ciding with Von Martius in the supposition that the Marajó mounds were made by Indians of Tupí descent. There are many resemblances between the pottery of Marajó and that of Peru and North America that will be worth study. I hope that future explorations will enable me to clear up some of the doubts expressed in this paper, and cast much needed light on the ancient races of the Amazonian valley.

APPLICATION OF THE DARWINIAN THEORY TO FLOWERS AND THE INSECTS WHICH VISIT THEM.*

THE first impression which flowers make upon us with the beauty of their radiate and symmetrical forms, their luxuriant display of colors and the variety and sweetness of their odors, easily begets in us the idea that they were created for delighting and gratifying our senses.

This, however, is a pleasing fancy which the Darwinian doctrine speedily annihilates. This doctrine teaches us that all the species of animals and plants now in existence are only the result of the same laws which, starting from the beginning of organic life on the earth and coming down to our day, have governed and continue to govern all animated things ; and these are the laws of hereditary transmission and variation, of the struggle for existence and the consequent necessity that only those forms survive which best respond to external circumstances.

According to the Darwinian doctrine all the characteristics and properties of animals and plants appeared at first only as simple, *individual variations*, which were a necessary consequence of determinate physical and chemical actions,† and which, if they have

*Discourse delivered by Dr. ERM. MULLER of Lippstadt at the 26th General Assembly of the Naturhistorischen Verein für Rheinland und Westphalen, 1869. Translated into Italian from the German with Annotations by Prof. FREDERIC DELPINO. Translated for the NATURALIST from the Italian by R. L. PACKARD.

† The lively sense of fraternal friendship which unites me with the able author of this discourse cannot dissuade me from expressing my own views whenever they differ from his. I also am profoundly convinced that all variations were at first merely phenomena of individual variations subsequently fixed by the laws of hereditary descent,

been perpetuated, owe it to the circumstance that, in the struggle for existence, they were advantageous to those individuals in which they appeared. From the Darwinian doctrine, then, there springs the following thesis, which is of general application; that *in all animals and in all plants there is not a single characteristic, a single property, which is not either useful to its possessor, or at least is not inherited from ancestors more or less remote, for whom, at some time, it procured a decided advantage in the battle of life.*

Therefore, if we wish to apply the Darwinian doctrine to the rich and varied kingdom of Flora, we should, in the first place, answer this question: in what manner and by what means have the brilliant colors, the diverse odors, and the variegated structure of their flowers been of use to plants? The solution of this question cannot be obtained from a consideration of the flowers alone, for their properties are not *immediately* useful, but only *mediately;* and the mediation is accomplished by insects.

That flowers are visited by insects in various ways, and that many of them—bees, for example—are constrained to visit them for food, is well known; but this fact does not suffice to explain how these visits can be advantageous to the plants. Colors, odors, pollen, and honey seem at first sight to be of utility only to insects. If, as did C. C. Sprengel towards the close of the last century, we should propose to consider how insects act upon plants, and the wonderful conformity of floral structure which certain plants have with certain insects, we, like Sprengel, would easily fall into the belief that such harmonies are the cause of the insects effecting, without either knowing or willing it, the transfer of pollen from the anthers to the stigmas, while seeking their food in the flowers. But why should nature have entrusted to insects the

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but can in no way admit that the causes of these variations were *only determinate chemico-physical actions.* For who has ever been able to determine them, and who will ever be able? I should rather say that the causal principle of these variations is an intrinsic and not external one; an intrinsic principle reacting during the whole of life against extrinsic influences, or chemical and physical agents. I am far from wishing to deny the action or influence of external circumstances; but I think that these, as long as life lasts, and within certain limits, are ruled over by that internal principle, intelligent and free, which I suppose incarnate in all living things. I candidly confess that my mode of thinking is purely and simply theoretical; but the contrary thesis maintained by Müller and all the naturalists of our age, is also purely and simply theoretical, and always will be! and theory for theory, I prefer my own.

As to which of the two theories, the dualistic or the monistic, will ultimately gain the victory, I think I do not err in saying that the question is and always has been insoluble.

accomplishment of this transfer, when it would have been much more simple to dispose the organs in such a way that the anthers might cast the pollen immediately upon the stigmas? The reason of this Sprengel failed to comprehend, nor should we be more successful without recognizing an important natural law recently detected by the author of the doctrine of natural selection.*

Charles Darwin saw, what Sprengel failed to see, that the principal effect of the action of insects upon plants is the transfer of the pollen of one individual to the stigma of another. To this conclusion he was led by his beautiful researches on the floral structure and the fecundation of Orchids. And from these he subsequently inferred that it is advantageous to every vegetable to have its pistils fecundated by the pollen of other individuals of the same species, rather than by its own. As soon as observation had made Darwin master of this great truth, he resorted to the control of experiment. The experiments made by him with unwearied diligence through a long series of years — scattering upon the stigmas of plants of the same species, sometimes their own pollen, sometimes that of others — placed it out of doubt that *the impollination of the stigmas with the pollen of other individuals, or the intercourse between distinct individuals, produces an offspring more numerous, more robust, and capable of greater development than if fecundation had been produced by its own pollen;* a thesis which subsequently became amply confirmed by the numerous experiments of Hildebrand, my brother Fritz, and others. The enigma of floral structure is then solved, and we will now pass to the

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*The author attributes to Charles Darwin the merit of having first formulated the law of the necessity of cross-fertilization even for hermaphrodites; but this law, already partially seen by Kœlreuter, was comprehended in nearly all its vigor by C. C. Sprengel.

Kœlreuter having in 1761 made the discovery that in the Malvaceæ, Epilobia and Polemonia, the stigmas are developed long after the anthers, and therefore have to be fecundated with pollen from other flowers, makes the following shrewd remark. "An id aliquid in recessu habeat, quod hujuscemodi flores nunquam proprio suo pulvere sed semper eo aliorum suæ speciei impregnentur, merito quæritur. Certe natura nil facit frustra."

C. C. Sprengel went further, and on p. 43 of his work, "Das entdeckte Geheimniss der Natur in Bau, und in der Befruchtung der Blumen" (1793) uses these memorable words: "Since there are so many unisexual flowers, and since among hermaphrodite flowers there are so many that do not mature the male and female organs at the same time, it *appears that nature does not wish that each flower should fecundate itself with its own pollen.*" And he cites as a support an experiment made by him upon the flowers of *Hemerocallis fulva* which, after being fecundated artificially with their own pollen never perfected the seeds.

principal applications of the foregoing thesis in the explanation of the forms and properties of flowers.

If it is true that intercourse between distinct individuals produces a more vigorous and numerous offspring, it is equally true that every variation in the flowers which favors the transfer of pollen from one individual to another secures a notable advantage to the individual in which it takes place, and therefore cannot fail to be fixed and perpetuated by means of natural selection.

Now, as far as we know, there are only two external agents which can effect this transfer, namely, the wind and insects; — naturally with the contingence of very different floral structure.*

The different species of plants, as concerns the variations which first appeared in them, would, by natural selection, accommodate themselves to the wind or the visits of insects, by suitably modelling their flowers either upon an anemophilous or an entomophilous type.† The action of the wind is simple and uniform, while that of insects is extremely varied: therefore their self-adaptation to the action of the wind presupposes a variation in a single and definite direction; whereas that to the visit of insects takes place in as many different ways as there are differences between individual insects; that is to say, differences in size, form, structure, habits, modes of life, sympathies, antipathies, seasons, etc. Therefore, from the Darwinian point of view, we should expect to find: first, that the variations of plants arising from adapting themselves to the multiform actions of insects should have taken place far more frequently than those due to their adapting themselves to the uniform action of the wind; second, that plants modified to receive

* The numerous observations made by me in this field of biological study put me in a condition to enlarge a little upon what the author says here. The fecundating agents of plants besides insects and the wind I think are the following natural agents: —

The humming birds (Trochilus, Ornismya, Nectarinia, etc.) for a great variety of tropical plants; snails for *Rhodea Japonica* and some Aroideæ; water for *Vallisneria spiralis*, probably for all the Zosteraceæ and all the Florideæ (according to the recent and beautiful observations of Thuret and Bornet).

