ON THE ORIGIN OF CERTAIN TYPES OF CRINOID STEMS.

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In a recent number of the American Naturalist[a] I brought forward what appears to me to be conclusive evidence of the very close relationship between the Echinoidea and the Crinoidea, which two groups I placed, together with the Holothuroidea, in the new sub-phylum Echinodermata Heteroradiata in contradistinction to the Echinodermata Astroradiata, which comprises the Asteroidea and the Ophiuroidea. The paper was necessarily short; only the major features of the interrelationships were considered, as in a dissertation of that character wealth of detail always means lack of strength; and many minor points connected with the homology in whole and in part between the urchins and the pelmatozoa yet remain to be elucidated. One of the most important of these minor considerations is the probable relationship between the column of the crinoid and the central or sur-anal plate of the echinoid; how may one of these structures reasonably be derived from the other? and how may widely different types of columns such as those of *Edriocrinus*, *Phrynocrinus*, *Platycrinus*, *Metacrinus*, *Holopus*, *Bathycrinus*, *Calamocrinus*, etc., be logically reduced to a primitive common ancestor?

First of all there is one feature which may, perhaps, require a word of explanation. I have homologized the column of the crinoid with the sur-anal plate of the urchins, and for this I have been criticized by my friend, Dr. Th. Mortensen, of Copenhagen, on the ground that the so-called "Palaeochinoidea," the oldest known echinoids, lack the sur-anal plate. I was aware of this fact at the time I wrote the paper, but it did not appear to me to have any weight whatever, for in the structure of the test the "Palaeochinoidea" are in certain ways far more specialized than any recent species, and, as specialization is usually accompanied to a greater or lesser degree with the suppression of more or less fundamental primitive structures, I assumed that, although the sur-anal plate was usually retained in a more or less reduced form by all recent types, there was no reason for supposing that, were the recent genera to attain multicolumnar ambulacral and

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interambulacral areas instead of their more primitive bicolumnar areas, such an advance would not be accompanied by the dwindling and disappearance of the sur-anal. Because the clavicles are small or entirely absent in the mostly extinct Ratitæ, while in all cases well-developed in the mainly recent Carinatæ we can not pronounce them unessential features of vertebrate morphology.

The common ancestor of the Heteroradiate Echinoderms was an unattached organism with a central dorsal plate surrounded by two, or possibly three, alternating circlets of plates. The Echinoidea, which have remained unattached, retain to-day the original arrangement in a slightly modified form; the Crinoidea, however, instead of maintaining a position in which the dorsal side is up and the mouth down, became inverted, so that the mouth and peristome is up and the dorsal side down. This brought the central plate into permanent contact with the sea floor, and, the central plate being a physiologically inert skeletal structure, a calcareous element whose shape and thickness are in no way confined within narrow limits by physiological or mechanical limitations, it became attached to the sea floor by a simple increase in thickness. The facility with which organisms with calcareous skeletons become attached, even though belonging to normally free groups, is graphically illustrated by *Ætheria*, *Mülleria*, *Spondylus*, *Ostrea*, *Balanus*, and various other genera, the developmental stages of which show that the sessile mode of existence is of comparatively late phylogenetic inception.

MacBride has observed that the larvæ of *Asterina gibbosa* in the early stages of development attach themselves for a short time by the præoral lobe, and from this circumstance it has been argued that the ancestors of all echinoderms were attached. I quite fail to see the force of this reasoning; the larva of *Asterina* at the time of its short attachment is at a very young stage. The larvæ of echinoderms are creatures of a high state of specialization, a specialization along entirely different lines from that of the adults, fitting them for a radically different mode of existence; and it seems to me that the only logical course is to treat the larvæ and the adults as different classes of animals, modified for an entirely different environment, each highly specialized in its own way. Thus I consider that the action of the *Asterina* larva is of interest only in comparison with other echinoderm larvæ of a corresponding stage of development, and is and can be of not the slightest significance as regards the adult life either of *Asterina* or of any other echinoderm; in other words, that, in general, echinoderm larvæ are only interesting or significant *as* echinoderm larvæ, and not as elucidating the phylogenetic path which has been traversed by the adults. For instance, the larvæ of *Echinus* are highly specialized pelagic plutei, those of *Antedon* almost annelidan in character and with a greatly reduced duration of free existence; this would seem to indicate a great phylogenetic difference; but the species of *Antedon* are of exceedingly limited distribution; those of *Tropiometra* have a very wide distribution, necessitating a prolonged free-swimming stage; are we justified in saying that the larvæ of *Tropiometra* may not turn out to be plutei or something like them? Echinoderm larvæ I consider to be in exactly the same category as arthropod larvæ, useful in some ways, highly deceptive in others.

