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Article XV.—BUDDING IN COMPOUND ASCIDIANS AND OTHER INVERTEBRATES, AND ITS BEARING ON THE QUESTION OF THE EARLY ANCESTRY OF THE VERTEBRATES

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It is one of the remarkable facts regarding the ascidians that, although they exhibit apparently unquestionable relationship to the highest group of animals, the vertebrates, and are classed with them in the phylum Chordata, many of them have an asexual method of reproduction in addition to the usual sexual one, namely, the power of reproduction by gemmation or budding and of forming colonies of connected individuals, a habit which is found elsewhere only in certain of the less highly organized branches of the animal kingdom. In the older classifications it was customary to divide the ascidians into two primary divisions, the simple and the compound, according to whether they possessed this faculty or not, and, on account of its convenience, this method of dividing them is still in common use, though it is now well appreciated that the division is not a natural one. This is proved by the fact that some of the compound ascidians show much closer relationship to particular families of simple ascidians than they do to each other, a circumstance which has commonly been explained by the theory that the compound ascidians were derived separately from two or more groups of simple ascidians by separately and independently acquiring the power of gemmation. The writer himself formerly accepted this view, which has been and undoubtedly still is the one held by most of those who are specialists in the study of the Tunicata, as well as by other zoologists, and which is apparently implied in a statement by Hartmeyer, at present the greatest authority on this group of animals, as recently as the year 1918 (Sitzungsber. Gesell. Nat. Freunde Berlin, 1918, pp. 395–396), and by de Selys-Longchamps, who has made important studies of the budding of Ascidians as recently as 1917 (Bull. Sci. France-Belgique, L, p. 271), although the last-named writer briefly alludes to the fact that the opposing theory, that budding was an ancestral character of the tunicates, requires consideration.

According to the classifications of ascidians now in common use by the more progressive authorities, budding and the resulting colony-formation occur in about half the families; in a majority of cases, if it occurs at all in a family, it occurs in all members of it, but there are

certain interesting exceptions. The large and well-known family Styelidæ contains both simple and compound forms, too closely similar to each other in structure to deserve separation into two distinct families in spite of this important difference in their life history. They have, however, often been divided on this basis into two subfamilies, Styelinæ comprising the simple and Polyzoinæ the compound forms.[1] But, on closer examination, we find here within narrower limits relationships of the same nature that proved the division of all the ascidians into simple and compound forms an untenable one. Some of the Polyzoinæ are unquestionably more closely related to certain Styelinæ than to others of their own subfamily. There are certain compound forms which, though separated as the genus *Polyandrocarpa* from the simple genus *Polycarpa* on the basis of their habit of budding, are distinguished from the latter genus by no other character of more than specific rank. Exactly the same condition prevails in another family of ascidians, the Diazonidæ, not at all closely related to the Styelidæ. Here there are two commonly accepted genera, *Rhopalæa* and *Rhopalopsis*, of practically identical character except that the former is reported as not being known to reproduce by budding, while the latter does it, though single individuals are formed also.

Evidently, then, if the common theory is correct, the simple ascidians or some groups of them are probably still in processes of acquiring this new power; it must evidently have appeared very recently in such genera as *Polyandrocarpa* and *Rhopalopsis*, since they have not perceptibly differentiated from their simple allies. Why may we not expect it to appear in others now known only as simple ascidians and perhaps even to develop before our eyes? It would certainly be an interesting observation if we could detect its first origin in some genus or family in which it is as yet unknown.

It is evident that this theory presupposes a sudden or at least an exceedingly rapid development of the function of bud formation somewhat after the manner of a mutation, with either a complete suppression of, or a very rapid transition through, the intermediate stages. We know of no ascidians which habitually produce functionless or incomplete buds that may be regarded as an intermediate stage in the acquiring of the budding function, nor can we image how such incomplete buds could have a utility that would insure their continued production with an increasing approximation toward a perfection permitting of their functioning as

[1]These subfamilies are no longer accepted in some of the latest works.

individuals. The ascidians always have the faculty of budding in a fully functional degree or they do not have it at all.

If we compare the ascidians that produce buds with those that do not, we find that the former are almost universally characterized by two features, first, the individuals or zooids are of simpler and less specialized structure and, second, they are of much smaller size than in most of the simple ascidians. None of the members of the two most highly specialized families of the Ascidiacea, the Molgulidæ and Pyuridæ [=Cynthiidæ of older classifications], which also contain many of the largest species of ascidians, ever bud at all, while those few compound ascidians whose zooids attain a size approaching to or equalling the smaller simple ascidians, or approach the latter in the increasing complexity of their organization, exhibit the power of budding only to a limited extent, forming as a rule only small or rather small groups instead of the extensive colonies which the smaller and more simply organized compound ascidians ordinarily produce. The ascidians being, as their ontogeny shows, a degraded or degenerate group, descended from more highly organized ancestors, it has been assumed that the forms with small, simply organized zooids were the result of the continued operation of the degenerating factors and that when the processes had gone far enough, reducing the animals to a condition corresponding to the members of some of the lower divisions of the animal kingdom, they became able, like these lower forms, to exercise the faculty of budding.