As to humming birds, never having been able to visit tropical countries I was obliged to limit myself to conjectures, which have subsequently been partly confirmed by letters from Charles Darwin as regards the fecundation of the genus Strelitzia, and from Fritz Müller as regards that of certain Passifloræ, Salviæ and other Brazilian plants.

† The terms anemophilous for plants fecundated by the wind, and entomophilous for those fecundated by insects were proposed on p. 34–35 of a work of mine upon the *arrangements for fecundation in anthocarpous plants* (Florence, 1867), and have been adopted by Severino Axell in his fine work *Om anordningarna för de fanerogama växternas befrutkning* (Stockholm, 1869) and by some others. That is why I permit myselt to translate with such words the compound nouns *Wind-blüthen* and *Insect-blüthen,* used by the author, which cannot be literally translated.

the visits of insects should offer a much greater variety of floral forms than plants adapted to the wind.

These two propositions which are necessary consequences of the Darwinian doctrine are effectually confirmed by observation, for anemophilous flowers are not only less numerous than entomophilous,* but are also much less varied in their conformation.

The transfer of pollen by means of the wind demands that the anthers and stigmas be well exposed to the air, and it is also necessary for the pollen to be subtile and very light and dry, so as to be more easily carried by the air, and to be produced in enormous quantities so as to insure fixing upon the stigmas some one of its grains. Remarkable examples of such a disposition are afforded by the Cupuliferæ, Coniferæ, Graminaceæ, Juncaceæ and Plantaginaceæ.† If, for example, a bush of hazel in flower is shaken, or if

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* If we think of the immense number of individuals belonging to the essentially anemophilous families of the Coniferæ, Amentaceæ, Graminaceæ, Cyperaceæ and Juncaceæ, and of the great number of flowers which every individual of them usually bears, the statement that anemophilous flowers are less numerous than entomophilous is subject to dispute.

At bottom, however, the principle maintained by Müller is most just; and the only change which occurs to me is to substantiate for his proposition this other; *anemophilous species are not only much less numerous, but also much less varied in the structure of their flowers than entomophilous species;* a most true and splendid generalization, which explains why in cold countries where the generation of insects is opposed by the climate, the whole of the vegetation is composed of anemophilous and gregarious plants (firs, birches, Graminaceæ and Cyperaceæ), and therefore desolately monotonous and poor in form; while in warm countries where myriads of insects abound, vegetation is most rich in diversity of forms and therefore composed of species not gregarious but entomophilous or ornithophilous.

† The genus Plantajo furnished me a most interesting subject of study, since by examining some of its species I saw how by gradual transitions an anemophilous species can change to an entomophilous.

Plantago lanceolata, as far as I could observe, develops in three forms. One of these has a stout and very high scape with whitish anthers which are quite broad and tremble in the wind, inhabits meadows and is exclusively anemophilous, as I have never seen it visited by insects. Another form is found upon hills, the stalk is not so high as in the first, and like it is essentially anemophilous. I saw, however, occasionally a species of Halictus light upon its spikes and try to gather the pollen; but the structure of the flower is so ill-adapted to such a purpose that the greater part of the pollen fell to the earth without being of use either to the insect or the plant. The third form is of small size, inhabits mountains, the spikes are very short, and the filaments shorter than in the others. In the pastures upon the Apennines of Chiavari I saw a great number of bees flying diligently from one spike to another, collecting pollen with perfect success and providing equally well for a promiscuous intercourse between the plants. There is, therefore, a form of *Plantago* perfectly intermediate between the anemophilous and entomophilous forms, and equally capable of being fecundated by the wind or bees.

Now if we suppose the filaments of this form to become rigid and colored, the pollen unctuous and sticky, and the anthers to lose their special tremulousness, we should reach the gradual metamorphosis of anemophilous into entomophilous characters, and witness the formation of an entomophilous from an anemophilous species. Exactly we blow upon one of its mature catkins, we see at once small clouds of pollen emitted and carried away, and if immediately after we examine the surrounding stigmas we find very few which have not some granules of pollen attached to them. In this example, as a condition of the easy dispersion of the pollen by means of the wind, we have the excellent form of inflorescence of the male flowers arranged in catkins freely suspended in the air, and, as a condition of an inevitable intercourse between individuals, we find a separation of the sexes, which is a quite general phenomenon in anemophilous flowers. In other cases, for example in the Plantaginaceæ, the parts shaken by the wind are the anthers which hang suspended from long and very weak filaments, and the intercourse between individuals is obtained not by a separation of the sexes, but by a difference of time in the development of the sexual organs. In these plants, while the anthers are yet immature and enclosed within the floral envelope, the stigmas, perfectly mature, have already appeared in the form of long, plumose stalks; and only when the stigmas have passed maturity do the anthers appear. Such are the principal characteristic differences of anemophilous flowers.

The flowers fecundated by the intervention of insects are far more highly differentiated in the disposition of their parts. Yet here, too, some general conditions necessary to secure the visits of insects, and the transfer of pollen by their means can easily be determined. And in the first place, it is necessary that the insects should be able to distinguish such flowers at a distance. Now this can only obtain in three ways, either by means of the colors, or the odors, or both colors and odors at the same time. And this *a priori* deduction from the Darwinian doctrine is in harmony with the facts; for entomophilous flowers are either colored, or odorous, or colored and odorous at the same time. In like manner, odors and colors are *a priori* perfectly useless to anemophilous flowers, or those fecundated by the wind, and are not, therefore, properties which can be fixed by natural selection. With this, too, the reality corresponds perfectly, for anemophilous flowers have neither colors nor odors.

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what we here merely suppose, takes place in reality. The *Plantago media* is a Plantago which has become entomophilous; its stamens are of a beautiful rose color; the tremulousness of the anthers is lessened, the pollen has lost its volatility, and the plant is normally visited by *Bombus terrestris*, as I ascertained in the mountains above mentioned.

A second condition which is absolutely necessary to obtain a regular and indefectible visit of insects is, that the flowers furnish them some substance which is agreeable and of use to them. In the more simple cases, for example in Anemone and Clematis,* such a substance is the pollen which the insects feed upon, or gather as food for their larvæ. In other cases it is not only the pollen which is presented to them, but also honey, as in the Ranunculi, the Rosaceæ and many other plants. In still other cases the stamens withdraw themselves more or less from the depredatorial action of insects which then take from the flowers only honey. This takes place in the genera Salvia, Pedicularis, and Iris.†

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*Not all the Anemoneæ nor all the Clematideæ are without honey. *A. coronaria, hortensis, pavonina, nemorosa,* and *Hepatica* are without nectaries, or seemed to me to be so, but in *A. pratensis* and probably in all the forms of the subgenus Pulsatilla, the outer row of stamens show different stages of atrophy, and have anthers more or less abortive and changed into nectaries. As to Clematis, it is true that some of the species are without honey, at least none has yet been found in them; but in *C. Balearica* and some others, the more external filaments are dilated and transmuted into real introrse honey-bearing receptacles, which Bombi and Xylocopæ visit. Finally in *C. integrifolia*, although the outer stamens, which are hairy and diluted, have no nectar, the much narrower and glabrous inner ones have nectarifluous filaments.

It is very difficult to determine whether a flower has or has not honey. It is frequently found where least expected and secreted by entirely different organs. I have been frequently mistaken in the search. For instance, although I have had occasion for three or four years to study the flower of *Caltha palustris*, it is only a short time since I discovered that from each one of its carpels honey transudes through two small rhomboidal spaces in its external surface. The discovery was made while observing the deportment of a Halictus in one of the flowers. I noticed that it not only gathered the pollen, but sought something else, turning its proboscis towards the centre of the flower. Then, instructed by the insect, I examined the flower more closely and found that its nectaries secreted a very dense and white honey. It is an incontestable fact that, in this kind of search honey-bees show greater sagacity than we ourselves. The same, however, cannot be said of Diptera, which are in general of obtuse intelligence. And, in fact, all the flowers which are destined to be preferably visited and impollinated by Diptera (flesh-flies, Eristalidæ, Syrphidæ, etc.), secrete honey in broad and open nectaries, easily discovered.

