

Colonial Organisms (Continued)

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shell beads; a few small copper beads; specimens of paint and plumbago; three skulls.

I am inclined to believe that these mounds are the work of the Cherokees, but cannot give my reasons for this belief in this article. Somewhat similar burials found in Kentucky point to the region of the Ohio as the former home of the builders of the North Carolina and East Tennessee mounds. It is possible, therefore, that further research will tend to confirm the Cherokee tradition mentioned by old John Lederer.

COLONIAL ORGANISMS.

BY CHARLES MORRIS.

(Continued from page 149.)

CONTINUED review of the subject of animal colonization leads next to the Annelida and the Arthropoda as its most advanced instances. This progression, indeed, is not so strongly marked in the Annelida, which are usually not only distinctly segmented, but each segment is an almost complete individual. Each segment possesses its own nerve fibers and ganglion, its own muscles, its own limbs, frequently its own breathing organs, and, in a partial degree, its own circulation. The intestines of the several segments unite into a common intestine. Indeed this retention of individuality, in some cases, goes still further. There are existing worms which possess eyes in each separate segment. Thus the indications are very marked that the Annelid began life as a colony of budded individuals in which subordination of some of the life functions had taken place. This subordination is yet, in many instances, very slight, the only distinctly specialized segment being the head, with its mouth and sense organs. The loss of individual completeness is not nearly so great as in the members of the Siphonophora.

In its reproductive phenomena the family of segmented worms presents some striking evidences of a colonial origin. In certain instances the worm is born as an individual segment, and gains its mature state by subsequent budding. This is the case with the tape worm, in which the budding process continues indefinitely throughout life. Among the Chætopoda some very significant phenomena are exhibited. A single worm is divided into two through fission between two of the body segments, one of

which becomes the anal region of the anterior worm, and the other develops into the head and several succeeding segments of the posterior worm. The anal region may, by growth and segmentation, give rise to an indefinite number of new segments. In the fresh-water worms, the Nais and Chætogaster, this phenomenon proceeds farther. After the division into two worms and subsequent growth by segmentation, fission again and again takes place, whenever four or five new segments are added in front of an anal zone, so that a chain of zoöids is formed, each with a few segments only and all fed from the mouth of the anterior one. Subsequently they break up into free individuals, each of which lengthens by budding.

This phenomenon strongly indicates an original possession of the full life functions by a single segment which formed, by asexual reproduction, a longitudinal colony. Each member of this colony, while subordinated in function, tends to complete development, as is shown by the fact that certain segments apparently regain lost organs and resume discarded functions. The seeming indications is that these organs and functions were part of their original life plan, and that their ordinary development is only a partial one.

In fact, in all these cases of individuals developed from colonies, the segments or organs present certain analogies to the larval state of other animals. The larva is an instance of retarded development in which the surrounding conditions check for a time the further unfoldment of the life plan, and cause the assumption of new temporary organs or functions. In the segment the unfoldment of the life plan is in like manner checked, and occasionally new organs or functions are developed to bring the organism into harmony with surrounding conditions. Ordinarily the larva enters into new conditions and resumes its checked development. Ordinarily the segment fails to enter into new conditions, and its development continues partial. Yet there are interesting instances in which the larval retardation continues for life, as in the Leptocephali, or embryonic fish. And to complete the analogy we have the above interesting instance of the Chætopoda, in which the developmental energies of the segments appear occasionally to triumph over the retarding conditions, and

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¹See paper on "Growth and Development," AMER. NATURALIST, July, 1883, p. 725.

to cause a nearly complete unfoldment of the original life plan. The main difference between the larva and the Annelid segment, or the Hydrozoan organ, is, that in the former the animal is checked in an embryonic stage, in which it possesses full life functions; in the latter it attains its mature stage, but with only a portion of the life functions. In the former it displays an independent immaturity, in the latter a subordinated maturity. But with these distinctions we seem to behold in all these phenomena the results of one law of nature, a checked development, under the force of circumstances, of forms which have an innate tendency to complete their development, which tendency becomes effective as soon as the retarding conditions are removed, and at times seemingly in spite of them. There appears to be a persistent strife between the active external conditions and the innate hereditary life energies.

The embryological development of the Annelids presents indications like those of the Hydrozoa. They leave the egg as globular masses of untransformed cells. This cell mass elongates and becomes segmented, while the head organs appear anteriorly. The number of segments increases by the interposition of new ones, the segmental organs appear, and the young animal gains the mature form. In this process the indication of an original colonial origin is evident, though perhaps less so than in the Hydrozoa. The asexual budding by which the mature animal is formed is certainly significant, and points to the character of its phylogenetic derivation.