But, if we stop to consider the question, difficulties in accepting this convenient theory at once arise. How is an animal, even one no more highly organized than an ascidian, suddenly able to acquire the power of producing buds? Of course the budding under consideration here consists, like other forms of growth and development, of cell division accompanied by differentiation, under control of guiding influences the nature of which we do not understand, but the character of these controlling influences is, in the case of the budding of a complex multicellular animal, apparently much more complicated and even farther beyond our understanding than in the case of those which govern the progressive differentiation taking place in the development of an egg into an embryo and eventually into an adult organism. If a mechanic is provided with the necessary tools and raw materials he may build a complex and serviceable machine, but give him the same machine and tell him to make two smaller yet serviceable similar machines out of it and he would very likely find it impossible. This illustration is only a remote parallel, but even if we were able to represent by a mathematical formula the

factors involved in the development of an egg into the adult, would not the representation of the budding of a complex multicellular animal into two or more similar ones require the introduction of additional unknown quantities into the equation which is already beyond our powers of solution?

The writer cannot believe that any ascidian or, for that matter, any of the numerous other invertebrates that reproduce asexually in analogous ways and form colonies of connected individuals ever suddenly "acquired" such a function, or that they now possess it unless they have continuously maintained it during the whole history of evolution, having inherited it from remote ancestors of such primitive structure that budding was then nothing more than cell division, and gradually developed the process in complexity as, in the course of their phylogenetic development, their own structure became more complex. Here, as in other cases, "natura non fecit saltem." Once an organism loses this function or allows it to remain latent during any period of extensive phylogenetic change and progress, it is improbable that the power can be secondarily acquired.

According to this view the simple ascidians have not given rise to the compound ones by a process of degeneration in size and in their complexity of organization. The indications are rather that budding was originally a faculty common to all ascidians and that the simple ascidians have lost that power.

Apparently, not only in the ascidians but in the other groups of invertebrates whose members bud and form colonies, an increase in the size of the individuals and in the multiplication and complexity of their anatomical parts beyond a certain point is accompanied by an abandonment of the budding function; in the cœlenterates, for instance, forms with large individuals, as the sea anemones, are commonly simple, those with small individuals, as most corals and alcyonarians and, in another phylum, the Bryozoa, are generally compound.

This circumstance may, of course, be explained in at least two ways, that the increase in size and complexity of structure made the budding physically and physiologically more difficult, so that the power was eventually lost, or that the failure to divide into several or many small individuals made possible the larger growth and higher development of the single individual. Probably both these suppositions are correct and the causes have mutually interacted. Neither of them is opposed to the theory of the development of the simple from the compound ascidians.

The writer believes, therefore, that the power of the budding and colony formation, where it exists at all, is always a continuously maintained inheritance from the earliest ancestors of the group. The fact that, even in such a small and homogeneous group as the ascidians, several quite important modifications in the manner and details of the budding process have been shown to exist does not furnish such a strong argument for this function having arisen independently as a late acquirement as it might seem to at first sight. We cannot doubt that the Tunicata living today are the survivors of an ancient group formerly of much more importance than it is now, and that the ascidians and other subdivisions of it are also ancient groups. The great differentiation that is shown among the Tunicata, comparatively few as they are, indicates a long phylogenetic history, even though on account of their soft-bodied character we have not found them as fossils. There probably has been ample time for modifications in the process of budding within the group of ascidians. Neither is the fact that the most simply organized tunicates living today, the appendicularians, do not reproduce by budding any valid argument against the theory above advocated, as they have probably lost the function, because reproduction by budding is not a convenient process for animals of free-swimming or other active habits, the resulting interference with locomotion and obtaining food being evident. Therefore we see budding and colony formation retained (except in specially modified forms of the process such as occurs for instance in *Salpa*) chiefly in animals that have a permanently attached stage in their life history or an alternation of a fixed and a free generation.

