**Colonial Organisms**

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abundant they are swept through the pharynx and into the body in a strong stream, the animal having sufficient intelligence to know and to reject what may be unpleasant or non-beneficial. With indigo it refuses to have anything to do; and a particle of any kind that may be too large, or otherwise unacceptable, scarcely passes the oral aperture before the current is reversed and the disagreeable substance dashed out.

Reproduction with the form referred to as *Tillina inflata*, n. sp., is accomplished, so far as I have observed, by encystment and subdivision of the body into four zoöids, which differ from the adult in no particular, except in their smaller size.

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## COLONIAL ORGANISMS.

BY CHARLES MORRIS.

THE remarkable resemblance which appears between the separate segments of an Annelid, the distinct units of a Hydrozoan, or in the sectional parts of other forms of the animal and vegetable kingdoms, is one that admits of two interpretations, and has in consequence given rise to two opposed theories. In the first, supported by several eminent scientists, it is assumed that each unit or segment represents an original individual, and that the existing individual arose through the subordination of the members of an original colony. In the second, supported by equally eminent authorities, it is assumed that the organs of an original individual gradually took on the form and functions of the parent body, and thus, though originally diverse in function, grew to closely resemble each other.

This latter theory, which is based on the assumed tendency of each cell or other portion of an organic form to develop into an exact reproduction of that form, is supported by Huxley, Van Beneden and other biologists. The opposite theory, which is based on the apparently direct indication of the facts, is sustained by Allman, Gegenbaur, Claus, Lankester, the Hertwigs, &c. Late discoveries seem to sustain the colonial rather than the individual theory. The probable fact is, however, that they are both, to a certain extent, true, and that both the colonizing habit and the reproductive power of single cells have had their share in the formation of the closely similar sections of Hydrozoan and Annelidan individuals.

It is proposed here to offer a general consideration of the subject in its application to both the vegetable and animal kingdoms, and mainly from the colonial point of view, though with full acknowledgment of the tendency of the generalized parts of an organic body to assume the form of the whole, and the power of each unspecialized cell to act as a reproductive germ. It is quite possible that some new arguments may be advanced, and the whole subject be placed in a clearer light, since, so far as the writer is aware, no complete treatment of it has been yet attempted.

Organic forms are reproduced in two methods: by asexual and by sexual generation. The first, the development of unfertilized germinal cells, is the most common in the lowest forms of life. The second, the development of fertilized germs, or of germinal cells into whose composition enters material from two separate individuals, gradually replaces the first as life attains a higher grade, and completely replaces it in the highest forms. In connection with this is another fact of importance here. The products of asexual reproduction very commonly remain attached to the mother form, and compose colonies. The products of sexual reproduction never remain attached, but always enjoy a free existence. This distinction is markedly displayed in vegetable life, in which the product of the leaf bud continues, with few exceptions, attached to the parent form, while the product of the flower bud is always set free, to give rise to a new parent stock.

There is reason to believe that generalized cells, capable of reproductive development under proper conditions, exist abundantly in every part of every organism. In all the higher animals, if the views advanced by the writer in a preceding paper[1] be correct, these mainly exist in the blood current, as the amœboid white corpuscles. In many of the lower animals, in which specialization has made no progress, most or all of the cells of the body possess this power, and reproductive budding may take place at any part of the organism, or if it be cut into minute portions, each of these may develop into a new individual. In vegetable forms the latter condition seems to prevail. In the lower plants every cell may be capable of asexual development. In the higher plants the process of specialization has taken this power from the great mass of cells, yet vast numbers of cells exist capable of germinal

[1] Organic Physics, AMER. NAT., July, 1882.

reproduction. We venture to offer the hypothesis that the meristem, or generalized active tissue, is made up of such reproductive cells, each capable of asexual development, or of being converted, through the medium of the flower organs, into sexual germs. If this be correct, the meristem cells of plants represent in their germinal powers the generalized tissue cells of the lower animals, and the wandering white corpuscles of the higher animals.

Abundant, however, as germinal cells may be in every part of every organism, yet only a limited number of them can develop since their growth acts to exhaust the strength and substance of the parent form. Only in the lower single-celled organisms do we find instances in which the whole body is converted into active germs, and the parent disappears in its offspring. In all the higher animals and plants this only partially takes place, and the less so the higher the organism.