It is singular how honey is secreted by the most different organs. Thus, in the single family of the Ranunculaceæ the honey is secreted, 1, by the reddish margins of the sepals in certain of the *Pæoniæ;* 2, by the petals in Ranunculus, Myosurus, Trollius, Isopyrum, Helleborum, Nigella, Delphinium, Aconitum, Coptis; 3, by the abortive anthers in *Anemone pratensis;* 4, by the filaments in some Clematideæ; 5, by the carpels in the genus Caltha. So that in the Ranunculaceæ we have the singular example of all the floral organs, petals, sepals, stamens, and carpels, assuming and abandoning alternately the function of secreting honey for the advantage of insects.

†This does not accord with my observations. Our species of Salvia are visited almost exclusively by bees. When they thrust their heads into the fauces of the flower to suck the honey, the anthers, by means of a curious hinge movement, scatter the pollen upon their backs. Now the honey bees and Bombi collect this pollen carefully, brushing their backs with their legs from time to time. The same is true of Iris. I have frequently surprised a Bombus (I am uncertain whether a *B. hortorum* or *terrestris*) and *Xylocopa violacea* entering one of the three mouths of the flowers of this plant, and covering its back with pollen; after visiting two or three flowers it would

In much rarer instances, insects seek in the flowers neither pollen nor honey, but a different substance. Some Coleoptera which are of comparatively little importance in the fecundation of flowers, suck the tissues of the floral organs. In the case of a small orchid from Brazil, according to my brother Fritz, the lip becomes filled with a kind of flour. In other Brazilian flowers there are fleshy excrescences which the insects visiting those flowers gnaw.* A

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rest a short time in order to brush itself with its legs and collect the pollen there accumulated. I have elsewhere described the admirable mechanism of the flowers of Pedicularineæ, by means of which bees in thrusting the proboscis into the melliferous coralline tube, cause all the pollen to fall upon their backs, which without doubt they collect with great diligence.

Thus the flowers in question, far from having dispositions tending to withdraw pollen from insects, have admirable adaptations for furnishing it to them with great speed and abundance. Nor are the flowers of Salvia, Pedicularis and Iris alone in this, but almost all those belonging to the labiate or papilionaceous types, which are characterized principally by being always irregular and more or less horizontal or pendent.

The flowers of the labiate type have the honey-food in the lower part and the pollen-food in the upper, so that insects visiting such flowers get the pollen upon their backs. To this type belong nearly all the plants which Linnæus calls *didynamous*, that is to say, nearly all the Labiatæ, Personatæ, Acanthaceæ, Lobeliaceæ, etc.

The flowers of the papilionaceous type have the position of the food curiously inverted; for the pollen is at the lower part and the honey at the upper, so that insects visiting these plants cover the abdomen and not the back with pollen. A large part of the Leguminaceæ are of this type, which is also seen in some Polygalæ, Fumariaceæ, in the genus Collinsia among the Personatæ, and in the genus Hyptis among Labiatæ, etc.

In flowers of the labiate type the anthers are guarded above by one or more petals shaped like a helmet; in those of the papilionaceous type they are guarded below by one or more petals shaped like a keel. Müller's error, which is very excusable, comes from not having well interpreted the scope or function of this protection of the anthers, which instead of keeping pollen from insects rather favors giving them the whole. And what is the purpose of this protection? It is the very important one of protecting the pollen from atmospheric agents, especially rain.

And while upon this I think it worth while to call to notice the fact that the flowers of the labiate and papilionaceous types are, at least in Europe, exclusively designed for bees, flies being too stupid to discover where the pollen and honey are, and the Lepidoptera (diurnal), which sometimes visit them not being able to open the carina or galea and thus contribute to cross fecundation. These plants, therefore, belong to that numerous class which I call melittophilous.

*In the flowers of Serapias there is a large, dark-purple protuberance, which I conjecture is designed to be attacked by some insect specially active in fecundating this plant. But in eastern Liguria, where this plant and *S. cordigera* abound, I never succeeded in surprising insects upon its flowers nor in discovering pollen-masses displaced or stigmas fecundated. But my friend Luigi Ricca, the distinguished botanist, succeeded in western Liguria in surprising a bee on *S. longipetala* with its head loaded with pollen-masses; but he did not notice whether it gnawed the protuberance or not.

One of the magnolias, *Illicium religiosum*, as I recently observed, produces in the centre of its flowers a group of very juicy *pseudostigmatic* papillæ, which doubtless furnish food to some particular Cetoniæ; which I am the more disposed to believe, as I have seen *C. aurata*, *stictaca* and others eagerly licking the stigmatic or circumstigmatic papillæ of *Magnolia grandiflora*, of which they are the real and peculiar fecundators.

In the same way the Ceteniæ, which are the normal fecundators of *Peonia montana*, small bee, formerly noticed by Réaumur, the *Anthocopa papaveris*, cuts from the flower of the wild poppy pieces of the petal for lining the walls of its cells.

A third condition is a suitable conformation of the pollen granules and the stigmas. The pollen should be able to attach itself to the bodies of insects, and the stigmas should be able to detach it therefrom.

This affixing the pollen to the bodies of insects could not occur except by means of a spinose surface of the pollen granules, as is the case in the genera Malva and Taraxacum, or a light viscous coating as in most plants: or unless, as in the Orchidaceæ and the Asclepiadaceæ, there is a singular mechanism which attaches to the bodies of the insects the entire mass of pollen contained in the anther-lobes. Hence we see why we should not expect to find in entomophilous flowers the dry and smooth pollen of the anemophilous.*

Instead of plumose stigmas, fitted to collect pollen diffused in the air, and appropriate to anemophilous plants, we find the stigmas of entomophilous flowers smooth or papillose, but always more or less viscid.

All the many differences in colors, odors, pollen and honey, and in the structure of the pollen and the stigmas, which characterize entomophilous flowers, can be explained with entire ease if we think how infinitely varied is the mode in which the numerous phalanx of anthophilous insects can transfer pollen from one flower to another. Therefore we should not expect to find perfection reached in this or that individual flower, for we see that different plants, in their relations with insects occupy different grades of perfection, which is in entire accord with the Darwinian doc-

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apparently suck by preference the red, fleshy disk (the morphological nature of which is so much in controversy) which encloses its carpels.

*Sometimes in the best pronounced entomophilous plants there is found pollen perfectly smooth, pulverulent, and light. But in these cases it is easy to account for the phenomenon. There is for instance a floral type essentially melittophilous common to the genera Borago, Cyclamen, Galanthus, etc. The flowers droop, and the connivent anthers enclose the style, forming a pyramid. The bees grasp this pyramid and pressing upon it, sprinkle the breast with pollen. It is clear that if the pollen had not been smooth and pulverulent, its discharge would not have been effected and the floral arrangement in question would be of no use.

For the same reason the pollen of *Rhinanthus* is pulverulent, smooth and dry, as it has to be scattered upon the backs of bees.

Likewise in the family of Melastomaceæ, and the genera Solanum, Cassia, Erica and others, the pulverosity of the pollen is in evident relation with the dehiscence of the anthers, having pores at their summits.

trine. It has not yet been satisfactorily shown whether or not there is any plant subject to a perennial self fecundation (selbst befruchtung), that is to say, any plant with hermaphrodite flowers where the stigmas are constantly and exclusively fecundated by their own anthers. This seems the most simple case, and was probably at first general.*

However it may be with many plants, in the case of the Ranunculaceæ, Papaveraceæ and Cruciferæ, the visits of insects effect with greater facility the impollination of the stigmas with the pollen of their own flowers (*homoclinous or homogamous impollination*) than the transfer of pollen from one flower to another (*heteroclinous impollination*).

