VI.—*The Genetic Succession of Zooids in the Hydroida.* By Professor ALLMAN.

(Read 16th May 1870.)

Though most of the terms employed in the following paper have already become part of the language of science, some definitions may be here given with the view of rendering the subject more intelligible.

The *Zooids* are the more or less individualised members of which the hydroid colony is composed.

The *Hydranth* is the proper nutritive zooid.

The *Blastostyle* is a columnar zooid destined not for nutrition, but for the origination of sexual buds.

The *Blastocheme* is a medusiform zooid which gives origin to generative elements, not immediately, but through the intervention of special sexual buds.

The *Gonophore* is the ultimate generative zooid, that which *immediately* produces the generative elements. It may be either medusiform or sacciform.

The *Trophosome* is the entire assemblage of nutritive zooids in a colony.

The *Gonosome* is the entire assemblage of generative zooids in a colony.

From all the facts which the study of the *Hydroida* has made apparent, we may regard it as certain that however long zooidal multiplication may continue, this is not sufficient for the perpetuation of the species, but that a period must at last come in the life of the hydroid when by an act of true sexual reproduction, new individuals are produced for the indefinite extension of the species through time.

This truth finds its expression in STEENSTRUP'S famous law of "Alternation of Generations,"—a law which, though not very correctly enunciated by its framer, may be regarded when properly expounded as a statement of the fact, that in certain animals every act of embryonal development is followed by one or more acts of zooidal development, which invariably conduct us to an ovum in which embryonal development followed by zooidal development again occurs, and the entire series becomes thus repeated.

Now the various series expressing this alternation of sexual with non-sexual development, exhibit among the *Hydroida* different degrees of complication, which will be more easily understood if we attempt to present them in the somewhat technical shape of formulæ.

Let t be the trophosome, and g the gonosome, then

$$\text{I.}\quad \underbrace{t+g} \times \underbrace{t+g} \times \underbrace{t+g} \times \ldots\ldots\ldots\ldots\&c.,$$

will be the general expression for the genetic succession in the life of the hydroid, the sign + indicating succession by zooidal development, and × by embryonal.

It is very seldom, however, that the trophosome consists of only a single zooid. Such rare instances are presented by *corymorpha* (fig. 1), and by certain allied forms, whose trophosomes never become developed into a colony of mutually dependent hydranths, and I believe it better to regard the hydrorhizal fibres here as elsewhere in the light of mere extensions of the hydrorhizal or fixed end of the colony, rather than in that of proper zooids—a view supported by their mode of development in the primordial hydranth. In almost every other case, the hydranths composing the trophosome become greatly multiplied by budding.

Still less tendency is there in the gonosome to present an absolutely simple condition. Indeed, the gonosome is perhaps never limited in its normal state to a single zooid, and we frequently find hundreds and even thousands of zooids entering into the composition of this portion of the hydroid colony.

But the zooids of which the colony is thus composed may not only be numerous, but may also vary in form. Those indeed which constitute the trophosome are always of a different form from those of the gonosome. In the trophosome it is rare to find any other form of zooid than that of the proper hydranth. In *Hydractinia*, however, there is associated with the ordinary hydranths the peculiarly modified ones, whose spiral form confers upon the trophosome of this genus one of its most striking features, while the nematophores of the *Plumularidæ* can scarcely be regarded otherwise than as special zooids whose morphological differentiation from the other zooids of the colony is carried to a maximum.

In the gonosome, on the other hand, the usual condition is that of variety of form among its component zooids; and it is quite common to find in one and the same gonosome, three different kinds of zooids, each with its special form among the associated zooids, and its special duty in the generative functions of the hydroid.

While the type of *heteromorphism*, or variety of form, among the zooids is fixed for every species, the *polymerism*, or simple multiplication of the component zooids, is indefinite, and varies with the age, perfection of nutrition, &c., of the individual.