The development of the germ cells usually occurs only at those points where favoring conditions most fully exist. In sexual reproduction these points are particularly limited in number, since the requisite meeting of germs from two organisms can only take place through the aid of a special mechanism. Asexual reproduction needs no such special mechanism, and may occur in most regions of the body. Yet, as life advances in grade, the favoring conditions of asexual development will be apt to exist more abundantly in some regions of the body than in others, and tend to become confined to these regions by hereditary transmission. In the higher plants these regions are usually the leaf axils, in which a degree of protection is afforded the bud, or partially developed germ. But if a tree be closely trimmed, and thus deprived of all its buds, new germs may develop at any point in the secondary meristem of the trunk or branches, and new shoots appear, the product of germinal cells which otherwise would have lacked the opportunity to develop.

In the development of the germs of the root fibers or shoots no such protection is requisite, and they may start from any point in the cambium layer. They are evidently the product of those meristem cells, which have been most successful in the general effort to develop.

The reason that certain cells alone succeed in developing, out of the great mass of cells that possess equal germinal powers, is

an interesting subject to which some further attention is desirable. As already said, each developing cell to a certain extent exhausts the organism and checks the reproductive activity of other cells. What is the principle of selection of these fortunate cells? It would seem as if they must possess superiority in nutrition, or be most favorably situated for assimilating nutriment from the vascular juices of the organism. Thus growing rich in protoplasm, their effort to develop must be not too greatly hampered by the crowding of surrounding cells. They must have some freedom of field in which to expand. The cell most favored in these particulars will be the most likely to develop. As for the germ cell of sexual reproduction, it possesses these requisites in a high degree. It develops in a region which is richly supplied with nutriment, and where there is no hindrance to its expansion. Of the many cells delivered into this region it would seem that those richest in protoplasm should, all things considered, have the best chance to develop and become the germs of new organisms. In sexual development, however, there must enter a certain element of chance, since the meeting of ova and spermatozoa is, to some extent, a matter of chance, and the earliest fertilized ova probably have a degree of advantage over their rivals.

With these preliminary remarks we may proceed to the consideration of the colonizing habit as usually displayed by the products of asexual generation. Colonial organisms occur abundantly in the single-celled field of life, as in the Diatomaceæ, the Volvocineæ, the Foraminifera, the Radiolaria, the Flagellata, &c. In the multicelled field it is indicated throughout the vegetable kingdom, and in the Spongida, the Hydrozoa, the Actinozoa, the Polyzoa, the Ascidia, the Annelida and the Arthropoda of the animal kingdom. But these indications of colonial origin are by no means all equally distinct, and in some of the sub-kingdoms mentioned they are but vaguely discernible. Yet there is a gradual movement from the less to the more questionable colonies which is significant of a common origin.

In the colonies of Rhizopod and Flagellate Protozoa no traces of differentiation appear. Each individual is like all the others, and each is capable of separate existence. We cannot, in any proper sense, consider these colonies as compound individuals, though in the Foraminifera there is a slight tendency in that direction. This tendency is more markedly displayed in the

Volvocineæ, as we shall show farther on. It will suffice to say here that these colonies are the product of continued asexual reproduction, and of the coherence of individuals thus produced.

Of colonies of Metazoa those of the sponges are similarly the result of asexual reproduction, are unattended by specialization of any members of the colony, and their members may be separated and pursue individual lives, and produce new colonies. The sexually generated sponge, on the contrary, begins life as a free individual.

But the subject of the sponge leads us deeper into the question of reproduction. As is well known there are two hypotheses extant in regard to the classification of the individual sponge. In the one it is viewed as a colony of Flagellate Protozoa. In the other it is viewed as a single Metazoan. The former hypothesis is based on the cellular organization of the sponge, since most of the cells of its epidermal layer are essentially Flagellate Infusoria. The latter is based on the character of its reproduction, since the germ develops in Metazoan fashion and not by a process of colonization.

It has been assumed that these hypotheses are mutually exclusive, and that only one of them can be true. Yet this does not necessarily follow. They may both be true. The strong argument which each advances may perhaps be reconciled by a third hypothesis, or by a fuller consideration of the essential character of reproduction.

The assumption that a compound organism which is born as a single cell, and grows by asexual budding, is a Protozoan colony, and that one which is born as a definite compound of cells is a Metazoan individual, has its uses for purposes of classification, but it declares a distinction that has no real existence. If we consider birth in its true relations, all organisms are born as single cells, and their complete development takes place after birth. For birth really occurs at the moment in which the germinal cell ceases to be a part of the parent organism, and begins its individual life. Whether it is delivered directly into the surrounding elements, or into an ovary within the maternal body, the essential fact remains the same. It has ceased to be a constituent part of the maternal body. It occupies an external locality, either in the exterior world or in a cavity communicating therewith, and

its nutrition and growth have become distinct from those of the mother. The only discoverable difference is that in the one case the nutriment is obtained independently of the mother, in the other case it is for a time provided by the mother.

