four ova, which grow from the embryo to maturity, and exclude their fertile ova in the same period. The same individual, producing in ten days forty eggs, developed with the rapidity above cited, this rate, raised to the tenth power, gives one million of individuals from one parent, on the eleventh day four millions, and on the twelfth day sixteen millions, and so on." Ascending from this extreme, the differences of organization and activity greatly complicate the inverse variation of fertility and bulk. Bearing in mind, however, that the rate of multiplication depends much less on the number of each brood than on the quickness with which maturity is reached and a new generation commenced, it will be obvious that though Annelids produce great numbers of ova, yet as they do this at comparatively long intervals, their rates of increase fall immensely below that just instanced in the Rotifers. And when at the other extreme we come to the large articulate animals, such as the Crab and the Lobster, the further diminution of fertility is seen in the still longer delay that occurs before each new generation begins to reproduce.

Perhaps the best examples are supplied by vertebrate animals, and especially those that are most familiar to us. Comparisons between Fishes are unsatisfactory, because of our ignorance of their histories. In some cases Fishes equal in bulk produce widely different numbers of eggs; as the Cod which spawns a million at once, and the Salmon by which nothing like so great a number is spawned. But then the eggs are very unlike in size; and if the ovaria of the two fishes be compared, the difference between their masses is comparatively moderate. There are, indeed, contrasts which seem at variance with the alleged relation; as that between the Cod and the Stickleback, which, though so much smaller, produces fewer ova. The Stickleback's ova, however, are relatively large; and their total bulk bears as great a ratio to the bulk of the Stickleback as does the bulk of the Cod's ova to that of the Cod. Moreover, if, as is not improbable, the reproductive age is arrived at earlier by the Stickleback than by the Cod, the fertility of the species may be greater notwithstanding the smaller number produced by each individual. Evidence that admits of being tolerably well disentangled is furnished by Birds. They differ but little in their grades of organization; and the habits of life throughout extensive groups of them are so similar, that comparisons may be fairly made. It is true that, as hereafter to be shown, the differences of expenditure which differences of bulk entail, have doubtless much to do with the differences of fertility. But we may set down under the present head some of those cases in which the activity, being relatively slight, does not greatly interfere with the relation we are considering; and may note that among such birds having similarly slight activities, the small produce more eggs than the large, and eggs that bear in their total mass a greater ratio to the mass of the parent. Consider, for example, the gallinaceous birds; which are like one another and unlike birds of most other groups in flying comparatively little. Taking first the wild members of this order, which rarely breed more than once in a season, we find that the Pheasant has from 6 to 10 eggs, the Black-cock from 5 to 10, the Grouse 8 to 12, the Partridge 10 to 15, the Quail still more, sometimes reaching 20. Here the only exception to the relation between decreasing bulk and increasing number of eggs, occurs in the cases of the Pheasant and the Black-cock; and it is to be remembered, in explanation, that the Pheasant inhabits a warmer region and is better fed—often artificially. If we pass to domesticated genera of the same order, we meet with parallel differences. From the numbers of eggs laid, little can be inferred; for under the favourable conditions artificially maintained, the laying is carried on indefinitely. But though in the sizes of their broods the Turkey and the Fowl do not greatly differ, the Fowl begins breeding at a much earlier age than the Turkey, and produces broods more frequently: a considerably higher rate of multiplication being the result. Now these contrasts among domestic creatures that are similarly conditioned, and closely-allied by constitution, may be held to show, more clearly than most other contrasts, the inverse variation between bulk and sexual genesis; since here the cost of activity is diminished to a comparatively small amount. There is little expenditure in flight—sometimes almost none; and the expenditure in walking about is not great: there is more of standing than of actual movement. It is true that young Turkeys commence their existences as larger masses than chickens; but it is tolerably manifest that the total weight of the eggs produced by a Turkey during each season, bears a less ratio to the Turkey's weight, than the total weight of the eggs which a Hen produces during each season, bears to the Hen's weight; and this is the fairest way of making the comparison. The comparison so made shows a greater difference than appears likely to be due to the different costs of locomotion; considering the inertness of the creatures. Remembering that the assimilating surface increases only as the squares of the dimensions, while the mass of the fabric to be built up by the absorbed nutriment increases as the cubes of the dimensions, it will be seen that the expense of growth becomes relatively greater with each increment of size; and that hence, of two similar creatures commencing life with different sizes, the larger one in reaching its superior adult bulk, will do this at a more than proportionate expense; and so will either be delayed in commencing its reproduction, or will have a diminished reserve for reproduction, or both. Other orders of Birds, active in their habits, show more markedly the connexion between augmenting mass and declining fertility. But in them the increasing cost of locomotion becomes an important, and probably the most important, factor. The evidence they furnish will therefore come better under another head. Contrasts among Mammals, like those which Birds present, have their meanings obscured by inequalities of the expenditure for motion. The smaller fertility which habitually accompanies greater bulk, must in all cases be partly ascribed to this. Still, it may be well if we briefly note, for as much as they are worth, the broader contrasts. While a large Mammal bears but a single young one at a time, is several years before it commences doing this, and then repeats the reproduction at long intervals; we find, as we descend to the smaller members of the class, a very early commencement of breeding, an increasing number at a birth, reaching in small Rodents to 10 or even more, and a much more frequent recurrence of broods: the combined result being a relatively prodigious fertility. If a specific comparison be desired between Mammals that are similar in constitution, in food, in conditions of life, and all other things but size, the Deer-tribe supplies it. While the large Red-deer has but one at a birth, the small Roe-deer has two at a birth.

§ 341. The antagonism between growth and sexual genesis, visible in these general contrasts, may also be traced in the history of each plant and animal. So familiar is the fact that sexual genesis does not occur early in life, and in all organisms which expend much begins only when the limit of size is nearly reached, that we do not sufficiently note its significance. It is a general physiological truth, however, that while the building-up of the individual is going on rapidly, the reproductive organs remain imperfectly developed and inactive; and that the commencement of reproduction at once indicates a declining rate of growth, and becomes a cause of arresting growth. As was shown in § 78, the exceptions to this rule are found where the limit of growth is indefinite; either because the organism expends little or nothing in action, or expends in action so moderate an amount that the supply of nutriment is never equilibrated by its expenditure.

We will pass over the inferior plants, and limiting ourselves to Phænogams, will not dwell on the less conspicuous evidence which the smaller types present. A few cases such as gardens supply will serve. All know that a Pear-tree continues to increase in size for years before it begins to bear; and that, producing but few pears at first, it is long before it fruits abundantly. A young Mulberry, branching out luxuriantly season after season, but covered with nothing but leaves, at length blossoms sparingly, and sets some small and imperfect berries, which it drops while they are green; and it makes these futile attempts time after time before it succeeds in ripening any seeds. But these multi-axial plants, or aggregates of individuals some of which continue to grow while others become arrested and transformed into seed-bearers, show us the relation less definitely than certain plants that are substantially, if not literally, uni-axial. Of these the Cocoa-nut may be instanced. For some years it goes on shooting up without making any sign of becoming fertile. About the sixth year it flowers; but the flowers wither without result. In the seventh year it flowers and produces a few nuts; but these prove abortive and drop. In the eighth year it ripens a moderate number of nuts; and afterwards increases the number until, in the tenth year, it comes into full bearing. Meanwhile, from the time of its first flowering its growth begins to diminish, and goes on diminishing till the tenth year, when it ceases. Here we see the antagonism between growth and sexual genesis under both its aspects—see a struggle between self-evolution and race-evolution, in which the first for a time overcomes the last, and the last ultimately overcomes the first. The continued aggrandisement of the parent-individual makes abortive for two seasons the tendency to produce new individuals; and the tendency to produce new individuals, becoming more decided, stops any further aggrandisement of the parent-individual.

Parallel illustrations occur in the animal kingdom. The eggs laid by a pullet are relatively small and few. Similarly, it is alleged that, as a general rule, "a bitch has fewer puppies at first, than afterwards." According to Burdach, as quoted by Dr. Duncan, "the elk, the bear, &c., have at first only a single young one, then they come to have most frequently two, and at last again only one. The young hamster produces only from three to six young ones, whilst that of a more advanced age produces from eight to sixteen. The same is true of the pig." It is remarked by Buffon that when a sow of less than a year old has young, the number of the litter is small, and its members are feeble and even imperfect. Here we have evidence that in animals growth checks sexual genesis. And then, conversely, we have evidence that sexual genesis checks growth. It is well known to breeders that if a filly is allowed to bear a foal, she is thereby prevented from reaching her proper size. And a like loss of perfection as an individual, is suffered by a cow that breeds too early.

§ 342. Notwithstanding the way in which the inverse variation of growth and sexual genesis is complicated with other relations, its existence is thus, I think, sufficiently manifest. Individually, many of the foregoing instances are open to criticism, and have to be taken with qualifications; but when looked at in the mass, their meaning is beyond doubt. Comparisons between the largest with the smallest types, whether vegetal or animal, yield results that are unmistakeable. On the one hand, remembering the fact that during its centuries of life an Oak does not produce as many acorns as a Fungus does spores in a single night, we see that the Fungus has a fertility exceeding that of the Oak in a degree literally beyond our powers of calculation or imagination. When, on the other hand, taking a microscopic protophyte which has millions of descendants in a few days, we ask how many such would be required to build up the forest tree that is years before it drops a seed, we are met by a parallel difficulty in conceiving the number, if not in setting it down. Similarly, if we turn from the minute and prodigiously-fertile Rotifer, to the Elephant, which approaches thirty years before it bears a solitary young one, we find the connexions between small size and great fertility and between great size and small fertility, too intensely marked to be much disguised by the perturbing relations that have been indicated. Finally, as this induction, reached by a survey of organisms in general, is verified by observations on the relation between decreasing growth and commencing reproduction in individual organisms, we may, I think, consider the alleged antagonism as proved.*

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* When, after having held for some years the general doctrine elaborated in these chapters, I agreed, early in 1852, to prepare an outline of it for the *Westminster Review*, I consulted, among other works, the just-issued third edition of Dr. Carpenter's *Principles of Physiology, General and Comparative*—seeking in it for facts illustrating the different degrees of fertility of different organisms. I met with a passage, quoted above in § 339, which seemed tacitly to assert that individual aggrandizement is at variance with the propagation of the race; but nowhere found a distinct enunciation of this truth. I did not then read the Chapter entitled "General View of the Functions," which held out no promise of such evidence as I was looking for. But on since referring to this chapter, I discovered in it the definite statement that—"there is a certain degree of antagonism between the Nutritive and Reproductive functions, the one being executed at the expense of the other. The reproductive apparatus derives the materials of its operations through the nutritive system, and is entirely dependent upon it for the continuance of its function. If, therefore, it be in a state of excessive activity, it will necessarily draw off from the individual fabric some portion of the aliment destined for its maintenance. It may be universally observed that, when the nutritive functions are particularly active in supporting the *individual*, the reproductive system is in a corresponding degree undeveloped,—and *vice versâ*."—*Principles of Physiology, General and Comparative*, Third Edition, 1851, p. 592.

# CHAPTER VII.

## THE ANTAGONISM BETWEEN DEVELOPMENT AND GENESIS, ASEXUAL AND SEXUAL.

§ 343. By Development, as here to be dealt with apart from Growth, is meant increase of structure as distinguished from increase of mass. As was pointed out in § 50, this is the biological definition of the word. In the following sections, then, we have to note how complexity of organization is hindered by reproductive activity, and conversely.

This relation partially coincides with that which we have just contemplated; for, as was shown in § 44, degree of growth is to a considerable extent dependent on degree of organization. But while the antagonism to be illustrated in this chapter, is much entangled with that illustrated in the last chapter, it may be so far separated as to be identified as an additional antagonism.

Besides the direct opposition between that continual disintegration which rapid genesis implies, and the fulfilment of that pre-requisite to extensive organization—the formation of an extensive aggregate, there is an indirect opposition which we may recognize under several aspects. The change from homogeneity to heterogeneity takes time; and time taken in transforming a relatively-structureless mass into a developed individual, delays the period of reproduction. Usually this time is merged in that taken for growth; but certain cases of metamorphosis show us the one separate from the other. An insect, passing from its lowly-organized caterpillar-stage into that of chrysalis, is afterwards a week, a fortnight, or a longer period in completing its structure: the recommencement of genesis being by so much postponed, and the rate of multiplication therefore diminished. Further, that re-arrangement of substance which development implies, entails expenditure. The chrysalis loses weight in the course of its transformation; and that its loss is not loss of water only, may be inferred from the fact that it respires, and that respiration indicates consumption. Clearly the matter consumed, is, other things equal, a deduction from the surplus that may go to reproduction. Yet again, the more widely and completely an organic mass becomes differentiated, the smaller the portion of it which retains the relatively-undifferentiated state that admits of being moulded into new individuals, or the germs of them. Protoplasm which has become specialized tissue, cannot be again generalized, and afterwards transformed into something else; and hence the progress of structure in an organism, by diminishing the unstructured part, diminishes the amount available for making offspring.

It is true that higher structure, like greater growth, may insure to a species advantages that eventually further its multiplication—may give it access to larger supplies of food, or enable it to obtain food more economically; and we shall hereafter see how the inverse variation we are considering is thus qualified. But here we are concerned only with the necessary and direct effects; not with those that are contingent and remote. These necessary and direct effects we will now look at as exemplified.

§ 344. Speaking generally, the simpler plants propagate both sexually and asexually; and, speaking comparatively, the complex plants propagate only sexually: their asexual propagation is usually incomplete—produces a united aggregate of individuals instead of numerous distinct individuals.

The Protophytes that perpetually subdivide, the merely-cellular *Algæ* that shed their tetraspores, the Acrogens that spontaneously separate their fronds and drop their gemmæ, show us an extra mode of multiplication which, among flowering plants, is exceptional. This extra mode of multiplication among these simpler plants, is made easy by their low development. Tetraspores arise only where the frond consists of untransformed cells; gemmæ bud out and drop off only where the tissue is comparatively homogeneous.

Should it be said that this is but another aspect of the antagonism already set forth, since these undeveloped forms are also the smaller forms; the reply is that though in part true, this is not wholly true. Various marine *Algæ* which propagate asexually, are larger than some Phænogams which do not thus propagate. The objection that difference of medium vitiates this comparison, is met by the fact that it is the same among land-plants themselves. Sundry of the lowly-organized Liverworts that are habitually gemmiparous, exceed in size many flowering plants. And the Ferns show us agamic multiplication occurring in plants which, while they are inferior in complexity of structure, are superior in bulk to a great proportion of annual Endogens and Exogens.

§ 345. In the ability of the lowly-organized, or almost unorganized, sarcode of a Sponge, to transform itself into multitudes of gemmules, we have an instance of this same direct relation in the animal kingdom. Moreover, the instance yields very distinct proof of an antagonism between development and genesis, independent of the antagonism between growth and genesis; for the Sponge which thus multiplies itself asexually, as well as sexually, is far larger than hosts of more complex animals which do not multiply asexually.

Once again may be cited the creature so often brought in evidence, the *Hydra*, as showing us how rapidity of agamic propagation is associated with inferiority of structure. Its power to produce young ones from nearly all parts of its body, is due to the comparative homogeneity of its body. In kindred but more-organized types, the gemmiparity is greatly restricted, or disappears. Among the free-swimming *Hydrazoa*, multiplication by budding, when it occurs at all, occurs only at special places. That increase of structure apart from increase of size, is here a cause of declining agamogenesis, we may see in the contrast between the simple and the compound *Hydroida;* which last, along with more-differentiated tissues, show us a gemmation which does not go on all over the body of each polype, and much of which does not end in separation.

It is, however, among the *Annulosa* that progressing organization is most conspicuously operative in diminishing agamogenesis. The segments or "somites" that compose an animal belonging to this class, are primordially alike; and, as before argued (§§ 205-7), are probably the homologues of what were originally independent individuals. The progress from the lower to the higher types of the class, is at once a progress towards types in which the strings of segments cease to undergo subdivision, and towards types in which the segments, no longer alike in their structures and functions, have become physiologically integrated or mutually dependent. Already this group of cases has been named as illustrating the antagonism between growth and asexual genesis; but it is proper also to name it here; since, on the one hand, the greater size due to the ceasing of fission, is made possible only by the specialization of parts and the development of a co-ordinating apparatus to combine their actions, and since, on the other hand, specialization and co-ordination can advance only in proportion as fission ceases.

§ 346. The inverse variation of development and sexual genesis is by no means easy to follow. One or two facts indicative of it may, however, be named.

Phænogams that have but little supporting tissue may fairly be classed as structurally inferior to those provided with stems formed of woody fibres; for these imply additional differentiations, and constitute wider departures from the primitive type of vegetal tissue. That the concomitant of this higher organization is a slower gamogenesis, scarcely needs pointing out. While the herbaceous annual is blossoming and ripening seed, the young tree is transforming its originally-succulent axis into dense fibrous substance; and year by year the young tree expends in doing the like, nutriment which successive generations of the annual expend in fruit. Here the inverse relation is between sexual reproduction and complexity, and not between sexual reproduction and bulk seeing that besides seeding, the annual often grows to a size greater than that reached by the young infertile tree in several years.

Proof of the antagonism between complexity and gamogenesis in animals, is still more difficult to disentangle. Perhaps the evidence most to the point is furnished by the contrast between Man and certain other Mammals approaching to him in mass. To compare him with the domestic Sheep, which, though not very unlike in size, is relatively prolific, is objecjectionable because of the relative inactivity of Sheep; and this, too, may be alleged as a reason why the Ox, though far more bulky, is also far more fertile, than Man. Further, against a comparison with the Horse, which, while both larger and more prolific, is tolerably active, it may be urged that, in his case, and the cases of herbivorous creatures generally, the small exertion required to procure food, joined with the great ratio borne by the assimilative organs to the organs they have to build up and repair, vitiates the result. We may, however, fairly draw a parallel between Man and a large carnivore. The Lion, superior in size, and perhaps equal in activity, has a digestive system not proportionately greater; and yet has a higher rate of multiplication than Man. Here the only decided want of parity, besides that of organization, is that of food. Possibly a carnivore gains an advantage in having a surplus nutriment consisting almost wholly of those nitrogenous materials from which the bodies of young ones are mainly formed. But, allowing for all other differences, it appears not improbable that the smallness of human fertility compared with the fertility of large feline animals, is due to the greater complexity of the human organization—more especially the organization of the nervous system. Taking degree of nervous organization as the chief correlative of mental capacity; and remembering the physiological cost of that discipline whereby high mental capacity is reached; we may suspect that nervous organization is very expensive: the inference being that bringing it up to the level it reaches in Man, whose digestive system, by no means large, has at the same time to supply materials for general growth and daily waste, involves a great retardation of maturity and sexual genesis.

# CHAPTER VIII.

## ANTAGONISM BETWEEN EXPENDITURE AND GENESIS.

§ 347. Under this head we have to set down no evidence derived from the vegetal kingdom. Plants are not expenders of force in such degrees as to affect the general relations with which we are dealing. They have not to maintain a heat above that of their environment; nor have they to generate motion; and hence consumption for these two purposes does not diminish the stock of material that serves on the one hand for growth and on the other hand for propagation.

It will be well, too, if we pass over the lower animals: especially those aquatic ones which, being nearly of the same temperature as the water, and nearly of the same specific gravity, lose but little in evolving motion, sensible and insensible. A further reason for excluding from consideration these inferior types, is, that we do not know enough of their rates of genesis to permit of our making, with any satisfaction, those involved comparisons here to be entered upon.

The facts on which we must mainly depend are those to be gathered from terrestrial animals; and chiefly from those higher classes of them which are at the same time great expenders and have rates of multiplication about which our knowledge is tolerably definite. We will restrict ourselves, then, to the evidence which Birds and Mammals supply

§ 348. Satisfactory proof that loss of substance in the maintenance of heat diminishes the rapidity of propagation, is difficult to obtain. It is, indeed, obvious that the warm-blooded *Vertebrata* are less prolific than the cold-blooded; but then they are at the same time more vivacious. Similarly, between Mammals and Birds (which are the warmer-blooded of the two) there is, other things equal, a parallel, though much smaller, difference; but here, too, the unlikenesses of muscular action complicate the evidence. Again, the annual return of generative activity has an average correspondence with the annual return of a warmer season, which, did it stand alone, might be taken as evidence that a diminished cost of heat-maintenance leads to such a surplus as makes reproduction possible. But then, this periodic rise of temperature is habitually accompanied by an increase in the quantity of food—a factor of equal or greater importance. We must be content, therefore, with such few special facts as admit of being disentangled.

Certain of these we are introduced to by the general relation last named—the habitual recurrence of genesis with the recurrence of spring. For in some cases a domesticated creature has its supplies of food almost equalized; and hence the effect of varying nutrition may be in great part eliminated from the comparison. The common Fowl yields an illustration. It is fed through the cold months, but nevertheless, in mid-winter, it either wholly leaves off laying or lays very sparingly. And then we have the further evidence that if it lays sparingly, it does so only on condition that the heat, as well as the food, is artificially maintained. Hens lay in cold weather only when they are kept warm. To which fact may be added the kindred one that "when pigeons receive artificial heat, they not only continue to hatch longer in autumn, but will recommence in spring sooner than they would otherwise do." An analogous piece of evidence is that, in winter, inadequately-sheltered Cows either cease to give milk or give it in diminished quantity. For though giving milk is not the same thing as bearing a young one, yet, as milk is part of the material from which a young one is built up, it is part of the outlay for reproductive purposes, and diminution of it is a loss of reproductive power. Indeed the case aptly illustrates, under another aspect, the struggle between self-preservation and race-preservation. Maintenance of the cow's life depends on maintenance of its heat; and maintenance of its heat may entail such reduction in the supply of milk as to cause the death of the calf.

Evidence derived from the habits of the same or allied genera in different climates, may naturally be looked for; but it is difficult to get, and it can scarcely be expected that the remaining conditions of existence will be so far similar as to allow of a fair comparison being made. The only illustrative facts I have met with which seem noteworthy, are some named by Mr. Gould in his work on *The Birds of Australia.* He says:—"I must not omit to mention, too, the extraordinary fecundity which prevails in Australia, many of its smaller birds breeding three or four times in a season; but laying fewer eggs in the early spring when insect life is less developed, and a greater number later in the season, when the supply of insect food has become more abundant. I have also some reason to believe that the young of many species breed during the first season, for among others, I frequently found one section of the Honey-eaters (the *Melithrepti*) sitting upon eggs while still clothed in the brown dress of immaturity; and we know that such is the case with the introduced *Gallinaceæ* (or poultry) three or four generations of which have been often produced in the course of a year." Though here Mr. Gould refers only to variation in the quantity of food as a cause of variation in the rate of multiplication, may we not suspect that the warmth is a part-cause of the high rate which he describes as general?

§ 349. Of the inverse variation between activity and genesis, we get clear proof. Let us begin with that which Birds furnish.

First we have the average contrast, already hinted, between the fertility of Birds and the fertility of Mammals. Comparing the large with the large and the small with the small, we see that creatures which continually go through the muscular exertion of sustaining themselves in the air and propelling themselves rapidly through it, are less prolific than creatures of equal weights which go though the smaller exertion of moving about over solid surfaces. Predatory Birds have fewer young ones than predatory Mammals of approximately the same sizes. If we compare Rooks with Rats, or Finches with Mice, we find like differences. And these differences are greater than at first appears. For whereas among Mammals a mother is able, unaided, to bear and suckle and rear halfway to maturity, a brood that probably weighs more in proportion than does the brood of a Bird; a Bird, or at least a Bird that flies much, is unable to do this. Both parents have to help; and this indicates that the margin for reproduction in each adult individual is smaller.

Among Birds themselves occur contrasts which may be next considered. In the Raptorial class, various species of which, differing in their sizes, are similarly active in their habits, we see that the small are more prolific than the large. The Golden Eagle has usually 2 eggs: sometimes only 1. As we descend to the Kites and Falcons, the number is 2 or or 3, and 3 or 4. And when we come to the Sparrow-Hawk, 3 to 5 is the specified number. Similarly among the Owls: while the Great Eagle-Owl has 2 or 3 eggs, the comparatively small Common Owl has 4 or 5. As before hinted, it is impossible to say what proportions of these differences are due to unlikenesses of bulk merely, and what proportions are due to unlikenesses in the costs of locomotion. But we may fairly assume that the unlikenesses in the costs of locomotion are here the more important factors. Weights varying as the cubes of the dimensions, while muscular powers vary as the squares, the expense of flight increases more rapidly than the size increases; and as motion through the air requires more effort than motion on the ground, this geometrical progression tells more rapidly on Birds than on Mammals. Be this as it may, however, these contrasts support the argument; as do various others that may be set down. The Finch family, for example, have broods averaging about 5 in number, and have commonly 2 broods in the season; while in the Crow family the number of the brood is on the average less, and there is but one brood in a season. And then on descending to such small birds as the Wrens and the Tits, we have 8, 10, 12 to 15 eggs, and often two broods in the year. One of the best illustrations is furnished by the Swallow-tribe, throughout which there is little or no difference in mode of life or in food. The Sand-Martin, much the least of them, has usually 6 eggs; the Swallow, somewhat larger, has 4 or 5; and the Swift, larger still, has but 2. Here we see a lower fertility associated in part with greater size, but associated still more conspicuously with greater expenditure. For the difference of fertility is more than proportionate to the difference of bulk, as shown in other cases; and for this greater difference there is the reason, that the Swift has to support not only the cost of propelling its larger mass through the air, but also the cost of propelling it at a higher velocity.

Omitting much evidence of like nature, let us note that disclosed by comparisons of certain groups of birds with other groups. "Skulkers" is the descriptive title applied to the Water-Rail, the Corn-Crake, and their allies, which evade enemies by concealment—consequently expending but little in locomotion. These birds have relatively large broods—6 to 11, 8 to 12, &c. Not less instructive are the contrasts between the Gallinaceous Birds and other Birds of like sizes but more active habits. The Partridge and the Wood-Pigeon are about equal in bulk, and have much the same food. Yet while the one has from 10 to 15 young ones, the other has but 2 young ones twice a-year: its annual reproduction is but one-third. It may be said that the ability of the Partridge to bring up so large a brood, is due to that habit of its tribe which one of its names, "Scrapers," describes; and to the accompanying habit of the young, which begin to get their own living as soon as they are hatched: so saving the parents' labour. Conversely, it may be said that the inability of the Pigeon to rear more than 2 at a time, is caused by the necessity of fetching everything they eat. But the alleged relation holds nevertheless. On the one hand, a great part of the food which the Partridge chicks pick up, is food which, in their absence, the mother would have picked up: though each chick costs her far less than a young Pigeon costs its parents, yet the whole of her chicks cost her a great deal in the shape of abstinence—an abstinence she can bear because she has to fly but little. On the other hand, the Pigeon's habit of laying and hatching but two eggs, must not be referred to any foreseen necessity of going through so much labour in supporting the young, but to a constitutional tendency established by such labour. This is proved by the curious fact that when domesticated, and saved from such labour by artificial feeding, Pigeons, says Macgillivray, "are frequently seen sitting on eggs long before the former brood is able to leave the nest, so that the parent bird has at the same time young birds and eggs to take care of."

§ 350. Made to illustrate the effect of activity on fertility, most comparisons among Mammals are objectionable: other circumstances are not equal. A few, however, escape this criticism. One is that between the Hare and the Rabbit. These are closely-allied species of the same genus, similar in their diet but unlike in their expenditures for locomotion. The relatively-inert Rabbit has 5 to 8 young ones in a litter, and several litters a-year; while the relatively-active Hare has but 2 to 5 in a litter. This is not all. The Rabbit begins to breed at six months old; but a year elapses before the Hare begins to breed. These two factors compounded, result in a difference of fertility far greater than can be ascribed to unlikeness of the two creatures in size.

Perhaps the most striking piece of evidence which Mammals furnish, is the extreme infertility of our common Bat. The *Cheiroptera* and the *Rodentia* are very similar in their internal structures. Diversity of constitution, therefore, cannot vitiate the comparison between Bats and Mice, which are about the same in size. Though their diets differ, the difference is in favour of the Bat: its food being exclusively animal while that of the Mouse is mainly vegetal. What now are their respective rates of genesis? The Mouse produces many young at a time, reaching even 10 or 12; while the Bat produces only one at a time. Whether the Bat repeats its one more frequently than the Mouse repeats its ten is not stated; but it is quite certain that even if it does so, the more frequent repetition cannot be such as to raise its fertility to anything like that of the Mouse. And this relatively-low rate of multiplication we may fairly ascribe to its relatively-high rate of expenditure.

Here let us note, in passing, an interesting example of the way in which a species that has no specially-great power of self-preservation, while its power of multiplication is extremely small, nevertheless avoids extinction because it has to meet an unusually-small total of race-destroying forces. Leaving out parasites, the only enemy of the Bat is the Owl; and the Owl is sparingly distributed.

