THE SYSTEMATIC POSITION OF THE CRINOID GENUS MARSUPITES.

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Some time ago I suggested the division of the great group of free living crinoids known as the comatulids into three suborders, as follows:

Innatantes: Families Marsupitidæ and Uintacrinidæ.

Oligophreata: Families Comasteridæ, Zygometridæ, Himerometridæ, Stephanometridæ, Pontiometridæ, Mariametridæ, Colobometridæ, Thalassometridæ, Calometridæ, and Tropiometridæ.

Macrophreata: Families Antedonidæ, Atelecrinidæ, and Pentametrocrinidæ.

At that time I was concerned mainly with the recent forms, and so I did not wish to go into detail in regard to the processes of deduction by which I had arrived at the conclusion that *Marsupites* is closely allied to the comatulids, the predominant type in the recent seas.

I owe it to my colaborators, however, to define my position, and to state the reasons for my conclusion, so that they may judge for themselves whether I am right or wrong.

As I understand it, *Marsupites* is a pelagic comatulid, derived from the common comatulid stock and owing its aberrant calyx structure solely to its pelagic mode of life; the calyx is the most primitive type of comatulid calyx, serving the original purpose of protecting the viscera; what development there has been was exactly the opposite of that seen in all other comatulids, and resulted in enlarging the dorsalmost plates instead of reducing them, as has happened in all other forms. The arms alone have developed along the lines followed by the other comatulids; judging from the material which I have been able to examine, the arms are not only exactly like those of the recent comatulid or pentacrinite, but are comparable only to the arms of the more specialized types, in the latter only to those in the genus *Endoxocrinus*.

It is in the arms that we get the only direct clue to the systematic position of *Marsupites;* but this clue is positive and unmistakable;

and, once we grasp the idea that *Marsupites* may be a comatulid, it is readily seen that, with due regard for contingent circumstances consequent on a curiously specialized mode of existence, the remaining structures point to the same conclusion.

When any member of a group of animals adopts a mode of life entirely different from that of all the other members of the same group we must be prepared to encounter extraordinary and unexpected changes in its organization which are not connected with the more normal type of organization by any intermediates; and it must be remembered that such changes affect first of all the general body form. Among such animals we almost always find the group characters developed in a most erratic manner; some structures will be very highly specialized, sometimes specialized far beyond what is seen in any other members of the group, while others will be in a very rudimentary or primitive state of development, or even absent altogether.

As instances of adaptation to a peculiar and phylogenetically unnatural environment I may mention the flying mammals (bats); the pelagic mammals (cetaceans); the terrestrial birds (kiwi, ostrich, etc.); the pelagic birds (penguins); the flying reptiles (pterodactyls); the pelagic reptiles (sea snakes, plesiosauri, ichthyosauri, etc.); the purely aquatic amphibians (*Amphiuma, Siredon, Triton, Siren,* etc.); the purely terrestrial amphibians (*Hylodes,* etc.); the semiterrestrial fishes; the flying fishes; the parasitic or symbiotic fishes; the purely pelagic fishes; the deep-sea fishes; the parasitic insects; the aquatic insects; the aquatic arachnids; the parasitic arachnids; the mud-inhabiting holothurians; the deep-sea holothurians; the pelagic holothurians; the mud-living echinoids; the sessile gastropods; the parasitic gastropods; the parasitic "worms;" the sessile ctenophores; the parasitic barnacles; the free-living barnacles; the parasitic crustacea; the pelagic crustacea; the deep-sea crustacea. A large number of additional instances could be brought forward, but a study of the types mentioned is sufficient to show at once that when an animal acquires a phylogenetically new environment a readjustment of its structure is induced which often leads to very remarkable changes, so that the real affinities of the animal are rendered very difficult of appreciation.

Among the echinoderms a few cases seem worthy of special attention. The elasipod holothurians, which live in deep water, are bilaterally symmetrical, with tube feet on the ventral side only, and with papillæ on the back; there are no respiratory trees or Cuvierian organs. The apodal holothurians, which commonly live in mud, have no radial canals, tube feet, or respiratory trees. The free-swimming pelagic holothurians have no calcareous deposits whatever, no respiratory trees, no Cuvierian organs, no retractor muscles, and single longitudinal muscles. Only those echinoids which have flexible tests possess longitudinal muscles; many of the species never develop teeth, while some do not develop the lantern apparatus; several genera of the Arbaciidæ never develop spines upon the apical surface, this permanently remaining as in the very young of *Arbacia*.