In the Arthropoda appears the highest known development of this principle of the formation of individuals by the transformation of colonies. Of these the Myriopoda alone present clear indications of colonization. In them the segments are as similar to each other as in the Annelida, and like the latter possess nearly all the life organs. Each segment has its own nerve ganglion and fibers, its breathing organs, muscles, intestine and vascular space. It lacks only the mouth and the sense organs of the head-segment to be a complete animal. And its formation by the indefinite budding of new segments is significant of its origin.

In the Crustacea, Insecta and Arachnida, the traces of the original colonial condition are much less evident, though they are ordinarily quite manifest in Crustacean and insect larvæ. And

even in the highest of the Arthropoda, the insects, the original individuality of the segments is not quite lost in the mature The primitively individual members of the colony stubbornly resist the cession of their separate functions, and only partially yield to the common needs. This persistent individuality of the segment is partly manifest in their legs and wings, which are appendages of separate segments; but more particularly in the segmental succession of their nervous, muscular and respiratory organs, and in their segmented chitinous armor. Indeed, the Crustaceans and Insects indicate a lateral as well as a longitudinal development of individual segments, for the limbs present significant traces of an origin in the budding process. They appear, in fact, to be a series of specialized segments which have become greatly degraded from their original organic completeness through disuse of the internal organs. Each possesses its muscles, its chitinous armor and what may represent its intestinal cavity. The successive joints of the limbs appear to result from a continuance of the budding process. This seems evidenced by their power of reproduction by budding, when broken off at the joint, and also by the lateral budding which frequently takes place at the extremities of the limbs.

As for the reproduction of the Arthropoda, it tends to disguise their colonial origin, yet only partly so. They are usually born as partially developed colonies, resembling the Annelida in general configuration. But this merely indicates an acceleration of development, or an embryological growth to a considerable extent through the aid of maternally-provided nutriment. In the highest insects, the ants and bees, the parental care is continued until maturity. The growth of the embryo from nutriment provided by the maternal body in no essential sense differs from its continued growth from nutriment provided by the workers, and it is not thrown upon its own resources until maturity. This is the final and highest outcome of the colonial method of animal formation, one in which the members of the colony have become so welded together and subordinated as to have almost vanished from observation, and in which the young begins its individual life in the mature state.1

The review we have here given of the method of development of individual animals through a process of colonization, and the

¹For a somewhat different consideration of this topic see "The Evolution of Organic Form," *Popular Science Monthly*, Nov., 1880.

reduction of the members of the colony to the condition of organs of an individual, may be briefly concluded and perhaps strengthened by a reference to the sub-kingdoms of animals whose members appear to develop as individuals and not through colonization, and whose organs arise from special modification of the tissues of the individual body, and not from subordination of the separate members of a colony. There are three of these sub-kingdoms, the Echinodermata, the Mollusca and the Vertebrata. Of these, indeed, the first is supposed by Haeckel to arise from a colony, since he ascribes the star-fish to the original junction of five worm-like animals. The evidence in favor of this, however, is not convincing, and is not sustained by any distinct evidence of budding in the development of the embryo. In regard to the Mollusca their individual derivation is unquestionable, and their organs present no indication of assuming the typical molluscan form. The segmental character of a part of the body of the Vertebrata has been adduced as an argument in favor of their colonial derivation, but this argument is unsustained by any other evidence. There is no indication of segmentation in the organs, none of which are successively repeated, as in the Arthropoda and Hydrozoa. These organs indeed present every indication of originating in the transformation of the tissues of an individual, and display no evidence whatever of a tendency to assume the parental form. The only indication of colonial aggregation is in the segmental repetition of the vertebrate bones and their accompanying nerve ganglia, but this segmentation may perhaps be better explained in another manner.¹

In vertebrate embryology there is no clear evidence of segmentation; and the lowest vertebrate, the lancelet, possesses the vertebral characteristics very imperfectly. The Tunicata yield some indication of a connection with the Vertebrata by the segmentation of their posterior body in the embryo state, but this very low stage in the line of vertebrate development is utterly unlike the accordant stage of articulate development. In the latter each segment is furnished with nearly all the organs necessary for individual life. In the former the functional organs develop within the anterior undivided body, and the segmentation is limited to the tissues of the tail, and is perhaps due to the need of flexibility in the swimming motion of a homogeneous organ.

¹ See " Evolution of Organic Form," Pop. Science Monthly, Nov., 1880.