Among primordial and homogamous plants every slightest variation which might open a way to the possibility of the transfer of pollen constituted a signal advantage; and therefore the variations of color, secretions of honey and viscosity of pollen, became fixed in the flower by natural selection. In other and more numerous cases to these simple dispositions others more complicated were added, and of such a nature as not only to favor the eventuality of heteroclinous fecundation, but render it inevitable and necessary. The sexes, for example, began to separate themselves as individuals or distinct flowers, as in the genus Salix and the

* Charles Darwin was the first to conjecture that primordial plants were essentially hermaphrodite or monoclinous, and that diclinous plants were later and had developed unisexual flowers in obedience to the grand principle of the division of physiological labor. Frederic Hildebrand (Die Geschlichter-Vertheilung bei den Pflanzen. Lips. 1867, p. 12–14), adopts the same opinion. In a work of mine (Atti della Soc. Ital. di Scienze nat. in Milano, vol. x, 1867, p. 275–277) I exposed summarily the reasons which caused me to embrace opinions diametrically opposite. Subsequently I collected a great number of data, all which confirmed me in my views. Severino Axell (on anordningarna för de fanerogama vaxternas befruktning, Stockholm, 1869, p. 89–93) strenuously defends my opinion to which he says he was led by a process of reasoning extremely like mine but entirely independent, since he heard of my work only after his own conclusions had been reached. This coincidence gives great weight to my argument, but as it is not a suitable place to develop it here, I will only mention that the families of plants received as primordial, for instance, the Coniferæ, Cycadeæ, and Amentaceæ are unisexual and anemophilous par excellence, while those which have experienced greater evolution and are more perfect, for instance, the Ranunculaceæ, Leguminosæ, Compositæ and the Corolliforæ in general, are eminently hermaphrodite and entomophilous.

Diœcious and monœcious plants form the primordial group (essentially anemophilous); from these are then developed polygamous plants (intermediate between anemophilous and entomophilous), and from these again the hermaphrodite plants (essentially entomophilous).

This harmonizes with paleontological data; but this important generalization I reserve to develop elsewhere with a sufficient amount of facts and arguments.

Cucurbitaceæ. Here it is obvious that the transfer of pollen by means of insects is rendered absolutely indispensable. In other plants, as in *Cerastium arvense*, the Umbelliferæ and Compositæ, although both sexes are united in the same flower, yet they are not developed contemporaneously; wherefore it is equally necessary for insects to transfer the pollen from one flower to another. Finally in many other plants the flowers are formed and disposed in such a way that the transfer of pollen by the agency of insects is greatly favored and frequently even rendered necessary.

From among the great number of floral arrangements which render heteroclinous impollination necessary, and which have been brought to light by the researches of Darwin, Hildebrand, Delpino and my brother Fritz, I will mention two which not long since appeared sufficiently enigmatical, which enigma, however, has recently been solved by direct observation of the fecundating insects; I mean the floral arrangements of the Orchis of our meadows, and *Cypripedium Calceolus*.

Orchis Morio, *mascula*, *latifolia* and *maculata* have a spur in their flowers in the cavity of which no honey is found. This absence of honey is a phenomenon without parallel in the vegetable kingdom. Sprengel on that account called them plants with *false nectaries* (Scheinsaft pflanzen), imagining that the insects which visit them are deceived by the odors, colors and form of the spur into inserting their heads into the fauces of the flower with the expectation of finding honey. He was never able, however, to observe how the fecundating insects conduct themselves in the flowers of these Orchises. He observed, indeed, frequently, masses of pollen displaced and sticking upon the stigma, and occasionally came upon dead flies in the flowers, whence he concluded that flies are the fecundators of these plants. Nevertheless, the floral arrangement of the Orchises remained somewhat mysterious to him. "It is inconceivable to me," he says on page 404 of his work, "how it is that such flowers produce no honey, when, as it seems to me, it would be much better for them to produce it with a view to enticing flies to visit them repeatedly and fecundate them."

It is clear that Sprengel himself was conscious of not having completely deciphered the enigma. Darwin, too, as we read in his work on the Orchids, never succeeded in surprising insects in the field Orchis, although he had observed them diligently not less than twenty years. Nevertheless, he proceeds to expose in detail the process of their fecundation, because his theory of natural selection, according to which only useful qualities can be fixed and preserved in living things, placed him in a condition to infer from simple inspection of the flowers, the details of the fecundative process.

As far as concerns the Orchis of our fields, Darwin had come to the conclusion that the insects visiting them might suck the honey enclosed between the inner and outer membranes of the spur, piercing the latter with their proboscis; that such an operation required the precise time necessary for the viscous stalks of the pollen-masses to attach themselves firmly upon the heads of the insects; and that the time occupied by the pollen-masses securely attached to the insects in becoming depressed upon their stalk so as to be able to rub against the stigma, corresponds nearly to the time employed by the insects in visiting one plant and passing to another. In this way, intercourse between two individuals would necessarily take place.

However, when we consider the immense number of such Orchids in the meadows, and reflect that insects have to perform several operations in order to fecundate them, it seems strange that they should never have been surprised at work by any one. Fortunately, I am able to fill up this gap and at the same time fully confirm Darwin's conclusions.

Towards the close of last spring I had taken a good many Bombi and some honey bees with several masses of pollen upon their heads, and I saw a *Bombus sylvarum* fly to the flowers of *Orchis Morio*, stick its proboscis into the spur and fly away with pollinaria upon its head. On another occasion, I saw at a distance a *Bombus lapidarius* fly to the flowers of *Orchis latifolia;* and I also saw a dipterous insect, *Volucella bombylans*, with the pollen-masses of *Orchis maculata* upon its head. However, during the spring I was not able to observe these insects closely enough to note exactly their movements and deportment.

But subsequently, on the sixth of this month (May, 1869) upon the heights of Stromberg, very abundant in Orchis, both I and my son Hermann were enabled with ease, and close at hand, to observe many Bombi at work. At a place full of *Orchis mascula* we saw a Bombus which appeared to be *B. terrestris* fly to the lowermost flower of a spike of this Orchis. It inserted its head into the flower, remaining about four seconds, and then withdrew it with two pollen-masses attached. Ascending from the bottom towards the top, it visited the second and third flowers of the same spike. After withdrawing its head from the third flower, it stopped a short time and endeavored to brush off the pollen-masses with its legs, but without success. It then continued its visit, climbing up the spike, and visited a fourth flower. At this point I tried to catch it in the net, but failed, and it flew away. After standing a short time we saw a *Bombus hortorum* visit three or four flowers from base to summit of a spike of *Orchis mascula*, after which it flew to another individual of the same species, visiting its flowers in the same way. Upon examining the stigmas of this second individual we found pollen scattered upon them, and the anther lobes emptied of their pollen-masses. In the space of about two hours, which we spent in observing this fecundation of *Orchis mascula*, we noted two visits of *Bombus lapidarius* and one *Psithyrus campestris*. The *Bombus lapidarius* did not remain in the flowers longer than from two to three seconds. We captured the *Psithyrus* and one *Bombus lapidarius*. Both had a quantity of pollen-masses upon their heads, some of which were already depressed upon their respective stalks, and therefore in a condition to rub against and fecundate the stigmas, while others were yet erect and therefore not in a condition to effect fecundation. Of ninety-seven bees collected by us in this excursion, thirty-two had pollen-masses stuck upon their heads. Sometimes we observed that the bees succeeded in freeing themselves from some of the pollen-masses, either by tearing them off with their mandibles or brushing them off with their fore-legs. Possibly, it is in this way that sometimes in the flowers of Orchis, pollen-masses are found in greater or less proximity to the stigma, out of place and, as it were, wasted.

At least a good third, then, of the bees collected on the heights of Stromberg were engaged in the fecundation of Orchises, and we can obtain an approximate measure of their activity by the following figures. At seven o'clock, A. M., in a meadow containing several thousand individuals of *Orchis mascula*, I collected ten spikes which had one hundred and seven open flowers, only three of which had the stigma smeared with pollen, and one alone was without pollen-masses. Towards five o'clock, P. M., I collected from the same meadow ten other spikes having ninety-seven flowers open. Fourteen of these flowers had the stigmas smeared with pollen, two of which still preserved the pollen-masses in place while the remaining twelve no longer had any. Two had a couple of pollen-masses stuck upon the edge of the stigma, and three were without any pollen-masses at all though the stigma was devoid of pollen. Thus at seven o'clock in the morning the fecundated flowers were in the ratio of two and one-half to one hundred, and at five o'clock in the evening the ratio had reached fourteen to one hundred.