§ 351. These general evidences may be enforced by some special evidences. We have few opportunities of observing how, within the same species, variations of expenditure are related to variations of fertility. But a fact or two showing the connexion may be named.

Doctor Duncan quotes a statement to the point respecting the breeding of dogs. Already in § 341 I have extracted a part of this statement, to the effect that before her growth is complete, a bitch bears at a birth fewer puppies than when she becomes full-grown. An accompanying allegation is, that her declining vigour is shown by a decrease in the number of puppies contained in a litter, "ending in one or two." And then it is further alleged that, "as regards the amount of work a dog has to perform, so will the decline be rapid or gradual; and hence, if a bitch is worked hard year after year, she will fail rapidly, and the diminution of her puppies will be accordingly; but if worked moderately and well kept, she will fail gradually, and the diminution will be less rapid."

In this place, more fitly than elsewhere, may be added a fact of like implication, though of a different order. Of course whether excessive expenditure be in the continual repairs of nervo-muscular tissues or in replacing other tissues, the reactive effects, if not quite the same, will be similar—there will be a decrease of the surplus available for genesis. If, then, in any animals there from time to time occur unusual outlays for self-maintenance, we may expect the periods of such outlays to be periods of diminished or arrested reproduction. That they are so the moulting of birds shows us. When hens begin to moult they cease to lay. While they are expending so much in producing new clothing, they have nothing to expend for producing eggs.

# CHAPTER IX.

## COINCIDENCE BETWEEN HIGH NUTRITION AND GENESIS.

§ 352. Under this head may be grouped various facts which, in another way, tell the same tale as those contained in the last chapter. The evidence there put together went to show that increased cost of self-maintenance entailed decreased power of propagation. The evidence to be set down here, will go to show that power of propagation is augmented by making self-maintenance unusually easy. For into this may be translated the effect of abundant food.

To put the proposition more specifically—we have seen that after individual growth, development, and daily consumption have been provided for, the surplus nutriment measures the rate of multiplication. This surplus may be raised in amount by such changes in the environment as bring a larger supply of the materials or forces on which both parental life and the lives of offspring depend. Be there, or be there not, any expenditure, a higher nutrition will make possible a greater propagation. We may expect this to hold both of agamogenesis and of gamogenesis; and we shall find that it does so.

§ 353. On multi-axial plants, the primary effect of surplus nutriment is a production of large and numerous leaf-shoots. How this asexual multiplication results from excessive nutrition, is well shown when the leading axis, or a chief branch, is broken off towards its extremity. The axillary buds below the breakage quickly swell and burst into lateral shoots, which often put forth secondary shoots: two generations of agamic individuals arise where there probably would have been none but for the local abundance of sap, no longer drawn off. In like manner the abnormal agamogenesis which we have in proliferous flowers, is habitually accompanied by a general luxuriance, implying an unusual plethora.

No less conclusive is the evidence furnished by agamogenesis in animals. Sir John Dalyell, speaking of *Hydra tuba,* whose peculiar metagenesis he was the first to point out, says—" It is singular how much propagation is promoted by abundant sustenance." This Polype goes on budding-out young polypes from its sides, with a rapidity proportionate to the supply of materials. So, too, is it with the agamic reproduction of the *Aphis.* As cited by Professor Huxley, Kyber " states that he raised viviparous broods of both this species (*Aphis Dianthi*) and *A. Rosæ* for four consecutive years, without any intervention of males or oviparous females, and that the energy of the power of agamic reproduction was at the end of that period undiminished. The rapidity of the agamic prolification throughout the whole period was directly proportional to the amount of warmth and food supplied."

In these cases the relation is not appreciably complicated by expenditure. The parent having reached its limit of growth, the absorbed food goes to asexual multiplication: scarcely any being deducted for the maintenance of parental life.

§ 354. The sexual multiplication of organisms under changed conditions, undergoes variations conforming to a parallel law. Cultivated plants and domesticated animals yield us proof of this.

Facts showing that in cultivated plants, sexual genesis increases with nutrition, are obscured by facts showing that a less rapid asexual genesis, and an incipient sexual genesis, accompany the fall from a high to a moderate nutrition. The confounding of these two relations has led to mistaken inferences. When treating of Genesis inductively, we reached the generalization that "the products of a fertilized germ go on accumulating by simple growth, so long as the forces whence growth results are greatly in excess of the antagonist forces; but that when diminution of the one set of forces, or increase of the other, causes a considerable decline in this excess, and an approach towards equilibrium, fertilized germs are again produced." (§ 78.) It was pointed out that this holds of organisms which multiply by heterogenesis, as well as those which multiply by homogenesis. And plants were referred to as illustrating, both generally and locally, the decline of agamic multiplication and commencement of gamic multiplication, along with a lessening rate of nutrition. Now the many cases that are given of fruitfulness caused in trees by depletion, are really cases of this change from agamogenesis to gamogenesis; and simply go to prove that what would naturally arise when decreased peripheral growth had followed increased size, may be brought about artificially by diminishing the supply of materials for growth. Cramping its roots in a pot, or cutting them, or ringing its branches, will make a tree bear very early: bringing about a premature establishment of that relative innutrition which would have spontaneously arisen in course of time. Such facts by no means show that in plants, sexual genesis increases as nutrition diminishes. When it has once set in, sexual genesis is scanty or imperfect unless nutrition is good. Though the starved plant may blossom, yet many of its blossoms will fail; and such seeds as it produces will be ill-furnished with those enveloping structures and that store of albumen, &c., needed to give good chances of successful germination—the number of surviving offspring will be diminished. Were it otherwise, the manuring of fields that are to bear seed-crops, would be not simply useless but injurious. Were it otherwise, dunging the roots of a fruit-tree would in all cases be impolitic; instead of being impolitic only where the growth of sexless axes is still luxuriant. Were it otherwise, a tree which has borne a heavy crop, should, by the consequent depletion, be led to bear a still heavier crop next year; whereas it is apt to be wholly or partially barren next year—has to recover a state of tolerably-high nutrition before its sexual genesis again becomes large.

But the best illustrations are those yielded by animals, in which we have, besides an increased supply of nutriment, a diminished expenditure. Two classes of comparisons, alike in their implications, may be made—comparisons between tame and wild animals of the same species or genus, and comparisons between tame animals of the same species differently treated.

To begin with Birds, let us first contrast the farm-yard *Gallinaceæ* with their kindred of the fields and woods. Notwithstanding their greater size, which, other things equal, should be accompanied by smaller fertility, the domesticated kinds have more numerous offspring than the wild kinds. A Turkey has a dozen in a brood, while a Pheasant has from 6 to 10. Twice or thrice in a season, a Hen rears as many chickens as a Partridge rears once in a season. Anserine birds show us parallel differences. The Tame Goose sits on 12 or more eggs, but the Wild Goose sits on 5, 6, or 7; and these are noted as considerably smaller. It is the same with Ducks: the domesticated variety lays and hatches twice as many eggs as the wild variety. And the like holds of Pigeons. After remarking of the *Columba livia* that "in spring when they have plenty of corn to pick from the newly-sown fields, they begin to get fat and pair; and again, in harvest, when the corn is cut down," Macgillivray goes on to say, that "the same pair when tamed generally breed four times" in the year. That between different poultry-yards, inequalities of fertility are caused by inequalities in the supplies of food, is a familiar truth. High feeding shows its effects not only in the continuous laying, but also in the sizes of the eggs. Among directions given for obtaining eggs from pullets late in the year, it is especially insisted on that they shall have a generous diet. Respecting Pigeons Macgillivray writes:—"that their breeding depends much on their having plenty of food to fatten them, seems, I think, evident from the circumstance that, when tamed, which they easily are, they are observed to breed in every month of the year. I do not mean that the same pair will breed every month; but some in the flock, if well fed, will breed at any season." There may be added a fact of like meaning which partially-domesticated birds yield. The Sparrow is one of the Finch tribe that has taken to the neighbourhood of houses; and by its boldness secures food not available to its congeners. The result is that it has several broods in a season, while its field-haunting kindred have none of them more than two broods, and some have only one.

Equally clear proof that abundant nutriment raises the rate of multiplication, occurs among Mammals. Compare the litters of the Dog with the litters of the Wolf and the Fox. Whereas those of the one range in number from 6 to 14, the others contain respectively 5 or 6 or occasionally 7, and 4 or 5 or rarely 6. Again, the wild Cat has 4 or 5 kittens; but the tame Cat has 5 or 6 kittens 2 or 3 times a-year. So, too, is it with the Weasel tribe. The Stoat has 5 young ones once a-year. The Ferret has 2 litters yearly, each containing from 6 to 9; and this notwithstanding that it is the larger of the two. Perhaps the most striking contrast is that between the wild and tame varieties of the Pig. While the one produces, according to its age, from 4 to 8 or 10 young ones, once a year, the other produces sometimes as many as 17 in a litter; or, in other cases, will bring up 5 litters of 10 each in two years—a rate of reproduction that is unparalleled in animals of as large a size. And let us not omit to note that this excessive fertility occurs where there is the greatest inactivity—where there is plenty to eat and nothing to do. There is no less distinct evidence that among domesticated Mammals themselves, the well-fed individuals are more prolific than the ill-fed individuals. On the high and comparatively-infertile Cotswolds, it is unusual for Ewes to have twins; but they very commonly have twins in the adjacent rich valley of the Severn. Similarly, among the barren hills of the west of Scotland, two lambs will be borne by about one Ewe in twenty; whereas in England, something like one Ewe in three will bear two lambs. Nay, in rich pastures, twins are more frequent than single births; and it occasionally happens that, after a genial autumn and consequent good grazing, a flock of Ewes will next spring yield double their number of lambs—the triplets balancing the uniparæ. So direct is this relation, that I have heard a farmer assert his ability to foretell, from the high, medium, or low, condition of an Ewe in the autumn, whether she will next spring bear two, or one, or none.

§ 355. An objection must here be met. Many facts may be brought to prove that fatness is not accompanied by fertility but by barrenness; and the inference drawn is that high feeding is unfavourable to genesis. The premiss may be admitted while the conclusion is denied.

There is a distinction between what may be called normal plethora, and an abnormal plethora, liable to be confounded with it. The one is a mark of constitutional wealth; but the other is a mark of constitutional poverty. Normal plethora is a superfluity of materials both for the building up of tissue and the evolution of force; and this is the plethora which we have found to be associated with unusual fecundity. Abnormal plethora, which, as truly alleged, is accompanied by infecundity, is a superfluity of force-evolving materials joined with either a positive or a relative deficiency of tissue-forming materials: the increased bulk indicating this state, being really the bulk of so much inert or dead matter. Note, first, a few of the facts which show us that obesity implies physiological impoverishment.

Neither in brutes nor men does it ordinarily occur either in youth or in that early maturity during which the vigour is the greatest and the digestion the best: it does not habitually accompany the highest power of taking up nutritive materials. When fatness arises in the prime of life, whether from peculiarity of food or other circumstance, it is not the sign of an increased total vitality. On the contrary, if great muscular action has to be gone through, the fat must be got rid of—either, as in a man, by training, or as in a horse that has grown bulky while out at grass, by putting him on such more nutritive diet as oats. The frequency of senile fatness, both in domesticated creatures and in ourselves, has a similar implication. Whether we consider the smaller ability of those who display it to withstand large demands on their powers, or whether we consider the comparatively-inferior digestion common among them, we see that the increased size indicates, not an abundance of materials which the organism requires, but an abundance of materials which it does not require. Of like meaning is the fact that women who have had several children, and animals after they have gone on bearing young for some time, frequently become fat; and lose their fecundity as they do this. In such cases, the fatness is not to be taken as the cause of the infecundity; but the constitutional exhaustion which the previous production of offspring has left, shows itself at once in the failing fecundity and the commencing fatness. There is yet another kind of evidence. Obesity not uncommonly sets in after the system has been subject to debilitating influences. Often a serious illness is followed by a corpulence to which there was previously no tendency. And the prolonged administration of mercury, constitutionally injurious as it is, sometimes produces a like effect.

Closer inquiry verifies the conclusion to which these facts point. The microscope shows that along with the increase of bulk common in advanced life, there goes on what is called "fatty degeneration:" oil-globules are deposited where there should be particles of flesh—or rather, we may say, the hydro-carbonaceous molecules locally produced by decomposition of the nitrogenous molecules, have not been replaced by other nitrogenous molecules, as they should have been. This fatty degeneration is, indeed, a kind of local death. For so regarding it we have not simply the reason that an active substance has its place occupied by an inert substance; but we have the reason that the flesh of dead bodies, under certain conditions, is transformed into a fatty matter called adipocere.

The infertility that accompanies fatness in domestic animals, has, however, other causes than that declining constitutional vigour which the fatness indicates. Being artificially fed, these animals cannot always obtain what their systems need. That which is given to them is often given expressly because of its fattening quality. And since the capacity of the digestive apparatus remains the same, the absorption of fat-producing materials in excess, implies defect in the absorption of materials from which the tissues are formed, and out of which young ones are built up. Moreover, this special feeding with a view to rapid and early fattening, continued as it is through generations, and accompanied as it is by a selection of individuals and varieties which fatten most readily, tends to establish a modified constitution, more fitted for producing fat and correspondingly-less fitted for producing flesh—a constitution which, from this relatively-deficient absorption of nitrogenous matters, is likely to become infertile; as, indeed, these varieties generally become. Hence, no conclusions respecting the effects of high nutrition, properly so called, can be drawn from cases of this kind. The cases are, in truth, of a kind that could not exist but for human agency. Under natural conditions no animal would diet itself in the way required to produce such results. And if it did, its race would quickly disappear.*

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* It is worth while inquiring whether unfitness of the food given to them, is not the chief cause of that sterility which, as Mr. Darwin says, "is the great bar to the domestication of animals." He remarks that "when animals and plants are removed from their natural conditions, they are extremely liable to

There is yet another mode in which accumulation of fat diminishes fertility. Even supposing it unaccompanied by a smaller absorption of nitrogenous materials, it is still a cause of lessening the surplus of nitrogenous materials. For the repair of the motor tissues becomes more costly. Fat stored-up is weight to be carried. A creature loaded with inert matter must, other things equal, consume a greater amount of tissue-forming substances for keeping its locomotive apparatus in order; and thus expending more for self-maintenance can expend less for race-maintenance. Abnormal plethora is thus antagonistic to reproduction in a double way. It ordinarily implies a smaller absorption of tissue-forming matters, and an increased demand on the diminished supply. Hence fertility decreases in a geometrical progression.

The counter-conclusion drawn from facts of this class, is, then, due to a misconception of their nature—a misconception arising partly from the circumstance that the increase of bulk produced by fat is somewhat like the increase of bulk which growth of tissues causes, and partly from the circumstance that abundance of good food normally produces a certain quantity of fat, which, within narrow limits, is a valuable store of force-evolving material. When, however, we limit the phrase high nutrition to its proper meaning—an abundance of, and due proportion among, all the substances which the organism needs—we find that, other things equal, fertility always increases as nutrition increases. And we see that these apparently-exceptional cases, are cases that really show us the same thing; since they are cases of relative innutrition.

have their reproductive systems seriously affected." Possibly the relative or absolute arrest of genesis, is less due to a direct effect on the reproductive system, than to a changed nutrition of which the reproductive system most clearly shows the results. The matters required for forming an embryo are in a greater proportion nitrogenous than are the matters required for maintaining an adult. Hence, an animal forced to live on insufficiently-nitrogenized food, may have its surplus for reproduction cut off, but still have a sufficiency to keep its own tissues in repair, and appear to be in good health—meanwhile increasing in bulk from excess of the non-nitrogenous matters it eats.

# CHAPTER X.

## SPECIALITIES OF THESE RELATIONS.

§ 356. Tests of the general doctrines set forth in preceding chapters, are afforded by organisms having modes of life that diverge widely from ordinary modes. Here, as elsewhere, aberrant cases yield crucial proofs.

If certain organisms are so circumstanced that highly-nutritive matter is supplied to them without stint, and they have nothing to do but absorb it, we may infer that their powers of propagation will be enormous.

If there are classes of creatures that expend very little for self-support in comparison with allied creatures, a relatively extreme prolificness may be expected of them.

Or if, again, we find species presenting the peculiarity that while some of their individuals have much to do and little to eat, others of their individuals have much to eat and little to do, we may look for great fertility in these last and comparative infertility or barrenness in the first.

These several anticipations we shall find completely verified.

§ 357. Plants which, like the *Rafflesiaceæ*, carry their parasitism to the extent of living on the juices they absorb from other plants, exhibit one of these relations in the vegetal kingdom. In them the organs for self-support being needless, are rudimentary; and the parts directly or indirectly concerned in the production and distribution of germs, constitute the mass of the organism. That small ratio which the race-preserving structures bear to the self-preserving structures in ordinary Phænogams, is, in these Phænogams, inverted. A like relation occurs in the common Dodder.

There may be added a kindred piece of evidence which the *Fungi* present. Those of them which grow on living plants, repeat the above connection completely; and those of them which, though not parasitic, nevertheless subsist on organized materials previously elaborated by other plants, substantially repeat it. The spore-producing part is relatively enormous; and the fertility is far greater than that of Cryptogams of like sizes, which have to form for themselves the organic compounds of which they and their germs consist.

§ 358. The same lesson is taught us by animal-parasites. Along with the decreased cost of Individuation, they similarly show us an increased expenditure for Genesis; and they show us this in the most striking manner where the deviation from ordinary conditions of life is the greatest.

Take, among the *Epizoa*, such an instance as the *Nicothœ*. Belonging to the *Entomostraca*, both males and females of this species are, in their early days, similar to their allies; and the males continue so throughout life. Each female, however, presently fixes herself on the skin of an aquatic animal, where she sits and sucks its juices, enlarges rapidly, and undergoes an extreme distortion from the growth of the ovaries. These, bulging out from her sides, become lateral sacs, each of which attains something like three times her size; and then a further distortion is produced by two vast egg-bags, severally larger than herself, which also are formed and become pendant. So that the germ-producing organs and their contents, eventually acquire a total bulk some eight or ten times that of the rest of the body. Numerous species of this type and habit, repeat this relation between a life of inaction with high feeding, and an enormous rate of genesis.

*Entozoa* yield us many examples of this causal relation, raised to a still higher degree. The *Gordius*, or Hair-worm, is a creature which, finding its way when young into the body of an insect, there grows rapidly, and afterwards emerging to breed, lays as many as 8,000,000 eggs in less than a day. Similarly with the larger types that infest the higher animals. It has been calculated by Dr. Eschricht, as quoted by Professor Owen, that there are "64,000,000 of ova in the mature female *Ascaris Lumbricoides.*" Even a still greater fertility occurs among the cestoid *Entozoa.* Immersed as a Tape-worm is in nutritive liquid, which it absorbs through its integument, it requires no digestive apparatus. The room which one would occupy, and the materials it would use up, are therefore available for germ-producing organs, which nearly fill each segment: each segment, sexually complete in itself, is little else than an enormous reproductive system, with just enough of other structures to bind it together. Remembering that the Tape-worm, retaining its hold, continues to bud-out such segments as fast as the fully-developed ones are cast off, and goes on doing this as long as the infested individual lives; we see that here, where there is no expenditure, where the cost of individuation is reduced to the greatest extent while the nutrition is the highest possible, the degree of fertility reaches its extreme. These *Entozoa* yield us further interesting evidence. Of their various species, most if not all undergo passive migration from animal to animal before they become nature. Usually, the form assumed in the body of the first host, is devoid of all that part in which the reproductive structures take their rise; and this part grows and develops reproductive structures, only in some predatory animal to which its first host falls a sacrifice. Occasionally, however, the egg gives origin to the sexual form in the animal that originally swallowed it, but the development remains incomplete—there is no sexual genesis, no formation of eggs in the rudimentary segments. That these may become fertile, it is needful, as before, for the containing animal to be devoured; so that the imperfect Tape-worm may find its way into the intestine of a higher animal. Thus the *Bothriocephalus solidus*, found in the abdominal cavity of the Stickleback, is barren while it remains there; but if the Stickleback is eaten by a Water-fowl, the reproductive system of the transferred *Bothriocephalus* becomes developed and active. So, too, a kind of Tape-worm which remains infertile while in the intestine of a Mouse, becomes fertile in the intestine of a Cat that devours the mouse. May we not regard these facts as again showing the dependence of fertility on nutrition? Barrenness here accompanies conditions unfavourable to the absorption of nutriment; and it gives way to fecundity where nutriment is large in quantity and superior in quality.

§ 359. Extremely significant are those cases of partial reversion to primitive forms of genesis, that occur under special conditions in some of the higher *Annulosa.* I refer to the pseudo-parthenogenesis and metagenesis in Insects.

Under what conditions do the *Aphides* exhibit this strange deviation from the habits of their order? Why among them should imperfect females produce, agamically, others like themselves, generation after generation, with great rapidity? There is the obvious explanation that they get plenty of easily-assimilated food without exertion. Piercing the tender coats of young shoots, they sit and suck—appropriating the nitrogenous elements of the sap and ejecting its saccharine matter as "honey dew." Along with a sluggishness strongly contrasted with the activity of their allies—along with a very low rate of consumption and a correlative degradation of structure; we have here a retrogression to asexual genesis, and a greatly-increased rate of multiplication.

The recently-discovered instance of internal metagenesis in the maggots of certain Flies has a like meaning. Incredible as it at first seemed to naturalists, it is now proved that the *Cecydomia*-larva develops in its interior a brood of larvæ of like structure with itself. In this case, as in the last, abundant food is combined with low expenditure. These larvæ are found in such habitats as the refuse of beet-root-sugar factories—masses of nitrogenous *débris* remaining after the extraction of the saccharine matter. Each larva has a practically-unlimited supply of sustenance imbedding it on all sides.

It is true that some other maggots, as those of the Flesh-fly, are similarly, or still better, circumstanced; and, it may be said, ought therefore to have the same habit. But this does not necessarily follow. Survival of the fittest will determine whether such specially-favourable conditions result in the aggrandisement of the individual or in the multiplication of the race. And in the case of the Flesh-fly, there is a reason why greater individuation rather than more rapid genesis will occur. For a decomposing animal body lasts so short a time, that were Flesh-fly larvæ to multiply agamically, the second generation would die from the disappearance of their food. Hence, individuals in which the excessive nutrition led to internal metagenesis, would leave no posterity; and natural selection would establish the variety in which greater growth resulted. All which the argument requires is, that when such reversion to agamogenesis *does* take place, it shall be where the food is unusually abundant and the expenditure unusually small; and this the cases instanced go to show.

§ 360. The physiological lesson taught us by Bees and Ants, not quite harmonizing with the moral lesson they are supposed to teach, is that highly-fed idleness is favourable to fertility, and that excessive industry has barrenness for its concomitant.

The egg of a Bee develops into a small barren female or into a large fertile female, according to the supply of food given to the larva hatched from it. We here see that the germ-producing action is an overflow of the surplus remaining after completion of the individual; and that the lower feeding which the larva of a working Bee has, results in a dwarfing of the adult and an arrested development of the generative organs. Further, we have the fact that the condition under which the perfect female, or mother-Bee, goes on, unlike insects in general, laying eggs continuously, is that she has plenty of food brought to her, is kept warm, and goes through no considerable exertion. While, contrariwise, it is to be noted that the infertility of the workers, is associated with the ceaseless labour of bringing materials for the combs and building them, as well as the labour of feeding the queen, the larvæ, and themselves.

Ants, and especially some of the tropical kinds, show us these relations in an exaggerated form. The difference of bulk between the fecund and infecund females is immensely greater. The mother-Ant has the reproductive system so enormously developed, that the remainder of her body is relatively insignificant. Entirely incapable of locomotion, she is unable to deposit her eggs in the places where they are to be hatched; so that they have to be carried away by the workers as fast as they are extruded. Her life is thus reduced substantially to that of a parasite—an absorption of abundant food supplied gratis, a total absence of expenditure, and a consequent excessive rate of genesis. "The queen-ant of the African *Termites* lays 80,000 eggs in twenty-four hours."

§ 361. It may be needful to say that these exceptional relations cannot be ascribed to the assigned causes acting alone. The extreme fertility which, among parasites and social insects, accompanies extremely high feeding, and an expenditure reduced nearly to zero, presupposes typical structures and tendencies of suitable kinds; and these are not directly accounted for. On creatures otherwise organized, unlimited supplies of food and total inactivity are not followed by such results. There of course requires a constitution fitted to the special conditions; and the evolution of this cannot be due simply to plethora joined with rest. These cases are given as illustrating the conditions under which extreme exaltations of fertility become possible. Their meanings, thus limited, are clear, and completely to the point. We see in them that the devotion of nutriment to race-preservation, is carried furthest where the cost of self-preservation is reduced to a minimum; and, conversely, that nothing is devoted directly to race-preservation by individuals on which falls an excessive expenditure for self-preservation and preservation of other's offspring.

# CHAPTER XI.

## INTERPRETATION AND QUALIFICATION.

§ 362. Considering the difficulties of inductive verification, we have, I think, as clear a correspondence between the *à priori* and *à posteriori* conclusions, as can be expected. The many factors co-operating to bring about the result in every case, are so variable in their absolute and relative amounts, that we can rarely disentangle the effect of each one; and have usually to be content with qualified inferences. Though in the mass, organisms show us an unmistakable relation between great size and small fertility; yet special comparisons among them are nearly always partially vitiated by differences of structure, differences of nutrition, differences of expenditure. Though it is beyond question that the more complex organisms are the less prolific; yet as complexity has a certain general connexion with bulk, and in animals with expenditure, we cannot often identify its results as independent of these. And, similarly, though the creatures that waste much matter in producing motion, sensible and insensible, have lower rates of multiplication than those which waste less; yet, as the creatures which waste much are generally larger and more complex, we are again met by an obstacle which limits our comparisons, and compels us to accept conclusions less definite than are desirable.

Such difficulties arise, however, only when we endeavour, as in foregoing chapters, to prove the inverse variation between Genesis and each separate element of Individuation —growth, development, activity. We are scarcely at all hampered by qualifications when, from contemplating these special relations, we return to the general relation. The antagonism between Individuation and Genesis, is shown by all the facts that have been grouped under each head. We have seen that in ascending from the lowest to the highest types, there is a decrease of fertility so great as to be absolutely inconceivable, and even inexpressible by figures; and whether the superiority of type consists in relative largeness, in greater complexity, in higher activity, or in some or all of these combined, matters not to the ultimate inference. The broad fact, enough for us here, is that organisms in which the integration and differentiation of matter and motion have been carried furthest, are those in which the rate of multiplication has fallen lowest. How much of the decline of reproductive power is due to the greater integration of matter, how much to its greater differentiation, how much to the larger amounts of integrated and differentiated motions generated, it may be impossible to say; and it is not needful to say. These are all elements of a higher degree of life, an augmented ability to maintain the organic equilibrium amid environing actions—an increased power of self-preservation; and we find their invariable accompaniment to be, a diminished expenditure of matter, or motion, or both, in race-preservation.

In brief, then, examination of the evidence shows that there *does* exist that relation which we inferred *must* exist. Arguing from general data, we saw that for the maintenance of a species, the ability to produce offspring must be great, in proportion as the ability of the individuals to contend with destroying forces is small; and conversely. Arguing from other general data, we saw that, derived as the self-sustaining and race-sustaining forces are from a common stock of force, it necessarily happens that, other things equal, increase of one involves decrease of the other. And then, turning to special facts, we have found that this inverse variation is clearly traceable throughout both the animal and vegetal kingdoms. We may therefore set it down as a law, that every higher degree of organic evolution, has for its concomitant a lower degree of that peculiar organic dissolution which is seen in the production of new organisms.

§ 363. Something remains to be said in reply to the inquiry—how is the ratio between Individuation and Genesis established in each case? This inquiry has been but partially answered in the course of the foregoing argument.

All specialities of the reproductive process are due to the natural selection of favourable variations. Whether a creature lays a few large eggs or many small ones equal in weight to the few large, is not determined by any physiological necessity: here the only assignable cause is the survival of varieties in which the matter devoted to reproduction, happens to be divided into portions of such size and number as most to favour multiplication. Whether in any case there are frequent small broods or larger broods at longer intervals, depends wholly on the constitutional peculiarity that has arisen from the dying out of families in which the sizes and intervals of the broods were least suited to the conditions of life. Whether a species of animal produces many offspring of which it takes no care or a few of which it takes much care—that is, whether its reproductive surplus is laid out wholly in germs or partly in germs and partly in labour on their behalf—must have been decided by that moulding of constitution to conditions, slowly effected through the more frequent preservation of descendants from those whose reproductive habits were best adapted to the circumstances of the species. Given a certain surplus available for race-preservation, and it is clear that by indirect equilibration only, can there be established the more or less peculiar distribution of this surplus which we see in each case. Obviously, too, survival of the fittest has a share in determining the proportion between the amount of matter that goes to Individuation and the amount that goes to Genesis. Whether the interests of the species are most subserved by a higher evolution of the individual joined with a diminished fertility, or by a lower evolution of the individual joined with an increased fertility, are questions ever being experimentally answered. If the more-developed and less-prolific variety has a greater number of survivors, it becomes established and predominant. If, contrariwise, the conditions of life being simple, the larger or more-organized individuals gain nothing by their greater size or better organization; then the greater fertility of the less evolved ones, will insure to their descendants an increasing predominance.