If we specialise the general expression already given (I.), so as to make it directly applicable to particular cases of heteromorphic succession in the life of the hydroid, we shall obtain the following formulæ, where *h* is used for the hydranth, *bls* for blastostyle, *blch* for blastocheme, and *gph* for gonophore—

$$\text{II. Binary.}\ \Big\}\ \underbrace{h + gph} \times \underbrace{h + gph} \times \ldots\ldots\ldots\ldots \&\text{c., } \textit{Corymorpha.}\quad \text{(fig. 1.)}$$

$$\text{III. Ternary.}\ \Big\}\ \underbrace{h + bls + gph} \times \underbrace{h + bls + gph} \times \ldots\ldots\ldots \&\text{c., } \textit{Dicoryne.}\quad \text{(fig. 2.)}$$

$$\text{IV. Quaternary.}\ \Big\}\ \underbrace{h + bls + blch + gph} \times \underbrace{h + bls + blch + gph} \times \ldots \&\text{c., } \textit{Campanularia.}\ \text{(fig. 3.)}$$

These formulæ present three types of heteromorphism. In II. the heteromorphism is *binary*, in III. *ternary*, in IV. *quaternary*.

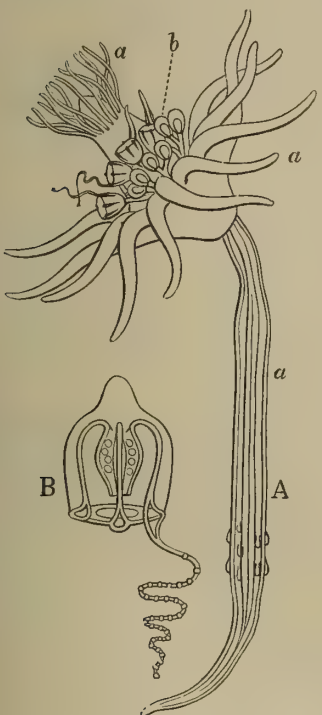

Fig. 1.—Diagram of *Corymorpha*. A, the entire colony composed of trophosome and gonosome; *aaa*, the trophosome, consisting of a solitary zooid; *b*, the gonosome, consisting of numerous zooids. B, a single zooid (gonophore) of the trophosome become free and mature.

Fig. 2.—Diagram of *Dicoryne*. *aaaa*, the trophosome, consisting of numerous zooids; *b c*, the gonosome, consisting of blastostyle, *b*, and gonophores, *c*.

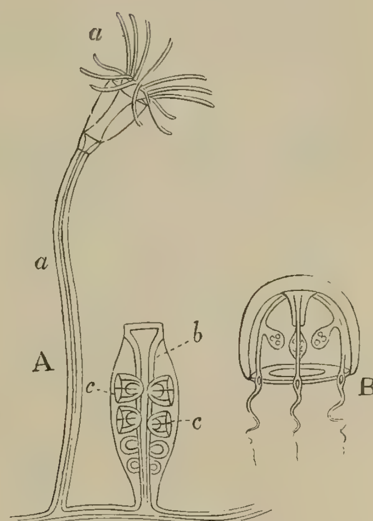

Fig. 3.—Diagram of *Campanularia* A, portion of the entire colony; *aa*, the trophosome; *bc*, the gonosome; *b*, blastostyle; *cc*, blastochemes. B, a blastocheme become free and mature, and carrying within its bell special zooids, which are the ultimate sexual buds or gonophores.

But the hydranth may and does in almost every instance—either directly or through the medium of the common basis or hydrophyton—repeat itself indefinitely by budding (fig. 2) before the time arrives when an element of the gonosome is to be budded off; and a series of homomorphic zooids may thus introduce themselves into the heteromorphic succession, as expressed in the following formulæ—

$$\text{V.}\quad \underbrace{h+h+h+\ldots\ldots\&\text{c.}+bls+gph}\times\underbrace{h+h+h+\ldots\ldots\&\text{c.}+bls+gph}\times\ldots\ldots\&\text{c.}$$

where the hydranth becomes indefinitely repeated in the formula of ternary heteromorphism (III.) given above; and the same will apply to each of the other two types of heteromorphism.

Now, in all these cases, the succession from the primordial nutritive zooid to the ultimate generative zooid, or gonophore, admits of being expressed in a continuous line; but one or more of the zooids of the trophosome may emit buds which will diverge from the direct line of succession, and which may then either form the starting-point for another similar line of succession, or may be destitute of all power of continuing the succession of the zooids. Thus, (figs. 4 and 7) the primordial hydranth, or any of those derived from it, may repeat itself by a bud which will diverge from the direct line, produce other zooids by gemmation, and thus start off a new series, as expressed in the following formula:—

$$\text{VI.}\quad \underbrace{h\left\{\begin{array}{l}+h+h+h+\ldots\ldots\&\text{c.}+bls+gph\\+h+h+h+\ldots\ldots\&\text{c.}+bls+gph\end{array}\right\}}\times h\left\{\ldots\right\}\times\ldots\&\text{c.}$$

And this state of things may also repeat itself indefinitely, giving rise to an indefinite number of collateral series diverging from one another, and from the primary axis of succession.