The phenomena succeeding birth are the same in both cases. Continued division of the germ cell takes place and a mass of cohering cells is formed. It is true that in the cases where this takes place within the ovary or the egg a definite form is assumed. But the same is the fact with the Foraminifera, the Radiolaria, the Fungi, and the other colonial organizations which arise exteriorly through the continued subdivision of a germinal cell. There is no essential distinction between the two processes. The only visible distinction is that in the one case all this subdivision takes place exteriorly to the maternal body, in the other a greater or lesser portion of it takes place in a cavity of the maternal body which communicates with the external world, or within a capsular inclosure provided by the mother.

The distinction, therefore, between Protozoa and Metazoa is by no means absolute, and the highest Metazoan is essentially a colony of Protozoa, since it is born as a single cell, and gains its mature form by a long series of asexual cell productions. Its main distinction is that many of these new cells are greatly specialized, while in the simpler cell colonies they are to a great extent generalized.

The most primitive organic differentiation is into free cell and coherent cell individuals. Of the former there are numerous instances in the Protozoan world, yet at a very low level of life asexually-born cells begin to cohere into colonies. From these, at a higher level, arises the only distinctive feature of the primitive Metazoan life, that of the formation of organized cell colonies within the maternal ovary or the egg, precedent to birth into the exterior world. However different this process may appear from the formation of the simpler cell colony, the difference is only in seeming, and the enclosed embryo perhaps very gradually succeeded to the external colony.

The first significant step in this direction is taken at the low level of the Volvocineæ. The globular colony of Volvox in fact acts as a sort of womb, into which are born asexual germs. These develop into embryo colonies within the maternal body. We have here an instance closely analogous to that of Metazoan

birth, and a significant indication of the origin of the latter. The sexual offspring of Volvox, however, is born as a single germinal cell.

In the vegetable world the free cell colony assumes a size and complexity considerably in advance of any animal instances, for the Algæ and Fungi begin their external life as single cells. Thus, however large and complex they become, the process of growth is distinctly that of cell colonization.

There is one important fact observable in all cell colonies. They do not display varying and indefinite expansion, but tend to assume specific forms. These organisms are probably results of natural selection, and possess the forms best adapted to the life conditions of the colony, which forms are hereditarily transmitted. Now we may readily conceive, in the numberless fluctuations of nature, the appearance of circumstances to which the mature colony would be well adapted, but in which the germinal cell and the growing colony would be in danger of extirpation. Under such circumstances it would be a decided advantage if the germ could pass through its first stages of division within the maternal body, and a still more decided advantage if it could be retained under the maternal protection until sufficiently developed to be able to take care of itself in the battle of life. Such, possibly, was the method in which the Protozoan cell colony became the Metazoan organism, namely, by the retention of the germinal cell under the maternal protection until it had unfolded into a self-sustaining organism. The degree to which this embryonic growth proceeds differs greatly in different cases. In all cases the new creature is born as a single cell. In the Protozoan colony it is shed into the external world at this stage. In the Metazoan it is retained until it has passed through a portion or the whole of its development, or, more usually, is born as an egg, in which the germ rests in a store of nutriment provided by the mother, and enclosed within a protective covering. Only in the case of the Mammalia is the development completed before external birth.

Thus the division of the germinal cell, in the formation of the Morula, is in no fundamental sense different from the division of the amœboid cell, in the formation of a colony of Foraminifera. The Flagellate colony, from which there is reason to believe that the sponge originated, may, in the process of evolution, have

gained a somewhat complex organization, protected by fibrous and mineral secretions. Perhaps primitively yielding its germs as free cells, to develop into colonies externally, it may, in the exigencies of the struggle for existence, have come to retain them until they had developed into organized colonies, capable of self-support. Yet during the long period in which these gradual changes took place, the cells of the sponge colony continued to retain the characteristics of the Amœbæ and the Flagellata, so that to-day they display the double character of a colony of Protozoa and of a Metazoan individual.