But direct equilibration all along maintains the limits within which indirect equilibration thus works. The necessary antagonism we have traced, rigidly restricts the changes that natural selection can produce, under given conditions, in either direction. A greater demand for Individuation, be it a demand caused by some spontaneous variation or by an adaptive increase of structure and function, inevitably diminishes the supply for Genesis; and natural selection cannot, other things remaining the same, restore the rate of Genesis while the higher Individuation is maintained. Conversely, survival of the fittest, acting on a species that has, by spontaneous variation or otherwise, become more prolific, cannot again raise its lowered Individuation, so long as everything else continues constant.

§ 364. Here, however, a qualification must be made. It was parenthetically remarked in § 327 that the inverse variation between Individuation and Genesis is not exact; and it was hinted that a slight modification of statement would be requisite at a more advanced stage of the argument. We have now reached the proper place for specifying this modification.

Each increment of evolution entails a decrement of reproduction that is not accurately proportionate, but somewhat less than proportionate. The gain in the one direction is not wholly canceled by a loss in the other direction, but only partially canceled: leaving a margin of profit to the species. Though augmented power of self-maintenance habitually necessitates diminished power of race-propagation, yet the product of the two factors is greater than before; so that the forces preservative of race become, thereafter, in excess of the forces destructive of race, and the race spreads. We shall soon see why this happens.

Each advance in evolution implies an economy. That any increase in bulk, or structure, or activity, may become established, the life of the organism must be to some extent facilitated by the change—the cost of self-support must be, on the average, reduced. If the greater complexity, or the larger size, or the more agile movement, entails on the individual an outlay that is not repaid in food more-easily obtained, or danger more-easily escaped; then the individual will be at a relative disadvantage, and its diminished posterity will disappear. If the extra outlay is but just made good by the extra advantage, the modified individual will not survive longer, or leave more descendants, than the unmodified individuals. Consequently, it is only when the expense of greater individuation is out-balanced by a subsequent saving, that it can tend to subserve the preservation of the individual; or, by implication, the preservation of the race. The vital capital invested in the alteration must bring a more than equivalent return. A few instances will show that, whether the change results from direct equilibration or from indirect equilibration, this must happen. Suppose a creature takes to performing some act in an unusual way—leaps where ordinarily its kindred crawl, eludes pursuit by diving instead of, like others of its kind, by swimming along the surface, escapes by doubling instead of by sheer speed. Clearly, perseverance in the modified habit will, other things equal, imply that it takes less effort. The creature's sensations will ever prompt desistance from the more laborious course; and hence a congenital habit is not likely to be diverged from unless an economy of force is achieved by the divergence. Assuming, then, that the new method has no advantage over the old in directly diminishing the chances of death, the establishment of it, and of the structural complications involved, nevertheless implies a physiological gain. Suppose, again, that an animal takes to some abundant food previously refused by its kind. It is likely to persist only if that the comparative ease in obtaining this food, more than compensates for any want of adaptation to its digestive organs; so that superposed modifications of the digestive organs are likely to arise only when an average economy results. What now must be the influence on the creature's system as a whole? Diminished expenditure in any direction, or increased nutrition however effected, will leave a greater surplus of materials. The animal will be physiologically richer. Part of its augmented wealth will go towards its own greater individuation—its size, or its strength, or both, will increase; while another part will go towards more active genesis. Just as a state of plethora directly produced enhances fertility; so will such a state indirectly produced.

In another way, the same thing must result from those additions to bulk or complexity or activity that are due to survival of the fittest. Any change which prolongs individual life, will, other things remaining the same, further the production of offspring. Even when it is not, like the foregoing, a means of economizing the forces of the individual, still, if it increases the chances of escaping destruction, it increases the chances of leaving posterity. Any further degree of evolution, therefore, will be so established only where the cost of it is more than repaid; part of the gain being shown in the lengthened life of the individual, and part in the greater production of other individuals.

We have here the solution of various minor anomalies by which the inverse variation of Individuation and Genesis is obscured. Take as an instance the fertility of the Blackbird as compared with that of the Linnet. Both birds lay five eggs, and both usually have two broods. Yet the Blackbird is far the larger of the two; and ought, according to the general law, to be much less prolific. What causes this nonconformity? We shall find an answer in their respective foods and habits. Except during the time that it is rearing its young, the Linnet collects only vegetal food—lives during the winter on the seeds it finds in the fields, or, when hard pressed, picks up around farms; and to obtain this spare diet is continually flying about. The result, if it survives the frost and snow, is a considerable depletion; and it recovers its condition only after some length of spring weather. The Blackbird, on the other hand, is omnivorous: while it eats grain and fruit when they come in its way, it depends largely on animal food. It cuts to pieces and devours the dew-worms which, morning and evening, it finds on the surface of a lawn, and, even discovering where they are, unearths them; it swallows slugs, and breaking snail-shells, either with its beak or by hammering them against stones, tears out their tenants; and it eats beetles and larvæ. Thus the strength of the Blackbird opens to it a store of good food, much of which is inaccessible to so small and weak a bird as a Linnet—a store especially helpful to it during the cold months, when the hybernating Snails in hedge-bottoms yield it abundant provision. The result is that the Blackbird is ready to breed very early in spring; and is able during the summer to rear a second, and sometimes even a third, brood. Here, then, a higher degree of Individuation secures advantages so great, as to much more than compensate its cost: it is not that the decline of Genesis is less than proportionate to the increase of Individuation, but there is no decline at all. Comparison of the Rat with the Mouse yields a parallel result. Though they differ greatly in size, yet the one is as prolific as the other. This absence of difference cannot be ascribed to their unlike degrees of activity. We must seek its cause in some facility of living secured to the Rat by its greater intelligence, greater power and courage, greater ability to utilize what it finds. The Rat is notoriously cunning; and its cunning gives success to its foraging expeditions. It is not, like the Mouse, limited mainly to vegetal food; but while it eats grain and beans like the Mouse, it also eats flesh and carrion, devours young poultry and eggs. The result is that, without a proportionate increase of expenditure, it gets a far larger supply of nourishment than the Mouse; and this relative excess of nourishment makes possible a large size without a smaller rate of multiplication. How clearly this is the cause, we see in the contrast between the common Rat and the Water-Rat. While the common Rat has habitually several broods a-year of from 10 to 12 each, the Water-Rat, though somewhat smaller, has but 5 or 6 in a brood, and but one brood, or sometimes two broods, a-year. But the Water-Rat lives on vegetal food—lacks all that its bold, sagacious, omnivorous congener, gains from the warmth as well as the abundance which men's habitations yield.

The inverse variation of Individuation and Genesis is, therefore, but approximate. Recognizing the truth that every increment of evolution which is appropriate to the circumstances of an organism, brings an advantage somewhat in excess of its cost; we see the general law, as more strictly stated, to be that Genesis decreases not quite so fast as Individuation increases. Whether the greater Individuation takes the form of a larger bulk and accompanying access of strength; whether it be shown in higher speed or agility; whether it consists in a modification of structure that facilitates some habitual movement, or in a visceral change that helps to utilize better the absorbed aliment; the ultimate effect is identical. There is either a more economical performance of the same actions, internal or external, or there is a securing of greater advantages by modified actions, which cost no more, or have an increased cost less than the increased gain. In any case, the result is a greater surplus of vital capital; part of which goes to the aggrandisement of the individual, and part to the formation of new individuals. While the higher tide of nutritive matters, everywhere filling the parent-organism, adds to its power of self-maintenance, it also causes a reproductive overflow larger than before.

Hence every type that is best adapted to its conditions, which on the average means every higher type, has a rate of multiplication that insures a tendency to predominate. Survival of the fittest, acting alone, is ever replacing inferior species by superior species. But beyond the longer urvival, and therefore greater chance of leaving offspring, which superiority gives, we see here another way in which the spread of the superior is insured. Though the more-evolved organism is the less fertile absolutely, it is the more fertile relatively.

## CHAPTER XII.

### MULTIPLICATION OF THE HUMAN RACE.

§ 365. The relative fertility of Man considered as a species, and those changes in Man's fertility which occur under changed conditions, must conform to the laws which we have traced thus far. As a matter of course, the inverse variation between Individuation and Genesis, holds of him as of all other organized beings. His extremely low rate of multiplication—far below that of all terrestrial Mammals except the Elephant, (which though otherwise less evolved, is, in extent of integration, more evolved)—we shall recognize as the necessary concomitant of his much higher evolution. And the causes of increase or decrease in his fertility, special or general, temporary or permanent, we shall expect to find in those changes of bulk, of structure, or of expenditure, which we have in all other cases seen associated with such effects.

In the absence of detailed proof that these parallelisms exist, it might suffice to contemplate the several communities between the reproductive function in human beings and other beings. I do not refer simply to the fact that genesis proceeds in a similar manner; but I refer to the similarity of the relation between the generative function and the functions that have for their joint end the preservation of the individual. In Man, as in other creatures that expend much, genesis commences only when growth and development are declining in rapidity and approaching their termination. Among the higher organisms in general, the reproductive activity, continuing during the prime of life, ceases when the vigour declines, leaving a closing period of infertility; and in like manner among ourselves, barrenness supervenes when middle age brings the surplus vitality to an end. So, too, it is found that in Man, as in beings of lower orders, there is a period at which fecundity culminates. In § 341, facts were cited showing that at the commencement of the reproductive period, animals bear fewer offspring than afterwards; and that towards the close of the reproductive period, there is a decrease in the number produced. In like manner it is shown by the tables of Dr. Duncan's recent work, that the fecundity of women increases up to the age of about 25 years; and continuing high with but slight diminution till after 30, then gradually wanes. It is the same with the sizes and weights of offspring. Infants born of women from 25 to 29 years of age, are both longer and heavier than infants born of younger or older women; and this difference has the same implication as the greater total weight of the offspring produced at a birth, during the most fecund age of a pluriparous animal. Once more, there is the fact that a too-early bearing of young produces on a woman the same injurious effects as on an inferior creature—an arrest of growth and an enfeeblement of constitution.

Considering these general and special parallelisms, we might safely infer that variations of human fertility conform to the same laws as do variations of fertility in general. But it is not needful to content ourselves with an implication. Evidence is assignable that what causes increase or decrease of genesis in other creatures, causes increase or decrease of genesis in Man. It is true that, even more than hitherto, our reasonings are beset by difficulties. So numerous are the inequalities in the conditions, that but few unobjectionable comparisons can be made. The human races differ considerably in their sizes, and notably in their degrees of cerebral development. The climates they inhabit entail on them widely different consumptions of matter for maintenance of temperature. Both in their qualities and quantities, the foods they live on are unlike; and the supply is here regular and there very irregular. Their expenditures in bodily action are extremely unequal; and even still more unequal are their expenditures in mental action. Hence the factors, varying so much in their amounts and combinations, can scarcely ever have their respective effects identified. Nevertheless there are a few comparisons, the results of which may withstand criticism.

§ 366. The increase of fertility caused by a nutrition that is greatly in excess of the expenditure, is to be detected by contrasting populations of the same race, or allied races, one of which obtains good and abundant sustenance much more easily than the other. Three cases may here be set down.

The traveller Barrow, describing the Cape-Boors, says:—"Unwilling to work and unable to think," * * * "indulging to excess in the gratification of every sensual appetite, the African peasant grows to an unwieldy size;" and respecting the other sex, he adds—"the women of the African peasantry lead a life of the most listless inactivity." Then, after illustrating these statements, he goes on to note "the prolific tendency of all the African peasantry. Six or seven children in a family are considered as very few; from a dozen to twenty are not uncommon." The native races of this region yield evidence to the same effect. Speaking of the cruelly-used Hottentots (he is writing sixty years ago), who, while they are poor and ill-fed, have to do all the work for the idle Boors, Barrow says that they "seldom have more than two or three children; and many of the women are barren." This unusual infertility stands in remarkable contrast with the unusual fertility of the Kaffirs, of whom he afterwards gives an account. Rich in cattle, leading easy lives, and living almost exclusively on animal food (chiefly milk with occasional flesh), these people were then reputed to have a very high rate of multiplication. Barrow writes:—"They are said to be exceedingly prolific; that twins are almost as frequent as single births, and that it is no uncommon thing for a woman to have three at a time." Probably both these statements are in excess of the truth; but there is room for large discounts without destroying the extreme difference. A third instance is that of the French Canadians. "*Nous sommes terribles pour les enfants!*" observed one of them to Prof. Johnston; who tells us that the man who said this "was one of fourteen children—was himself the father of fourteen, and assured me that from eight to sixteen was the usual number of the farmers' families. He even named one or two women who had brought their husbands five-and-twenty, and threatened '*le vingt-sixième pour le prêtre.*'" From these large families, joined with the early marriages and low rate of mortality, it results that, by natural increase, "there are added to the French-Canadian population of Lower Canada four persons for every one that is added to the population of England." Now these French-Canadians are described by Prof. Johnston as home-loving, contented, unenterprising; and as living in a region where "land and subsistence are easily obtained." Very moderate industry brings to them liberal supplies of necessaries; and they pass a considerable portion of the year in idleness. Hence the cost of Individuation being much reduced, the rate of Genesis is much increased. That this uncommon fertility is not due to any direct influence of the locality, is implied by the fact that along with the "restless, discontented, striving, burning energy of their Saxon neighbours" no such rate of multiplication is observed; while further south, where the physical circumstances are more favourable if anything, the Anglo-Saxons, leading lives of excessive activity, have a fertility below the average. And that the peculiarity is not a direct effect of race, is proved by the fact that in Europe, the rural French are certainly not more prolific than the rural English.

To every reader there will probably occur the seemingly adverse evidence furnished by the Irish; who, though not well fed, multiply fast. Part of this more rapid increase is due to the earlier marriages common among them, and consequent quicker succession of generations—a factor which, as we have seen, has a larger effect than any other on the rate of multiplication. Part of it is due to the greater generality of marriage—to the comparative smallness of the number who die without having had the opportunity of producing offspring. The effects of these causes having been deducted, we may doubt whether the Irish, individually considered, would be found more prolific than the English. Perhaps, however, it will be said that, considering their diet, they ought to be less prolific. This is by no means obvious. It is not simply a question of nutriment absorbed: it is a question of how much remains after the expenditure in self-maintenance. Now a notorious peculiarity in the life of the Irish peasant, is, that he obtains a return of food that is large in proportion to his outlay in labour. The cultivation of his potatoe-ground occupies each cottager but a small part of the year; and the domestic economy of his wife is not of a kind to entail on her much daily exertion. Consequently, the crop, tolerably abundant in quantity though innutritive in quality, very possibly suffices to meet the comparatively-low expenditure, and to leave a good surplus for genesis—perhaps a greater surplus than remains to the males and females of the English peasantry, who, though fed on better food, are harder worked.

We conclude, then, that in the human race, as in all other races, such absolute or relative abundance of nutriment as leaves a large excess after defraying the cost of carrying on parental life, is accompanied by a high rate of genesis.*

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* This is exactly the reverse of Mr. Doubleday's doctrine; which is that throughout both the animal and vegetal kingdoms, "over-feeding checks increase; whilst, on the other hand, a limited or deficient nutriment stimulates and adds to it." Or, as he elsewhere says—"Be the range of the

§ 367. Evidence of the converse truth, that relative increase of expenditure, leaving a diminished surplus, reduces the degree of fertility, is not wanting. Some of it has been set down for the sake of antithesis in the foregoing section. Here may be grouped a few facts of a more special kind having the same implication.

To prove that much bodily labour renders women less prolific, requires more evidence than is obtainable. Some evidence, however, may be set down. De Boismont in France and Dr. Szukits in Austria, have shown by extensive statistical comparisons, that the reproductive age is reached a year later by women of the labouring class than by middle-class women; and while ascribing this delay in part to inferior

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natural power to increase in any species what it may, the *plethoric* state invariably checks it, and the *deplethoric* state invariably develops it; and this happens in the exact ratio of the intensity and completeness of each state, until each state be carried so far as to bring about the actual death of the animal or plant itself."

I have space here only to indicate the misinterpretations on which Mr. Doubleday has based his argument.

In the first place, he has confounded normal plethora with what I have, in § 355, distinguished as abnormal plethora. The cases of infertility accompanying fatness, which he cites in proof that over-feeding checks increase, are not cases of high nutrition properly so called; but cases of such defective absorption or assimilation as constitutes low nutrition. In Chap. IX, abundant proof was given that a truly plethoric state is an unusually fertile state. It may be added that much of the evidence by which Mr. Doubleday seeks to show that among men, highly-fed classes are infertile classes, may be outbalanced by counter-evidence. Many years ago Mr. Lewes pointed this out: extracting from a book on the peerage, the names of 16 peers who had, at that time, 186 children; giving an average of 11·6 in a family.

Mr. Doubleday insists much on the support given to his theory by the barrenness of very luxuriant plants, and the fruitfulness produced in plants by depletion. Had he been aware that the change from barrenness to fruitfulness in plants, is a change from agamogenesis to gamogenesis—had it been as well known at the time when he wrote as it is now, that a tree which goes on putting out sexless shoots, is so producing new individuals; and that when it begins to bear fruit, it simply begins to produce new individuals after another manner—he would have perceived that facts of this class do not tell in his avour.

In the law which Mr. Doubleday alleges, he sees a guarantee for the main-nutrition, we may suspect that it is in part due to greater muscular expenditure. A kindred fact, admitting of a kindred interpretation, may be added. Though the comparatively-low rate of increase in France is attributed to other causes, yet, very possibly, one of its causes is the greater proportion of hard work entailed on French women, by the excessive abstraction of men for non-productive occupations, military and civil. The higher rate of multiplication in England than in continental countries generally, is not improbably furthered by the easier lives which English women lead.

That absolute or relative infertility is generally produced in women by mental labour carried to excess, is more clearly shown. Though the regimen of upper-class girls is not what it should be, yet, considering that their feeding is

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tenance of species. He argues that the plethoric state of the individuals constituting any race of organisms, presupposes conditions so favourable to life that the race can be in no danger; and that rapidity of multiplication becomes needless. Conversely, he argues that a deplethoric state implies unfavourable conditions—implies, consequently, unusual mortality; that is—implies a necessity for increased fertility to prevent the race from dying out. It may be readily shown, however, that such an arrangement would be the reverse of self-adjusting. Suppose a species, too numerous for its food, to be in the resulting deplethoric state. It will, according to Mr. Doubleday, become unusually fertile; and the next generation will be more numerous rather than less numerous. For, by the hypothesis, the unusual fertility due to the deplethoric state, is the cause of undue increase of population. But if the next generation is more numerous while the supply of food has remained the same, or rather has decreased under the keener competition for it, then this next generation will be in a still more deplethoric state, and will be still more fertile. Thus there will go on an ever-increasing rate of multiplication, and an ever-decreasing supply of food, until the species disappears. Suppose, on the other hand, the members of a species to be in an unusually plethoric state. Their rate of multiplication, ordinarily sufficient to maintain their numbers, will become insufficient to maintain their numbers. In the next generation, therefore, there will be fewer to eat the already abundant food, which, becoming relatively still more abundant, will render the fewer members of the species still more plethoric, and still less fertile, than their parents. And the actions and reactions continuing, the species will presently die out from absolute barrenness.

better than that of girls belonging to the poorer classes, while, in most other respects, their physical treatment is not worse, the deficiency of reproductive power among them may be reasonably attributed to the overtaxing of their brains—an overtaxing which produces a serious reaction on the physique. This diminution of reproductive power is not shown only by the greater frequency of absolute sterility; nor is it shown only in the earlier cessation of child-bearing; but it is also shown in the very frequent inability of such women to suckle their infants. In its full sense, the reproductive power means the power to bear a well-developed infant, and to supply that infant with the natural food for the natural period. Most of the flat-chested girls who survive their high-pressure education, are incompetent to do this. Were their fertility measured by the number of children they could rear without artificial aid, they would prove relatively very infertile.

The cost of reproduction to males being so much less than it is to females, the antagonism between Genesis and Individuation is not often shown in men by suppression of generative power consequent on unusual expenditure in bodily action. Nevertheless, there are indications that this results in extreme cases. We read that the ancient *athletæ* rarely had children; and among such of their modern representatives as acrobats, an allied relation of cause and effect is alleged. Indirectly this truth, or rather its converse, appears to have been ascertained by those who train men for feats of strength—they find it needful to insist on continence.

Special proofs that in men, great cerebral expenditure diminishes or destroys generative power, are difficult to obtain. It is, indeed, asserted that intense application to mathematics, requiring as it does extreme concentration of thought, is apt to have this result; and it is asserted, too, that this result is produced by the excessive emotional excitement of gambling. Then, again, it is a matter of common remark how frequently men of unusual mental activity leave no offspring. But facts of this kind admit of another interpretation. The reaction of the brain on the body is so violent—the overtaxing of the nervous system is so apt to prostrate the heart and derange the digestion; that the incapacities caused in these cases, are probably often due more to constitutional disturbance than to the direct deduction which excessive action entails. Such instances harmonize with the hypothesis; but how far they yield it positive support we cannot say.

§ 368. An objection must here be guarded against. It is likely to be urged that since the civilized races are, on the average, larger than many of the uncivilized races; and since they are also somewhat more complex as well as more active; they ought, in conformity with the alleged general law, to be less prolific. There is, however, no evidence to prove that they are so: on the whole, they seem rather the reverse.

The reply is that were all other things equal, these superior varieties of men should have inferior rates of increase. But other things are not equal; and it is to the inequality of other things that this apparent anomaly is attributable. Already we have seen how much more fertile domesticated animals are than their wild kindred; and the causes of this greater fertility are also the causes of the greater fertility, relative or absolute, which civilized men exhibit when compared with savages.

There is the difference in amount of food. Australians, Fuegians, and sundry races that might be named as having low rates of multiplication, are obviously underfed. The sketches of natives contained in the volumes of Livingstone, Baker, and others, yield clear proofs of the extreme depletion common among the uncivilized. In quality as well as in quantity, their feeding is bad. Wild fruits, insects, larvæ, vermin, &c., which we refuse with disgust, often enter largely into their dietary. Much of this inferior food they eat uncooked; and they have not our elaborate appliances for mechanically-preparing it, and rejecting its useless parts. So that they live on matters of less nutritive value, which cost more both to masticate and to digest. Further, to uncivilized men supplies of food come very irregularly: long periods of scarcity are divided by short periods of abundance. And though by gorging when opportunity occurs, something is done towards compensating for previous want, yet the effects of prolonged starvation cannot be neutralized by occasional enormous meals. Bearing in mind, too, that improvident as they are, savages often bestir themselves only under pressure of hunger, we may fairly consider them as habitually ill-nourished—may see that even the poorer classes of civilized men, making regular meals on food separated from innutritive matters, easy to masticate and digest, tolerably good in quality and adequate if not abundant in quantity, are much better nourished.

Then, again, though a much greater consumption in muscular action appears to be undergone by civilized men than by savages; and though it is probably true that among our labouring people the daily repairs cost more; yet in many cases there does not exist so much difference as we are apt to suppose. The chase is very laborious; and great amounts of exertion are gone through by the lowest races in seeking and securing the odds and ends of wild food on which they largely depend. We naturally assume that because barbarians are averse to regular labour, their muscular action is less than our own. But this is not necessarily true. The monotonous toil is what they cannot tolerate; and they may be ready to go through as much or more exertion when it is joined with excitement. If we remember that the sportsman who gladly scrambles up and down rough hill-sides all day after grouse or deer, would think himself hardly used had he to spend as much effort and time in digging; we shall see that a savage who is the reverse of industrious. may nevertheless be subject to a muscular waste not very different in amount from that undergone by the industrious. When it is added that a larger physiological expenditure is entailed on the uncivilized than on the civilized by the absence of good appliances for shelter and protection—that in some cases they have to make good a greater loss of heat, and in other cases suffer much wear from irritating swarms of insects—we shall see that the total cost of self-maintenance among them is probably in many cases little less, and in some cases more, than it is among ourselves.

So that though, on the average, the civilized are probably larger than the savage; and though they are, in their nervous systems at least, somewhat more complex; and though, other things equal, they ought to be the less prolific; yet, other things are so unequal, as to make it quite conformable to the general law that they should be more prolific. In § 365 we observed how, among inferior animals, higher evolution sometimes makes self-preservation far easier, by opening the way to resources previously unavailable: so involving an undiminished, or even an increased, rate of genesis. And similarly we may expect among races of men, that those whose slight further developments have been followed by habits and arts that immensely facilitate life, will not exhibit a lower degree of fertility, and may even exhibit a higher.

§ 369. One more objection has to be met—a kindred objection to which there is a kindred reply. Cases may be named of men conspicuous for activity, bodily and mental, who were also noted, not for less generative power than usual, but for more. As their superiorities indicate higher degrees of evolution, it may be urged that such men should, according to the theory, have lower degrees of reproductive activity. The fact that here, along with increased powers of self-preservation, there go increased powers of race-propagation, seems irreconcilable with the general doctrine. Reconciliation is not difficult however.

The cases are analogous to some before named, in which more abundant food simultaneously aggrandizes the individual and adds to the production of new individuals—the difference between the cases being, that instead of a better external supply of materials there is here a better internal utilization of materials. Creatures of the same species notoriously differ in goodness of constitution. Here there is some visceral defect, showing itself in feebleness of all the functions; while here some peculiarity of organic balance, some high quality of tissue, some abundance or potency of the digestive juices, gives to the system a perpetual high tide of rich blood, that serves at once to enhance the vital activities and to raise the power of propagation. Such variations, however, are quite independent of changes in the *proportion* between Individuation and Genesis: this remains the same, while both are increased or decreased by the increase or decrease of the common stock of materials.

An illustration will best clear up any perplexity. Let us say that the fuel burnt in the furnace of a locomotive steam-engine, answers to the food which a man consumes; let us say that the produced steam expended in working the engine, corresponds to that portion of absorbed nutriment which carries on the man's functions and activities; and let us say that the steam blowing off at the safety-valve, answers to that portion of the absorbed nutriment which goes to the propagation of the race. Such being the conditions of the case, several kinds of variations are possible. All other circumstances remaining the same, there may be changes of proportion between the steam used for working the engine and the steam that escapes by the safety-valve. There may be a structural or organic change of proportion. By enlarging the safety-valve or weakening its spring, while the cylinders are reduced in size, there may be established a constitutionally-small power of locomotion and a constitutionally-large amount of escape-steam; and inverse variations so produced, will answer to the inverse variations between

Individuation and Genesis which different types of organisms show us. Again, there may be a functional change of proportion. If the engine has to draw a considerable load, the abstraction of steam by the cylinders greatly reduces the discharge by the safety-valve; and if a high velocity is kept up, the discharge from the safety-valve entirely ceases. Conversely, if the velocity is low, the escape-steam bears a large ratio to the steam consumed by the motor apparatus; and if the engine becomes stationary the whole of the steam escapes by the safety-valve. This inverse variation answers to that which we have traced between Expenditure and Genesis, as displayed in the contrasts between species of the same type but unlike activities, and in the contrasts between active and inactive individuals of the same species. But now beyond these inverse variations between the quantities of consumed steam and escape-steam, that are structurally and functionally caused, there are coincident variations, producible in both by changes in the quantity of steam supplied—changes that may be caused in several ways. In the first place, the fuel thrown into the furnace may be increased or made better. Other things equal, there will result a more active locomotion as well as a greater escape; and this will answer to that simultaneous addition to its individual vigour and its reproductive activity, caused in an animal by a larger quantity, or a superior quality, of food. In the second place, the steam generated may be economized. Loss by radiation from the boiler may be lessened by a covering of non-conducting substances; and part of the steam thus prevented from condensing, will go to increase the working power of the engine, while part will be added to the quantity blowing off. This variation corresponds to that simultaneous addition to bodily vigour and propagative power, which results in animals that have to expend less in keeping up their temperatures. In the third place, by improvement of the steam-generating apparatus, more steam may be obtained from a given weight of fuel. A better-formed evaporating surface, or boiler plates which conduct more rapidly, or an increased number of tubes, may cause a larger absorption of heat from the burning mass or the hot gases it gives off; and the extra steam generated by this extra heat, will, as before, augment both the motive force and the emission through the safety-valve. And this last case of coincident variation, is parallel to the case with which we are here concerned—the augmentation of individual expenditure and of reproductive energy, that may be caused by a superiority of some organ on which the utilizing or economizing of materials depends.