Thus the conclusions of Darwin are fully confirmed by my observations. The bees must seek something in the spur of the flower or else they would not stop to visit them repeatedly. Since the honey is not free in the interior of the spur but is contained between its inner and outer membranes, the insects have to pierce this latter, which is very delicate and cannot offer the least difficulty.* Direct observation has shown that a stay of three or four sec-

* My studies thus far made upon field Orchis would lead me to different conclusions from those of Darwin and Müller. In the acts of the Italian Society of Natural Sciences of Milan (vol. 12, 1869, p. 129) I said: "this asserted deficiency of fecundation, together with the phenomenon of the absence of honey in many species of Orchis which have an enormous development of an *illusory* spur, *formerly* honey-bearing but now dry, produces the conviction that such Orchids are degenerate forms and more or less near extinction.

There is here a manifest example of imperfection or rather, organic degeneration, the pernicious effects of which are very obvious if we compare the scanty number of capsules in orchids, with the abundant fructificatión of *Spiranthes autumnalis*, *Loroglossum secundiflorum* and other Orchids which secrete a sweet fluid."

Darwin and Müller suppose that there is a secretion of nectar between the inner and outer membranes of the spur. Now, in all my observation, I never could see this honey. I indeed saw frequently, but not always, that the inside of the spur is vescicular, but when examined by the microscope I found that there is absolutely no trace of that glandulose tissue which is a constant characteristic of nectar-producing surfaces. Bèsides, reasons deduced from close analogy are against such a condition of things. Gymnadenia and Platanthera, which are closely related to them, have a spur entirely analogous to that of the Orchids, yet the honey they produce is not secreted in a vescicular hypodermis, but transudes in a normal manner.

I willingly admit that some liquid is frequently met with in such pores. In the vescicular parts of plants, e. g., in the summits of the inner petals of Dielytra, in the bladdery fruits of Colutea, Vesicaria, etc., drops of liquid are found, but these are only water of transpiration, or rather lymph, but never honey. It may happen that this lymph, which was found in abundance by Darwin in *Orchis pyramidalis* alone, really attracts *Acontia luctuosa* (one individual of which was found with its proboscis loaded with seven couples of pollen-masses), and other diurnal and nocturnal lepidoptera. But on the whole it seems improbable to me that the spurs, although lymphatic, yet not honey-bearing, of *Orchis morio*, *latifolia*, *maculata*, etc., should attract bees.

But bees, according to the positive observations of Müller, frequent and fecundate the flowers of Orchis. This fact signifies, according to my view, that they resort to them for some other purpose, which is to collect pollen which they find already prepared in a convenient form. It is more than probable that upon entering their hives loaded with bundles of pollen, they are soon freed by their companions from the annoyance they experience.

Sprengel calls the spur of Orchis a false nectary. Although in some plants I have onds is sufficient to stick the pollen-masses firmly upon the heads of the insects, and any one can easily convince himself of the fact by introducing into the flower a sharpened pencil, and holding it for three or four seconds when, upon withdrawing it, pollen-masses will be found adhering to it. It will also be found that in about forty seconds after drawing it out, these masses will have completed that movement of declination by virtue of which they can come in contact with the stigma. Now, as a bee, from what we observed, does not remain on a given spike longer than twenty or twenty-two seconds, it is clear that it cannot fecundate it with its own pollen, but only with that of spikes previously visited.

On the 11th of May, 1869, in the neighborhood of Lippstadt near Overhagen, I repeatedly saw bees effecting the fecundation of *Orchis latifolia*, but I observed nothing new, or in any way different from what I noted in the case of *Orchis mascula.*

Towards the close of last year I published in the acts of this Society an observation made in May, 1867, upon the fecundation of Cypripedium, which was in many respects incomplete because made under unpropitious circumstances, although I succeeded with the aid of the Darwinian theory, in completely explaining the part the different floral organs play in securing the fecundative process. But on the 16th of May, 1868, in the same locality, I was able to make a greater number of observations, and confirm all my conclusions. This place which was of limited extent had only six flowers of Cypripedium. Passing and repassing in the examination of the slipper-like flowers peculiar to this plant, I found in one of them, which half a minute before was empty, an *Andrena pratensis* which by its violent agitation could be perceived at the distance of several feet. Visibly disquieted by its imprisonment it tried at least twenty times to climb up the walls of the slipper, but these are so contorted, and of such a shape, that after every attempt the Andrena slipped back again into the flower. Finally, it retired to the base of the flower and pushed its head into one of the two small apertures there; but this being too narrow, it attempted to scale the walls anew, and not succeeding, ran back

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come upon organs or parts of organs, which really merit this appellation, it does not seem to me applicable here. I ascribed to Orchids an illusory spur, once perhaps honey-bearing, but now dry, and I think that is the better view. It is in favor of this view that orchids, at least in eastern Liguria, are almost entirely passed over by insects, and offer an incredibly small number of transformed pollen-masses and fecundated ovaries.

again to the small aperture, and then again climbed up with no better success than before. Then, after a short pause, it ran with greater impetus to one of the small apertures (to the left) and using all its strength, at length succeeded in pressing down the lip and pushing its head, thorax, fore legs, and finally its whole body through this aperture, and so was again at liberty. In this passage, its right shoulder rubbed against the anther overhanging the aperture and carried away a good deal of the pollen.

The flower of Cypripedium, then, must be considered as a trap for Andrenas which enter it, allured by a sweet exhalation, and the minute drops of honey exuding from the apices of certain hairs in the lip. If an Andrena visits this snare during the warmer hours of the day, that is to say, when it possesses its maximum vital energy, it easily succeeds after a few minutes in freeing itself from its prison, but not without first getting some pollen upon its back which will fecundate the stigma of the next flower it visits. But if it is caught in the cool of the evening, it must perforce make up its mind to take lodgings there for the night, and be content to escape from its unwelcome quarters during the warm hours of the next day.*

If small Andrenas falling into this trap have not strength enough to push aside the lip so as to escape through the small apertures,

*The structure of the flowers of *Cypripedium* relatively to the mode in which promiscuous intercourse is effected by means of insects, has been studied, in order of time, by Charles Darwin, Asa Gray, by myself, and by E. Müller.

Darwin (On the Contrivances, . . by which . . Orchids are fertilized by Insects) believed at first that the fecundation of the species of this genus took place by means of the proboscis of certain insects which, in being introduced by one of the two small holes of the sac, became covered with pollen which was then communicated to the stigma.

Gray soon after, from an examination of some American Cypripedia concluded that fecundation was effected by small insects entering the flower by the large opening, and leaving it covered with pollen by the small ones.

In 1866 I examined some exotic Cypripedia in Florence, and, though ignorant of Gray's observations, reached the same conclusion (On the arrangements for fecund. of anthoc., plants 1867, p. 20, 22).

The next year E. Müller (Beobacht. an West fälisch. Orchidera p. 1-6), established the truth of my conjectures, observing and describing the mode of action of certain andrenas in visiting and fertilizing the flowers of *C. Calceolus*.

In 1868 and 1869, having had occasion to study anew the flowers of some foreign Cypripedia (*C. barbatum* and others), I observed the manner in which large flies are imprisoned in them. It should be noted that not unfrequently in the Boboli botanical gardens the ovaries of Cypripedia ripen, without doubt, in consequence of the visits and imprisonment of these flies.

Ultimately Darwin (notes on the fertilization of Orchids, 1869, p. 16 and 17) cited the observations made on Cypripedium by Gray, myself, and Müller, fully admitting the results.

they die with hunger; and on the 17th of May, of this year (1869) I saw two dead individuals of *Andrena parvula* in the flowers of Cypripedium.

I here leave the first part of my subject, the application of the Darwinian doctrine to flowers, and pass to the second, which is the application of the same doctrine to the insects which visit the flowers.