As already said, however, the diverging zooid may have no power of continuing the succession. Thus, the spiral hydranth of *Hydractinia* is not intercalated in the direct succession of zooids. It is a diverging zooid, like that which starts off the collateral series in formula VI., but one which here never gives rise to buds, and is therefore incapable of either continuing or originating a new succession.*

The following formula, where h' is the spiral hydranth, will express the place and power of this zooid in Hydractinia:—

$$\text{VII.}\quad \underbrace{h\left\{\begin{array}{l}+bls+gph\\+h'\end{array}\right.}\times\underbrace{h\left\{\begin{array}{l}+bls+gph\\+h'\end{array}\right.}\times\ldots\ldots\ldots\ldots\&\text{c.}$$

The case expressed in the formulæ given above is the simple one, where only the last hydranth in the succession of buds composing a period is supposed to

* The bifurcation occasionally observed in the spiral hydranth of *Hydractinia* is evidently abnormal, and cannot be regarded as invalidating the above statement.

give origin to a bud of the gonosome. But any other hydranth in the succession may just as well bud off a member of the gonosome, which may thus form a collateral gonosomal axis. This, indeed, is by far the most usual case, and is what is actually represented in the diagrams (see figs. 2, 4, 7). The axis, however, thus produced will be necessarily definite, and will contrast in this respect with the indefinitely extended axis of the trophosome, while it will differ from the diverging bud, h' in formula VII., by the fact of its having the power of repeating the colony by sexual reproduction, while h' has no power of reproduction, either sexual or non-sexual.

This condition may be expressed by the following formula, in which not only the last hydranth of the period gives off a bud of the gonosome, but the primordial hydranth emits a collateral gonosomal axis :—

$$\text{VIII.}\quad \underbrace{h \left\{ \begin{matrix} + h + h + h + \ldots\ldots\&c. + bls + gph \\ + bls + gph \qquad\qquad\qquad\qquad\qquad \end{matrix} \right\}} \times h \left\{ \quad \right\} \times \ldots\ldots\&c.$$

Besides the particular cases now given, certain other modifications of the plan of gemmation will at once occur to any one who has made the *Hydroida* a subject of study. Those here adduced, however, will serve to convey an adequate idea of the essential features in hydroid gemmation.

It is thus, by the combination of heteromorphic and homomorphic multiplication, and of direct and diverging series indefinitely repeated, that the animal attains to the condition of those wonderful complex colonies which impress themselves so strongly on the mind of the observer.

So also the gonosome may present not only a heteromorphic but a homomorphic multiplication of zooids. In no case, however, so far as I am aware, does any zooid of the gonosome repeat itself by homomorphic gemmation, except in some comparatively rare instances of budding in the medusa; for though the homomorphic repetition of zooids may be in the gonosome as in the trophosome, carried to a great extent, it is almost always the result of budding from a zooid of a different form. Thus the blastostyle never emits buds destined to repeat its own form, and this form, however frequently repeated in the gonosome, is always budded off from the hydranthal element in the trophosome, its own buds, however numerous, being always heteromorphic with itself.

In the formulæ now given, one fact is obvious, namely, that the groups included between every two acts of embryonal development are exactly similar to one another in the nature and succession of their heteromorphic elements; in other words, that the life series of the hydroid may be represented by definite groups of zooids exactly repeated after each generative act.* We are indebted to HUXLEY for having assigned to our conception of the biological individual its

* The mere *number* of zooids in two or more of these groups may of course vary, depending as this does on the accident of abundant or deficient nutrition and the like.

proper limits, when he defined it as "the total result of the development of a single ovum," and compared the definite groups of zooids which constitute the life series of animals presenting the phenomenon of "alternation of generations" to the single organisms known as the *individuals*, which make up the *species* in other animals. These groups form the periods of the series; the period repeats itself by true generation, and this repetition continues itself indefinitely, like a circulating decimal, so as to represent the indefinitely extended life of the *species*, while the life of the *individual*—in its technical sense as the component of the species—is expressed by each period singly.