Manifestly, therefore, an increased expenditure for Genesis, or an increased expenditure for Individuation, may arise in one of two quite different ways—either by diminution of the antagonistic expenditure, or by addition to the store which supplies both expenditures; and confusion results from not distinguishing between these. Given the ratio 4 to 20, as expressive of the relative costs of Genesis and Individuation, and the expenditure for Genesis may be raised to 5 while the expenditure for Individuation is raised to 25, without any alteration of type; merely by favourable circumstances or superiority of constitution. On the other hand, circumstances remaining the same, the expenditure for Genesis may be raised from 4 to 5, by lowering the expenditure for Individuation from 20 to 19: which change of ratio may be either functional and temporary, or structural and permanent. And only when it is the last does it illustrate that inverse variation between degree of evolution and degree of procreative dissolution, which we have everywhere seen.

§ 370. There is no reason to suppose, then, that the laws of multiplication which hold of other beings, do not hold of the human being. On the contrary, there are special facts which unite with general implications, to show that these laws do hold of the human being. The absence of direct evidence in some cases where it might be looked for, we find fully explained when all the factors are taken into account.

And certain seemingly-adverse facts, prove, on examination, to be facts belonging to a different category from that in which they are placed, and harmonize with the rest when rightly interpreted.

The conformity of human fertility to the laws of multiplication in general, being granted, it remains to inquire what effects must be caused by permanent changes in men's natures and circumstances. Thus far we have observed how, by their extremely-high evolution and extremely-low fertility, mankind display the inverse variation between Individuation and Genesis, in one of its extremes. And we have also observed how mankind, like other kinds, are functionally changed in their rates of multiplication by changes of conditions. But we have not observed how alteration of structure in Man entails alteration of fertility. The influence of this factor is so entangled with the influences of other factors which are for the present more important, that we cannot recognize it. Here, if we proceed at all, we must proceed deductively.

# CHAPTER XIII.

## HUMAN POPULATION IN THE FUTURE.

§ 371. Any further evolution in the most-highly evolved of terrestrial beings, Man, must be of the same nature as evolution in general. Structurally considered, it may consist in greater integration, or greater differentiation, or both—augmented bulk, or increased heterogeneity and definiteness, or a combination of the two. Functionally considered, it may consist in a larger sum of actions, or more multiplied varieties of actions, or both—a larger amount of sensible and insensible motion generated, or motions more numerous in kind and more intricate and exact in co-ordination, or motions that are greater alike in quantity, complexity, and precision.

Expressing the change in terms of that more special evolution displayed by organisms; we may say that it must be one which further adapts the moving equilibrium of organic actions. As it was pointed out in *First Principles*, § 133, "the maintenance of such a moving equilibrium, requires the habitual genesis of internal forces corresponding in number, directions, and amounts to the external incident forces—as many inner functions, single or combined, as there are single or combined outer actions to be met." And it was also pointed out that, "the structural complexity accompanying functional equilibration, is definable as one in which there are as many specialized parts as are capable, separately and jointly, of counteracting the separate and joint forces amid which the organism exists." Clearly, then, since all incompletenesses in Man as now constituted, are failures to meet certain of the outer actions, mostly involved, remote, irregular, to which he is exposed; every advance implies additional co-ordinations of actions and accompanying complexities of organization.

Or once more, to specialize still further this conception of future progress, we may consider it as an advance towards completion of that continuous adjustment of internal to external relations, which constitutes Life. In Part I. of this work, where it was shown that the correspondence between inner and outer actions called Life, is a particular kind of what, in terms of Evolution, we called a moving equilibrium; it was shown that the degree of life varies as the degree of correspondence. Greater evolution or higher life, implies, then, such modifications of human nature as shall make more exact the existing correspondences, or shall establish additional correspondences, or both. Connexions of phenomena of a rare, distant, unobtrusive, or intricate kind, which we either suffer from or do not take advantage of, have to be responded to by new connexions of ideas, and acts properly combined and proportioned: there must be increase of knowledge, or skill, or power, or of all these. And to effect this more extensive, more varied, and more accurate, co-ordination of actions, there must be organization of still greater heterogeneity and definiteness.

§ 372. Let us before proceeding, consider in what particular ways this further evolution, this higher life, this greater co-ordination of actions, may be expected to show itself.

Will it be in strength? Probably not to any considerable degree. Mechanical appliances are fast supplanting brute force, and doubtless will continue doing this. Though at present civilized nations largely depend for self-preservation on vigour of limb, and are likely to do so while wars continue; yet that progressive adaptation to the social state which must at last bring wars to an end, will leave the amount of muscular power to adjust itself to the requirements of a peaceful regime. Though, taking all things into account, the muscular power then required may not be less than now, there seems no reason why more should be required.

Will it be in swiftness or agility? Probably not. In the savages these are important elements of the ability to maintain life; but in the civilized man they aid self-preservation in quite a minor degree, and there seems no circumstance likely to necessitate an increase of them. By games and gymnastic competitions, such attributes may indeed be artificially increased; but no artificial increase which does not bring a proportionate advantage can be permanent; since, other things equal, individuals and societies that devote the same amounts of energy in ways that subserve life more effectually, must by and by predominate.

Will it be in mechanical skill, that is, in the better-coordination of complex movements? Most likely in some degree. Awkwardness is continually entailing injuries and deaths. Moreover, the complicated tools which civilization brings into use, are constantly requiring greater delicacy of manipulation. All the arts, industrial and æsthetic, as they develop, imply a corresponding development of perceptive and executive faculties in men—the two necessarily act and react.

Will it be in intelligence? Largely, no doubt. There is ample room for advance in this direction, and ample demand for it. Our lives are universally shortened by our ignorance. In attaining complete knowledge of our own natures and of the natures of surrounding things—in ascertaining the conditions of existence to which we must conform, and in discovering means of conforming to them under all variations of seasons and circumstances—we have abundant scope for intellectual progress.

Will it be in morality, that is, in greater power of self-regulation? Largely also: perhaps most largely. Right conduct is usually come short of more from defect of will than defect of knowledge. To the due co-ordination of those complex actions which constitute human life in its civilized form, there goes not only the pre-requisite—recognition of the proper course; but the further pre-requisite—a due impulse to pursue that course. And on calling to mind our daily failures to fulfil often-repeated resolutions, we shall perceive that lack of the needful desire, rather than lack of the needful insight, is the chief cause of faulty action. A further endowment of those feelings which civilization is developing in us—sentiments responding to the requirements of the social state—emotive faculties that find their gratifications in the duties devolving on us—must be acquired before the crimes, excesses, diseases, improvidences, dishonesties, and cruelties, that now so greatly diminish the duration of life, can cease.

Thus, looking at the several possibilities, and asking what direction this further evolution, this more complete moving equilibrium, this better adjustment of inner to outer relations, this more perfect co-ordination of actions, is likely to take; we conclude that it must take mainly the direction of a higher intellectual and emotional development.

§ 373. This conclusion we shall find equally forced on us if we inquire for the causes which are to bring about such results. No more in the case of Man than in the case of any other being, can we presume that evolution either has taken place, or will hereafter take place, spontaneously. In the past, at present, and in the future, all modifications, functional and organic, have been, are, and must be immediately or remotely consequent on surrounding conditions. What, then, are those changes in the environment to which, by direct or indirect equilibration, the human organism has been adjusting itself, is adjusting itself now, and will continue to adjust itself? And how do they necessitate a higher evolution of the organism?

Civilization, everywhere having for its antecedent the increase of population, and everywhere having for one of its consequences a decrease of certain race-destroying forces, has for a further consequence an increase of certain other race-destroying forces. Danger of death from predatory animals lessens as men grow more numerous. Though, as they spread over the Earth and divide into tribes, men become wild beasts to one another, yet the danger of death from this cause also diminishes as tribes coalesce into nations. But the danger of death which does not diminish, is that produced by augmentation of numbers itself—the danger from deficiency of food. Supposing human nature to remain unchanged, the mortality hence resulting would, on the average, rise as human beings multiplied. If mortality, under such conditions, does not rise, it must be because the supply of food also augments; and this implies some change in human habits wrought by the stress of human needs. Here, then, is the permanent cause of modification to which civilized men are exposed. Though the intensity of its action is ever being mitigated in one direction, by greater production of food; it is, in the other direction, ever being added to by the greater production of individuals. Manifestly, the wants of their redundant numbers constitute the only stimulus mankind have to obtain more necessaries of life: were not the demand beyond the supply, there would be no motive to increase the supply. And manifestly, this excess of demand over supply is perennial: this pressure of population, of which it is the index, cannot be eluded. Though by the emigration that takes place when the pressure arrives at a certain intensity, temporary relief is from time to time obtained; yet as, by this process, all habitable countries must become peopled, it follows that in the end, the pressure, whatever it may then be, must be borne in full.

This constant increase of people beyond the means of subsistence, causes, then, a never-ceasing requirement for skill, intelligence, and self-control—involves, therefore, a constant exercise of these and gradual growth of them. Every industrial improvement is at once the product of a higher form of humanity, and demands that higher form of humanity to carry it into practice. The application of science to the arts, is the bringing to bear greater intelligence for satisfying our wants; and implies continued progress of that intelligence. To get more produce from the acre, the farmer must study chemistry, must adopt new mechanical appliances, and must, by the multiplication of processes, cultivate both his own powers and the powers of his labourers. To meet the requirements of the market, the manufacturer is perpetually improving his old machines, and inventing new ones; and by the premium of high wages incites artizans to acquire greater skill. The daily-widening ramifications of commerce entail on the merchant a need for more knowledge and more complex calculations; while the lessening profits of the ship-owner force him to build more scientifically, to get captains of higher intelligence, and better crews. In all cases, pressure of population is the original cause. Were it not for the competition this entails, more thought and energy would not daily be spent on the business of life; and growth of mental power would not take place. Difficulty in getting a living is alike the incentive to a higher education of children, and to a more intense and long-continued application in adults. In the mother it induces foresight, economy, and skilful house-keeping; in the father, laborious days and constant self-denial. Nothing but necessity could make men submit to this discipline; and nothing but this discipline could produce a continued progression.

In this case, as in many others, Nature secures each step in advance by a succession of trials; which are perpetually repeated, and cannot fail to be repeated, until success is achieved. All mankind in turn subject themselves more or less to the discipline described; they either may or may not advance under it; but, in the nature of things, only those who *do* advance under it eventually survive. For, necessarily, families and races whom this increasing difficulty of getting a living which excess of fertility entails, does not stimulate to improvements in production—that is, to greater mental activity—are on the high road to extinction; and must ultimately be supplanted by those whom the pressure does so stimulate. This truth we have recently seen exemplified in Ireland. And here, indeed, without further illustration, it will be seen that premature death, under all its forms and from all its causes, cannot fail to work in the same direction. For as those prematurely carried-off must, in the average of cases, be those in whom the power of self-preservation is the least, it unavoidably follows that those left behind to continue the race, must be those in whom the power of self-preservation is the greatest—must be the select of their generation. So that, whether the dangers to existence be of the kind produced by excess of fertility, or of any other kind, it is clear that by the ceaseless exercise of the faculties needed to contend with them, and by the death of all men who fail to contend with them successfully, there is ensured a constant progress towards a higher degree of skill, intelligence, and self-regulation—a better co-ordination of actions—a more complete life.*

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* A good deal of this chapter retains its original form; and the above paragraph is reprinted verbatim from the *Westminster Review* for April, 1852, in which the views developed in the foregoing hundred pages were first sketched out. This paragraph shows how near one may be to a great generalization without seeing it. Though the process of natural selection is recognized; and though to it is ascribed a share in the evolution of a higher type; yet the conception must not be confounded with that which Mr. Darwin has worked out with such wonderful skill, and supported by such vast stores of knowledge. In the first place, natural selection is here described only as furthering direct adaptation—only as aiding progress by the preservation of individuals in whom functionally-produced modifications have gone on most favourably. In the second place, there is no trace of the idea that natural selection may, by co-operation with the cause assigned, or with other causes, produce *divergences*

§ 374. The proposition at which we have thus arrived, is, then, that excess of fertility, through the changes it is ever working in Man's environment, is itself the cause of Man's further evolution; and the obvious corollary here to be drawn, is, that Man's further evolution so brought about, itself necessitates a decline in his fertility.

That future progress of civilization which the never-ceasing pressure of population must produce, will be accompanied by an enhanced cost of Individuation, both in structure and function; and more especially in nervous structure and function. The peaceful struggle for existence in societies ever growing more crowded and more complicated, must have for its concomitant an increase of the great nervous centres in mass, in complexity, in activity. The larger body of emotion needed as a fountain of energy for men who have to hold their places and rear their families under the intensifying competition of social life, is, other things equal, the correlative of larger brain. Those higher feelings presupposed by the better self-regulation which, in a better society, can alone enable the individual to leave a persistent posterity, are, other things equal, the correlatives of a more complex brain; as are also those more numerous, more varied, more general, and more abstract ideas, which must also become increasingly

of structure; and of course, in the absence of this idea, there is no implication, even, that natural selection has anything to do with the origin of species. And in the third place, the all-important factor of variation—"spontaneous," or incidental as we may otherwise call it—is wholly ignored. Though use and disuse are, I think, much more potent causes of organic modification than Mr. Darwin supposes—though, while pursuing the inquiry in detail, I have been led to believe that direct equilibration has played a more active part even than I had myself at one time thought; yet I hold Mr. Darwin to have shown beyond question, that a great part of the facts—perhaps the greater part—are explicable only as resulting from the survival of individuals which have deviated in some indirectly-caused way from the ancestral type. Thus, the above paragraph contains merely a passing recognition of the selective process; and indicates no suspicion of the enormous range of its effects, or of the conditions under which a large part of its effects are produced.

requisite for successful life as society advances. And the genesis of this larger quantity of feeling and thought, in a brain thus augmented in size and developed in structure, is, other things equal, the correlative of a greater wear of nervous tissue and greater consumption of materials to repair it. So that both in original cost of construction and in subsequent cost of working, the nervous system must become a heavier tax on the organism. Already the brain of the civilized man is larger by nearly thirty per cent. than the brain of the savage. Already, too, it presents an increased heterogeneity—especially in the distribution of its convolutions. And further changes like these which have taken place under the discipline of civilized life, we infer will continue to take place. But everywhere and always, evolution is antagonistic to procreative dissolution. Whether it be in greater growth of the organs which subserve self-maintenance, whether it be in their added complexity of structure, or whether it be in their higher activity, the abstraction of the required materials, implies a diminished reserve of materials for race-maintenance. And we have seen reason to believe that this antagonism between Individuation and Genesis, becomes unusually marked where the nervous system is concerned, because of the costliness of nervous structure and function. In § 346 was pointed out the apparent connexion between high cerebral development and prolonged delay of sexual maturity; and in § § 366, 367, the evidence went to show that where exceptional fertility exists there is sluggishness of mind, and that where there has been during education excessive expenditure in mental action, there frequently follows a complete or partial infertility. Hence the particular kind of further evolution which Man is hereafter to undergo, is one which, more than any other, may be expected to cause a decline in his power of reproduction.

The higher nervous development and greater expenditure in nervous action, here described as indirectly brought about by increase of numbers, and as thereafter becoming a check on the increase of numbers, must not be taken to imply an intenser strain—a mentally-laborious life. The greater emotional and intellectual power and activity above contemplated, must be understood as becoming, by small increments, organic, spontaneous and pleasurable. As, even when relieved from the pressure of necessity, large-brained Europeans voluntarily enter on enterprises and activities which the savage could not keep up even to satisfy urgent wants; so, their still larger-brained descendants will, in a still higher degree, find their gratifications in careers entailing still greater mental expenditures. This enhanced demand for materials to establish and carry on the psychical functions, will be a constitutional demand. We must conceive the type gradually so modified, that the more-developed nervous system irresistibly draws off, for its normal and unforced activities, a larger proportion of the common stock of nutriment; and while so increasing the intensity, completeness, and length of the individual life, necessarily diminishing the reserve applicable to the setting up of new lives—no longer required to be so numerous.

Though the working of this process will doubtless be interfered with and modified in the future, as it has been in the past, by the facilitation of living which civilization brings; yet nothing beyond temporary interruptions can so be caused. However much the industrial arts may be improved, there must be a limit to the improvement; while, with a rate of multiplication in excess of the rate of mortality, population must continually tread on the heels of production. So that though, during the earlier stages of civilization, an increased amount of food may accrue from a given amount of labour; there must come a time when this relation will be reversed, and when every additional increment of food will be obtained by a more than proportionate labour: the disproportion growing ever higher, and the diminution of the reproductive power becoming greater.

§ 375. There now remains but to inquire towards what limit this progress tends. So long as the fertility of the race is more than sufficient to balance the diminution by deaths, population must continue to increase. So long as population continues to increase, there must be pressure on the means of subsistence. And so long as there is pressure on the means of subsistence, further mental development must go on, and further diminution of fertility must result. Thus, the change can never cease until the rate of multiplication is just equal to the rate of mortality; that is, can never cease until, on the average, each pair has as many children as are requisite to produce another generation of child-bearing adults, equal in number to the last generation. At first sight, this would seem to imply that eventually each pair will rarely have more than two offspring; but a little consideration shows that this is a lower degree of fertility than is likely ever to be reached.

Supposing the Sun's light and heat, on which all terrestrial life depends, to continue abundant, for a period long enough to allow the entire evolution we are contemplating; there are still certain slow astronomic and geologic changes which must prevent such complete adjustment of human nature to surrounding conditions, as would permit the rate of multiplication to fall so low. As before pointed out (§ 148) during an epoch of 21,000 years, each hemisphere goes through a cycle of temperate seasons and seasons extreme in their heat and cold—variations that are themselves alternately exaggerated and mitigated in the course of far longer cycles; and we saw that these caused perpetual ebbings and flowings of species over different parts of the Earth's surface. Further, by slow but inevitable geologic changes, especially those of elevation and subsidence, the climate and physical characters of every habitat are modified; while old habitats are destroyed and new are formed. This, too, we noted as a constant cause of migrations and of consequent alterations of environment. Now though the human race differs from other races in having a power of artificially counteracting external changes, yet there are limits to this power; and, even were there no limits, the changes could not fail to work their effects indirectly, if not directly. If, as is thought probable, these astronomic cycles entail recurrent glacial periods in each hemisphere, then, parts of the Earth that are at one time thickly peopled, will at another time, be almost deserted, and *vice versâ*. The geologically-caused alterations of climate and surface, must produce further slow re-distributions of population; and other currents of people, to and from different regions, will be necessitated by the rise of successive centres of higher civilization. Consequently, mankind cannot but continue to undergo changes of environment, physical and moral, analogous to those which they have thus far been undergoing. Such changes may eventually become slower and less marked; but they can never cease. And if they can never cease, there can never arise a perfect adaptation of human nature to its conditions of existence. To establish that complete correspondence between inner and outer actions which constitutes the highest life and greatest power of self-preservation, there must be a prolonged converse between the organism and circumstances that remain the same. If the external relations are being altered while the internal relations are being adjusted to them, the adjustment can never become exact. And in the absence of exact adjustment, there cannot exist that theoretically-highest power of self-preservation with which there would co-exist the theoretically-lowest power of race-production.

Hence though the number of premature deaths may ultimately become very small, it can never become so small as to allow the average number of offspring from each pair to fall so low as two. Some average number between two and three may be inferred as the limit—a number, however, that is not likely to be quite constant, but may be expected at one time to increase somewhat and afterwards to decrease somewhat, according as variations in physical and social conditions lower or raise the cost of self-preservation.

Be this as it may, however, it is manifest that in the end, pressure of population and its accompanying evils will disappear; and will leave a state of things requiring from each individual no more than a normal and pleasurable activity. Cessation in the decrease of fertility implies cessation in the development of the nervous system; and this implies a nervous system that has become equal to all that is demanded of it—has not to do more than is natural to it. But that exercise of faculties which does not exceed what is natural, constitutes gratification. In the end, therefore, the obtainment of subsistence and discharge of all the parental and social duties, will require just that kind and that amount of action needful to health and happiness.

The necessary antagonism of Individuation and Genesis, not only, then, fulfils with precision the *à priori* law of maintenance of race, from the Monad up to Man, but ensures final attainment of the highest form of this maintenance—a form in which the amount of life shall be the greatest possible, and the births and deaths the fewest possible. This antagonism could not fail to work out the results we see it working out. The excess of fertility has itself rendered the process of civilization inevitable; and the process of civilization must inevitably diminish fertility, and at last destroy its excess. From the beginning, pressure of population has been the proximate cause of progress. It produced the original diffusion of the race. It compelled men to abandon predatory habits and take to agriculture. It led to the clearing of the Earth's surface. It forced men into the social state; made social organization inevitable; and has developed the social sentiments. It has stimulated to progressive improvements in production, and to increased skill and intelligence. It is daily thrusting us into closer contact and more mutually-dependent relationships. And after having caused, as it ultimately must, the due peopling of the globe, and the raising of all its habitable parts into the highest state of culture—after having brought all processes for the satisfaction of human wants to perfection—after having, at the same time, developed the intellect into complete competency for its work, and the feelings into complete fitness for social life—after having done all this, the pressure of population, as it gradually finishes its work, must gradually bring itself to an end.

§ 377. In closing the argument let us not overlook the self-sufficingness of those universal processes by which the results reached thus far have been wrought out, and which may be expected to work out these future results.

Evolution under all its aspects, general and special, is an advance towards equilibrium. We have seen that the theoretical limit towards which the integration and differentiation of every aggregate advances, is a state of balance between all the forces to which its parts are subject, and the forces which its parts oppose to them (*First Prin.* § 130). And we have seen that organic evolution is a progress towards a moving equilibrium completely adjusted to environing actions.

It has been also pointed out that, in civilized Man, there is going on a new class of equilibrations—those between his actions and the actions of the societies he forms (*First Prin.* § 135). Social restraints and requirements are ever altering his activities and by consequence his nature; and as fast as his nature is altered, social restraints and requirements undergo more or less re-adjustment. Here the organism and the conditions are both modifiable; and by successive conciliations of the two, there is effected a progress towards equilibrium.

More recently we have seen that in every species, there establishes itself an equilibrium of an involved kind between the total race-destroying forces and the total race-preserving forces—an equilibrium which implies that where the ability to maintain individual life is small, the ability to propagate must be great, and *vice versâ*. Whence it follows that the evolution of a race more in equilibrium with the environment, is also the evolution of a race in which there is a correlative approach towards equilibrium between the number of new individuals produced and the number which survive and propagate.

The final result to be observed, is, that in Man, all these equilibrations between constitution and conditions, between the structure of society and the nature of its members, between fertility and mortality, advance simultaneously towards a common climax. In approaching an equilibrium between his nature and the ever-varying circumstances of his inorganic environment, and in approaching an equilibrium between his nature and all the requirements of the social state, Man is at the same time approaching that lowest limit of fertility at which the equilibrium of population is maintained by the addition of as many infants as there are subtractions by death in old age. Changes numerical, social, organic, must, by their mutual influences, work unceasingly towards a state of harmony—a state in which each of the factors is just equal to its work. And this highest conceivable result must be wrought out by that same universal process which the simplest inorganic action illustrates.

THE END.

# APPENDIX.

# APPENDIX A.

## SUBSTITUTION OF AXIAL FOR FOLIAR ORGANS IN PLANTS.

I APPEND here the evidences referred to in § 190. The most numerous and striking I have met with among the *Umbelliferæ*. Monstrosities having the alleged implication, are frequent in the common Cow-Parsnep—so frequent that they must be familiar to botanists; and wild Angelica supplies many over-developments of like meaning. Omitting numerous cases of more or less significance, I will limit myself to two.

One of them is that of a terminal umbel, in which nine of the outer umbellules are variously transformed—here a single flower being made monstrous by the development of some of its members into buds; there several such malformed flowers being associated with rays that bear imperfect umbellules; and elsewhere, flowers being replaced by umbellules: some of which are perfect, and others imperfect only in the shortness of the flower-stalks. The annexed Fig. 69, representing in a somewhat conventionalized way, a part of the dried speci-

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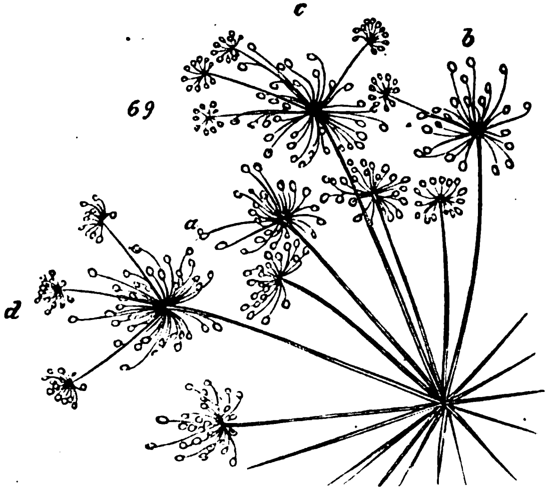

men, will give an idea of this Angelica. At *a* is shown a single flower partially changed; in the umbellule marked *b*, one of the rays bears a secondary umbellule; and there may be seen at *c* and *d*, several such over-developments.

But the most conclusive instance is that of a Cow-Parsnep, in which a single terminal umbel, besides the transformations already mentioned, exhibits higher degrees of such transformations.* The components of this complex growth are;—three central umbellules, abnormal only in minor points; one umbellule, external to these, which is partially changed into an umbel; one rather more out of the centre, which is so far metamorphosed as to be more an umbel than an umbellule: nine peripheral clusters formed by the development of umbellules into umbels, some of which are partially compounded still further. Examined in detail, these structures present the following facts:—1. The innermost umbellule is normal, save in having a peripheral flower of which one member (apparently a petal) is transformed into a flower-bud. 2. The next umbellule, not quite so central, has one of its peripheral flowers made monstrous by the growth of a bud from the base of the calyx. 3. The third of the central umbellules has two abnormal outer flowers. One of them carries a flower-bud on its edge, in place of a foliar member. The other is half flower and half umbellule: being composed of three petals, three stamens, and five flower-buds growing where the other petals and stamens should grow. 4. Outside of these umbellules comes one of the mixed clusters. Its five central flowers are normal. Surrounding these are several flowers transformed in different degrees: one having a stamen partially changed into a flower bud. And then, at the periphery of this mixed cluster, come three complete umbellules and an incomplete one in which some petals and stamens of the original flower remain. 5. A mixed cluster, in which the umbel-structure predominates, stands next. Its three central flowers are normal. Surrounding them are five flowers over-developed in various ways, like those already described. And on its periphery are seven complete umbellules in place of flowers; besides an incomplete umbellule that contains traces of the original flower, one of them being a petal imperfectly twisted up into a bud. 6. Of the nine external clusters, in which the development of simple into compound umbels is most decided, nearly all present anomalies. Three of them have each a central flower untransformed; and in others, the central

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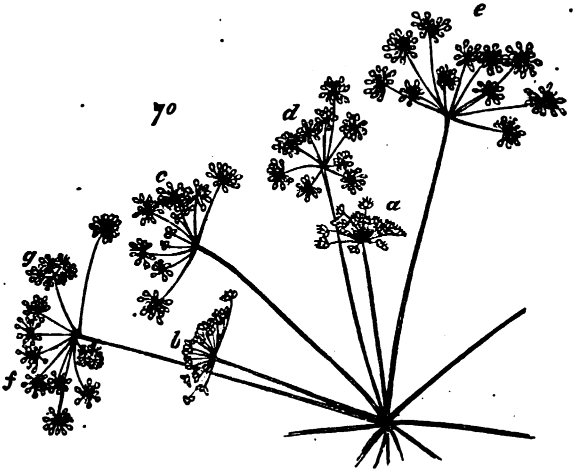
* For the information of those who may wish to examine metamorphoses of these kinds, I may here state that I have found nearly all the examples described, in the neighbourhood of the sea—the last-named, on the shore of Locheil, near Fort William. Whether it is that I have sought more diligently for cases when in such localities, or whether it is that the sea-air favours that excessive nutrition whence these transformations result, I am unable to say.

umbellule is composed of two, three, or four flowers. 7. But the most remarkable fact is, that in sundry of these peripheral clusters, resulting from the metamorphosis of simple umbels into compound umbels, the like metamorphosis is carried a stage higher. Some of the component rays, are themselves the bearers of compound umbels



instead of simple umbels. In Fig. 70, a portion of the dried specimen is represented. Two of the central umbellules are marked *a* and *b*; those marked *c* and *d* are mixed clusters; at *e* and *f* are compound umbels replacing simple ones; and *g* shows one of the rays on which the over-development goes still further.