Attached by the central plate, our theoretical ancestral crinoid has two possible courses to follow: (1) It may increase the area of its attached base, or (2) it may increase its thickness, thus forming a column. In recent forms the first possibility is realized in the young of *Holopus* as figured by Mr. Agassiz; the base has spread out enormously, so that the animal presents a striking similarity to certain low species of *Balanus*, the ten arms being countersunk, as it were, in a depression at the apex of a broad low truncated cone. The second possibility is exemplified among recent forms by the adult *Holopus;* the base, instead of further spreading out, gradually becomes elongated, so that the animal is raised up for a considerable distance on a thick stalk. I can see no other explanation of the origin of the base and the stalk in *Holopus*.

Now, a stalk like that of Holopus is limited in its availability for elongation; if it should grow to more than three or four times as long as the minimum diameter, it would rapidly become exceedingly brittle and liable to fracture by the contact of the animal with other organisms, or even from the effects of wave motion. There are, again, two possible lines of development: (1) The animal may break off and thus secondarily become free, or (2) the column may break in so far as the calcareous substance is concerned, yet remain in continuity through the organic base, thus developing an articulation which would admit of a very considerable additional elongation, at least double that of the original column. No recent crinoids are known in which the first line of development obtains; but it is seen in the fossil *Edriocrinus*. No crinoids are known in which the stem is composed simply of two columnars, as would be the case in the first stage of the second line of development. But suppose we carry this line further; we have a crinoid attached by a stalk in which an articulation has developed in the middle; such an articulation would of necessity develop a fulcral ridge running across the joint faces and embracing the central canal, admitting of motion in a single plane, perpendicular to that in which the original blow causing the fracture was received. Stem growth would continue; but, as new deposition occurs only just under the calyx, only the outer columnar would increase in length. Soon the outer columnar would become so long as to become brittle, as did the original stem, and fracture would again occur midway between the first articulation and the calyx. Now, this fracture would almost certainly differ from the original fracture in being formed at right angles to it; for any force exerted in the same plane as that which caused the original fracture would be taken up by the articulation which has formed; but, owing to the definite direction of, and close union along, the fulcral ridge, any force coming parallel to the fulcral ridge, that is, at right angles to the original force, would meet with resistance, as for a force exerted in this direction the original articulation would be practically nonexistent, and a second fracture would occur in the weakest spot, namely, halfway between the original articulation and the calyx, developing into a second articulation in which the fulcral ridge would run at right angles to the direction taken by that of the first. A still further increase in stem length would mean a progressive increase in the number of articulations, each of which would, in the direction taken by its fulcral ridge, alternate with those on either side; and thus would eventually be formed the primitive polycolumnar crinoid stem, a stem exactly comparable to the stem of *Rhizocrinus*, *Bathycrinus*, or the young of *Antedon*.

Now, there is a definite limit to the possibilities of further growth in a stem composed of long columnars fastened end to end by alternating articulations consisting of two ligament masses separated by a fulcral ridge; if the animal remains small with a small light crown, such a stem may attain a length of one hundred or more columnars safely; but if the crown should become of large size and heavy, a stem of this type would not be able to support it; the growing tendency to "buckle" would therefore limit the available length of a stem of this nature.

There are four possible ways of escape from such a calamity: (1) The stem may be discarded; (2) the individual columnars may become greatly shortened, the motion lost through the great diminution of the original beveling at the articulations being compensated by the greatly increased number of articulations in a given section of stem, and the columnars may become enlarged along these lines; (3) they may alter the direction of their fulcral ridges, so that, instead of each being at right angles to those preceding and succeeding, they may each lie at only a slight angle to the preceding (all diverging toward the same side), thus mutually bracing each other and attaining a collective rigidity like a pile of narrow boards built up spirally; or (4) the original fulcral ridge may disintegrate, each half breaking up longitudinally and spreading out fanlike, the two fanlike figures eventually uniting to form an articular surface composed of numerous uniform radiating lines.