As for the reproductive phenomena of the animals here considered, there is no essential distinction from those of the colonial class. In the low forms the young are born immature, in the high forms they are born mature, but in all cases their real birth is as a single cell into the ovary, while the after development is gained partly within the maternal body or the egg, partly in the external world. Yet in this respect the highest vertebrate presents an interesting parallelism with the highest arthropod. As the ants continue to feed the embryo after birth until it has assumed the mature form and is able to obtain its own subsistence in the method of the mature animals, the same may be said of the birds and the Mammalia, which continue to supply their young with food after birth until they are able to provide for their own needs in the parental method. Thus at the summit of the organic series the young begins its individual life as an animal mature in every function except the reproductive.

The colonial origin of the higher plants is equally significant with that of the animals mentioned. As compared with the animal world their closest analogy is with the colonies of the fixed Hydrozoa, in which, from a common stem attached to the surface, outgrow successive nutritive and reproductive individuals. This description applies exactly to the highest plants, with the exception that they are attached to the ground by roots, which are also transformed individuals.

Even the escape of the reproductive members of the Hydrozoan colonies as free Medusæ is not without its analogies in the vegetable world, whose shed spores become reproductive individuals. The fact is that all high development in plants is attained by the method of colonization, and that the advancement in this direction is far inferior to that gained by the higher animal colonies.

The lower sub-kingdoms of plants are not clearly distinct from cell colonies. They are born as single cells, which subsequently develop into cell masses. These, particularly in some of the higher Fungi, become very complexly organized, yet they display little or no cell differentiation, and may properly be considered as cell colonies. The spores, which are shed by all the lower orders of plants, are free asexual offspring probably peculiar only in being specially rich in protoplasm, and thus well adapted to active growth. Such an asexual growth takes place

in the spores of all plants from the Fungi to the Ferns, and sexual propagation arises through a combination of two cells produced by this secondary growth.

As the gastrula seems to be the primitive form of the manycelled animal, so we might reasonably look for some parallel typical form in plants. In all higher plants the leaf is the most apparent fundamental form. Yet the leaf is the result of a considerable degree of evolution, and is preceded in the lowest plants by a mere mass of undifferentiated cells which assumes no typical form. There is no requirement of a digestive cavity to which the fundamental form of animals is due. This cell mass assumes the leaf shape in some of the Algæ. In the mosses the leaf becomes more definitely organized, and still more so in the ferns, but gains its highest condition only in the phanerogams. embryological development passes through conditions analogous to those of animals. Birth consists in the extrusion of a single cell which, after fertilization, develops into a cell colony, and subsequently, in the higher plants, produces embryo leaves, stem and root in its ovarian development. In all plants a mass of unorganized tissue represents the early cell colony, while the leaf and the flower appear in the higher plants as the ultimate results of vegetable evolution. But these higher plants are in no proper sense individuals. They are colonies of but slightly subordinated members. The mosses, the ferns and their congeners, are little more than leaf colonies. An Endogen is an organic colony, each of whose members is a single leaf. In the Exogen the final step of progression is made, and the individual member of the colony is a group of leaves, attached alternately to an unbranched stem.

In all plant colonies a stock-mass or stem is formed, which serves as a reservoir of nutriment and a vascular organ. In the mosses and lower ferns this stem lies under ground, while the germs which it produces unfold into colonies of individual stems or leaves. The colonies are annually reproduced, and each adds something to the dimensions of the stock mass, which, in the higher ferns, emerges from the ground, and gradually extends upwards into the air. This fern stem has no power of self-growth. It is made up of the bases of old leaves, of vascular bundles which serve to supply the new leaves with nutriment, and of aërial roots which grow abundantly from its sides, and add much to its thickness.

In the Endogen the colonial character of the tree is equally or perhaps yet more evident. The stem is, as it were, a fertile soil, in which annual colonies of leaf individuals take root. leaf is not properly an organ of the tree, but is an individual which is rooted in the tree, as the tree itself in the soil. The vascular bundles or the root fibers of the leaves force their way far down into the trunk, as if in search of nutriment, and thus add new tissue to the stem throughout its whole length. Neither in the Fern nor the Endogen has the stem any power of selfgrowth (except in some special instances), there being no germinal tissue except at the extremity of the stem. The tree fern adds new tissue mainly to the extremity of the stem, which increases in diameter only by the outgrowth of adventitious roots. The Endogen, by the downward growth of vascular bundles from the leaves, adds new tissue throughout the stem, which in consequence becomes exceedingly dense and hard, but which has no growth in diameter.