We see, therefore, that it is a very common thing for a genus or other group living under special conditions to suffer an arrest in the development of some organ or set of organs, and in very many cases, best illustrated among the echinoderms, perhaps, by the well-known instances among the Arbaciidæ (*Arbaciella*, *Podocidaris*, *Dialithocidaris*, etc.), this arrest in development is chiefly evident in the very primitive condition of the general body form, as shown by a comparison of the adults of these genera with the very young of *Arbacia*.

In the very young of *Antedon*, as has been demonstrated by Bury and by Seeliger, there are:

(1) An apical system, consisting of a central plate, or dorsocentral, and a few columnars;

(2) A circlet of underbasals surrounding this apical system;

(3) A circlet of basals outside of and alternating with the underbasals;

(4) A circlet of radials beyond and alternating with the basals.

(5) A circlet of orals, each oral lying directly beyond a basal.

The differences between the calyx of the young *Antedon* and that of *Marsupites* are:

(1) In *Marsupites* the apical system is composed of a single plate instead of one large plate and a series of smaller ones;

(2) In *Marsupites* the underbasals are very large, as large as the basals, instead of being very small, as in *Antedon*.

This latter difference is easily shown to be of no especial significance by a study of the calyx development among the recent crinoids, and especially among the comatulids. Primarily the calyx is composed of four circlets of plates, all the plates being approximately equal in size; these circlets are (1) the underbasals, (2) the basals, (3) the radials, and (4) the orals. Phylogenetic development is in the direction of a reduction in the size of the calyx cavity and of a progressive extrusion of the visceral mass. The underbasals are first affected; instead of forming, as in the primitive condition, an important integral part of the body wall, they move inward, reducing their circlet in size, so that their inner borders, instead of abutting on the sides of the topmost columnar, slip inward over it; at the same time they gradually become more and more recumbent, finally attaining a horizontal position and, instead of functioning as a part of the lateral calyx wall, become merely a sort of flooring upon which the contents of the calyx rest. The basals are next affected; they become reduced in size, and their lower edges slip inward over the inner side of the horizontal underbasals, so that they eventually form a horizontal circlet of plates superimposed upon the similar circlet composed of underbasals; this condition is seen in *Antedon* just before the transformation of the basals into the rosette. A somewhat similar state of affairs is seen in the pentacrinites, though here the basals are not quite so reduced and, instead of covering the underbasals, as in *Antedon*, they imbricate over them. The radials travel the same path as did the basals and underbasals before them, and in most of the comatulids have become quite horizontal, serving merely as a platform upon which the visceral mass rests, and for the attachment of the arms.

This developmental path is very plain and easily demonstrated; but in *Antedon* the underbasals at their first appearance are very small and irregular in number, while in *Comactinia*, *Comanthus*, *Hathrometra*, and *Compsometra*, according to the investigations of Mortensen and myself, no underbasals ever appear. It seems clear that in the recent comatulids acceleration of development has operated to push the metamorphosis of the underbasal circlet so far forward in the ontogeny that it either only appears as a transient, usually imperfect, circlet or not at all; from what we know of the transformation of the basals and of the radials we must assume that the underbasals were of equal importance. This reasoning demonstrates that there is no tangible difference between the calyx of *Marsupites* and that of a comatulid in the younger stages, excepting only for the occurrence of a central plate, end to end with the underbasals, in the former.

The central plate in *Marsupites*, like the similar central plate in *Uintacrinus*, I believe to be the homologue of the dorso-central (terminal stem plate) plus all the columnars of the comatulid. In a previous paper I traced out the development of the crinoid stem from a hypothetical primitive central plate such as is seen in certain echinoids. I assumed that the central plate in *Marsupites* and in *Uintacrinus* was a primitive central plate, and in no way comparable to the comatulid centrodorsal (the topmost columnar of a subsequently discarded stem) for the following reasons: It lies in the body wall flush with the surrounding underbasals, and therefore can not be a columnar, for in all stalked crinoids the topmost columnar supports more or less of the lower margin of the basals or of the underbasals; this is a mechanical necessity, as otherwise the weight of all the calcareous structures would have to be taken up by the soft interior structures immediately above the stem and by the sutures between the topmost columnar and the underbasals. As the underbasals of the young *Antedon* surround its apical system in just the way that the underbasals of *Marsupites* and of *Uintacrinus* surround their central plates, I see no escape from the conclusion that these central plates are the equivalents of the entire apical system (the dorsocentral plus the columnars) of the developing *Antedon*.