The Comatulida fulfill the conditions of the first possibility; before the animal is large enough to cause any danger of "buckling" the stem is discarded at the articulation between the topmost columnar (which becomes the centro-dorsal) and the next following. *Phrynocrinus* is the only known instance of the second case. The curious fossil *Platycrinus* typifies the third. Among the recent forms *Hyocrinus*, *Ptilocrinus*, *Calamocrinus*, and the genera of Pentacrinitidæ are examples of the fourth. The change from the type of stem characteristic of the young of *Antedon* to that characteristic of *Phrynocrinus* may be traced step by step in the genus *Rhizocrinus*, beginning with *R. lofotensis* and ending with the gigantic *R. weberi*, very near in stem structure, though vastly inferior in size of crown, to *Phrynocrinus nudus*. The transition from the primitive type of stem to the curiously twisted column of *Platycrinus* may be easily followed in a good series of the young of any species of that genus, or even in single specimens in which the young stem is preserved. I have observed the change from the *Antedon*-like young stem to the radially arranged adult stem in *Isocrinus*, and have noticed that in the largest species of *Bathycrinus* the fulcral ridges of the articulations broaden out on each side of the central canal, becoming more or less wedge shaped or triangular, and breaking up into radiating lines, the articulations thus approaching the uniformly radiated type found in *Calamocrinus* and *Ptilocrinus* so closely as to leave no possible doubt as to their mode of origin.

It might be urged that the articular faces of the columnars of the Pentacrinitidæ, with their petaloid markings, could not be placed in the same class with articulations like those of *Calamocrinus*, where the joint faces are uniformly marked with radiating lines; but in the Pentacrinitidæ it is merely a case of the columnars, primarily with articular faces bearing regular radiating lines, being moulded or cast into petaloid sectors by the under surface of the basals against which they are formed, these basals being in a curiously reduced condition, midway between the normal type of basal, as seen in *Calamocrinus* or *Ptilocrinus*, and the atrophied and metamorphosed condition seen in *Antedon*.[a]

I can see no other way of deriving the stems of the recent and most fossil crinoids than by supposing them to be the homologue of the central plate of the crinoid-echinoid ancestor which has gradually become thickened and elongated and developed transverse alternating fractures which have metamorphosed into definite articulations. The fact that, when viewed by polarized light, the axis of crystallization is seen to follow the axis of the stem while in the basals and radials it passes at right angles to the plane of their surfaces, and therefore also in the same direction toward the center of the calyx would seem to suggest that the sum of the columnars was

[a] Since the above was put in type there has come to light a remarkable genus, *Proisocrinus*, in which the lower part of the stem resembles that of *Calamocrinus*, but the upper that of *Isocrinus* showing that this transition, foretold by deduction, actually occurs.

equivalent to a single calyx plate. Of course many animals, as for instance *Boltenia*, attach by a small portion of their external covering which becomes pulled out into a more or less slender stalk of greater or lesser length; this elongation of the external covering would carry with it any calcareous structures which happened to be included in it. Numerous cases of such elongation of the external body wall are found in echinoderms, for instance in *Caulaster*, or in the Elasipoda.

Dr. F. A. Bather believes that the stems of crinoids originated thus, from the prolongation of the posterior part of the body of a more or less irregularly plated hypothetical ancestor, the plates carried out into the primitive stem becoming later regularly arranged. I can see no reason for assuming that the stems of crinoids were derived from the stems of blastoids by any such process; they probably originated independently in each. I consider the type of crinoid stem composed of pentameres to represent a different sort of structure from that in the recent crinoids; whereas the latter is the equivalent of the central plate alone, the former is derived from a somewhat more extensive primitive base, not confined to the central plate, but involving the first circlet of five plates. A stem composed of pentameres, then, is made up of a series of repetitions of the lowest circlet of plates in the crinoid calyx, and the original central plate would be retained within the first of these extra circlets laid down, that is, instead of remaining at the calyx, the central plate has become fastened to the sea floor forming, as it were, a plug in the end of a long tube composed of morphological repetitions of the circlet of plates surrounding it. These pentameres, as described by Doctor Bather, gradually came into closer and closer contact so that eventually columnars were formed resembling those of *Calamocrinus*, though morphologically entirely different. So far as I know, sections of pentameres and of columnars derived through pentameres have not been examined to determine the axis of crystallization. It seems probable that in these cases the axis of crystallization will be found to run inward direct from the periphery of the stem toward the center instead of parallel to the main axis of the stem as in the other type.

The stalk of *Holopus* has been cited as an example of attachment by the central plate, and of an elongation of that attachment; but in reality the case is not quite so simple; in fact, *Holopus* is something of a combination of these two types of stem formation, for, in addition to the expanded and elongated base, the basals and the radials have become pulled downward so that instead of forming a cup they form a tube continuous with the expanded base and join with the expanded base in producing the stalk. If the stalk of *Holopus* should become greatly elongated it is a question whether a *Rhizocrinus*-like stem would be formed, or whether the basals would elongate and, by progressively developing a series of sutures, result in a stem formed of pentameres.