We have dwelt at considerable length on this one case, as it involves the principle at the basis of all organic development. There is one other matter of interest connected with it to which we may here refer. The retention of the embryo within the maternal body, or within the egg, has an important bearing on the question of evolution. This latter retention is a true "acceleration of development."[1] The embryo, while thus retained, is specially favored in its growth. Provided with food without personal exertion, as in the case of free cell colonization, none of its energies are exhausted, and that organic development which is so greatly favored by complete rest proceeds rapidly. Its condition resembles that of the insect in the pupa stage, in which, supplied with abundant nutriment, and in a state of complete rest, organic development is rapidly attained. Such is the case with the embryo within the egg or the maternal womb. Its development is strongly accelerated, its larval stages passed through so rapidly that many of them are slurred over, and only the more marked stages are discoverable, and the new individual, when at length forced to depend on its own exertions, begins its free life at a much higher stage than in the case of the germ that is shed into the external world as a single cell, or a very immature colony.

If now we come to the consideration of Metazoan colonies, we find a gradual variation from simple to complex conditions closely analogous to the parallel case of cell colonies. Many of the colonies of the Metazoa are nearly as simple as those of the Protozoa. Such is the case with the Ascidia and the Polyzoa. These colonies are compounds of precisely similar, asexually-born individuals, each of which pursues life as an individual, though

[1] Cope. Origin of Genera. 1868.

they seem to possess some degree of vascular and sensory connection.

A somewhat more progressed case is presented by the Actinozoa, in which the colony is united by a common stem, which is fed by the united labors of the feeding individuals, and through which these individuals possess some degree of vascular, sensitive and motor connection. The separate members of the colony here take a first step towards reduction into the organs of a complex individual.

In the Hydrozoa this subordination is much more declared. Each member of the colony has lost a portion of its life powers, and is thus an incomplete individual. Some feed only, and have ceased to reproduce. Others reproduce only, and have ceased to feed. The colonial life is a necessity, since each individual has lost a portion of its life powers. From being individuals possessed of all the life functions, they have become organs of a composite individual, but organs which are as yet, in nearly a complete sense, individual animals. If now we consider the swimming Hydrozoan colonies, the Siphonophora, a remarkable development of this principle of subordination makes its appearance. These complex animals yield strong indications of an origin in colonies of individuals, which have become quite incapable of a separate life. Each has lost not one only but several of its organic powers, and is reduced to the performance of a single duty, while dependent on its differently-developed neighbors for aid in its other duties. The original individuals have become degraded into organs through this loss of ability and limitation of their field of labor. Thus, at the extremity of the general stem of the Siphonophora, there is usually an individual converted into a simple bladder, and useful only for purposes of flotation. Beneath it are a number of others which act only as swimming bells, their sole duty being to rythmically contract and expand. On the remaining portion of the stem are individuals, some of which act as food catchers, others as mouths and digestive organs, others are limited to reproductive activity, and others again are reduced to mere covering pieces, in which all the life organs have disappeared, and which seem intended merely to protect the more active individuals. The common connecting stem acts as a vascular system, and probably possesses some degree of sensory and motor activity.

In the Siphonophora, then, the reduction of a colony of budded individuals to the condition of a single composite individual has greatly progressed, so far as indications go. Their embryological development points to such an origin. In fact, the Hydrozoa generally are born from the egg as ciliated planulæ, which, after a period of free-swimming existence, become fixed and develop the mouth and tentacles of the Hydroid type. Only later the polyp buds sprout and the polypary is formed. Thus their embryological development indicates the character of their phylogenetic evolution.

*(To be continued.)*

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## REVIEW OF THE PROGRESS OF NORTH AMERICAN BATRACHOLOGY IN THE YEARS 1880–1883.

BY W. N. LOCKINGTON.

IN this department little has been done in the direction of descriptive zoölogy—probably little remains to be done in the limits of the United States, while the researches of Sumichrast Bocourt, Cope and others, must have nearly exhausted the riches of Mexico and Central America in batrachian forms. Fortunately the batrachia are still, as they have been, favorite subjects with the anatomist and embryologist, and to this fact we owe much of the material presented in this article.

The most important addition to North American Batrachology within the two years to which we are confined is certainly that of M. Brocchi, forming one of the quarto numbers of the magnificent work which for several years has been published under the direction of M. H. Milne Edwards, by order of the Minister of Public Instruction, and entitled "Mission Scientifique au Mexique et dans l'Amerique Centrale." The part already published, though containing only the Raniformia and a portion of the Hylæformia, comprises descriptions of seventy species, eleven of which are new. The classification adopted is unfortunately that of Dumeril and Bibron. The primary division of the Anura is into Phaneroglossa and Aglossa. The former group is divided into Hylæformia, Raniformia, Hemiphractiformia (having teeth in both jaws), Bufoniformia and Hylapesiformia, the last section containing forms which are toothless like the toads, but are without the dilated sacral vertebræ of the latter. The Aglossa are