Does not this evidence, enforced as it is by much more of like kind, go far to prove that foliar organs may be developed into axial organs? Even were not the transitional forms traceable, there would still, I think, be no other legitimate interpretation of the facts last detailed. The only way of eluding the conclusion here drawn, is by assuming that where a cluster of flowers replaces a single flower, it is because the axillary buds which hypothetically belong to the several foliar organs of the flower, become developed into axes; and assuming this, is basing an hypothesis on another hypothesis that is directly at variance with facts. The foliar organs of flowers do *not* bear buds in their axils; and it would never have been supposed that such buds are typically present, had it not been for that mistaken conception of "type" which has led to many other errors in Biology. Goethe writes: "Now as we cannot realize the idea of a leaf apart from the node out of which it springs, or of a node without a bud, we may venture to infer," &c. See here an example of a method of philosophizing not uncommon among the Germans.

The method is this—Survey a portion of the facts, and draw from them a general conception; project this general conception back into the objective world, as a mould in which Nature casts her products; expect to find it everywhere fulfilled; and allege potential fulfilment where no actual fulfilment is visible.

If instead of imposing our ideal forms on Nature, we are content to generalize the facts as Nature presents them, we shall find no warrant for the morphological doctrine above enunciated. The only conception of type justified by the logic of science, is—that correlation of parts which remains constant under all modifications of the structure to be defined. To ascertain this, we must compare all these modifications, and note what traits are common to them. On doing so with the successive segments of a phænogamic axis, we are brought to a conclusion widely different from that of Goethe. Axillary buds are almost universally absent from the cotyledons; they are habitually present in the axils of fully-developed leaves higher up the axis; they are often absent from leaves that are close to the flower; they are nearly always absent from the bracts; absent from the sepals; absent from the petals; absent from the stamens; absent from the carpels. Thus, out of eight leading forms which folia assume, one has the axillary bud and seven are without it. With these facts before us, it seems to me not difficult to "realize the idea" "of a node without a bud." If we are not possessed by a foregone conclusion, the evidence will lead us to infer, that each node bears a foliar appendage and *may* bear an axillary bud.

Even, however, were it granted that the typical segment of a Phænogam includes an axillary bud, which must be regarded as always potentially present, no legitimate counter-interpretation of the monstrosities above described could thence be drawn. If when an umbellule is developed in place of a flower, the explanation is, that its component rays are axillary to the foliar organs of the flower superseded; we may fairly require that these foliar organs to which they are axillary, shall be shown. But there are none. In the last specimen figured, the inner rays of each such umbellule are without them; most of the outer rays are also without them; and in one cluster, only a single ray has a bract at its point of origin. There is a rejoinder ready, however: the foliar organs are said to be suppressed. Though Goethe could not "realize the idea" "of a node without a bud," those who accept his typical form appear to find no difficulty in realizing the idea of an axillary bud without anything to which it is axillary. But letting this pass, suppose we ask what is the warrant for this assumed suppression. Axillary buds normally occur where the nutrition is high enough to produce fully-developed leaves; and when axillary buds are demonstrably present in flowers, they accompany foliar organs that are more leaf-like than usual—always greener if not always larger. That is to say, the normal and the abnormal axillary buds, are alike the concomitants of foliar organs coloured by that chlorophyll which habitually favours foliar development. How, then, can it be supposed that when, out of a flower there is developed a cluster of flower-bearing rays, the implied excess of nutrition causes the foliar organs to abort? It is true that very generally in a branched inflorescence, the bracts of the several flower-branches are very small (their smallness being probably due to that defective supply of certain chlorophyll-forming matters, which is the proximate cause of flowering); and it is true that, under these conditions, a flowering axis of considerable size, for the development of which chlorophyll is less needful, grows from the axil of a dwarfed leaf. But the inference that the foliar organ may therefore be entirely suppressed, seems to me irreconcilable with the fact, that the foliar organ is always developed to some extent *before* the axillary bud appears. Until it has been shown that in some cases a lateral bud first appears, and a foliar organ *afterwards* grows out beneath it, to form its axil, the conception of an axillary bud of which the foliar organ is suppressed, will remain at variance with the established truths of development.

The above originally formed a portion of § 190. I have transferred it to the Appendix, partly because it contains too much detail to render it fit for the general argument, and partly because the interpretations being open to some question, it seemed undesirable to risk compromising that argument by including them. The criticisms passed upon these interpretations have not, however, sufficed to convince me of their incorrectness. Unfortunately, I have since had no opportunity of verifying the above statements by microscopic examinations, as I had intended.

Though unable to enforce the inference drawn by further facts more minutely looked into, I may add some arguments based on facts that are well known. One of these is the fact that the so-called axillary bud is not universally axillary—is not universally seated in the angle made by the axis and an appended foliar organ. In certain plants the axillary bud is placed far above the node, half-way between it and the succeeding node. So that not only may a segment of a phænogamic axis be without the axillary bud, but the axillary bud, when present, may be removed from that place in which, according to Goethe, it necessarily exists. Another fact not congruous with the current doctrine, is the common occurrence of "adventitious" buds—the buds that are put out from roots and from old stems or branches bare of leaves. The name under which they are thus classed, is meant to imply that they may be left out of consideration. Those, however, who have not got a theory to save by putting anomalies out of sight, may be inclined to think that the occurrence of buds where they are avowedly unconnected with nodes, and are axillary to nothing, tells very much against the assumption that every bud implies a node and a corresponding foliar organ. And they may also see that the development of these adventitious buds at places where there is excess of nutritive materials, favours the view above set forth. For if a bud thus arises at a place where it is not morphologically accounted for, simply because there happens to be at that place an abundance of unorganized protoplasm; then, clearly, it is likely that if the mass of protaplasm from which a leaf would usually arise, is greatly increased in mass by excess of nutrition, it may develop into an axis instead of a leaf.

# APPENDIX B.

## A CRITICISM ON PROF. OWEN'S THEORY OF THE VERTEBRATE SKELETON.

[*From the* BRITISH & FOREIGN MEDICO-CHIRURGICAL REVIEW FOR OCT., 1858.]

I. *On the Archetype and Homologies of the Vertebrate Skeleton. By* RICHARD OWEN, *F.R.S.—London*, 1848. *pp.* 172.

II. *Principes d'Ostéologie Comparée, ou Recherches sur l'Archétype et les Homologies du Squelette Vertébré. Par* RICHARD OWEN.—*Paris.*

*Principles of Comparative Osteology; or, Researches on the Arcnetype and the Homologies of the Vertebrate Skeleton. By* RICHARD OWEN.

III. *On the Nature of Limbs. A Discourse delivered on Friday, February* 9, *at an Evening Meeting of the Royal Institution of Great Britain. By* RICHARD OWEN, *F.R.S.—London*, 1849. *pp.* 119.

JUDGING whether another proves his position is a widely different thing from proving your own. To establish a general law requires an extensive knowledge of the phenomena to be generalized; but to decide whether an alleged general law is established by the evidence assigned, requires merely an adequate reasoning faculty. Especially is such a decision easy where the premises do *not* warrant the conclusion. It may be dangerous for one who has but little previous acquaintance with the facts, to say that a generalization is demonstrated; seeing that the argument may be one-sided: there may be many facts unknown to him which disprove it. But it is not dangerous to give a negative verdict when the alleged demonstration is manifestly insufficient. If the data put before him do not bear out the inference, it is competent for every logical reader to say so.

From this stand-point, then, we venture to criticize some of Professor Owen's osteological theories. For his knowledge of comparative osteology we have the highest respect. We believe that no living man has so wide and detailed an acquaintance with the bony structure of the *Vertebrata*. Indeed, there probably has never been any one whose information on the subject was so nearly exhaustive. Moreover, we confess that nearly all we know of this department of biology has been learnt from his lectures and writings. We pretend to no independent investigations, but merely to such knowledge of the phenomena as he has furnished us with. Our position, then, is such that, had Professor Owen simply enunciated his generalizations, we should have accepted them on his authority. But he has brought forward evidence to prove them. By so doing he has tacitly appealed to the judgments of his readers and hearers—has practically said, "Here are the facts; do they not warrant these conclusions?" And all we propose to do, is to consider whether the conclusions *are* warranted by the facts brought forward.

Let us first limit the scope of our criticisms. On that division of comparative osteology which deals with what Professor Owen distinguishes as "special homologies," we do not propose to enter. That the wing of a bird is framed upon bones essentially parallel to those of a mammal's fore-limb; that the cannon-bone of a horse's leg answers to the middle metacarpal of the human hand; that various bones in the skull of a fish are homologous with bones in the skull of a man—these and countless similar facts, we take to be well established. It may be, indeed, that the doctrine of special homologies is at present carried too far. It may be that, just as the sweeping generalization at one time favoured, that the embryonic phases of the higher animals represent the adult forms of lower ones, has been found untrue in a literal sense, and is acceptable only in a qualified sense; so the sweeping generalization that the skeletons of all vertebrate animals consist of homologous parts, will have to undergo some modification. But that this generalization is substantially true, all comparative anatomists agree.

The doctrine which we are here to consider, is quite a separate one—that of "general homologies." The truth or falsity of this may be decided on quite apart from that of the other. Whether certain bones in one vertebrate animal's skeleton correspond with certain bones in another's, or in every other's, is one question; and whether the skeleton of every vertebrate animal is divisible into a series of segments, each of which is modelled after the same type, is another question. While the first is answered in the affirmative, the last may be answered in the negative; and we propose to give reasons why it should be answered in the negative.

In so far as his theory of the skeleton is concerned, Professor Owen is an avowed disciple of Plato. At the conclusion of his *Archetype and Homologies of the Vertebrate Skeleton*, he quotes approvingly the Platonic hypothesis of ἰδέαι, "a sort of models, or moulds in which matter is cast, and which regularly produce the same number and diversity of species." The vertebrate form in general (see diagram of the *Archetypus*), or else the form of each kind of vertebrate animal (see p. 172, where this seems implied), Professor Owen conceives to exist as an "idea"—an "archetypal exemplar on which it has pleased the Creator to frame certain of his living creatures." Whether Professor Owen holds that the typical vertebra also exists as an "idea," is not so certain. From the title given to his figure of the "ideal typical vertebra," it would seem that he does; and at p. 40 of his *Nature of Limbs*, and indeed throughout his general argument, this supposition is implied. But on the last two pages of the *Archetype and Homologies*, it is distinctly alleged that "the repetition of similar segments in a vertebral column, and of similar elements in a vertebral segment, is analogous to the repetition of similar crystals as the result of polarizing force in the growth of an inorganic body;" it is pointed out that, "as we descend the scale of animal life, the forms of the repeated parts of the skeleton approach more and more to geometrical figures;" and it is inferred that "the Platonic ἰδέα or specific organizing principle or force, would seem to be in antagonism with the general polarizing force, and to subdue and mould it in subserviency to the exigencies of the resulting specific form." If Professor Owen's doctrine is to be understood as expressed in these closing paragraphs of his *Archetype and Homologies*—if he considers that "the ἰδέα" "which produces the diversity of form belonging to living bodies of the same materials," is met by the "counter-operation" of "the polarizing force pervading all space," which produces "the similarity of forms, the repetition of parts, the signs of unity of organization," and which is "*subdued*" as we ascend "in the scale of being;" then we may pass on with the remark that the hypothesis is too cumbrous and involved to have much *vraisemblance*. If, on the other hand, Professor Owen holds, as every reader would suppose from the general tenor of his reasonings, that not only does there exist an archetypal or ideal vertebrate skeleton, but that there also exists an archetypal or ideal vertebra; then he carries the Platonic hypothesis much further than Plato does. Plato's argument, that before any species of object was created it must have existed as an idea of the Creative Intelligence; and that hence all objects of such species must be copies of this original idea, is tenable enough from the anthropomorphic point of view. But while those who, with Plato, think fit to base their theory of creation upon the analogy of a carpenter designing and making a table, must yield assent to Plato's inference, they are by no means committed to Professor Owen's expansion of it. To say that before creating a vertebrate animal, God must have had the conception of one, does not involve saying that God gratuitously bound himself to make a vertebrate animal out of segments all moulded after one pattern. As there is no conceivable advantage in this alleged adhesion to a fundamental pattern—as, for the fulfilment of the intended ends, it is not only needless, but often, as Professor Owen argues, less appropriate than some other construction would be (see *Nature of Limbs*, pp. 39, 40), to suppose the creative processes thus regulated, is not a little startling. Even those whose conceptions are so anthropomorphic as to think they honour the Creator by calling him "the Great Artificer," will scarcely ascribe to him a proceeding which, in a human artificer, they would consider a not very worthy exercise of ingenuity.

But whichever of these alternatives Professor Owen contends for —whether the typical vertebra is that more or less crystalline figure which osseous matter ever tends to assume in spite of "the ἰδέα or organizing principle," or whether the typical vertebra is itself an "ἰδέα or organizing principle"—there is alike implied the belief that the typical vertebra has an abstract existence apart from actual vertebræ. It is a form which, in every endoskeleton, strives to embody itself in matter—a form which is potentially present in each vertebra; which is manifested in each vertebra with more or less clearness; but which, in consequence of antagonizing forces, is nowhere completely realized. Apart from the philosophy of this hypothesis, let us here examine the evidence which is thought to justify it.

And first as to the essential constituents of the "ideal typical vertebra." Exclusive of "*diverging appendages*" which it "may also support," "it consists in its typical completeness of the following elements and parts":—A *centrum* round which the rest are arranged in a somewhat radiate manner; above it two *neurapophyses* —converging as they ascend, and forming with the centrum a trianguloid space containing the neural axis; a *neural spine* surmounting the two neurapophyses, and with them completing the neural arch; below the centrum two *hæmapophyses* and a *hæmal spine*, forming a hæmal arch similar to the neural arch above, and enclosing the hæmal axis; two *pleurapophyses* radiating horizontally from the sides of the centrum; and two *parapophyses* diverging from the centrum below the pleurapophyses. "These," says Professor Owen, "being usually developed from distinct and independent centres, I have termed 'autogenous elements.'" The remaining elements, which he classes as "exogenous," because they "shoot out as continuations from some of the preceding elements," are the *diapophyses* diverging from the upper part of the centrum as the parapophyses do below, and the *zygapophyses* which grow out of the distal ends of the neurapophyses and hæmapophyses.

If, now, these are the constituents of the vertebrate segment "in its typical completeness;" and if the vertebrate skeleton consists of a succession of such segments; we ought to have in these constituents, representatives of all the elements of the vertebrate skeleton—at any rate, all its essential elements. Are we then to conclude that the "diverging appendages," which Professor Owen regards as rudimental limbs, and from certain of which he considers actual limbs to be developed, are typically less important than some of the above-specified exogenous parts—say the zygapophyses?

That the meaning of this question may be understood, it will be needful briefly to state Professor Owen's theory of *The Nature of Limbs;* and such criticisms as we have to make on it must be included in the parenthesis. In the first place, he aims to show that the scapular and pelvic arches, giving insertion to the fore and hind limbs respectively, are displaced and modified hæmal arches, originally belonging in the one case to the occipital vertebra, and in the other case to some trunk-vertebra not specified. In support of this assumption of displacement, carried in some cases to the extent of *twenty-seven* vertebræ, Professor Owen cites certain acknowledged displacements which occur in the human skeleton to the extent of half a vertebra—a somewhat slender justification. But for proof that such a displacement *has* taken place in the scapular arch, he chiefly relies on the fact that in fishes, the pectoral fins, which are the homologues of the fore-limbs, are directly articulated to certain bones at the back of the head, which he alleges are parts of the occipital vertebra. This appeal to the class of fishes is avowedly made on the principle that these lowest of the *Vertebrata* approach closest to archetypal regularity, and may therefore be expected to show the original relations of the bones more nearly. Simply noting the facts that Professor Owen does not give us any transitional forms between the alleged normal position of the scapular arch in fishes, and its extraordinary displacement in the higher *Vertebrata;* and that he makes no reference to the embryonic phases of the higher *Vertebrata*, which might be expected to exhibit the progressive displacement; we go on to remark that, in the case of the pelvic arch, he abandons his principle of appealing to the lowest vertebrate forms for proof of the typical structure. In fishes, the rudimentary pelvis, widely removed from the spinal column, shows no signs of having belonged to any vertebra; and here Professor Owen instances the perennibranchiate *Batrachia* as exhibiting the typical structure: remarking that "mammals, birds, and reptiles show the rule of connexion, and fishes the exception." Thus in the case of the scapular arch, the evidence afforded by fishes is held of great weight, *because* of their archetypal regularity; while in the case of the pelvic arch, their evidence is rejected as exceptional. But now, having, as he considers, shown that these bony frames to which the limbs are articulated are modified hæmal arches, Professor Owen points out that the hæmal arches habitually bear certain "diverging appendages;" and he aims to show that the "diverging appendages" of the scapular and pelvic arches respectively, are developed into the fore and hind limbs. There are several indirect ways in which we may test the probability of this conclusion. If these diverging appendages are "rudimental limbs"—"future possible or potential arms, legs, wings, or feet," we may fairly expect them always to bear to the hæmal arches a relation such as the limbs do. But they by no means do this. "As the vertebræ approach the tail, these appendages are often transferred gradually from the pleurapophysis to the parapophysis, or even to the centrum and neural arch." (*Arch. and Hom.*, p. 93.) Again, it might naturally be assumed that in the lowest vertebrate forms, where the limbs are but little developed, they would most clearly display their alliance with the appendages, or "rudimental limbs," by the similarity of their attachments. Instead of this, however, Professor Owen's drawings show that whereas the appendages are habitually attached to the pleurapophyses, the limbs, in their earliest and lowest phase, alike in fishes and in the *Lepidosiren*, are articulated to the hæmapophyses. Most anomalous of all, however, is the process of development. When we speak of one thing as being developed out of another, we imply that the parts next to the germ are the first to appear, and the most constant. In the evolution of a tree out of a seed, there come at the outset the stem and the radicle; afterwards the branches and divergent roots; and still later the branchlets and rootlets; the remotest parts being the latest and most inconstant. If, then, a limb is developed out of a "diverging appendage" of the hæmal arch, the earliest and most constant bones should be the humerus and femur; next in order of time and constancy should come the coupled bones based on these; while the terminal groups of bones should be the last to make their appearance, and the most liable to be absent. Yet, as Professor Owen himself shows, the actual mode of development is the very reverse of this. At p. 16 of the *Archetype and Homologies*, he says:—

> "The earlier stages in the development of all locomotive extremities are permanently retained or represented in the paired fins of fishes. First the essential part of the member, the hand or foot, appears: then the fore-arm or leg, both much shortened, flattened, and expanded, as in all fins and all embryonic rudiments of limbs: finally come the humeral and femoral segments; but this stage I have not found attained in any fish."

That is to say, alike in ascending through the *Vertebrata* generally, and in tracing up the successive phases of a mammalian embryo, the last-developed and least constant division of the limb, is that basic one by which it articulates with the hæmal arch. It seems to us that, so far from proving his hypothesis, Professor Owen's own facts tend to show that limbs do not belong to the vertebræ at all; that they make their first appearance peripherally; that their development is centripetal; and that they become fixed to such parts of the vertebrate axis as the requirements of the case determine.

But now, ending here this digressive exposition and criticism, and granting the position that limbs "are developments of costal appendages," let us return to the question above put—Why are not these appendages included as elements of the "ideal typical vertebra?" It cannot be because of their comparative inconstancy; for judging from the illustrative figures, they seem to be as constant as the hæmal spine, which is one of the so-called autogenous elements: in the diagram of the *Archetypus*, the appendage is represented as attached to every vertebrate segment of the head and trunk, which the hæmal spine is not. It cannot be from their comparative unimportance; seeing that as potential limbs they are essential parts of nearly all the *Vertebrata*—much more obviously so than the diapophyses are. If, as Professor Owen argues, "the divine mind which planned the archetype also foreknew all its modifications;" and if, among these modifications, the development of limbs out of diverging appendages was one intended to characterize all the higher *Vertebrata;* then, surely, these diverging appendages must have been parts of the "ideal typical vertebra." Or, if the "ideal typical vertebra" is to be understood as a crystalline form in antagonism with the organizing principle; then why should not the appendages be included among its various offshoots? We do not ask this question because of its intrinsic importance. We ask it for the purpose of ascertaining Professor Owen's method of determining what are true vertebral constituents. He presents us with a diagram of the typical vertebra, in which are included certain bones, and from which are excluded certain others. If relative constancy is the criterion, then there arises the question—What degree of constancy entitles a bone to be included? If relative importance is the criterion, there comes not only the question —What degree of importance suffices? but the further question —How is importance to be measured? If neither of these is the criterion, then what is it? And if there is no criterion, does it not follow that the selection is arbitrary?

This question serves to introduce a much wider one:—Has the "ideal typical vertebra" any essential constituents at all? It might naturally be supposed that though some bones are so rarely developed as not to seem worth including, and though some that are included are very apt to be absent; yet that certain others are invariable: forming, as it were, the basis of the ideal type. Let us see whether the facts bear out this supposition. In his "summary of modifications of corporal vertebræ" (p. 96), Professor Owen says—"The *hæmal spine* is much less constant as to its existence, and is subject to a much greater range of variety, when present, than its vertical homotype above, which completes the neural arch." Again he says—"The *hæmapophyses*, as osseous elements of a vertebra, are less constant than the pleurapophyses." And again—"The *pleurapophyses* are less constant elements than the neurapophyses." And again—"Amongst air-breathing vertebrates the *pleurapophyses* of the trunk segments are present only in those species in which the septum of the heart's ventricle is complete and imperforate, and here they are exogenous and confined to the cervical and anterior thoracic vertebræ." And once more, both the *neurapophyses* and the *neural spine* "are absent under both histological conditions, at the end of the tail in most air-breathing vertebrates, where the segments are reduced to their central elements." That is to say, of all the peripheral elements of the "ideal typical vertebra," there is not one which is always present. It will be expected, however, that at any rate the *centrum* is constant: the bone which "forms the axis of the vertebral column, and commonly the central bond of union of the peripheral elements of the vertebra (p. 97), is of course an invariable element. No: not even this is essential.

> "The centrums do not pass beyond the primitive stage of the notochord (undivided column) in the existing lepidosiren, and they retained the like rudimental state in every fish whose remains have been found in strata earlier than the permian æra in Geology, though the number of vertebræ is frequently indicated in Devonian and Silurian ichthyolites by the fossilized neur- and hæmapophyses and their spines" (p. 96).

Indeed, Professor Owen himself remarks that "the neurapophyses are more constant as osseous or cartilaginous elements of the vertebræ than the centrums" (p. 97). Thus, then, it appears that the several elements included in the "ideal typical vertebra" have various degrees of constancy, and that no one of them is essential. There is no one part of a vertebra which invariably answers to its exemplar in the pattern-group. How does this fact consist with the hypothesis? If the Creator saw fit to make the vertebrate skeleton out of a series of segments, all formed on essentially the same model—if, for the maintenance of the type, one of these bony segments is in many cases formed out of a coalesced group of pieces, where, as Professor Owen argues, a single piece would have served as well or better; then we ought to find this typical repetition of parts uniformly manifested. Without any change of shape, it would obviously have been quite possible for every actual vertebra to have contained all the parts of the ideal one—rudimentally where they were not wanted. Even one of the terminal bones of a mammal's tail might have been formed out of the nine autogenous pieces, united by suture but admitting of identification. As, however, there is no such uniform typical repetition of parts, it seems to us that to account for the typical repetition which *does* occur, by supposing the Creator to have fixed on a pattern-vertebra, is to ascribe to him the inconsistency of forming a plan and then abandoning it.

If, on the other hand, Professor Owen means that the "ideal typical vertebra" is a crystalline form in antagonism with "the idea or organizing principle;" then we might fairly expect to find it most clearly displaying its crystalline character, and its full complement of parts, in those places where the organizing principle may be presumed to have "subdued" it to the smallest extent. Yet in the *Vertebrata* generally, and even in Professor Owen's *Archetypus*, the vertebræ of the tail, which must be considered as, if anything, less under the influence of the organizing principle than those of the trunk, do not manifest the ideal form more completely. On the contrary, as we approach the end of the tail, the successive segments not only lose their remaining typical elements, but become as uncrystalline-looking as can be conceived.

Supposing, however, that the assumption of suppressed or undeveloped elements be granted—supposing it to be consistent with the hypothesis of an "ideal typical vertebra," that the constituent parts may severally be absent in greater or less number, sometimes leaving only a single bone to represent them all; may it not be that such parts as *are* present, show their respective typical natures by some constant character: say their mode of ossification?

To this question some parts of the *Archetype and Homologies* seem to reply, "Yes;" while others clearly answer, "No." Criticising the opinions of Geoffroy St. Hilaire and Cuvier, who agreed in thinking that ossification from a separate centre was the test of a separate bone, and that thus there were as many elementary bones in the skeleton as there were centres of ossification, Professor Owen points out that, according to this test, the human femur, which is ossified from four centres, must be regarded as four bones; while the femur in birds and reptiles, which is ossified from a single centre, must be regarded as a single bone. Yet, on the other hand, he attaches weight to the fact that the skull of the human fœtus presents "the same ossific centres" as do those of the embryo kangaroo and the young bird. (*Nature of Limbs*, p. 40.) And at p. 104 of the *Homologies*, after giving a number of instances, he says—

'These and the like correspondences between the points of ossification of the human fœtal skeleton, and the separate bones of the adult skeletons of inferior animals, are pregnant with interest, and rank among the most striking illustrations of unity of plan in the vertebrate organization."

It is true that on the following page he seeks to explain this seeming contradiction by distinguishing

> "between those centres of ossification that have homological relations, and those that have teleological ones—*i.e.*, between the separate points of ossification of a human bone which typify vertebral elements, often permanently distinct bones in the lower animals; and the separate points which, without such signification, facilitate the progress of osteogeny, and have for their obvious final cause the well-being of the growing animal."

But if there are thus centres of ossification which have homological meanings, and others which have not, there arises the question—How are they always to be distinguished? Evidently independent ossification ceases to be a homological test, if there are independent ossifications that have nothing to do with the homologies. And this becomes the more evident when we learn that there are cases where neither a homological nor a teleological meaning can be given. Among various modes of ossification of the centrum, Professor Owen points out that "the body of the human atlas is sometimes ossified from two, rarely from three, distinct centres placed side by side" (p. 89); while at p. 87 he says:—"In osseous fishes I find that the centrum is usually ossified from six points." It is clear that this mode of ossification has here no homological signification; and it would be difficult to give any teleological reason why the small centrum of a fish should have more centres of ossification than the large centrum of a mammal. The truth is, that as a criterion of the identity or individuality of a bone, mode of ossification is quite untrustworthy. Though, in his "ideal typical vertebra," Professor Owen delineates and classifies as separate "autogenous" elements, those parts which are "usually developed from distinct and independent centres;" and though by doing so he erects this characteristic into some sort of criterion; yet his own facts show it to be no criterion. The parapophyses are classed among the autogenous elements; yet they are autogenous in fishes alone, and in these only in the trunk vertebræ, while in all air-breathing vertebrates they are, when present at all, exogenous. The neurapophyses, again, "lose their primitive individuality by various kinds and degrees of confluence:" in the tails of the higher *Vertebrata* they, in common with the neural spine, become exogenous. Nay, even the centrum may lose its autogenous character. Describing how, in some batrachians, "the ossification of the centrum is completed by an extension of bone from the bases of the neurapophyses, which effects also the coalescence of these with the centrum," Professor Owen adds:— "In *Pelobates fuscus* and *Pelobates cultripes*, Müller found the centire centrum ossified from this source, without any independent points of ossification" (p. 88). That is to say, the centrum is in these cases an exogenous process of the neurapophyses. We see, then, that these so-called typical elements of vertebræ have no constant developmental character by which they can be identified. Not only are they undistinguishable by any specific test from other bones not included as vertebral elements; not only do they fail to show their typical characters by their constant presence; but, when present, they exhibit no persistent marks of individuality. The central element may be ossified from six, four, three, or two points; or it may have no separate point of ossification at all: and similarly with various of the peripheral elements. The whole group of bones forming the "ideal typical vertebra" may severally have their one or more ossific centres; or they may, as in a mammal's tail, lose their individualities in a single bone ossified from one or two points.

Another fact which seems very difficult to reconcile with the hypothesis of an "ideal typical vertebra," is the not infrequent presence of some of the typical elements in duplicate. Not only, as we have seen, may they severally be absent; but they may severally be present in greater number than they should be. When we see, in the ideal diagram, one centrum, two neurapophyses, two pleurapophyses, two hæmapophyses, one neural spine, and one hæmal spine, we naturally expect to find them always bearing to each other these numerical relations. Though we may not be greatly surprised by the absence of some of them, we are hardly prepared to find others multiplied. Yet such cases are common. Thus the neural spine "is double in the anterior vertebræ of some fishes" (p. 98). Again, in the abdominal region of extinct saurians, and in crocodiles, "the freely-suspended hæmapophyses are compounded of two or more overlapping bony pieces" (p. 100). Yet again, at p. 99, we read—"I have observed some of the expanded pleurapophyses in the great *Testudo elephantopus* ossified from two centres, and the resulting divisions continuing distinct, but united by suture." Once more "the neurapophyses, which do not advance beyond the cartilaginous stage in the sturgeon, consist in that fish of two distinct pieces of cartilage; and the anterior pleurapophyses also consist of two or more cartilages, set end on end" (p. 91). And elsewhere referring to this structure, he says:—

> "Vegetative repetition of perivertebral parts not only manifests itself in the composite neurapophyses and pleurapophyses, but in a small accessory (interneural) cartilage, at the fore and back part of the base of the neurapophysis; and by a similar (interhæmal) one at the fore and back part of most of the parapophyses" (p. 87).