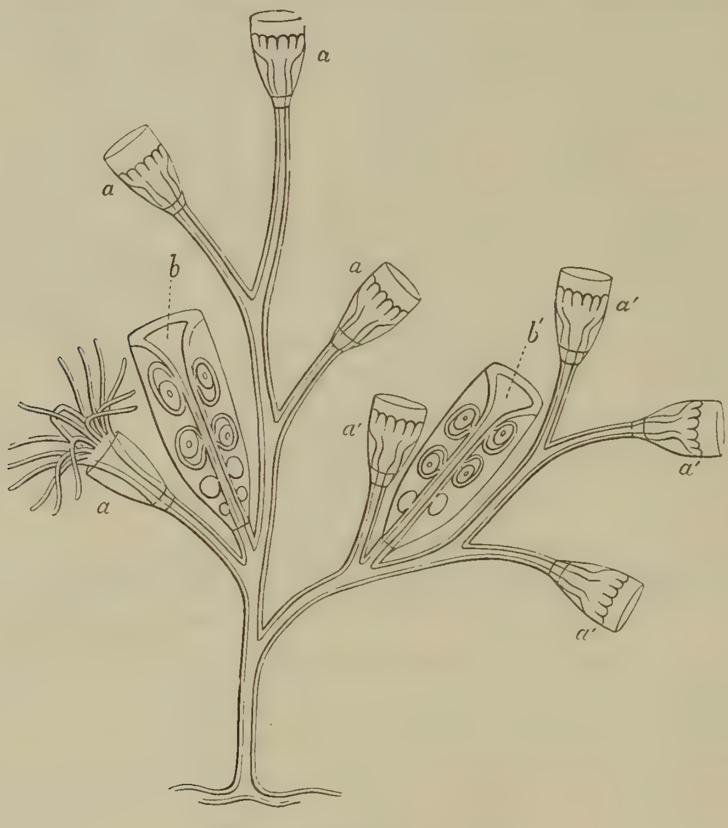

Fig. 4.—Diagram of *Laomedea*.
a a a a, hydranths belonging to the primary or direct line of succession; *a′a′a′a′*, hydranths belonging to a secondary or diverging line of succession; *b*, blastostyle of the primary line of succession, bearing gonophores, and surrounded by a gonangium; *b′*, blastostyle with gonophores and gonangium of the diverging line.

It is a universal law in the succession of zooids, that no retrogression ever takes place in the series. In other words, no bud ever becomes developed into a zooid which is of a different form from the budder, and has at the same time preceded it in the line of succesion. Thus, true hydranths are never emitted either by blastostyle, blastocheme, or gonophore; and to this law the peculiar gemminate hydriform bodies which are found on the summit of the female blastostyle in certain species of *Halecium* form no exception; for though closely resembling true hydranths, they appear to have a different signification, contributing probably in some way as yet unknown to the generative functions of the hydroid, while they have no power of continuing the succession in a direct or collateral line like the proper hydranths of the trophosome.

The hydranth normally continues the axis in the hydroid colony, just as the leaf-bud in the plant continues the vegetable axis; the gonophore, on the other hand, has no power of continuing the axis, and constitutes the terminal zooid in each period of the series, just as the flower-bud stops the elongation of the axis in the plant. This analogy, however, must not be pushed too far, for while the hydranths and gonophores are simple zooids, the leaf-buds and flower-buds are complex associations of the corresponding element of individuality in the plant.

The normal order of succession of the buds in the trophosome is from the proximal or fixed to the distal or free end of the hydrosoma, so that the older buds are met with towards the base or hydrorhizal end of the main stem and branches, the younger ones towards the summit. In the gonosome, on the other hand, the order of succession is sometimes towards the distal, sometimes towards the proximal end of the axis. In the calyptoblastic genera, represented by campanularian, sertularian, and allied forms, the order of succession of the sporosacs or blastochemes is invariably from the distal towards the proximal extremity of the blastostyle on which in these genera they are always borne. When a blastostyle is present in the gymnoblastic or tubularian genera, the gonophores succeed one another, sometimes from the proximal towards the distal end (*Hydractinia echinata*), sometimes from the distal towards the proximal (*Dicoryne conferta*). In *Tubularia* their succession is from the distal towards the proximal end of the common peduncle, which is more or less developed in the various species of this genus; and the same order of succession occurs in *Corymorpha*.