As flowers are accommodated to the visits of insects, and as the meaning of the structure of flowers can only be comprehended by thoroughly knowing their entomological relations, so the insects which derive nutriment from flowers are accommodated to them, and the structure of their bodies cannot be well understood except in the relation of adaptation to flowers. And since, according to the Darwinian doctrine, the adaptations of insects to floral food can only be considered as characteristics slowly acquired by hereditary descent, we are necessarily led to distinguish inferior or primitive, and superior or posthumous forms. We are thus led to some indications of a genealogical tree of the insects which visit flowers.

These insects belong principally to three orders, the Hymenoptera, Diptera and Lepidoptera. The incentives, however, which urge them to visit flowers are different for each. The Lepidoptera suck honey exclusively; the Diptera devour pollen and are in the habit of sucking not only honey, but any sort of liquid; and, finally, the Hymenoptera which visit flowers, that is, bees, feed exclusively on honey and pollen, not only in their perfect state, but also as larvæ, so that they suck honey, eat pollen, and collect both for their young.

Of the three orders cited, that of Lepidoptera is the only one which is composed of families all of which are adapted to floral food, although only in the perfect state. Hence, it is that their buccal organs have a very uniform structure. The labrum and mandibles are entirely atrophied;* the maxillæ are transformed into two tubular [nearly], cylindrical and spirally twisted filaments which perform the function of a sucking tube; and at the base of these filaments are two rudimentary palpi. The inferior lip or labium is atrophied, and as a compensation its palpi are greatly developed.

*Their rudiments are readily seen, except in certain silk-worm moths, in which the labrum is entirely atrophied.— EDS. NATURALIST.

If we turn from those Lepidoptera, which, endowed with a long proboscis, hover without alighting, and suck honey from the bottom of flowers with the longest tubes, and regard those which are of an inferior grade of adaptation, we find all possible gradations from a long proboscis to a rudimentary one, where the buccal parts are yet recognizable under the form of small fleshy papillæ equally unsuited either to bite or suck. According to the Darwinian doctrine, all Lepidoptera are derived from a single stock, and their characteristic spiral proboscis must have been formed gradually by slight and innumerable variations, which in the struggle for existence, were advantageous to those individuals in which they appeared, and were, therefore, able to accumulate and become fixed in their posterity in accordance with the laws of hereditary transmission. Therefore, as a necessary consequence of this doctrine, we should expect to find that the order Lepidoptera offers in its lowest stage this characteristic of a spiral proboscis, and possesses those fleshy protuberances or rudimentary buccal organs which we see to-day possessed by not a few of its representatives. This conjecture, strictly deduced from the Darwinian doctrine, accords wonderfully with the opinion of entomologists of great authority, who admit that there is the closest affinity between the Phryganeidæ and Lepidoptera; and the Phryganeidæ have the buccal organs precisely in that rudimentary state which we should pre-suppose appropriate to the primordial race or type of Lepidoptera. And, further, to consider this affinity of the Phryganeidæ with butterflies, Réaumur deduced it from general considerations upon the analogies of the insects; De Geer from the analogous form of the wings, and from the internal structure of the larvæ; Kirby from analogies in the buccal organs, and Westwood from the habits of the case-bearing larvæ of the genera *Psyche* and *Tinea*, from the analogous covering of the wings in the Phryganeidæ and some Papilios, and from the tibiæ analogously spinose in the two groups.

The expression, "*close affinity*," employed by these entomologists is changed and resolved, in the language of the Darwinian doctrine, into *close relationship*, and signifies that both Lepidoptera and Phryganeidæ proceed from a single stock, which, both in the internal structure of its larvæ and their habit of dragging a sheath about with them, in the venation and covering of the wings, the spinose character of the tibiæ, the buccal organs reduced to fleshy protuberances, and in the long antennæ, would quite closely resemble the Phryganeidæ of to-day. The posterity of this stock separated into two parts. One of these continuing to live either in, or near the water, diverged little from the primitive customs, habits and forms, and came to constitute the group of Phryganeidæ. The other accustomed itself to suck the honey of flowers, withdrew itself little by little from the water, and, finding its new diet entirely acceptable, adapted itself to it completely, modifying the buccal organs, step by step, by successive variations always more convenient and more in harmony with its new mode of life, until in this way it gradually acquired a proboscis sufficiently long and dexterous to suck honey. It moreover, greatly developed its æsthetic sense of colors, at first in correspondence with the lively coloring of the flowers, and then in reference to sexual election. As soon as the hairy system of wings and body began to vary, which can happen the more easily the greater the surface of the hairs themselves becomes, until their complete conversion into variously tinted scales, the females would prefer those males which were adorned with the liveliest colors, and, vice versa, the males would select the most brilliantly adorned females.*

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* The relations of colors and odors which occur between flowers and their fertilizers, may to many appear a chimerical product of the imagination. But after a long series of observations I can assert that, however unexpected and surprising they may be, they are yet undeniable and real.

It is believed by many that the æsthetic sense belongs only to the human race. Nothing is more erroneous. The sense of music alone, however much it has been and perfected in birds through sexual selection, is beyond comparison more perfect in man. In the senses of taste and smell man is, by a singular coincidence, like bees and butterflies. Sweet things please our young not less than bees, and the ancient poets designated with the same word, nectar, the food of the gods and the honey of bees. By a no less singular coincidence the odors which allure bees and butterflies allure us too, and those which repel us repel bees. The graveolent flower of rue, which is so excessively disagreeable to us, although visited by flies, repels bees and Lepidoptera although it produces honey.

As to the æsthetic sense of colors and form, then, if we speak the plain truth, man is inferior to many living things.

Passing in review the most beautiful forms, and those adorned with the most attractive colors, we have on one side flowers, and on the other their fertilizers, that is, birds, flies, humming birds, Nectarineæ, lepidoptera, Bombylii, Syrphidæ and some Cetoniæ.

The most beautiful forms and brilliant tints in the world are without question those of the humming birds. They visit the most splendid and beautiful flowers on the earth, and the reason why the magnificent flowers of the tropical zone do not enter our climate is certainly correlative to the causes which exclude from temperate and cold countries the humming birds and gorgeous lepidoptera which are peculiar to warm regions.

But not all flowers are beautiful; there are some which have livid and repulsive

As to flies, it has been until now generally admitted that they are exclusively destined to fluid nutriment. But in the summer of 1867, I was somewhat surprised while observing in my garden an *Eristalis tenax* upon a flower of *Œnothera media*, to discover that it was eating the pollen. Resting upon its middle and hind legs, it thrust out its fleshy proboscis like an arm, seized a morsel of pollen with the two valves which terminate the proboscis, and tore it away from the anther. Since the pollen granules of Œnothera are tied together by elastic threads, that bit of pollen torn from the anther was attached to others by a band of threads, and the insect, in order to free its mouth from that inconvenient appendage began to use its fore-legs. Raising both together towards its mouth, it seized between them the cordon of threads, and rapidly rubbing them one against the other, much as we do in washing our hands, succeeded in cutting the threads and clearing them from its mouth and legs. Then it raised them again, and seized the two valves of the proboscis, thoroughly cleaning them of pollen, and the threads yet adhering to it; and in about three seconds this work of cleaning was complete. At the same time the valves of the proboscis, by rubbing against each other, had masticated the morsel of pollen, and had conveyed the single granules into the channel of the labium, whence they were pushed into the mouth. It had hardly finished cleaning its proboscis and eating the first mouthful of pollen, when it seized another portion and repeated each and all the operations I have described. It was so intent upon its meal, that I was able to observe it in the closest proximity without its manifesting the slightest fear.

The quantity of pollen which an Eristalis can devour in this way is surprising. Upon making a section of one and examining

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colors. Nor do all flowers emit a pleasant odor, since some have a fetid smell, or one like that of decaying animal matter.

All the flowers which have this (those, e. g., of Arum, Dracanculus, of the Stapeliæ, of some American Aristolochiæ, of the Rafflesiæ, Sapriæ, Brugmansiæ, Sapranthus, etc.) have without exception livid colors, and, like the skins of some serpents, are speckled with dark-purple and yellowish-black spots. Now all these flowers are fertilized exclusively by the flies which feed upon dead animals (*Sarcophaga carnaria*, *Musca vomitoria*, and the like).