Thus the neural and hæmal spines, the neurapophyses, the pleurapophyses, the hæmapophyses, may severally consist of two or more pieces. This is not all: the like is true even of the centrums.

> "In *Heptanchus* (*Squalus cinereus*) the vertebral centres are feebly and vegetatively marked out by numerous slender rings of hard cartilage in the notochordal capsule, the number of vertebræ being more definitely indicated by the neurapophyses and parapophyses. . . . In the piked dog-fish (*Acanthias*) and the spotted dog-fish (*Scyllium*) the vertebral centres coincide in number with the neural arches" (p. 87).

Is it not strange that the pattern vertebra should be so little adhered to, that each of its single typical pieces may be transformed into two or three?

But there are still more startling departures from the alleged type. The numerical relations of the elements vary not only in this way, but in the opposite way. A given part may be present not only in greater number than it should be, but also in less. In the tails of homocercal fishes, the centrums "are rendered by centripetal shortening and bony confluence fewer in number than the persistent, neural, and hæmal arches of that part"—that is, there is only a fraction of a centrum to each vertebra. Nay, even this is not the most heteroclite structure. Paradoxical as it may seem, there are cases in which the same vertebral element is, considered under different aspects, at once in excess and defect. Speaking of the hæmal spine, Professor Owen says:—

> "The horizontal extension of this vertebral element is sometimes accompanied by a median division, or in other words, it is ossified from two lateral centres; this is seen in the development of parts of the human sternum; the same vegetative character is constant in the broader thoracic hæmal spines of birds; though, sometimes, as *e.g.*, in the struthionidæ, *ossification extends from the same lateral centre lengthwise—i.e., forwards and backwards, calcifying the connate cartilaginous homologues of halves of four or five hæmal spines, before these finally coalesce with their fellows at the median line*" (p. 101).

So that the sternum of the ostrich, which according to the hypothesis, should, in its cartilaginous stage, have consisted of *four or five transverse* pieces, answering to the vertebral segments, and should have been ossified from four or five centres, one to each cartilaginous piece, shows not a trace of this structure; but instead, consists of *two longitudinal* pieces of cartilage, each ossified from one centre, and finally coalescing on the median line. These four or five hæmal spines have at the same time doubled their individualities transversely, and entirely lost them longitudinally!

There still remains to be considered the test of relative position. It might be held that, spite of all the foregoing anomalies, if the typical parts of the vertebræ always stood towards each other in the same relations—always preserved the same connexions, something like a case would be made out. Doubtless, relative position is an important point; and it is one on which Professor Owen manifestly places great dependence. In his discussion of "moot cases of special homology," it is the general test to which he appeals. The typical natures of the alisphenoid, the mastoid, the orbitosphenoid, the prefrontal, the malar, the squamosal, &c., he determines almost wholly by reference to the adjacent nerve-perforations and the articulations with neighbouring bones (see pp. 19 to 72): the general form of the argument being—This bone is to be classed as such or such, *because* it is connected thus and thus with these others, which are so and so. Moreover, by putting forth an "ideal typical vertebra," consisting of a number of elements standing towards each other in certain definite arrangement, this persistency of relative position is manifestly alleged. The essential attribute of this group of bones, considered as a typical group, is the constancy in the connexions of its parts: change the connexions, and the type is changed. But the constancy of relative position thus tacitly asserted, and appealed to as a conclusive test in "moot cases of special homology," is clearly negatived by Professor Owen's own facts. For instance, in the "ideal typical vertebra," the hæmal arch is represented as formed by the two hæmapophyses and the hæmal spine; but at p. 91 we are told that

> "The contracted hæmal arch in the caudal region of the body may be formed by different elements of the typical vertebra: *e.g.*, by the parapophyses (fishes generally); by the pleurapophyses (lepidosiren); by both parapophyses and pleurapophyses (*Sudis*, *Lepidosteus*), and by hæmapophyses, shortened and directly articulated with the centrums (reptiles and mammals)."

And further, in the thorax of reptiles, birds, and mammals, "the hæmapophyses are removed from the centrum, and are articulated to the distal ends of the pleurapophyses; the bony hoop being completed by the intercalation of the hæmal spine" (p. 82). So that there are *five* different ways in which the hæmal arch may be formed—four modes of attachment of the parts different from that shown in the typical diagram! Nor is this all. The pleurapophyses "may be quite detached from their proper segment, and suspended to the hæmal arch of another vertebra;" as we have already seen, the entire hæmal arch may be detached and removed to a distance, sometimes reaching the length of twenty-seven vertebræ; and, even more remarkable, the ventral fins of some fishes, which theoretically belong to the pelvic arch, are so much advanced forward as to be articulated to the scapular arch—"the ischium elongating to join the coracoid." With these admissions it seems to us that relative position and connexions cannot be appealed to as tests of homology, nor as evidence of any original type of vertebra.

In no class of facts, then, do we find a good foundation for the hypothesis of an "ideal typical vertebra." There is no one conceivable attribute of this archetypal form which is habitually realised by actual vertebræ. The alleged group of true vertebral elements is not distinguished in any specified way from bones not included in it. Its members have various degrees of inconstancy; are rarely all present together; and no one of them is essential. They are severally developed in no uniform way: each of them may arise either out of a separate piece of cartilage, or out of a piece continuous with that of some other element; and each may be ossified from many independent points, from one, or from none. Not only may their respective individualities be lost by absence, or by confluence with others; but they may be doubled, or tripled, or halved, or may be multiplied in one direction and lost in another. The entire group of typical elements may coalesce into one simple bone representing the whole vertebra; and even, as in the terminal piece of a bird's tail, half-a-dozen vertebræ, with all their many elements, may become entirely lost in a single mass. Lastly, the respective elements, when present, have no fixity of relative position: sundry of them are found articulated to various others than those with which they are typically connected; they are frequently displaced and attached to neighbouring vertebræ; and they are even removed to quite remote parts of the skeleton. It seems to us that if this want of congruity with the facts does not disprove the hypothesis, no such hypothesis admits of disproof.

Unsatisfactory as is the evidence in the case of the trunk and tail vertebræ, to which we have hitherto confined ourselves, it is far worse in the case of the alleged cranial vertebræ. The mere fact that those who have contended for the vertebrate structure of the skull, have differed so astonishingly in their special interpretations of it, is enough to warrant great doubt as to the general truth of their theory. From Professor Owen's history of the doctrine of general homology, we gather that Duméril wrote upon "la tête considérée comme *une* vertèbre;" that Kielmeyer, "instead of calling the skull a vertebra, said each vertebra might be called a skull;" that 'Oken recognized in the skull *three* vertebræ and a rudiment; that Professor Owen himself makes out *four* vertebræ; that Goethe's idea, adopted and developed by Carus, was, that the skull is composed of *six* vertebræ; and that Geoffroy St. Hilaire divided it into *seven*. Does not the fact that different comparative anatomists have arranged the same group of bones into *one*, *three*, *four*, *six*, and *seven* vertebral segments, show that the mode of determination is arbitrary, and the conclusions arrived at fanciful? May we not properly entertain great doubts as to any one scheme being more valid than the others? And if out of these conflicting schemes we are asked to accept one, ought we not to accept it only on the production of some thoroughly conclusive proof—some rigorous test showing irrefragably that the others must be wrong and this alone right? Evidently where such contradictory opinions have been formed by so many competent judges, we ought, before deciding in favour of one of them, to have a clearness of demonstration much exceeding that required in any ordinary case. Let us see whether Professor Owen supplies us with any such clearness of demonstration.

To bring the first or occipital segment of the skull into correspondence with the "ideal typical vertebra," Professor Owen argues, in the case of the fish, that the parapophyses are *displaced*, and wedged between the neurapophyses and the neural spine—removed from the hæmal arch and built into the upper part of the neural arch. Further, he considers that the pleurapophyses are *teleologically compound.* And then, in all the higher vertebrata, he alleges that the hæmal arch is *separated* from its centrum, taken to a distance, and transformed into the scapular arch. Add to which, he says that in mammals the displaced parapophyses are mere processes of the neurapophyses (p. 133): these vertebral elements, typically belonging to the lower part of the centrum, and in nearly all cases confluent with it, are not only removed to the far ends of elements placed above the centrum, but have become exogenous parts of them!

Conformity of the second or parietal segment of the cranium with the pattern-vertebra, is produced thus:—The petrosals are *excluded* as being partially-ossified sense-capsules, not forming parts of the true vertebral system, but belonging to the "splanchno-skeleton." A centrum is *artificially* obtained by sawing in two the bone which serves in common as centrum to this and the preceding segment; and this though it is admitted that in fishes, where their individualities ought to be best seen, these two hypothetical centrums are not simply coalescent, but connate. Next, a similar *arbitrary bisection* is made of certain elements of the hæmal arches. And then, "the principle of *vegetative repetition* is still more manifest in this arch than in the occipital one:" each pleurapophysis is double; each hæmapophysis is double; and the hæmal spine consists of six pieces!

The interpretation of the third and fourth segments being of the same general character, need not be detailed. The only point calling for remark being, that in addition to the above various modes of getting over anomalies, we find certain bones referred to the *dermo-skeleton.*

Now it seems to us, that even supposing no antagonist interpretations had been given, an hypothesis reconcilable with the facts only by the aid of so many questionable devices, could not be considered satisfactory; and that when, as in this case, various comparative anatomists have contended for other interpretations, the character of this one is certainly not of a kind to warrant the rejection of the others in its favour; but rather of a kind to make us doubt the possibility of all such interpretations. The question which naturally arises is, whether by proceeding after this fashion, groups of bones might not be arranged into endless typical forms. If, when a given element was not in its place, we were at liberty to consider it as *suppressed*, or *connate* with some neighbouring element, or *removed* to some more or less distant position;—if, on finding a bone in excess, we might consider it, now as part of the *dermo-skeleton*, now as part of the *splanchno-skeleton*, now as *transplanted* from its typical position, now as resulting from *vegetative repetition*, and now as a bone *teleologically compound* (for these last two are intrinsically different, though often used by Professor Owen as equivalents);—if, in other cases, a bone might be regarded as *spurious* (p. 91), or again as having *usurped* the place of another;—if, we say, these various liberties were allowed us, we should not despair of reconciling the facts with various diagrammatic types besides that adopted by Professor Owen.

When, in 1851, we attended a course of Professor Owen's lectures on Comparative Osteology, beginning though we did in the attitude of discipleship, our scepticism grew as we listened, and reached its climax when we came to the skull; the reduction of which to the vertebrate structure, reminded us very much of the interpretation of prophecy. The delivery, at the Royal Society, of the Croonian Lecture for 1858, in which Professor Huxley, confirming the statements of several German anatomists, has shown that the facts of embryology do not countenance Professor Owen's views respecting the formation of the cranium, has induced us to reconsider the vertebral theory as a whole. Closer examination of Professor Owen's doctrines, as set forth in his works, has certainly not removed the scepticism generated years ago by his lectures. On the contrary, that scepticism has deepened into disbelief. And we venture to think that the evidence above cited shows this disbelief to be warranted.

There remains the question—What general views are we to take respecting the vertebrate structure? If the hypothesis of an "ideal typical vertebra" is not justified by the facts, how are we to understand that degree of similarity which vertebræ display?

We believe the explanation is not far to seek. All that our space will here allow, is a brief indication of what seems to us the natural view of the matter.

Professor Owen, in common with other comparative anatomists, regards the divergences of individual vertebræ from the average form, as due to adaptive modifications. If here one vertebral element is largely developed, while elsewhere it is small—if now the form, now the position, now the degree of coalescence, of a given part varies; it is that the local requirements have involved this change. The entire teaching of comparative osteology implies that differences in the conditions of the respective vertebræ necessitate differences in their structures.

Now, it seems to us that the first step towards a right conception of the phenomena, is to recognize this general law in its converse application. If vertebræ are unlike in proportion to the unlikeness of their circumstances, then, by implication, they will be like in proportion to the likeness of their circumstances. While successive segments of the same skeleton, and of different skeletons, are all in some respects more or less differently acted on by incident forces, and are therefore required to be more or less different; they are all, in other respects, similarly acted on by incident forces, and are therefore required to be more or less similar. It is impossible to deny that if differences in the mechanical functions of the vertebræ involve differences in their forms; then, community in their mechanical functions, must involve community in their forms. And as we know that throughout the *Vertebrata* generally, and in each vertebrate animal, the vertebræ, amid all their varying circumstances, *have* a certain community of function, it follows necessarily that they will have a certain general resemblance—there will recur that average shape which has suggested the notion of a pattern vertebra.

A glance at the facts at once shows their harmony with this conclusion. In an eel or a snake, where the bodily actions are such as to involve great homogeneity in the mechanical conditions of the vertebræ, the series of them is comparatively homogeneous. On the contrary, in a mammal or a bird, where there is considerable heterogeneity in their circumstances, their similarity is no longer so great. And if, instead of comparing the vertebral columns of different animals, we compare the successive vertebræ of any one animal, we recognize the same law. In the segments of an individual spine, where is there the greatest divergence from the common mechanical conditions? and where may we therefore expect to find the widest departure from the average form? Obviously at the two extremities. And accordingly it is at the two extremities that the ordinary structure is lost.

Still clearer becomes the truth of this view, when we consider the genesis of the vertebral column as displayed throughout the ascending grades of the *Vertebrata*. In its first embryonic stage, the spine is an undivided column of flexible substance. In the early fishes, while some of the peripheral elements of the vertebræ were marked out, the central axis was still, a continuous unossified cord. And thus we have good reason for thinking that in the primitive vertebrate animal, as in the existing *Amphioxus*, the notochord was persistent. The production of a higher, more powerful, more active creature of the same type, by whatever method it is conceived to have taken place, involved a change in the notochordal structure. Greater muscular endowments presupposed a firmer internal fulcrum

—a less yielding central axis. On the other hand, for the central axis to have become firmer while remaining continuous, would have entailed a stiffness incompatible with the creature's movements. Hence, increasing density of the central axis necessarily went hand in hand with its segmentation: for strength, ossification was required; for flexibility, division into parts. The production of vertebræ resulting thus, there obviously would arise among them a general likeness, due to the similarity in their mechanical conditions, and more especially the muscular forces bearing on them. And then observe, lastly, that where, as in the head, the terminal position and the less space for development of muscles, entailed smaller lateral bendings, the segmentation would naturally be less decided, less regular, and would be lost as we approached the front of the head.

But, it may be replied, this hypothesis does not explain all the facts. It does not tell us why a bone whose function in a given animal requires it to be solid, is formed not of a single piece, but by the coalescence of several pieces, which in other creatures are separate; it does not account for the frequent manifestations of unity of plan in defiance of teleological requirements. This is quite true. But it is not true, as Professor Owen argues respecting such cases, that "if the principle of special adaptation fails to explain them, and we reject the idea that these correspondences are manifestations of some archetypal exemplar, on which it has pleased the Creator to frame certain of his living creatures, there remains only the alternative that the organic atoms have concurred fortuitously to produce such harmony." This is not the only alternative: there is another, which Professor Owen has overlooked. It is a perfectly tenable supposition that all higher vertebrate forms have arisen by *the superposing of adaptations upon adaptations.* Either of the two antagonist cosmogonies consists with this supposition. If, on the one hand, we conceive species to have resulted from acts of special creation; then it is quite a fair assumption that to produce a higher vertebrate animal, the Creator did not begin afresh, but took a lower vertebrate animal, and so far modified its pre-existing parts as to fit them for the new requirements; in which case the original structure would show itself through the superposed modifications. If, on the other hand, we conceive species to have resulted by gradual differentiations under the influence of changed conditions; then, it would manifestly follow that the higher, heterogeneous forms, would bear traces of the lower and more homogeneous forms from which they were evolved.

Thus, besides finding that the hypothesis of an "ideal typical vertebra" is irreconcilable with the facts, we find that the facts are interpretable without gratuitous assumptions. The average community of form which vertebræ display, is explicable as resulting from natural causes. And those typical similarities which are traceable under adaptive modifications, must obviously exist if, throughout creation in general, there has gone on that continuous superposing of modifications upon modifications which goes on in every unfolding organism.

[I might with propriety have added to the foregoing criticisms, the remark that Professor Owen has indirectly conferred a great benefit by the elaborate investigations he has made with the view of establishing his hypothesis. He has himself very conclusively proved that the teleological interpretation is quite irreconcilable with the facts. In gathering together evidence in support of his own conception of archetypal forms, he has disclosed adverse evidence which I think shows his conception to be untenable. The result is that the field is left clear for the hypothesis of Evolution as the only tenable one.]

# APPENDIX C.

[*From the* TRANSACTIONS OF THE LINNEAN SOCIETY, VOL. XXV.]

## XV. *On Circulation and the Formation of Wood in Plants. By* HERBERT SPENCER, *Esq. Communicated by* GEORGE BUSK, *Esq., F.R.S., Sec. L.S.*

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OPINIONS respecting the functions of the vascular tissues in plants appear to make but little progress towards agreement. The supposition that these vessels and strings of partially-united cells, lined with spiral, annular, reticulated, or other frameworks, are carriers of the plant-juices, is objected to on the ground that they often contain air: as the presence of air arrests the movement of blood through arteries and veins, its presence in the ducts of stems and petioles is assumed to unfit them as channels for sap. On the other hand, that these structures have a respiratory office, as some have thought, is certainly not more tenable, since, if the presence of air in them negatives the belief that their function is to distribute liquid, the presence of liquid in them equally negatives the belief that their function is to distribute air. Nor can any better defence be made for the hypothesis which I find propounded, that these parts serve "to give strength to the parenchyma." Tubes with fenestrated and reticulated internal skeletons have, indeed, some power of supporting the tissue through which they pass; but tubes lined with spiral threads can yield extremely little support, while tubes lined with annuli, or spirals alternating with annuli, can yield no support whatever. Though all these types of internal framework are more or less efficient for preventing closure by lateral pressure, they are some of them quite useless for holding up the mass through which the vessels pass; and the best of them are for this purpose mechanically inferior to the simple cylinder. The same quantity of matter made into a continuous tube would be more effective in giving stiffness to the cellular tissue around it.

In the absence of any feasible alternative, the hypothesis that these vessels are distributors of sap claims reconsideration. The objections are not, I think, so serious as they seem. The habitual presence of air in the ducts that traverse wood, can scarcely be held anomalous if when the wood is formed their function ceases. The canals which ramify through a Stag's horn, contain air after the Stag's horn is fully developed; but it is not thereby rendered doubtful whether it is the function of arteries to convey blood. Again, that air should frequently be found even in the vessels of petioles and leaves, will not appear remarkable when we call to mind the conditions to which a leaf is subject. Evaporation is going on from it. The thinner liquids pass by osmose out of the vessels into the tissues containing the liquids thickened by evaporation. And as the vessels are thus continually drained, a draught is made upon the liquid contained in the stem and roots. Suppose that this draught is unusually great, or suppose that around the roots there exists no adequate supply of moisture. A state of capillary tension must result—a tendency of the liquid to pass into the leaves resisted below by liquid cohesion. Now, had the vessels impermeable coats, only their upper extremities would under these conditions be slowly emptied. But their coats, in common with all the surrounding tissues, are permeable by air. Hence, under this state of capillary tension, air will enter; and as the upper ends of the tubes, being both smaller in diameter and less porous than the lower, will retain the liquids with greater tenacity, the air will enter the wider and more porous tubes below—the ducts of the stem and branches. Thus the entrance of air no more proves that these ducts are not sap-carriers, than does the emptiness of tropical river-beds in the dry season prove that they are not channels for water. There is, however, a difficulty which seems more serious. It is said that air, when present in these minute canals, must be a great obstacle to the movement of sap through them. The investigations of Jamin have shown that bubbles in a capillary tube resist the passage of liquid, and that their resistance becomes very great when the bubbles are numerous—reaching, in some experiments, as much as three atmospheres. Nevertheless the inference that any such resistance is offered by the air-bubbles in the vessels of a plant, is, I think, an erroneous one. What happens in a capillary tube having impervious sides, with which these experiments were made, will by no means happen in a capillary tube having pervious sides. Any pressure brought to bear on the column of liquid contained in the porous duct of a plant, must quickly cause the expulsion of a contained air-bubble through the minute openings in the coats of the duct. The greater molecular mobility of gases than liquids, implies that air will pass out far more readily than sap. Whilst, therefore, a slight tension on the column of sap will cause it to part and the air to enter, a slight pressure upon it will force out the air and reunite the divided parts of the column.

To obtain data for an opinion on this vexed question, I have lately been experimenting on the absorption of dyes by plants. So far as I can learn, experiments of this kind have most, if not all of them, been made on stems, and, as it would seem from the results, on stems so far developed as to contain all their characteristic structures. The first experiments I made myself were on such parts, and yielded evidence that served but little to elucidate matters. It was only after trying like experiments with leaves of different ages and different characters, and with undeveloped axes, as well as with axes of special kinds, that comprehensible results were reached; and it then became manifest that the appearances presented by ordinary stems when thus tested, are in a great degree misleading. Let me briefly indicate the differences.

If an adult shoot of a tree or shrub be cut off, and have its lower end placed in an alumed decoction of logwood or a dilute solution of magenta,* the dye will, in the course of a few hours, ascend to a distance varying according to the rate of evaporation from the leaves. On making longitudinal sections of the part traversed by it, the dye is found to have penetrated extensive tracts of the woody tissue; and on making transverse sections, the openings of the ducts appear as empty spaces in the midst of a deeply-coloured prosenchyma. It would thus seem that the liquid is carried up the denser parts of the vascular bundles; neglecting the cambium layer, neglecting the central pith, and neglecting the spiral vessels of the medullary sheath. Apparently the substance of the wood has afforded the readiest channel. When, however, we examine these appearances critically, we find reasons for doubting this conclusion. If a transverse section of the lower part, into which the dye passed first and has remained longest, be compared with a transverse section of the part which the dye has but just reached, a marked difference is visible. In the one case the whole of the dense tissue is stained; in the other case it is not. This uneven distribution of stain in the part which the dye has incompletely permeated is not at random; it admits of definite description. A tolerably regular continuous ring of colour distinguishes the outer part of the wood from the inner mass, implying a passage of liquid up the elongated cells next the cambium layer. And the inner mass is coloured more round the mouths of the pitted ducts than elsewhere: the dense tissue is darkest close to the edges of these ducts; the colour fades away gradually on receding from their edges; there is most colour where there are several ducts together; and the dense tissue which

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* These two dyes have affinities for different components of the tissues, and may be advantageously used in different cases. Magenta is rapidly taken up by woody matter and other secondary deposits; while logwood colours the cell-membranes, and takes but reluctantly to the substances seized by magenta. By trying both of them on the same structure, we may guard ourselves against any error arising from selective combination.

is fully dyed for some space, is that which lies between two or more ducts. These are indications that while the layer of pitted cells next the cambium has served as a channel for part of the liquid, the rest has ascended the pitted ducts, and oozed out of these into the prosenchyma around. And this conclusion is confirmed by the contrast between the appearances of the lowest part of a shoot under different conditions. For if, instead of allowing the dye time for oozing through the prosenchyma, the end of the shoot be just dipped into the dye and taken out again, we find, on making transverse sections of the part into which the dye has been rapidly taken up, that, though it has diffused to some distance round the ducts, it has left tracts of wood between the ducts uncoloured—a difference which would not exist had the ascent been through the substance of the wood. Even still stronger is the confirmation obtained by using one dye after another. If a shoot that has absorbed magenta for an hour be placed for five minutes in the logwood decoction, transverse sections of it taken at a short distance from its end show the mouths of the ducts surrounded by dark stains in the midst of the much wider red stains.

Based on these comparisons only, the inference pointed out has little weight; but its weight is increased by the results of experiments on quite young shoots, and shoots that develope very little wood. The behaviour of these corresponds perfectly with the expectation that a liquid will ascend capillary tubes in preference to simple cellular tissue or tissue not differentiated into continuous canals. The vascular bundles of the medullary sheath are here the only channels which the coloured liquid takes. In sections of the parts up to which the dye has but just reached, the spiral, fenestrated, scalariform, or other vessels contained in these bundles are alone coloured; and lower down it is only after some hours that such an exudation of dye takes place as suffices partially to colour the other substances of the bundle. Further, it is to be noted that at the terminations of shoots, where the vessels are but incompletely formed out of irregularly-joined fibrous cells which still retain their original shapes, the dye runs up the incipient vessels and does not colour in the smallest degree the surrounding tissue.

Experiments with leaves bring out parallel facts. On placing in a dye a petiole of an adult leaf of a tree, and putting it before the fire to accelate evaporation, the dye will be found to ascend the midrib and veins at various rates, up even to a foot per hour. At first it is confined to the vessels; but by the time it has reached the point of the leaf, it will commonly be seen that at the lower part it has diffused itself into the sheaths of the vessels. In a quite young leaf from the same shoot, we find a much more rigorous restriction of the dye to the vessels. On making oblique sections of its petiole, midrib, and veins, the vessels have the appearance of groups of sharply defined coloured rods imbedded in the green prosenchyma; and this marked contrast continues with scarcely an appreciable change after plenty of time has been allowed for exudation.

The facts thus grouped and thus contrasted seem, at first sight, to imply that while they are young the coats of these ramifying canals lined with spiral or allied structures are not readily permeable, but that, becoming porous as they grow old, they allow the liquids they carry to escape with increasing facility; and hence a possible interpretation of the fact that, in the older parts, the staining of the tissue around the vessels is so rapid as to suggest that the dye has ascended directly through this tissue, whereas in the younger parts the reverse appearance necessitates the reverse conclusion. But now, is this difference determined by difference of age, or is it otherwise determined? The evidence as presented in ordinary stems and leaves shows us that the parts of the vascular system at which there is a rapid escape of dye are not simply older parts, but are parts where a deposit of woody matter is taking place. Is it, then, that the increasing permeability of the ducts, instead of being directly associated with their increasing age, is directly associated with the increasing deposit of dense substance around them?

To get proof that this last connexion is the true one, we have but to take a class of cases in which wood is formed only to a small extent. In such cases experiments show us a far more general and continued limitation of the dye to the vessels. Ordinary herbs and vegetables, when contrasted with shrubs and trees, illustrate this; as instance the petioles of Celery, or of the common Dock, and the leaves of Cabbages or Turnips. And then in very succulent plants, such as *Bryophyllum calycinum*, *Kalanchoë rotundifolia*, the various species of *Crassula*, *Cotyledon*, *Kleinia*, and others of like habit, the ducts of old and young leaves alike retain the dye very persistently: the concomitant in these cases being the small amount of prosenchyma around the ducts, or the small amount of deposit in it, or both. More conclusive yet is the evidence which meets us when we turn from very succulent leaves to very succulent axes. The tender young shoots of *Kleinia ante-euphorbium*, or *Euphorbia Mauritanica*, which for many inches of their lengths have scarcely any ligneous fibres, show us scarcely any escape of the coloured liquid from the vessels of the medullary sheath. So, too, is it with *Stapelia Buffonia*, a plant of another order, having soft swollen axes. And then we have a repetition of the like connexion of facts throughout the *Cactaceæ:* the most succulent showing us the smallest permeability of the vessels. In two species of *Rhipsalis*, in two species of *Cereus*, and in two species of *Mammillaria*, which I have tried, I have found this so. *Mammillaria gracilis* may be named as exemplifying the relation under its extreme form. Into one of these small spheroidal masses, the dye ascends through the large bundles of spiral or annular ducts, or cells partially united into such ducts, colouring them deeply, and leaving the feebly-marked sheath of prosenchyma, together with the surrounding watery cellular tissue, perfectly uncoloured.

The most conclusive evidence, however, is furnished by those *Cactaceæ* in which the transition from succulent to dense tissue takes place variably, according as local circumstances determine. *Opuntia* yields good examples. If a piece of it including one of the joints at which wood is beginning to form, be allowed to absorb a coloured liquid, the liquid, running up the irregular bundles of vessels and into many of their minute ramifications, is restricted to these where they pass through the parenchyma forming the mass of the stem; but near the joints the hardened tissue around the vessels is coloured. In one of these fleshy growths we get clear evidence that the escape of the dye has no immediate dependence on the age of the vessels, since, in parts of the stem that are alike in age, some of the vessels retain their contents while others do not. Nay, we even find that the younger vessels are more pervious than the older ones, if round the younger ones there is a formation of wood.