Where no special gonosomal axis is developed, the succession is usually from the proximal to the distal extremity of the branch (*Bougainvillia, Perigonimus*), thus corresponding to that of the zooids of the trophosome. Sometimes, however (*Syncoryne, Gemmaria*), it is from the distal to the proximal.

We have thus, then, in the gonosome of the *Hydroida*, as in the inflorescence of plants, both a centripetal and a centrifugal order of development. It is possible, however, that irregularities may occur, and that a new bud may be abnormally emitted at the distal side of a centrifugal series, or at the proximal side of a centripetal one, so as to disturb in individual cases the normal sequence of the zooids.

Some further points admitting of comparison with the inflorescence of plants may be noticed in the gonosome of such hydroids as possess a special gonosomal axis. In *Tubularia indivisa* (fig. 5), and in the male colonies of *Tubularia larynx*, the gonophores are—like the flowers of a raceme—carried on short pedicels along the sides of a long common peduncle, which springs from the body of the hydranth. Their order of development, however, is centrifugal, or

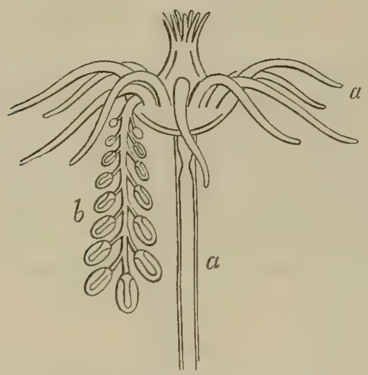

Fig. 5.—Diagram of *Tubularia indivisa*.
a a, hydranth on its stalk ; *b*, shortly stalked gonophores borne on a common peduncle, and increasing in maturity from the proximal to the distal extremity of the peduncle.

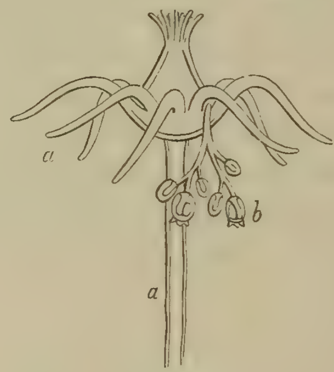

Fig. 6.—Diagram of *Tubularia larynx* (Female).
a a, a hydranth on its stalk ; *b*, gonophores attached by short stalks to a common branched peduncle, and increasing in maturity from the proximal to the distal extremities of the branches.

from the distal to the proximal extremity of the peduncle, so that the whole group may be compared to a reversed raceme. In the female colonies of *Tubularia larynx* (fig. 6), and in *Corymorpha nutans*, the pedicels become branched

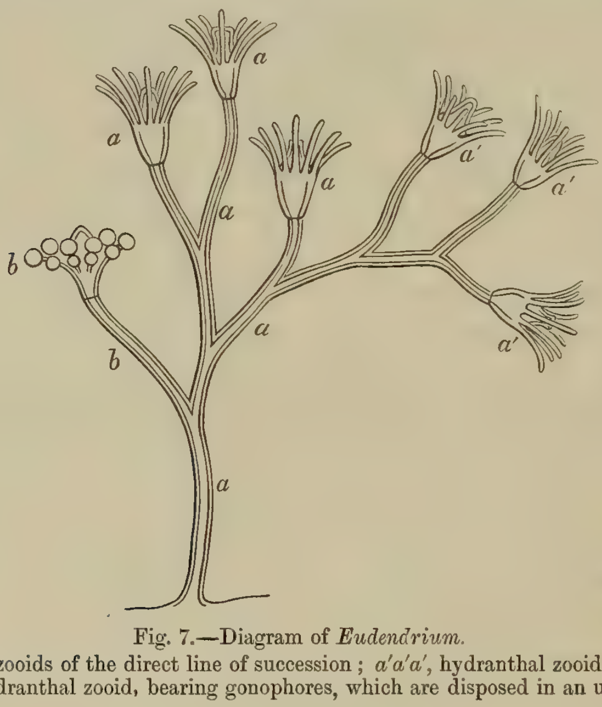

Fig. 7.—Diagram of *Eudendrium*.
a a a a a, hydranthal zooids of the direct line of succession ; *a′a′a′*, hydranthal zooids of a diverging line ; *b b*, suppressed hydranthal zooid, bearing gonophores, which are disposed in an unbelliform group.

with a similar order of development, which thus gives us the compound reversed raceme or cyme.