The flowers of the Ceropegiæ, one *Aristolochia*, *Asarum*, and *Ambrosinia Bassii*, are fecundated exclusively by gnats (Phora, Ceratopogon, Cecydomya, Oscinis, etc.). All these have a generally livid tint speckled or striped with dark-purplish spots, and a putrid odor, for the most part like that of urine.

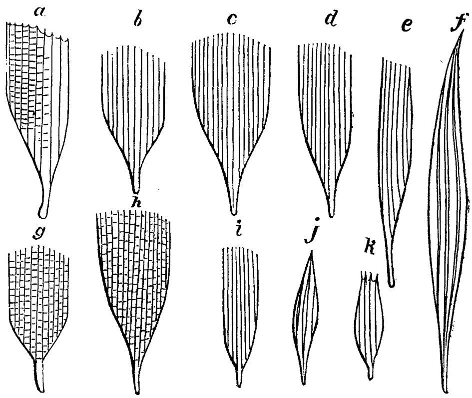
These few instances suffice to give an idea of the wonderful relations which occur between flowers and their fertilizing agents with reference to colors and odors.

the stomach, it appeared very large and was full of a yellow substance which consisted of hundreds of thousands of pollen-grains. I have had since then many opportunities to observe this eating of pollen, not only in all the species of Eristalis, but also in the genera Rhingia, Syrphus, Volucella and Scatophaga. This chewing of pollen alternates with sucking honey if the flowers have any, and I am of the opinion that the singular structure of the proboscis of flies cannot be fully explained without taking into account its double function of sucking honey and eating pollen. In the Tipulariæ and also in those flies which do not eat pollen but live exclusively upon juices, for instance, Bombylius, the two valves of the proboscis serve no other purpose than to protect and guide the sucking tubes, but in the flies which devour pollen besides this function there is also that of grinding the pollen, for which they have special adaptations, for the margins of the two valves at the point of union are transversely dentate with fine and parallel bands of chitine. Probably the greater or less distance of these bands in different species is related to the different size of the pollen upon which they feed.

Since the proboscis of the Tipulariæ often possesses one simple function and has in accordance with that a very simple organization, we may consider these Tipulariæ as the most ancient branch of the stock from which Diptera are derived. A fact casually discovered by me and of which I find no mention hitherto, seems to me of great importance in the systematic disposition of this order. In the spring of 1868, while engaged in examining the head of a gnat, with a view to ascertain whether or not the valves of its proboscis had the transverse bands of chitine, I was surprised to discover that the proboscis and palpi were clothed with scales entirely like those of butterflies.

I find no mention of this important fact in the special works of Meigen and Schiner which are in my possession. Meigen simply points out that in Culex, Anopheles, and Corethra, scaly productions are observed on the venation of the wings, and he figures some of them which, however, being quite narrow and with two sharp points, have no analogy with real lepidopterous scales. The gnat-scales observed by me and figured accurately (fig. 73) closely resemble the most characteristic lepidopterous scales. They suddenly dilate from a short and narrow peduncle to a large scutiform surface which is traversed longitudinally by a few parallel ridges between which, when more highly magnified, transverse wavy lines, very fine and numerous, are seen. The only difference which these scales present compared with those of butterflies is, that in the former the transverse lines are not so fine, so regular, nor so regularly distributed over the whole surface; also these lines are entirely wanting upon the scales of some species of Tipulariæ. Finally, while the real lepidopterous scales are always deeply crenate at their truncated extremity, the scales of gnats are not; and their truncated extremity terminates in a very fine margin, from which the points of the longitudinal ribs sometimes project.

Fig. 73.



Scales of two species of *Culex*.

a, e, Scales of the veins of the wings.
j, f, " " " margins of the wings.
i, g, " " " legs.
b, c, " " proboscis and palpi.
d, k, h, " " " of the second species of *Culex*.

These scales are partly dark and opaque, partly colored and transparent. It is in the latter that the transverse striæ frequently appear. All the figures are magnified 400 diameters.

I have examined several species of gnats and have found the proboscis, palpi, legs and abdomen clothed with scales of the same sort, while the thorax and the veins of the wings had forms intermediate between hairs and scales. I observed this in a magnificent Tipula from Brazil given to me by my brother Fritz. Besides this it had as a particular ornament a long tassel of scales upon its legs.

The presence of these scales upon the Tipulariæ shows that there is a close relationship between them and Lepidoptera, a relationship which is further attested by the lepidopterous appearance of the genus Psychoda, the tipulaceous habits of Pterophorus, the similar venation of the wings in many Tipulariæ (Limnobia, Ctenophora,) and the Phryganeidæ, the aquatic habitat of the larvæ of the Tipulæ, and, finally the circumstance that it is far easier to deduce morphologically the proboscis of the Tipulæ from the buccal organs of the Phyganeidæ than from those of any other order of insects.

Therefore, according to my opinion, the stock or kindred common to the Diptera, Lepidoptera, and Phryganeidæ, in its manner of life, and the structure of its body would be very closely allied to the Phryganeidæ of to-day, living in water in the form of sheath-bearing larvæ, and in the perfect state remaining in the vicinity of the water. Its posterity divided at first into two branches, to wit, the *conservative* one *par excellence*, of the Phryganeidæ, which continuing in the same mode of life as its ancestors, has undergone very few variations; and the branch of those insects which suck the honey of flowers, which have gradually removed from their aquatic abode, have developed by natural selection the sense of colors, and acquired through sexual selection a squamose covering. This second branch again divided into two, one of which accustomed itself to feed exclusively upon the honey of flowers and produced Lepidoptera; while the other, less exclusive in its tastes adapted itself to imbibe all sorts of fluids as well as to pierce the more tender tissues, and produced the Tipulariæ. One part of these besides sucking different juices, grew accustomed to eating pollen and thus little by little the proboscis of the Tipulæ was transmuted by natural selection into that of flies equally well adapted to suck honey or eat pollen.

The Hymenoptera which visit flowers, the bees, being given exclusively to floral food not only in the perfect state but also while larvæ, present the greatest possible variety of adaptation. Starting from the mouth of the fossorial Hymenoptera adapted only to bite and provided with a very short tongue, we arrive, through numerous transitions, to the highly developed proboscis of the Anthophoræ and Bombi which can extrude their tongue to a length equal to that of their body, and then coiling it up, draw it back again into its cavity so as to give free play to the action of the mandibles. Furthermore, in different ways, according to the different species, this or that part of the body has undergone special adaptations so as to be able to collect pollen with greater ease and in greater abundance. A sure criterion by which to comprehend these differences thoroughly as well as to estimate correctly the different grades of affinity between forms so varied, can be given only by the Darwinian doctrine. But we have no space to particularize.

We will conclude by discussing some objections which can be urged against the explanations of facts, and against the general principles advanced in this discourse.

It may be asked, what advantage can flowers and insects derive from having elongated respectively the melliferous tube and the proboscis instead of having them remain of a constant length? I answer that in order to comprehend the advantage of this elongation, it is necessary to consider in one view the benefits and the injuries which different tribes of insects bring to plants. The Lepidoptera are the only insects which, while aiding the plants by transferring pollen from one flower to another, do not cause injury by devouring the pollen. Therefore a plant which has modified its flowers so as to exclude bees and flies while admitting Lepidoptera, has obtained a signal advantage.

Suppose a plant develops a floral tube longer than usual so that the honey remains at a lower level; this variation will be an advantage for that tribe of insects which lives on honey alone and can therefore adapt itself more diligently to this variation. The advantage in this case is for the Lepidoptera and will last until the proboscis of certain bees and flies equals that of the Lepidoptera. When this equalization has been completed, a further elongation of the floral tube will be useful to the plant, which will immediately be followed by a corresponding elongation of the proboscis of the Lepidoptera, and so on. In this way, by means of the rivalry between the Lepidoptera, bees, and flies, the fact that the Lepidoptera do not consume pollen and can sooner adapt their proboscis to the variations of the flowers than their rivals coöperating, a gradual augmentation in the length of the tubes and spurs of flowers would become established, followed by a proportional elongation of the proboscis, concomitant in the Lepidoptera, later in bees and last of all in flies. It may be well to give in this place the measure of the longest proboscides of some of the Lepidoptera, bees and flies of our country.