The tunicates and the vertebrates being apparently of common origin, and in modern classifications included in the same phylum or primary division of the animal kingdom, the Chordata, the conclusions that we reach regarding the history of the Tunicata are not without interest as of possible bearing on the early history of the vertebrates, and it seems plausible that the chordate stock at the time of the separation of the tunicate and the vertebrate lines of descent still retained the habit of budding and colony formation which it had kept from its earliest beginnings. The ancestral vertebrates and later the appendicularians lost the faculty through their losing the fixed stage or generation in their life history and maintaining a free-swimming and active existence throughout their lives; more recently, the simple ascidians have also lost the faculty, in their case because of the increasing size and complexity of structure of the individual.

All permanently attached organisms and those which do not have some fairly efficient means of locomotion must provide not only for the reproduction but for the wider distribution of their species. The penalty for failure to do this is certain extinction. We find, therefore, in such organisms, a free-swimming or at least an easily transportable stage; sometimes there may be an alternation of generations between a fixed and a free-swimming form, but usually the distribution of the species is provided for at the time when it can most conveniently and effectively be done, that is while the individual is young and small; in the case of aquatic animals, by means of a free-swimming larval stage which the individual passes through immediately after hatching from the egg. Such a stage may be short or long; if it is prolonged, a development of the reproductive organs to a functional condition may occur and the animal may be able to reproduce without ever attaining the original adult attached stage. The latter, accordingly, becomes superfluous and may eventually be lost, and with it is lost also the power of asexual reproduction which may have been maintained in the attached stage. Apparently this is what has happened in the appendicularians among the tunicates and in the vertebrate branch of the chordate stock; possibly this process has been of still more general operation and many others of the Metazoa which lead a free and active existence may have arisen from the larvæ of attached forms rather than directly from ancestors leading an active existence throughout their life history. If we may base any speculations on the existing Tunicata, manifestly quite aberrant descendants of the original chordate stock, there was in the latter a prolonged larval free-swimming stage possessing such chordate characters as the dorsal central nervous system, notochord, and pharyngeal gill clefts; this stage alone has survived in the appendicularians and vertebrates. Both the larval and the attached stages have survived in the typical ascidians, though only in a degenerate and greatly altered form.

The conclusions to which this line of reasoning leads or to which it lends support may be summed up as follows.

1. The simple ascidians are not the ancestors of, but are derived from, the compound forms.

2. Reproduction by budding is a character originally inherited by the ascidians from their remotest ancestors, though it has since been lost by some of them.

3. Increase in size and complexity of structure and an active, free-swimming existence are two factors which cause loss of the faculty of budding.

4. Budding is not a faculty that can be acquired secondarily. It is a complex physiological and morphological process that must be maintained and gradually elaborated along with the phylogenetic development of the stock to which the organism belongs. If lost, it is lost permanently.

5. Other invertebrates, as cœlenterates and bryozoans, that reproduce by budding and form colonies in a manner analogous to the ascidians, are governed by these same laws.

6. The ancestors of the vertebrates may have had, like the ascidians, a fixed adult stage capable of reproduction by budding; the existing vertebrates may be a development of the free-swimming larvæ of such organisms, not of the fixed stage.

7. That many of the existing groups of free-living animals may be the descendants of larval stages of attached forms. Attached organisms were probably much more numerous and important in the early period of the development of the animal kingdom than they are now.

Although the reader may not be inclined to agree with most of the hypotheses here advanced, the views above expressed concerning the relationships between the simple and compound ascidians seem too strongly supported by observable facts to be regarded as mere guesses, and the inquiry may naturally be raised as to why the opposite views are the prevailing ones and are accepted by at least a large majority of the most competent authorities.

The reason seems to be that the generally recognized connection between the ascidian and vertebrate stocks, coupled with the present insignificance of the ascidian branch as compared with the vertebrate branch, has led to the former being regarded a mere offshoot of the ancestral vertebrates, and those characters common to both branches (exhibited in the ascidians only in the larvæ) have been accordingly regarded as the only fundamentally important characters, while any others, such as the possession of an attached adult stage and the function of budding, have been regarded as secondary ones, both in significance and in date of acquirement. Added to this we have the merely incidental circumstance of the comparatively degenerate character of the adult ascidian, which tends to make the attached stage appear a secondarily acquired condition, leading us to forget that in their corresponding adult stage the ancestral ascidians of past ages may have been animals of much higher organization.

It is possible, then, that the compound ascidians of today may represent, in spite of their considerable degree of degeneracy, a nearer

approach to the ancestral vertebrates than is generally supposed, and that in our search for the earliest type of that most important phylum we must look for it in an attached colony-forming organism rather than in the worm-like form with which our hypothetical histories of the group usually begin. If the common ancestors of the existing Chordata had been of active habits throughout their life, the subsequent development of an attached adult stage in one group (the Tunicata) would not be remarkable, but we would not expect to find in it the power of reproduction by budding.