In certain proliferous medusæ, the buds are borne on the manubrum with a centripetal order of development, thus giving us, according as the buds are sessile or pedunculated, the true spike, or the true raceme.

The reversed spike, or spike with a centrifugal development, shows itself in such forms as *Dicoryne conferta* (fig. 2, *b c*); while in *Campanularia* (fig. 3), *Laomedea* (fig. 4, *b b′*), *Obelia*, and other calyptoblastic forms, we have a reversed spike surrounded by the gonangial sheath; and were it not for the centrifugal development of the generative buds upon the blastostyle, and the complete closure of the gonangium, strongly recalling the spadix with its spathe in the inflorescence of an araceous plant.

In *Eudendrium* the male gonophores are disposed in an umbel (fig. 7, *b*) with the axis, in some cases prolonged beyond it, while in others there is little or no extension of the axis beyond the depressed portion which carries the gonophores. Though we cannot here recognise any difference in the order of development among the gonophores composing the umbel, we are justified in assuming this order to be as in the true umbel—a centripetal one; for in the female colonies of most species of this genus, such as *Eudendrium ramosum*,

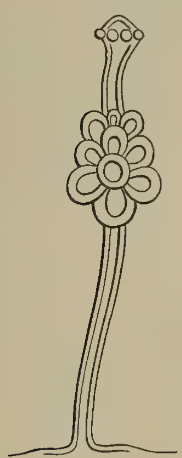

Fig. 8.
A blastostyle of *Hydractinia*, carrying its gonophores, which increase in maturity towards the proximal or attached end.

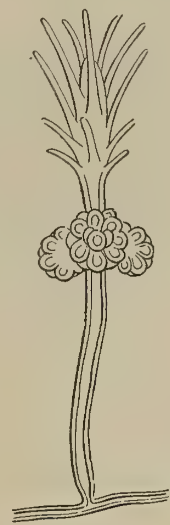

Fig. 9.
A hydranth of *Clava* with its gonophores surrounding it in globular clusters.

the gonophores are separated from distance to distance upon the stem immediately below the hydranth; and here their order of development is plainly seen to be centripetal.

In *Hydractinia echinata* (fig. 8) we have the closely approximated gonophores sessile on a blastostyle, and the development centripetal, as in the true spike, while the axis extends beyond it as a naked prolongation, reminding us of the naked prolongation of the spadix in certain *Araceæ*.

In *Clava squamata*, and in *Clava multicornis*, the gonophores form dense clusters, surrounding the hydranth in a sort of verticil (fig. 9). Each cluster consists of sessile gonophores, borne on a greatly depressed common peduncle, and thus recalling the form of inflorescence known as a capitulum. The order of development, however, appears to be centrifugal, instead of being, as in the true capitulum, centripetal, and would therefore, perhaps, more truly suggest a comparison with the depressed cyme which constitutes the axillary inflorescence in many *Labiatæ*.

In the comparison just instituted between the gonsome of the *Hydroida* and the inflorescence of plants, it will be noticed, that whenever in the *Hydroida* the generative buds are borne upon a special gonsomal axis, like the flowers in an inflorescence, the order of succession is far more frequently a centrifugal than a centripetal one. In the calyptoblastic forms, indeed, it is always centrifugal. This is exactly the opposite of what prevails in plants; for here the centripetal forms of inflorescence greatly exceed the centrifugal ones.

We must be careful, however, not to assign to the resemblances which may be noticed more importance than they are justly entitled to. But yet, after setting aside such as are merely superficial and accidental, many still remain which have their origin in certain deep-seated properties, and may be referred to the common phenomenon of gemmation, which by agamic multiplication in the animal as well as in the plant, gives rise to colonies whose members in each case, mutually dependent on one another, continue to be organically associated into definitely arranged and determinate groups.