In the Exogen other features of progression appear, and the colonial character has become less evident. The individual member of the Exogen colony is no longer a single leaf, but a group of leaves, seated on an unbranched connecting stem. And the vascular bundles proceeding from these leaves can be traced but a short distance into the substance of the stem. The members of the colony seek less for individual service by aid of their fibrous roots, but trust more to the general vascular service of the stem. This service is more easily performed from the fact that the exogenous trunk retains active tissue throughout its whole length. Thus cell reproduction is constant, and the stem increases annually in diameter. In addition the presence of germinal tissue throughout the stem permits asexual reproduction elsewhere than at the apex, as in Ferns and Endogens, and reproductive buds may be formed at any point in the cambium layer. Thus the Exogen, though a colony in origin, has made a decided movement towards a composite individuality, though it is far from having attained the definite individuality attained by the higher animal colonial groups.

We have, thus far, considered only the leaf members of the plant colony. There are two other members, the root and the flower, both produced by asexual budding, the former representing an earlier stage in vegetable evolution than the leaf, the latter

the most highly evolved members of the plant colony. The plant stem which connects these individuals resembles the stem of the Cœlenterate colony in its vascular function. But the plant colony has the peculiar feature that it includes two distinct forms of nutritive individuals, each absorbing a special kind of nutriment. The water and the nitrogenous elements of the food are absorbed by the roots, the carbonaceous by the leaves. Just where the chemical combination of these various elements into protoplasm takes place, whether in the leaves or the stem, is not known.

It appears, from these considerations, that the tree is not a colony in a simple sense, as in the Polyzoa, in which precisely similar individuals are aggregated; but in a complex sense, as in the Hydrozoa, in which each individual performs but a part of the life functions, and is dependent upon other individuals for the remainder. Thus the tree is, in one sense, an individual, with three kinds of organs, but in a truer sense, a colony of partly subordinated individuals.

The third form of organ, or member of the colony, the reproductive, is in its origin a modified leaf group. It has no nutritive powers, its sole duty being sexual reproduction. This reproductive function we need to consider in conclusion. The plant colony, like the animal colony, is built up by asexual budding. These buds, in the higher plants, attain a considerable degree of development ere their individual life begins. They enter upon their life duties neither as simple cells nor as simple leaf organs, but as leaf colonies. Thus the product of a Phanerogamous bud is not a single leaf, but a group of leaves, each of which, however, retains its individuality in the Endogens, but loses it in great measure in the Exogens, in which the twig with its leaves acts as a compound individual. This is another instance of "Acceleration of Development," an advanced degree of development being attained under the parental care, ere the offspring is thrown upon its own resources as an active individual.

In regard to the sexual individuals a still more declared acceleration is evident. In this respect the history of plants runs parallel with that of animals. In the lowest forms the product of sexual "conjugation" is a single cell, which is at once thrown upon its own resources for development. In somewhat higher forms, as in the higher Fungi, asexual germs, perhaps rich in protoplasm, are shed as free individuals, and grow into the fila-

ments of the mycelium ere sexual reproduction takes place. There seems here a preliminary gathering of nutriment for the use of the sexual germ. In the Ferns this process is repeated in a fuller degree. The asexual spore develops into a *proembryo*, or mass of cell tissue, within which arise the ova and spermatozoa of sexual reproduction. Thus the new-born sexual germ is provided with a stock of nutriment to aid in its embryo development, and the proembryo is in this sense the primitive form of the seed of the higher plants. It, indeed, in a fuller sense, represents the flower of the higher plants, since it acts as a reproductive organ, and produces fertilized germs.

But in the Phanerogams the development of the embryo under the parental care proceeds considerably farther than in the Cryptogams. The young is not shed as a germinal cell, nor as a mass of unorganized cell tissue, nor even as a leaf colony as in the asexual bud, but as a mature plant, with stem, leaf and root all clearly indicated, and surrounded by a store of nutriment to aid in the early stages of its subsequent growth. Thus the seed of the plant is directly parallel to the egg of the animal, and acceleration of development has attained to as high a stage in the one case as in the other. In the highest phases of both plant and animal life the young begins its individual life as a copy of the mature form. In the seed of the Endogen the simple nature of its individual is apparent in the presence of a single seed-leaf, while the double, or the yet more numerous cotyledons of the Exogens, point to the composite character of the exogenous individual.

This paper has grown to too great a length, and yet the subject is but briefly treated. A fuller consideration could have included many other facts in aid of the doctrine of the colonial origin of the organisms reviewed, and also have made more apparent the fact that the organs of individually-developing classes of animals, as the mollusks and the vertebrates, present no indication of a tendency to assume the typical form of the animal, as required by the opposite theory. It is offered but as a partial contribution to the subject, with little value beyond its extension of the inquiry to the whole field of animal and vegetable life, and possibly its effort to place the phenomena of reproduction, and the essential distinctions between the Protozoa and the Metazoa, in a somewhat clearer light.