Among flies the proboscis of *Bombylius discolor* is 10 millimetres long; that of *Rhingia rostrata* from 11 to 12 mm.; among bees that of *Bombus hortorum* is 21 mm., and that of *Anthophora pilipes* 25mm.; the proboscis of *Sphinx Elpinor* among the Lepidoptera is from 20 to 24 mm. long, that of *Sphinx pinastri* from 28 to 32 mm., and that of *Sphinx ligustri* from 37 to 42 mm. But the longest proboscis is that of *Sphinx convolvuli* which is from 70 to 80 mm.. This exceptional size led me to infer that *Sphinx convolvuli* may have acquired its long proboscis by competition with the flies and bees with a long proboscis inhabiting warm climates. This conjecture is confirmed by information as to the geographical distribution of *Sphinx convolvuli* afforded me by Dr. Speyer.

In order to eliminate the visits of bees and flies which prey upon pollen and permit only those of Lepidoptera, a variation still more advantageous than the elongation of the melliferous tube is manifestly that of flowering at night. And this is precisely what many plants do, which keep their flowers closed during the day and open them in the evening when with the disappearance of the sun the activity of bees and flies is entirely destroyed. It is in the hours of the evening and night that the flowers of such plants by the brilliancy of their colors and the pungency of their odors attract sphinxes and other moths, showing in an eloquent way how advantageous to themselves is the preference they show for the visits of insects which are only useful to those of insects which are at the same time useful and hurtful. But it will be said; why cannot bees and flies as well as Lepidoptera adapt themselves *pari passu* to the noctifloral variations of plants? It is not difficult to see why. Lepidoptera feed only upon honey, and hence are obliged to follow *pari passu* the variations of the plants which nourish them with analogous variations on their part. Flies, however, do not live exclusively upon honey, but suck by instinct any sort of liquid, and bees after collecting honey and pollen have to make complicated manipulations in the hive. Whence it is plain why Lepidoptera only and not bees and flies as well, can acquire nocturnal habits, and adapt themselves to night-flowering plants.*

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* However ingenious and seductive may be the theory here developed by the author to explain the genesis of evening or nocturnal flowers, and of flowers with a long, honey-bearing tube, it nevertheless seems contradicted by a multitude of facts collected by me, and by arguments which I here briefly subjoin.

The whole theory of the author reposes upon the fact that Lepidoptera do not feed

There is yet a general objection which can be advanced against the application of the Darwinian doctrine to flowers and insects. Even conceding, it may be said, that this doctrine can be applied to all the phenomena of the organized world, and that in many points its *a priori* deductions are confirmed *a posteriori* by observation, it does not follow from that that it should be preferred to the teleological mode of view which explains every property of organisms as created with a view to the well-being of a given individual or of other individuals as well.

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upon the pollen, and that their visits are consequently of greater utility to plants than those of bees and flies.

If the theory is in harmony with truth the following phemonena would necessarily be verified.

First, the flowers fecundated exclusively by Lepidoptera, that is, evening or nocturnal flowers, as contrasted with flowers fecundated by bees or flies, would constantly manifest a considerable saving in the production of pollen. Let us see if this saving takes place in the conspicuous examples of night-flowering plants. *Mirabilis jalapa* and *M. longiflora* for every ovule to be fertilized offer not less than five anthers furnished with numerous pollen-grains. *Œnothera biennis*, furnished with eight large anthers, offers to the proboscis of the Lepidoptera festoons of pollen, the greater part of which is of use neither to the insects nor the plant. *Cereus grandiflorus* has an excessively large number of stamens and consequently of pollen. Striking a mean of these and other lepidopterophilous flowers and comparing it with a mean of melittophilous flowers it must be admitted that there is not the least appearance of pollen-saving in the former.

Secondly, the flowers with long tubes, or those fertilized *preferably* by Lepidoptera or Trochili, if the author's theory is true, would constantly harbor the anthers within the tube so as to withdraw them from the depredation of bees and flies. Now this is precisely what does not occur in the great majority of such flowers, the anthers of which protrude beyond the tube, evidently to make bees and flies, as well as Lepidoptera, contribute to the transfer of pollen. This form of flowers, which can be said to be absolutely wanting to the flora of Europe, is, however, frequent in tropical plants.

Thirdly, if the theory in question is true, plants with flowers exclusively lepidopterophilous would take, or would tend to take, the advantage over plants with exclusively melittophilous or myophilous flowers. But precisely the opposite of this is true, and, limiting myself to European flora, while not more than from ten to twenty species are exclusively lepidopterophilous (species of *Pancratium*, *Calystegia*, some Caryophyllaceæ, and the like), the exclusively myophilous species are numerous (almost all the Umbelliferæ, Rhammaceæ, Aristolochiaceæ, Euphorbiaceæ, Celastrineæ, etc.), and most numerous of all are those which are exclusively melittophilous, that is, all the Leguminosæ and the greater part of the Labiatæ, Personatæ, Borragineæ, Cynarocephalæ, Lactucæ, etc.

From all this we conclude that the theory of the author of the genesis of lepidopterophilous flowers, although ingenious, does not seem admissible. I am as profoundly pursuaded as Erm. Müller that both the possession of long, honey-bearing tubes, and the habit of flowering at night in plants, stand in a causal relation with the Lepidoptera and their proboscis; but not that the reason of this reciprocal adaptation only has to do with the greater or less depredation of pollen on the part of the insects; since it must be referred to other contingencies.

It would seem opportune to state the result of the studies I have made with a view to elucidate the genesis of lepidopterophilous flowers; but as this special theme is connected with the whole theory touching the genesis of anemophilous, ornithophilous, melittophilous, etc., flowers, I am constrained to refer to my other writings, as there is no space here to enlarge.

Without stopping to mention that every teleological explanation involves an absurdity inasmuch as it suppresses in the order of the phenomena the bond between cause and effect, I will here briefly adduce some facts which render the acceptance of the doctrine of final causes impossible. I have already touched upon the errors into which Sprengel fell in thinking that the arrangements in flowers were so disposed for the benefit of insects. Nor can a single example be adduced of a living being whose properties are advantageous to other species and not to its own.

The other supposition then, that every property of individuals has been created for their well-being, in the greater number of instances answers as well for the interpretation of phenomena as the Darwinian system. But there are cases in which it does not answer at all. The abortive stamens and the anthers without pollen in some flowers of Glechoma, Thymus, and other polygamous Labiatæ, the tibiæ of Apathus dilated like those of Bombus, although the former do not collect pollen, the retrorse teeth of the sting of bees which cause the death of those insects if they use it, are a few examples drawn from an inexhaustible mine of facts, all easily explained by the Darwinian doctrine, and inexplicable by the teleological.

All the numerous instances where the functions and conditions of life have been changed in such a way that many of the inherited properties become of no use or even injurious, offer an insoluble difficulty to the teleological doctrine, while they are in full harmony with the Darwinian theory.*

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* I must here, as always, declare myself a teleologist and vitalist. Now teleology and vitalism, far from being vanquished by the Darwinian doctrine, find in it their most solid support. What do teleology and vitalism mean? They mean that we believe that there is in all living things an innate, specific principle, intelligent, free and teleological. This principle is the hidden cause of the variability of organized beings, as well as the wonderful harmonies which have been established between one being and another.

Every man is conscious of proposing continually a determinate end for his actions and of seeking the best means for attaining it. Therefore, every man is free and teleological; and every man has the profoundest conviction of this fact, nor can all the sophisms of the materialists of the present day against human liberty stand against the verdict of consciousness. And if man is teleological and free, how can other living things, each in its proper sphere, which are united to him by a more or less remote relationship, not likewise be free?

Man and other living beings vary because they are free, and are free because, if they had not varied they could not have been free; if they had not been free, they could not have varied. Liberty and variability are inseparably conjoined. The different worlds, stones, and crystals obey fixed, indeclinable, mathematical laws. Therefore they do not vary. They are not free because they do not vary, and do not vary because they