There is additional evidence that *Marsupites* never at any stage possessed a stalk, nor did *Uintacrinus*. This evidence is purely circumstantial, but appears to be none the less good. The enormous range of *Uintacrinus socialis* is well known, and recently *Marsupites* has been shown to have a range equally as extensive. Now we find among the jellyfishes forms which are purely pelagic and other forms which are fixed for varying periods. The extent of the distribution of these different types is very varied, the pelagic species having the greatest and the longest fixed the least range. When we compare the distribution of *Marsupites* and *Uintacrinus* with that of the recent jellyfish we find that the parallel is distinctly with those types which are exclusively pelagic and pass through no fixed stage, and we therefore appear to be justified in assuming that *Marsupites* and *Uintacrinus*, like them, were always, at all stages, free swimming.

Marsupites has large orals, and the arms are attached to a comparatively small portion of the distal border of the radials. Both these features are characteristic of the young *Antedon*, as well as of the young of all other genera in which the young have been observed. The orals undergo a metamorphosis just as do the underbasals, basals, and radials; but this metamorphosis merely takes the form of gradual resorption. In general, the resorption of the orals is correlated with the metamorphosis of the basals in the comatulids, as exemplified by *Antedon*. It would be presupposed, therefore, that, were we to discover a comatulid with persistent unmetamorphosed basals, it would also possess persistent unmetamorphosed orals.

Correlated with the presence of orals and unmetamorphosed basals in the young *Antedon*, we find the arms occupying only a small portion of the distal border of the radials; and therefore the same feature in *Marsupites* occasions no surprise.

Mr. Frank Springer first pointed out the correspondence between the structure of *Uintacrinus* and that of the comatulids, in particular to those belonging to the Comasteridæ. *Uintacrinus* has the same globular float-like body as *Marsupites*, but it is differently formed; *Uintacrinus* has progressed much farther along the phylogenetic comatulid path; both agree in having a centrale instead of a centrodorsal and in the possession of underbasals, though these are not always present in *Uintacrinus*. They should, therefore, be united in the same group, a group parallel to those which I have called Oligophreata and Macrophreata.

Uintacrinus has an eccentric mouth; if we can judge from the analogy with the eccentric mouth of most of the Comasteridæ, it also had a many-coiled digestive tube. The long digestive tube of the comasterid species is necessary on account of the habits of those animals, for a large amount of inorganic matter is ingested with the food, necessitating a large absorption surface; the comasterids of deep water have short digestive tubes and central mouths, like the species of other families. *Uintacrinus,* being a pelagic form, probably lived at or near the surface, and therefore its food consisted largely of minute plants. This would be sufficient to induce a very considerable increase in the length of the digestive tract over that necessary for the assimilation of purely animal nutriment. *Marsupites* had a central mouth; we can not say that it did not have a long digestive tube; if it had a short one, it may have been strongly plicated like that of some of the recent endocyclic forms.

The position of the mouth is of no particular importance, systematically, in regard to the question of the relationships of these genera. Among the Comasteridæ most of the species have a marginal or a submarginal mouth, though a number have it perfectly central as in *Antedon,* as, for instance, *Comatilia.* Moreover, in those comasterids in which the mouth is marginal it is always central in the young, and does not begin to move from its central location until the orals have become entirely resorbed. Thus in *Marsupites,* with its large orals, we should not expect to find the mouth eccentric, no matter what might be its position in nearly related genera.

The crinoids are primarily fixed types inhabiting shallow water, derived, not remotely, from free living littoral bottom inhabiting animals. A pelagic crinoid, or a crinoid in the deep sea, is a crinoid living under conditions not normal for its class, and in such a crinoid we must always be prepared to find some structural inconformity which, unless we are careful, will prevent us from appreciating its true affinities.