Thus, then, is confirmed the inference before drawn, that in ordinary stems the staining of the wood by an ascending coloured liquid is due, not to the passage of the coloured liquid up the substance of the wood, but to the permeability of its ducts and such of its pitted cells as are united into irregular canals. And the facts showing this, at the same indicate with tolerable clearness the process by which wood is formed. What in these cases is seen to take place with a dye, may be fairly presumed to take place with sap. Where the dye exudes but slowly, we may infer that the sap exudes but slowly; and it is a fair inference that where the dye leaks rapidly out of the vessels, the sap does the same. Inferring, thus, that wherever there is a considerable formation of wood there is a considerable escape of the sap, we see in the one the result of the other. The thickening of the prosenchyma is proportionate to the quantity of nutritive liquid passing into it; and this nutritive liquid passes into it from the vessels, ducts, and irregular canals it surrounds.

But an objection is made to such experiments as the foregoing, and to all the inferences drawn from them. It is said that portions of plants cut off and thus treated, have their physiological actions arrested, or so changed as may render the results misleading; and it is said that when detached shoots and leaves have their cut ends placed in solutions, the open mouths of their vessels and ducts are directly presented with the liquids to be absorbed, which does not happen in their natural states. Further, making these objections look serious, it is alleged that when solutions are absorbed through the roots, quite different results are obtained: the absorbed matters are found in the tissues and not in the vessels. Clearly, were the experiments yielding these adverse results conducted in unobjectionable ways, the conclusion implied by them would negative the conclusions above drawn. But these experiments are no less objectionable than those to which they are opposed. Such mineral matters as salts of iron, solutions of which have in some cases been supplied to the roots for their absorption, are obviously so unlike the matters ordinarily absorbed, that they are likely to interfere fatally with the physiological actions. If experiments of this kind are made by immersing the roots in a dye, there is, besides the difficulty that the mineral mordant contained by the dye is injurious to the plant, the further difficulty that the colouring matter, being seized by the substances for which it has an affinity, is left behind in the first layers of root tissues passed through, and that the decolorized water passing up into the plant is not traceable. To be conclusive, then, an experiment on absorption through roots must be made with some solution which will not seriously interfere with the plant's vital processes, and which will not have its distinctive element left behind. To fulfil these requirements I adopted the following method. Having imbedded a well-soaked broad-bean in moist sand, contained in an inverted cone of cardboard with its apex cut off for the radicle to come through—having placed this in a wide-mouthed dwarf bottle, partly filled with water, so that the protruding radicle dipped into the water—and having waited until the young bean had a shoot some three or more inches high, and a cluster of secondary rootlets from an inch to an inch and a-half long—I supplied for its absorption a simple decoction of logwood, which, being a vegetal matter, was not likely to do it much harm, and which, being without a mordant, would not leave its suspended colour in the first tissues passed through. To avoid any possible injury, I did not remove the plant from the bottle, but slightly raising the cone out of its neck, I poured away the water through the crevice and then poured in the logwood decoction; so that there could have been no broken end or abraded surface of a rootlet through which the decoction might enter. Being prepared with some chloride of tin as a mordant, I cut off, after some three hours, one of the lowest leaves, expecting that the application of the mordant to the cut surface would bring out the characteristic colour if the logwood decoction had risen to that height. I got no reaction, however. But after eight hours I found, on cutting off another leaf, that the vessels of its petiole were made visible as dark streaks by the colour with which they were charged—a colour differing, as was to be expected, from that of the logwood decoction, which spontaneously changes even by simple exposure. It was then too late in the day to pursue the observations; but next morning the vessels of the whole plant, as far as the petioles of its highest unfolded leaves, were full of the colouring-matter; and on applying chloride of tin to the cut surfaces, the vessels assumed that purplish red which this mordant produces when directly mixed with the logwood decoction. Subsequently, when one of the cotyledons was cut open by Prof. Oliver, to whom, in company with Dr. Hooker, I showed the specimen, we found that the whole of its vascular system was filled with the decoction, which everywhere gave the characteristic reaction. And it became manifest that the liquid absorbed through the rootlets, in the central vessels of which it was similarly traceable, had part of it passed directly up the vessels of the axis, while part of it had passed through other vessels into the cotyledon, out of which, no doubt, the liquid ordinarily so carried returns charged with a supply of the stored nutriment. I have since obtained a verification by varying the method. Digging up some young plants (Marigolds happened to afford the best choice) with large masses of soil round them, placing them in water, so as gradually to detach the soil without injuring the rootlets, planting them afresh in a flower-pot full of washed sand, and then, after a few days, watering them with a logwood decoction, I found, as before, that in less than twenty-four hours the colouring-matter had run up into the vessels of the leaves. Though the reaction produced by the mordant was not so strong as before, it was marked enough to be quite unquestionable.

As these experiments were so conducted that there was no access to the vessels except through the natural channels, and as the vital actions of the plants were so little interfered with that at the end of twenty-four hours they showed no traces of disturbance, I think the results must be held conclusive.

Taking it, then, as a fact that in plants possessing them the vessels and ducts are the channels through which sap is distributed, we come now to the further question—What determines the varying permeability of the walls of the vessels and ducts, and the consequent varying formation of wood? To this question I believe the true reply is—The exposure of the parts to intermittent mechanical strains, actual or potential, or both. By actual strains I of course mean those which the plant experiences in the course of its individual life. By potential strains I mean those which the form, attitude, and circumstances common to its kind involve, and which its inherited structure is adapted to meet. In plants with stems, petioles, and leaves, having tolerably constant attitudes, the increasing porosity of the tubes and consequent deposit of dense tissue takes place in anticipation of the strains to which the parts of the individual are liable, but takes place at parts which have been habitually subject to such strains in ancestral individuals. But though in such plants the tendency to repeat that distribution of dense tissue caused by mechanical actions on past generations, goes on irrespective of the mechanical actions to which the developing individual is subject, these direct actions, while they greatly aid the assumption of the typical structure, are the sole causes of those deviations in the relative thickenings of parts which distinguish the individual from others of its kind. And then, in certain irregularly growing plants, such as Cactuses and Euphorbias, where the strains fall on parts that do not correspond in successive individuals, we distinctly trace a direct relation between the degrees of strain and the rates of these changes which result in dense tissue. I will not occupy space in detailing the evidence of this relation, which is conspicuous in the orders named, but will pass to the question—What are the physical processes by which intermittent mechanical strains produce this deposit of resistant substance at places where it is needed to meet the strains? We have not to seek far for an answer. If a trunk, a bough, a shoot, or a petiole, is bent by a gust of wind, the substance of its convex side is subject to longitudinal tension: the substance of its concave side being at the same time compressed. This is the primary mechanical effect. There is, however, a secondary mechanical effect, which here chiefly concerns us. That bend by which the tissues of the convex side are stretched, also produces lateral compression of them. Buttoning on a tight glove and then closing the hand, will make this necessity clear: the leather, while it is strained along the backs of the fingers, presses with considerable force on the knuckles. It is demonstrable that the tensions of the outer layer of a mass made convex by bending, must, by composition of forces, produce at every point a resultant at right angles to the layer beneath it; that, similarly, the joint tensions of these two layers must throw a pressure on the next deeper layer; and so on. Hence, if at some little distance beneath the surface of a stem, twig, or leaf-stalk, there exist longitudinal tubes, these tubes must be squeezed each time the side of the branch they are placed on becomes convex. Modifying the illustration just drawn from the clenched hand will make this clear. When, on forcibly grasping something, the skin is drawn tightly over the back of the hand, the whitening of the knuckles shows how the blood is expelled from the vessels below the surface by the pressure of the tightened skin. If, then, the sap-vessels must be thus compressed, what will happen to the liquid they contain? It will move away along the lines of least resistance. Part, and probably the greater part, will escape lengthways from the place of greatest pressure: some of it being expelled downwards, and some of it upwards. But, at the same time, part of it will be likely to ooze through the walls of the tubes. If these walls are so perfect as to permit the passage of liquid only by osmose, it may still be inferred that the osmose will increase under pressure; and probably, under recurrent pressure, the places at which the osmotic current passes most readily will become more and more permeable, until they eventually form pores. At any rate it is manifest that where pores and slits exist, whether thus formed or formed in any other way, the escape of sap into the adjacent tissue at each bend will become easy and rapid. What further must happen? When the branch or shoot recoils, the vessels on the side that was convex, being relieved from pressure, will tend to resume their previous diameters; and will be helped to do this by the elasticity of the surrounding tissue, as well as by those spiral, annular, and allied structures which they contain. But this resumption of their previous diameters must cause an immediate rush of sap back into them. Whence will it come? Not to any considerable extent from the surrounding tissues into which part of it has been squeezed, seeing that the resistance to the return of liquid through small pores will be greater than the resistance to its return along the vessels themselves. Manifestly the sap which was thrust up and down the vessels from the place of compression will return—the quantities returning from above and from below varying, as we shall hereafter see, according to circumstances. But this is not all. From some side a greater quantity must come back than was sent away; for the amount that has escaped out of the tube into the prosenchyma has to be replaced. Thus during the time when the side of the branch or twig becomes concave, more sap returns from above or below than was expelled upwards or downwards during the previous compression. The refilled vessels, when the next bend renders their side convex, again have part of their contents forced through their parietes, and are again refilled in the same way. There is thus set up a draught of sap to the place where these intermittent strains are going on, an exudation proportionate to the frequency and intensity of the strains, and a proportionate nutrition or thickening of the wood-cells, fitting them to resist the strains. A rude idea of this action may be obtained by grasping in one hand a damp sponge, having its lower end in water, while holding a piece of blotting-paper in contact with its upper end, and then giving the sponge repeated squeezes. At each squeeze some of the water will be sent into the blotting-paper; at each relaxation the sponge will refill from below, to give another portion of its contents to the blotting paper when again squeezed.

But how does this explanation apply to roots? If the formation of wood is due to intermittent transverse strains, such as are produced in the aërial parts of upright plants by the wind, how does it happen that woody matter is deposited in roots, where there are no lateral oscillations, no transverse strains? The answer is, that longitudinal strains also are capable of causing the effects described. It is true that perfectly straight fibres united into a bundle and pulled lengthways would not exert on one another any lateral pressure, and would not laterally compress any similarly-straight canals running along with them. But if the fibres united into a bundle are variously bent or twisted, they cannot be longitudinally strained without compressing one another and structures imbedded in them. It needs but to watch a wet rope drawn tight by a capstan, to see that an action like that which squeezes the water out of its strands, will squeeze the sap out of the vessels of a root into the surrounding tissue, as often as the root is pulled by the swaying of the plant it belongs to. Here, too, as before, the vessels will refill when the pull intermits; and so, in the roots as in the branches, this rude pumping process will produce a growth of hard tissue proportionate to the stress to be borne.

These conclusions are supported by the evidence which exceptional cases supply. If intermittent mechanical strains thus cause the formation of wood where wood is found, then where it is not found, there should be an absence of intermittent mechanical strains. There is such an absence. Vascular plants characterized by little or no deposit of dense substance, are those having vessels so conditioned that no considerable pressures are borne by them. The more succulent a petiole or leaf becomes, the more do the effects of transverse strains fall on its outer layers of cells. Its mechanical support is chiefly derived from the ability of these minute vesicles, full of liquid, to resist bursting and tearing under the compressions and tensions they are exposed to. And just as fast as this change from a thin leaf or foot-stalk to a thick one entails increasing stress on the superficial tissue, so fast does it diminish the stress on the internally-seated vascular tissue. The succulent leaf cannot be swayed about by the wind as much as an ordinary leaf; and such small bends as can be given to it and its foot-stalk are prevented from affecting in any considerable degree the tubes running through its interior. Hence the retentiveness of the vessels in these fleshy leaves, as shown by the small exudation of dye; and hence the small thickening of their surrounding prosenchyma by woody deposit. Still more conspicuously is this connexion of facts shown when, from the soft thick leaves before named and such others as those of *Echeveria*, *Rochea*, *Pereskia*, we turn to the thick leaves that have strong exo-skeletons. *Gasteria* serves as an illustration. The leathery or horny skin here evidently bears the entire weight of the leaf, and is so stiff as to prevent any oscillation. Here, then, the vessels running inside are protected from all mechanical stress; and accordingly we find that the cells surrounding them are not appreciably thickened.

Equally clear, and more striking because more obviously exceptional, is the evidence given by succulent stems which are leafless. *Stapelia Buffonia*, having soft procumbent axes not liable to be bent backwards and forwards in any considerable degree by the wind, has, ramifying through its tissue, vessels that allow but an extremely slow escape of dye and have unthickened sheaths. Such of the Euphorbias as have acquired the fleshy character while retaining the arborescent growth, like *Euphorbia Canariensis*, teach us the same truth in another way. In them the formation of wood around the vessels is inconspicuous where the intermittent strains are but slight; but it is conspicuous at those joints on which lateral oscillations of the attached branches throw great extensions and compressions of tissue. Throughout the *Cactaceæ* we find varied examples of the alleged relation. *Mammillaria* furnishes a very marked one. The substance of one of these globular masses, resting on the ground, admits of no bending from side to side; and accordingly its large bundles of spiral and annular vessels, or partially-united cells, have very feebly-marked sheaths not at all thickened. In such types as *Cereus* and *Opuntia* we see, as in the Euphorbias, that where little stress falls on the vessels, little deposit takes place around them; while there is much deposit where there is much stress. Here let me add a confirmation obtained since writing the above. After observing among the Cactuses the very manifest relation between strain and the formation of wood, I inquired of Mr. Croucher, the intelligent foreman of the Cactus-house at Kew, whether he found this relation a constant one. He replied that he did, and that he had frequently tested it by artificially subjecting parts of them to strains. Neglecting at the time to inquire how he had done this, it afterwards occurred to me that if he had so done it as to cause constant strains, the observed result would not tell in favour of the foregoing interpretation. Subsequently, however, I learned that he had produced the strains by placing the plants in inclined attitudes—a method which, by permitting oscillations of the strained joints, allowed the strains to intermit. And then, making the proof conclusive, Mr. Croucher volunteered the statement that where he had produced constant strains by tying, no formation of wood took place.

Aberrant growths of another class display the same relations of phenomena. Take first the underground stems, such as the Potato and the Artichoke. The vessels which run through these, slowly take up the dye without letting it pass to any considerable extent into the surrounding tissues.* Only after an interval of many hours does the prosenchyma become stained in some places. Here, as before, an absence of rapid exudation accompanies an absence of woody deposit; and both these go along with the absence of intermittent strains. Take again the fleshy roots. The Turnip, the Carrot, and the Beetroot, have vessels that retain very persistently the coloured liquids they take up. And differing in this, as these roots do, from ordinary roots, we see that they also differ from them in not being woody, and in not being appreciably subject to the

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* Those who repeat these experiments must be prepared for great irregularities in the rates of absorption. Succulent structures in general absorb much more slowly than others, and sometimes will scarcely take up the dye at all. The differences between different structures, and the same structure at different times, probably depend on the degrees in which the tissues are charged with liquid and the rates at which they are losing it by evaporation.

usual mechanical actions. In these cases, as in the others, parts that ordinarily become dense, deviate from this typical character when they are not exposed to those forces which produce dense tissue by increasing the extravasation of sap.

To complete the proof that such a relation exists, let me add the results of some experiments on equal and similarly-developed parts, kept respectively at rest and in motion. I have tested the effects on large petioles, on herbaceous shoots, and on woody shoots. If two such petioles as those of Rhubarb, with their leaves attached, have their cut ends inserted in bottles of dye, and the one be bent backwards and forwards while the other remains motionless, there arises, after the lapse of an hour, scarcely any difference in the states of their vessels: a certain proportion of these are in both cases charged with the dye, and little exudation has been produced by the motion. Here, however, it is to be observed that the causes of exudation are scarcely operative; the vascular bundles are distributed all through the mass of the petiole, which is formed of soft watery tissue; and they are, therefore, not so circumstanced as to be effectually compressed by the bends. In herbaceous stems, such as those of the Jerusalem Artichoke and of the Foxglove, an effect scarcely more decided is produced; and here, too, when we seek a reason, we find it in the non-fulfilment of the mechanical conditions; for the vascular bundles are not so seated between a tough layer of bark and a solid core as to be compressed at each bend. When, however, we come to experiment upon woody shoots, we meet with conspicuous effects, though by no means uniformly. In some cases oscillations produce immense amounts of exudation—parallel transverse sections of the compared shoots showing that where, in the one that has been at rest, there are spots of colour round but a few pitted ducts, in the one that has been kept in motion the substance of the wood is soaked almost uniformly through with dye. In other cases, especially where there is much undifferentiated tissue remaining, the exudation is not very marked. The difference appears to depend on the quantity of liquid contained in the shoot. If its substance is relatively dry, the exudation is great; but it is comparatively small if all the tissues are fully charged with sap. This contrast of results is one which contemplation of the mechanical actions will lead us to expect.

And now, with these facts to aid our interpretation, let us return to ordinary stems. If the upper end of a growing shoot, the prosenchyma of which is but little thickened, be allowed to imbibe the dye, the vessels of its medullary sheath alone become charged; and from them there takes place but a slow oozing. If a like experiment be tried with a lower part of the shoot, where the wood in course of formation has its inner boundary marked but not its outer boundary, we find that the pitted ducts, and more especially the inner ones, come into play. And then lower still, where the wood has its periphery defined and its histological characters decided, the appearances show that the tissue forming its outer surface begins to take a leading part in the transmission of liquid. What now is the explanation of these changes, mechanically considered? In the young soft part of the shoot, as in all normal and abnormal growths that have not formed wood, the channels for the passage of sap are the spiral, annular, fenestrated, or reticulated vessels. These vessels, here included in the bundles of the medullary sheath, are, in common with the tissues around them, subject, by the bendings of the shoot, to slight intermittent compressions, and, especially the outermost of them, are thus forced to give the prosenchyma an extra supply of nutritive liquid. The thickening of the prosenchyma, spreading laterally as well as outwards from each bundle of the medullary sheath, goes on until it meets the thickenings that spread from the other bundles; and there is so formed an irregular cylinder of hardened tissue, surrounding the medulla and the vascular bundles of its sheath. As soon as this happens, these vascular bundles become, to a considerable extent, shielded from the effects of transverse strains, since the tensions and compressions chiefly fall on the developing wood outside of them. Clearly, too, the greatest stress must be felt by the outer layer of the developing wood: being further removed from the neutral axis, it must be subject to severer strains at each bend; and lying between the bark and the layer of wood first formed, it must be most exposed to lateral compressions. Among the elongated cells of this outer layer, some unite to form the pitted ducts. Being, as we see, better circumstanced mechanically, they become greater carriers of sap than the original vessels, and, in consequence of this, as well as in consequence of their relative proximity, become the sources of nutrition to the still more external layers of wood-cells. The same causes and the same effects hold with each new indurated coat deposited round the previously indurated coats.

This description may be thought to go far towards justifying the current views respecting the course taken by the sap. But the justification is more apparent than real. In the first place, the implication here is that the sap-carrying function is at first discharged entirely by the vessels of the medullary sheath, and that they cease to discharge this function only as fast as they are relatively incapacitated by their mechanical circumstances. And the second implication is, that it is not the wood itself, but the more or less continuous canals formed in it, which are the subsequent sap-distributors. This, though readily made clear by microscopic examination of the large pitted ducts in a partially lignified shoot that has absorbed the dye, is less manifestly true of the peripheral layer of sap-carrying tissue finally formed. But it is really true here. For this layer, though nominally a layer of wood, is practically a layer of inosculating vessels. It is formed out of irregular lines and networks of elongated pitted cells, obliquely united by their ends. Examination of them after absorption of a dye, shows that it is only along the continuous channels they unite to form that the current has passed. But the essentially vascular character of this outer and latest-formed layer of the alburnum is best seen in the fact that the vascular systems of new axes take their rise from it, and form with it continuous canals. If a shoot of last year in which growth is recommencing, be cut lengthways after it has imbibed a dye, clear proof is obtained that the passage of the dye into a lateral bud takes place from this outermost layer of pitted cells, and that the channels taken by the dye through the new tissue are composed of cells that pass through modified forms into the spiral vessels of the new medullary sheath. This transition may be still more clearly traced in a terminal bud that continues the line of last year's shoot. A longitudinal section of this shows that the vessels of the new medullary sheath do not obtain their sap from the vessels of last year's sheath (which, as shown by the non-absorption of dye, have become inactive), but that their supplies are obtained from those inosculating canals formed out of last year's outermost layer of prosenchyma, and that between the component cells of this and those of the new vascular system there are all gradations of structure.*

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* It may be added here that, on considering the mechanical actions that must go on, we are enabled in some measure to understand both how such inosculating channels are initiated, and how the structures of their component cells are explicable. What must happen to one of these elongated prosenchyma-cells if, in the course of its development, it is subject to intermittent compressions? Its squeezed-out liquid while partially escaping laterally, will more largely escape upwards and downwards; and while repeated lateral escape will tend to form lateral channels communicating with laterally-adjacent cells, repeated longitudinal escape will tend to form channels communicating with longitudinally-adjacent cells—so producing continuous though irregular longitudinal canals. Meanwhile each cell into and out of which the nutritive liquid is from time to time squeezed through small openings in its walls, cannot thicken internally in an even manner: deposition will be interfered with by the passage of the currents through the pores. The rush to or from each pore will tend to maintain a funnel-shaped depression in the deposit around; and the opening from cell to cell will so acquire just that shape which the microscope shows up—two hollow cones with their apices meeting at the point where the cell-membranes are in contact. Moreover, as confirming this interpretation, it may be remarked that we are thus supplied with a reason for the differences of shape between these passages from one pitted cell to another, and the analogous passages that exist between cells otherwise formed and otherwise conditioned. In the cells of the medulla, and others which are but little exposed to compression, the passages are severally formed more like a tube with two trumpet-mouths, one in each cell. This is just the form which might be expected where the nutritive fluid passes from cell to cell in moderate currents, and not by the violent rushes caused by intermittent pressures. Of course it is not meant that in each

It is not the aim of the foregoing reasoning to show that mechanical actions are the sole causes of the formation of dense tissue in plants. Dense tissue is in many cases formed where no such causes have come into play—as, for example, in thorns and in the shells of nuts. Here the natural selection of variations can alone have operated. It is manifest, too, that even those supporting structures the building up of which is above ascribed to intermittent strains, may, in the individual plant of a species that ordinarily has them, be developed to a great extent when intermittent strains are prevented. We see this in trees that are artificially supported by nailing to walls; and we also see a kindred fact in natural climbers. Though in these cases the formation of wood is obviously less than it would be were the stem and branches habitually moved about by the wind, it nevertheless goes on. Clearly the tendency of the plant to repeat the structure of its type (in the one case the structure of its species, and in the other case that of the order from which it has diverged in becoming a climber) is here almost the sole cause of wood-formation. But though in plants so circumstanced intermittent mechanical strains have little or no direct share, it may still be true, and I believe is true, that intermittent mechanical strains are the original cause; for, as before hinted, the typical structure which the individual thus repeats irrespective of its own conditions, is interpretable as a typical structure that is itself the product of these actions and reactions between the plant and its environment. Grant the inheritance of functionally-produced modifications; grant that natural selection will always co-operate in such way as to favour those individuals and families in which functionally-produced modifications have progressed most advantageously; and it will follow that this mechanically-caused formation of dense substance, accumulating from generation to generation by the survival of the fittest, will result in an organic habit of forming dense tissue at the required places. The deposit arising from exudation at the places of greatest strain, recurring from generation to generation at the same places, will come to be reproduced in anticipation of strain, and will continue to be reproduced for a long time after a changed habit of the species prevents the strain—eventually, however, decreasing, both through functional inactivity and natural selection, to the point at which it is in equilibrium with the requirement.

individual cell these structures are determined by these mechanical actions. The facts clearly negative any such conclusion, showing us, as they in many cases do, that these structures are assumed in advance of these mechanical actions. The implication is, that such mechanical actions initiated modifications that have, with the aid of natural selection, been accumulated from generation to generation; until, in conformity with ordinary embryological laws, the cells of the parts exposed to such actions assume these special structures irrespective of the actions—the actions, however, still serving to aid and complete the assumption of the inherited type.

Another side of the general question may now be considered. We have seen how, by intermittent pressures on capillary vessels and ducts and inosculating canals, there must be produced a draught of sap towards the point of compression to replace the sap squeezed out. But we have still to inquire what will be the effect on the distribution of sap throughout the plant as a whole. It was concluded that out of the compressed vessels the greater part of the liquid would escape longitudinally—the longitudinal resistance to movement being least. In every case the probabilities are infinity to one against the resistances being equal upwards and downwards. Always, then, more sap will be expelled in one direction than in the other. But in whichever direction least sap is expelled, from that same direction most sap will return when the vessels are relieved from pressure—the force which is powerful in arresting the back current in that direction being the same force which is powerful in producing a forward current. Ordinarily, the more abundant supply of liquid being from below, there will result an upward current. At each bend a portion of the contents will be squeezed out through the sides of the vessels—a portion will be squeezed downwards, reversing the current ascending from the roots, but soon stopped by its resistance; while a larger portion will be squeezed upwards towards the extremities of the vessels, where consumption and loss are most rapid. At each recoil the vessels will be replenished, chiefly by the repressed upward current; and at the next bend more of it will be thrust onwards than backwards. Hence we have everywhere in action a kind of rude force-pump, worked by the wind; and we see how sap may thus be raised to a height far beyond that to which it could be raised by capillary action, aided by osmose and evaporation.

Thus far, however, the argument proceeds on the asumption that there is liquid enough to replenish every time the vessels subject to this process. But suppose the supply fails—suppose the roots have exhausted the surrounding stock of moisture. Evidently the vessels thus repeatedly having their contents squeezed out into the surrounding tissue, cannot go on refilling themselves from other vessels without tending to empty the vascular system. On the one hand, evaporation from the leaves causing a draught on the capillary tubes that end in them, continually generates a capillary tension upwards; while, on the other hand, the vessels below, expanding after their sap has been squeezed out, produce a tension both upwards and downwards towards the point of loss. Were the limiting membranes of the vessels impermeable, the movement of sap would, under these conditions, soon be arrested. But these membranes are permeable; and the surrounding tissues readily permit the passage of air. This state of tension, then, will cause an entrance of air into the tubes: the columns of liquid they contain will be interrupted by bubbles. It seems, indeed, not improbable that this entrance of air may take place even when there is a good supply of liquid, if the mechanical strains are so violent and the exudation so rapid that the currents cannot refil the half-emptied vessels with sufficient rapidity. And in this case the intruding air may possibly play the same part as that contained in the air-chamber of a force-pump—tending, by moderating the violence of the jets, and by equalizing the strains, to prevent rupture of the apparatus. Of course when the supply of liquid becomes adequate, and the strains not too violent, these bubbles will be expelled as readily as they entered.

Here, as before, let me add the conclusive proof furnished by a direct experiment. To ascertain the amount of this propulsive action, I took from the same tree, a Laurel, two equal shoots, and placing them in the same dye, subjected them to conditions that were alike in all respects save that of motion: while one remained at rest, the other was bent backwards and forwards, now by switching and now by straining with the fingers. After the lapse of an hour, I found that the dye had ascended the oscillating shoot three times as far as it had ascended the stationary shoot—this result being an average from several trials. Similar trials brought out similar effects in other structures. The various petioles and herbaceous shoots experimented upon for the purpose of ascertaining the amount of exudation produced by transverse strains, showed also the amount of longitudinal movement. It was observable that the height ascended by the dye was in all cases greater where there had been oscillation than where there had been rest—the difference, however, being much less marked in succulent structures than in woody ones.

It need scarcely be said that this mechanical action is not here assigned as the sole cause of circulation, but as a cause co-operating with others, and helping others to produce effects that could not otherwise be produced. Trees growing in conservatories afford us abundant proof that sap is raised to considerable heights by other forces. Though it is notorious that trees so circumstanced do not thrive unless, through open sashes, they are frequently subject to breezes sufficient to make their parts oscillate, yet there is evidently a circulation that goes on without mechanical aid. The *causes* of circulation are those actions only which disturb the liquid equilibrium in a plant, by permanently abstracting water or sap from some part of it; and of these the first is the absorption of materials for the formation of new tissue in growing parts; the second is the loss by evaporation, mainly through adult leaves; and the third is the loss by extravasation, through compressed vessels. Only so far as it produces this last, can mechanical strain be regarded as truly a cause of circulation. All the other actions concerned must be classed as *aids* to circulation—as facilitating that redistribution of liquid that continually restores the equilibrium continually disturbed; and of these, capillary action may be named as the first, osmose as the second, and the propulsive effect of mechanical strains as the third. The first two of these aids are doubtless capable by themselves of producing a large part of the observed result—more of the observed result than is at first sight manifest; for there is an important indirect effect of osmotic action which appears to be overlooked. Osmose does not aid circulation only by setting up, within the plant, exchange currents between the more dense and the less dense solutions in different parts of it; but it aids circulation much more by producing distention of the plant as a whole. In consequence of the average contrast in density between the water outside of the plant and the sap inside of it, the constant tendency is for the plant to absorb a quantity in excess of its capacity, and so to produce distention and erection of its tissues. It is because of this that the drooping plant raises itself when watered; for capillary action alone could only refill its tissues without changing their attitudes. And it is because of this that juicy plants with collapsible structures bleed so rapidly when cut, not only from the cut surface of the rooted part, but from the cut surface of the detached part—the elastic tissues tending to press out the liquid which distends them. And manifestly if osmose serves thus to maintain a state of distention throughout a plant, it indirectly furthers circulation; since immediately evaporation or growth at any part, by abstracting liquid from the neighbouring tissues, begins to diminish the liquid pressure within such tissues, the distended structures throughout the rest of the plant thrust their liquid contents towards the place of diminished pressure. This, indeed, may very possibly be the most efficient of the agencies at work. Remembering how great is the distention producible by osmotic absorption—great enough to burst a bladder—it is clear that the force with which the distended tissues of a plant urge forward the sap to places of consumption, is probably very great. We must therefore regard the aid which mechanical strains give as being one of several. Oscillations help directly to restore any disturbed liquid equilibrium; and they also help indirectly, by facilitating the redistribution caused by capillary action and the process just described; but in the absence of oscillations the equilibrium may still be restored, though less rapidly and within narrower limits of distance.

One half of the problem of the circulation, however, has been left out of sight. Thus far our inquiry has been, how the ascending current of sap is produced. There remains the rationale of the descending current. What forces cause it, and through what tissues it takes place, are questions to which no satisfactory answers have been given. That the descent is due to gravitation, as some allege, is difficult to conceive, since, as gravitation acts equally on all liquid columns contained in the stem, it is not easy to see why it should produce downward movements in some while permitting upward movements in others—unless, indeed, there existed descending tubes too wide to admit of much capillary action, which there do not. Moreover, gravitation is clearly inadequate to cause currents towards the roots out of branches that droop to the ground. Here the gravitation of the contained liquid columns must nearly balance that of the connected columns in the stem, leaving no appreciable force to cause motion. Nor does there seem much probability in the assumption that the route of the descending sap is through the cambium layer, since experiments on the absorption of dyes prove that simple cellular tissue is a very bad conductor of liquids: their movement through it does not take place with one-fiftieth of the rapidity with which it takes place through vessels.*

Of course the defence for these hypotheses is, that there must be a downward current, which must have a course and a cause; and the very natural assumption has been that the course and the cause must be other than those which produce the ascending current. Nevertheless there is an alternative supposition, to which the foregoing considerations introduce us. It is quite possible for the same vascular system to serve as a channel for movement in opposite directions at different times. We have among animals well-known cases in which the blood-vessels carry a current first in one direction and then, after a brief pause, in the reverse direction. And there seems an *à priori* probability that, lowly organized as they are, plants are more likely to have distributing appliances of this imperfect kind than to have two sets of channels for two simultaneous currents. If, led by this suspicion, we inquire whether among the forces which unite to produce movements of sap, there are any variations or intermissions capable of determining the currents in different directions, we quickly discover that there are such, and that the hypothesis of an alternating motion of the sap, now centrifugal and now centripetal, through the same vessels, has good warrant. What are the several forces at work? First may be set down that tendency existing in every part of a plant to expand into its typical form, and to absorb nutritive liquids in doing this. The resulting competition

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* Some exceptions to this occur in plants that have retrograded in the character of their tissues towards the simpler vegetal types. Certain very succulent leaves, such as those of *Sempervivum*, in which the cellular tissue is immensely developed in comparison with the vascular tissue, seem to have resumed to a considerable extent what we must regard as the primitive form of vegetal circulation—simple absorption from cell to cell. These, when they have lost much of their water, will take up the dye to some distance through their general substance, or rather through its interstices, even neglecting the vessels. At other times, in the same leaves, the vessels will become charged while comparatively little absorption takes place through the cellular tissue. Even in these exceptional cases, however, the movement through cellular tissue is nothing like as fast as the movement through vessels.

for sap will, other things being equal, cause currents towards the most rapidly-growing parts—towards unfolding shoots and leaves, but not towards adult leaves. Next we have evaporation, acting more on the adult leaves than on those which are in the bud, or but partially developed. This evaporation is both regularly and irregularly intermittent. Depending chiefly on the action of the sun, it is, in fine weather, greatly checked or wholly arrested every evening; and in cloudy weather must be much retarded during the day. Further, every hygrometric variation, as well as every variation in the movement of the air, must vary the evaporation. This chief action, therefore, which, by continually emptying the ends of the capillary tubes, makes upward currents possible, is one which intermits every night, and every day is strong or feeble as circumstances determine. Then, in the third place, we have this rude pumping process above described, going on with greater vigour when the wind is violent, and with less vigour when it is gentle — drawing liquid *towards* different parts according to their degrees of oscillation, and *from* different parts according as they can most readily furnish it. And now let us ask what must result under changing conditions from these variously-conflicting and conspiring forces. When a warm sunshine, causing rapid evaporation, is emptying the vessels of the leaves, the osmotic and capillary actions that refill them will be continually aided by the pumping action of the swaying petioles, twigs, and branches, provided their oscillations are moderate. Under these conditions the current of sap, moving in the direction of least resistance, will set towards the leaves. But what will happen when the sun sets? There is now nothing to determine currents either upwards or downwards, except the relative rates of growth in the parts and the relative demands set up by the oscillations; and the oscillations acting alone, will draw sap to the oscillating parts as much from above as from below. If the resistance to be overcome by a current setting back from the leaves is less than the resistance to be overcome by a current setting up from the roots, then a current will set back from the leaves. Now it is, I think, tolerably manifest that in the swaying twigs and minor branches, less force will be required to overcome the inertia of the short columns of liquid between them and the leaves than to overcome the inertia of the long columns between them and the roots. Hence during the night, as also at other times when evaporation is not going on, the sap will be drawn out of the leaves into the adjacent supporting parts; and their nutrition will be increased. If the wind is strong enough to produce a swaying of the thicker branches, the back current will extend to them also; and a further strengthening will result from their absorption of the elaborated sap. And when the great branches and the stem are bent backwards and forwards by a gale, they too will share in the nutrition. It may at first sight seem that these parts, being nearer to the roots than to the leaves, will draw their supplies from the roots only. But the quantity which the roots can furnish is insufficient to meet so great a demand. Under the conditions described, the exudation of sap from the vessels will be very great, and the draught of liquid required to refill them, not satisfied by that which the root-fibres can take in, will extend to the leaves. Thus sap will flow to the several parts according to their respective degrees of activity—to the leaves while light and heat enable them to discharge their functions, and back to the twigs, branches, stem, and roots when these become active and the leaves inactive, or when their activity dominates over that of the leaves. And this distribution of nutriment, varying with the varying activities of the parts, is just such a distribution as we know must be required to keep up the organic balance.

To this explanation it may be objected that it does not account for the downward current of sap in plants that are sheltered. The stem and roots of a drawing-room Geranium display a thickening which implies that nutritive matters have descended from the leaves, although there are none of those oscillations by which the sap is said to be drawn downwards as well as upwards. The reply is, that the stem and roots tend to repeat their typical structures, and that the absorption of sap for the formation of their respective dense tissues, is here the force which determines the descent. Indeed it must be borne in mind that the mechanical strains and the pumping process which they keep up, as well as the distention caused by osmose, do not in themselves produce a current either upwards or downwards: they simply help to move the sap towards that place where there is the most rapid abstraction of it—the place towards which its motion is least resisted. Whether there is oscillation or whether there is not, the physiological demands of the different parts of the plant determine the direction of the current; and all which the oscillations and the distention do is to facilitate the supply of these demands. Just as much, therefore, in a plant at rest as in a plant in motion, the current will set downwards when the function of the leaves is arrested, and when there is nothing to resist that abstraction of sap caused by the tendency of the stem- and root-tissues to assume their typical structures. To which admission, however, it must be added that since this typical structure assumed, though imperfectly assumed, by the hot-house plant, is itself interpretable as the inherited effect of external mechanical actions on its ancestors, we may still consider the current set up by the assumption of the typical structure to be indirectly due to such actions.

Interesting evidence of another order here demands notice. In the course of experiments on the absorption of dyes by leaves, it happened that in making sections parallel to the plane of a leaf, with the view of separating its middle layer containing the vessels, I came upon some structures that were new to me. These structures, where they are present, form the terminations of the vascular system. They are masses of irregular and imperfectly united fibrous cells, such as those out of which vessels are developed; and they are sometimes slender, sometimes bulky—usually, however, being more or less club-shaped. In transverse sections of leaves their distinctive characters are not shown: they are taken for the smaller veins. It is only by carefully slicing away the surface of a leaf until we come down to that part which contains them, that we get any idea of their nature. Fig. 1 represents a specimen taken from a leaf of *Euphorbia neriifolia.* Occupying one of the interspaces of the ultimate venous network, it consists of a spirally-lined duct or set of ducts, which connects with the neighbouring vein a cluster of half-reticulated, half-scalariform cells. These cells have projections, many of them tapering, that insert themselves into the adjacent intercellular spaces, thus producing an extensive surface of contact between the organ and the imbedding tissues. A further trait is, that the ensheathing prosenchyma is either but little developed or wholly absent; and consequently this expanded vascular structure, especially at its end, comes immediately in contact with the tissues concerned in assimilation. The leaf of *Euphorbia neriifolia* is a very fleshy one; and in it these organs are distributed through a compact, though watery, cellular mass. But in any leaf of the ordinary type which possesses them, they lie in the network parenchyma composing its lower layer; and wherever they occur in this layer its cells unite to enclose them. This arrangement is shown in fig. 2, representing a sample from the Caoutchouc-leaf, as seen with the upper part of its envelope removed; and it is shown still more clearly in a sample from the leaf of *Panax Lessonii*, fig. 3. Figures 4 and 5 represent, without their sheaths, other such organs from the leaves of *Panax Lessonii* and *Clusia flava.* Some relation seems to exist between their forms and the thicknesses of the layers in which they lie. Certain very thick leaves, such as those of *Clusia flava*, have them less abundantly distributed than is usual, but more massive. Where the parenchyma is developed not to so great an extreme, though still largely, as in the leaves of Holly, *Aucuba*, *Camellia*, they are not so bulky; and in thinner leaves, like those of Privet, Elder, &c., they become longer and less conspicuously club-shaped. Some adaptations to their respective positions seem implied by these modifications; and we may naturally expect that in many thin leaves these free ends, becoming still narrower, lose the distinctive and suggestive characters possessed by those shown in the diagrams. Relations of this kind are not regular, however. In various other genera, members of which I have examined, as *Rhus*, *Viburnum*, *Griselinia*, *Brexia*, *Botryodendron*, *Pereskia*, the variations in the bulk and form of these structures are not directly determined by the spaces which the leaves allow: obviously there are other modifying causes. It should be added that while hese expanded free extremities graduate into tapering free extremities, not differing from ordinary vessels, they also pass insensibly into the ordinary inosculations. Occasionally, along with numerous free endings, there occur loops; and from such loops there are transitions to the ultimate meshes of the veins.

These organs are by no means common to all leaves. In many that afford ample spaces for them they are not to be found. So far as I have observed, they are absent from the thick leaves of plants which form very little wood. In *Sempervivum*, in *Echeveria*, in *Bryophyllum*, they do not appear to exist; and I have been unable to discover them in *Kalanchoë rotundifolia*, in *Kleinia ante-euphorbium* and *ficoides*, in the several species of *Crassulà*, and in other succulent plants. It may be added that they are not absolutely confined to leaves, but occur in stems that have assumed the functions of leaves. At least I have found, in the green parenchyma of *Opuntia*, organs that are analogous though much more rudely and irregularly formed. In other parts, too, that have usurped the leaf-function, they occur, as in the phyllodes of the Australian Acacias. These have them abundantly developed; and it is interesting to observe that here, where the two vertically-placed surfaces of the flattened-out petiole are equally adapted to the assimilative function, there exist two layers of these expanded vascular terminations, one applied to the inner surface of each layer of parenchyma.

Considering the structures and positions of these organs, as well as the natures of the plants possessing them, may we not form a shrewd suspicion respecting their function? Is it not probable that they facilitate absorption of the juices carried back from the leaf for the nutrition of the stem and roots? They are admirably adapted for performing this office. Their component fibrous cells, having angles insinuated between the cells of the parenchyma, are shaped just as they should be for taking up its contents; and the absence of sheathing tissue between them and the parenchyma facilitates the passage of the elaborated liquids. Moreover there is the fact that they are allied to organs which obviously have absorbent functions. I am indebted to Dr. Hooker for pointing out the figures of two such organs in the "Icones Anatomicæ" of Link. One of them is from the end of a dicotyledonous root-fibre, and the other is from the prothallus of a young Fern. In each case a cluster of fibrous cells, seated at a place from which liquid has to be drawn, is connected by vessels with the parts to which liquid has to be carried. There can scarcely be a doubt, then, that in both cases absorption is effected through them. I have met with another such organ, more elaborately constructed, but evidently adapted to the same office, in the common Turnip-root. As shown by the end view and longitudinal section in figs. 6 and 7, this organ consists of rings of fenestrated cells, arranged with varying degrees of regularity into a funnel, ordinarily having its apex directed towards the central mass of the Turnip, with which it has, in some cases at least, a traceable connexion by a canal. Presenting as it does an external porous surface terminating one of the branches of the vascular system, each of these organs is well fitted for taking up with rapidity the nutriment laid by in the Turnip-root, and used by the plant when it sends up its flower-stalk. Nor does even this exhaust the analogies. The cotyledons of the young bean, experimented upon as before described, furnished other examples of such structures, exactly in the places where, if they are absorbents, we might expect to find them. Amid the branchings and inosculations of the vascular layer running through the mass of nutriment deposited in each cotyledon, there are conspicuous free terminations that are club-shaped, and prove to be composed, like those in leaves, of irregularly formed and clustered fibrous cells; and some of them, diverging from the plane of the vascular layer, dip down into the mass of starch and albumen which the young plant has to utilize, and which these structures can have no other function but to take up.

Besides being so well fitted for absorption, and besides being similar to organs which we cannot doubt are absorbents, these vascular terminations in leaves afford us yet another evidence of their functions. They are seated in a tissue so arranged as specially to facilitate the abstraction of liquid. The centripetal movement of the sap must be set up by a force that is comparatively feeble, since, the parietes of the ducts being porous, air will enter if the tension on the contained columns becomes considerable. Hence it is needful that the exit of sap from the leaves should meet with very little resistance. Now were it not for an adjustment presently to be described, it would meet with great resistance, notwithstanding the peculiar fitness of these organs to take it in. Liquid cannot be drawn out of any closed cavity without producing a collapse of the cavity's sides; and if its sides are not readily collapsible, there must be a corresponding resistance to the abstraction of liquid from it. Clearly the like must happen if the liquid is to be drawn out of a tissue which cannot either diminish in bulk bodily or allow its components individually to diminish in bulk. In an ordinary leaf, the upper layer of parenchyma, formed as it is of closely-packed cells that are without interspaces, and are everywhere held fast within their framework of veins, can neither contract easily as a mass, nor allow its separate cells to do so. Quite otherwise is it with the network-parenchyma below. The long cells of this, united merely by their ends and having their flexible sides surrounded by air, may severally have their contents considerably increased and decreased without offering appreciable resistances; and the network-tissue which they form will, at the same time, be capable of undergoing slight expansions and contractions of its thickness. In this layer occur these organs that are so obviously fitted for absorption. Here we find them in direct communication with its system of collapsible cells. The probability appears to be, that when the current sets into the leaf, it passes through the vessels and their sheaths chiefly into the upper layer of cells (this upper layer having a larger surface of contact with the veins than the lower layer, and being the seat of more active processes); and that the juices of the upper layer, enriched by the assimilated matters, pass into the network parenchyma, which serves as a reservoir from which they are from time to time drawn for the nutrition of the rest of the plant, when the actions determine the downward current. Should it be asked what happens where the absorbents, instead of being inserted in a network parenchyma, are, as in the leaves of *Euphorbia neriifolia*, inserted in a solid parenchyma, the reply is, that such a parenchyma, though not furnished with systematically arranged air-chambers, nevertheless contains air in its intercellular spaces; and that when there occurs a draught upon its contents, the expansion of this air and the entrance of more from without, quickly supply the place of the abstracted liquid.

If then, returning to the general argument, we conclude that these expanded terminations of the vascular system in leaves are absorbent organs, we find a further confirmation of the views set forth respecting the alternating movement of the sap along the same channels. These spongioles of the leaves, like the spongioles of the roots, being appliances by which liquid is taken up to be carried into the mass of the plant, we are obliged to regard the vessels that end in these spongioles of the leaves as being the channels of the down current whenever it is produced. If the elaborated sap is abstracted from the leaves by these absorbents, then we have no alternative but to suppose that, having entered the vascular system, the elaborated sap descends through it. And seeing how, by the help of these special terminations, it becomes possible for the same vessels to carry back a quality of sap unlike that which they bring up, we are enabled to understand tolerably well how this rhythmical movement produces a downward transfer of materials for growth.

The several lines of argument may now be brought together; and along with them may be woven up such evidences as remain. Let me first point out the variety of questions to which the hypothesis supplies answers.

It is required to account for the ascent of sap to a height beyond that to which capillary action can raise it. This ascent is accounted for by the propulsive action of transverse strains, joined with that of osmotic distention. A cause has to be assigned for that rise of sap which, in the spring, while yet there is no considerable evaporation to aid it, goes on with a power which capillarity does not explain. The co-operation of the same two agencies is assignable for this result also.* The circumstance that vessels and ducts here contain sap and there contain air, and at the same place contain at different seasons now air and now sap is a fact calling for explanation. An explanation is furnished by these mechanical actions which involve the entrance or expulsion of air according to the supply of liquid. That vessels and ducts which were originally active sap-carriers go completely out of use, and have their function discharged by other vessels or ducts, is an anomaly that has to be solved. Again, we are supplied with a solution: these deserted vessels and ducts are those which, by the formation of dense tissue outside of them, become so circumstanced that they cannot be compressed as they originally were. A channel has to be found for the downward current of sap, which, on any other hypothesis than the foregoing, must be a channel separate from that taken by the upward current; and yet no good evidence of a separate channel has been pointed out. Here, however, the difficulty disappears, since one channel suffices for the current alternating upwards and downwards according to the conditions. Moreover there has to be found a force producing or facilitating the downward current, capable even of drawing sap out of drooping branches; and no such force is forthcoming. The hypothesis set forth dispenses with this necessity: under the recurring change of conditions, the same distention and oscillation which before raised the sap to the places of consumption, now bring it down to the places of consumption. A physical process has to be pointed out by which the material that forms dense tissue is deposited at the places where it is wanted, rather than at other places. This physical process the hypothesis indicates. It is requisite to find an explanation of the fact that, when plants ordinarily swayed about by the wind are grown indoors, the formation of wood is so much diminished that they become abnormally slender. Of this an explanation is supplied. Yet a further

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* It seems probable, however, that osmotic distention is here, especially, the more important of the two factors. The rising of the sap in spring may indirectly result, like the sprouting of the seed, from the transformation of starch into sugar. During germination, this change of an oxy-hydro-carbon from an insoluble into a soluble form, leads to rapid endosmose; consequently to great distention of the seed; and therefore to a force which thrusts the contained liquids into the plumule and radicle, and gives them power to displace the soil in their way: it sets up an active internal movement when neither evaporation nor the change which light produces can be operative. And similarly, if, in the spring, the starch stored up in the roots of a tree passes into the form of sugar, the unusual osmotic absorption that arises will cause an unusual distention—a distention which, being resisted by the tough bark of the roots and stem, will result in a powerful upward thrust of the contained liquid.

fact to be interpreted is, that in the same individual plant homologous parts, which, according to the type of the plant, should be equally woody, become much thicker one than another if subject to greater mechanical stress. And of this too an interpretation is similarly afforded.

Now the sufficiency of the assigned actions to account for so many phenomena not otherwise explained, would be strong evidence that the rationale is the true one, even were it of a purely hypothetical kind. How strong, then, becomes the reason for believing it the true one when we remember that the actions alleged demonstrably go on in the way asserted. They are ever operating before our eyes; and that they produce the effects in question is a conclusion deducible from mechanical principles, a conclusion established by induction, and a conclusion verified by experiment. These three orders of proof may be briefly summed up as follows.

That plants which have to raise themselves above the earth's surface, and to withstand the actions of the wind, must have a power of developing supporting structure, is an *à priori* conclusion which may be safely drawn. It is an equally safe *à priori* conclusion, that if the supporting structure, either as a whole or in any of its parts, has to adapt itself to the particular strains which the individual plant is subject to by its particular circumstances, there must be at work some process by which the strength of the supporting structure is everywhere brought into equilibrium with the forces it has to bear. Though the typical distribution of supporting structure in each kind of plant may be explained teleologically by those whom teleological explanations satisfy; and though otherwise this typical distribution may be ascribed to natural selection acting apart from any directly adaptive process; yet it is manifest that those departures from the typical distribution which fit the parts of each plant to their special conditions are explicable neither teleologically nor by natural selection. We are, therefore, compelled to admit that, if in each plant there goes on a balancing of the particular strains by the particular strengths, there must be a physical or physico-chemical process by which the adjustments of the two are effected. Meanwhile we are equally compelled to admit, *à priori*, that the mechanical actions to be resisted, themselves affect the internal tissues in such ways as to further the increase of that dense substance by which they are resisted. It is demonstrable that bending the petioles, shoots, and stems must compress the vessels beneath their surfaces, and increase the exudation of nutritive matters from them, and must do this actively in proportion as the bends are great and frequent; so that while, on the one hand, it is a necessary deduction that, if the parts of each plant are to be severally strengthened according to the several strains, there must be some direct connexion between strains and strengths, it is, on the other hand, a necessary deduction from mechanical principles that the strains do act in such ways as to aid the increase of the strengths. How a like correspondence between two *à priori* arguments holds in the case of the circulation, needs not to be shown in detail. It will suffice to remind the reader that while the raising of sap to heights beyond the limit of capillarity implies some force to effect it, we have in the osmotic distention and the intermittent compressions caused by transverse strains, forces which, under the conditions, cannot but tend to effect it; and similarly with the requirement for a downward current, and the production of a downward current.

Among the inductive proofs we find a kindred agreement. Different individuals of the same species, and different parts of the same individual, do strengthen in different degrees; and there is a clearly traceable connexion between their strengthenings and the intermittent strains they are exposed to. This evidence, derived from contrasts between growths on the same plant or on plants of the same type, is enforced by evidence derived from contrasts between plants of different types. The deficiency of woody tissue which we see in plants called succulent, is accompanied by a bulkiness of the parts which prevents any considerable oscillations; and this character is also habitually accompanied by a dwarfed growth. When, leaving these relations as displayed externally, we examine them internally, we find the facts uniting to show, by their agreements and differences, that between the compression of the sap-canals and the production of wood there is a direct relation. We have the facts, that in each plant, and in every new part of each plant, the formation of sap-canals precedes the formation of wood; that the deposit of woody matter, when it begins, takes place around these sap-canals, and afterwards around the new sap-canals successively developed; that this formation of wood around the sap-canals takes place where the coats of the canals are demonstrably permeable, and that the amount of wood-formation is proportionate to the permeability. And then that the permeability and extravasation of sap occur wherever, in the individual or in the type, there are intermittent compressions, is proved alike by ordinary cases and by exceptional cases. In the one class of cases we see that the deposit of wood round the vessels begins to take place when they come into positions that subject them to intermittent compressions, while it ceases when they become shielded from compressions. And in the other class of cases, where, from the beginning, the vessels are shielded from compression by surrounding fleshy tissue, there is a permanent absence of wood-formation.

To which complete agreement between the deductive and inductive inferences has to be added the direct proof supplied by experiments. It is put beyond doubt by experiment that the liquids absorbed by plants are distributed to their different parts through their vessels—at first by the spiral or allied vessels originally developed, and then by the better-placed ducts formed later. By experiment it is demonstrated that the intermittent compressions caused by oscillations urge the sap along the vessels and ducts. And it is also experimentally proved that the same intermittent compressions produce exudation of sap from vessels and ducts into the surrounding tissue.

That the processes here described, acting through all past time, have sufficed of themselves to develope the supporting and distributing structures of plants, is not alleged. What share the natural selection of variations distinguished as spontaneous, has had in establishing them, is a question which remains to be discussed. Whether acting alone natural selection would have sufficed to evolve these vascular and resisting tissues, I do not profess to say. That it has been a co-operating cause, I take to be self-evident: it must all along have furthered the action of any other cause, by preserving the individuals on which such other cause had acted most favourably. Seeing, however, the conclusive proof which we have that another cause has been in action—certainly on individuals, and, in all probability, by inheritance on races—we may most philosophically ascribe the genesis of these internal structures to this cause, and regard natural selection as having here played the part of an accelerator.

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## EXPLANATION OF PLATE.

Fig. 1. Absorbent organ from the leaf of *Euphorbia neriifolia.* The cluster of fibrous cells forming one of the terminations of the vascular system is here imbedded in a solid parenchyma.

Fig. 2. A structure of analogous kind from the leaf of *Ficus elastica.* Here the expanded terminations of the vessels are imbedded in the network parenchyma, the cells of which unite to form envelopes for them.

Fig. 3. Shows on a larger scale one of these absorbents from the leaf of *Panax Lessonii.* In this figure is clearly seen the way in which the cells of the network parenchyma unite into a closely-fitting case for the spiral cells.

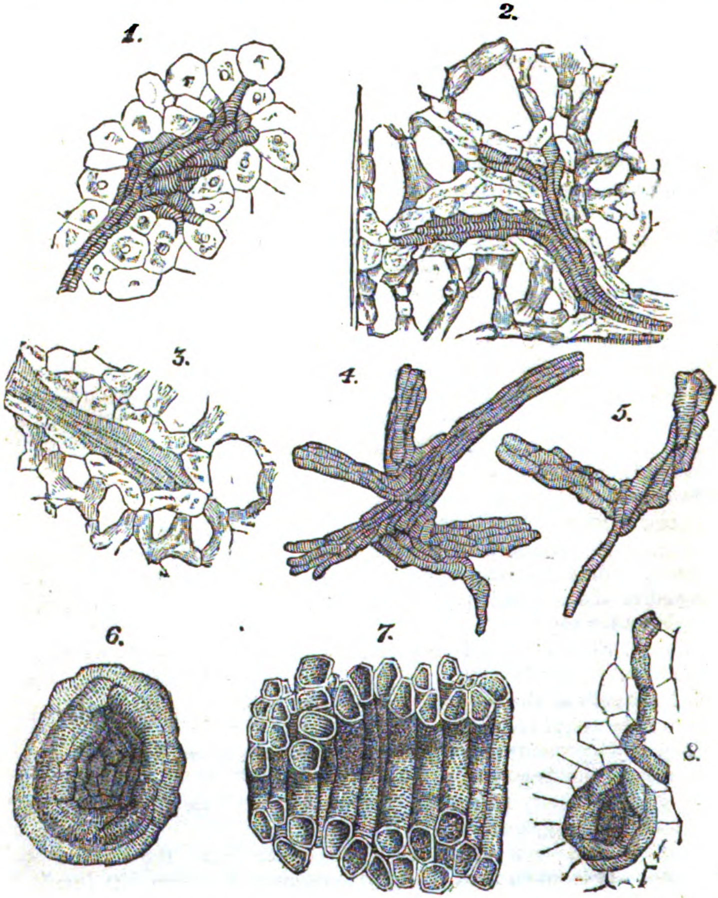
Fig. 4. Represents a much more massive absorbent from the same leaf, the surrounding tissues being omitted.

Fig. 5. Similarly represents, without its sheath, an absorbent from the leaf of *Clusia flava.*

Fig. 6. End view of an absorbent organ from the root of a Turnip. It is taken from the outermost layer of vessels. Its funnel-shaped interior is drawn as it presents itself when looked at from the outside of this layer; its narrow end being directed towards the centre of the Turnip.

Fig. 7 A longitudinal section through the axis of another such organ, showing its annuli of reticulated cells when cut through. The cellular tissue which fills the interior is supposed to be removed.

Fig. 8. A less-developed absorbent, showing its approximate connexion with a duct. In their simplest forms, these structures consist of only two fenestrated cells, with their ends bent round so as to meet. Such types occur in the central mass of the Turnip, where



the vascular system is relatively imperfect. Besides the comparatively regular forms of these absorbents, there are forms composed of amorphous masses of fenestrated cells. It should be added that both the regular and irregular kinds are very variable in their numbers: in some turnips they are abundant, and in others scarcely to be found. Possibly their presence depends on the age of the Turnip.