THE HOMOLOGIES OF THE ARM JOINTS AND ARM DIVISIONS IN THE RECENT CRINOIDS OF THE FAMILIES OF THE COMATULIDA AND THE PENTACRINITIDÆ.

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Hitherto, most writers on the recent crinoids have considered the arms as beginning with the first joints beyond the ("primary") radials; but so far no one has pointed out the exact relations between the arms and arm joints of the different genera and families.

Dr. P. H. Carpenter, in his most admirable essay on the genus "*Actinometra*"[a] (i. e., *Comaster* and *Comatula*), pointed out that in the Comatulida the first two joints beyond each axillary are always articulated in the same way as the two first post-radial joints, no matter how many axillaries may intervene between the radials and the free, undivided arms. He does not here mention the genus *Eudiocrinus*, as understood by him, but in his monograph of the recent stalked crinoids[b] he says:

In the five-armed *Eudiocrinus indivisus* the next joints beyond the radials are syzygial, with pinnules on the epizygals, which clearly shows that they must be considered as arm joints and not as belonging to the calyx, although they undoubtedly represent the so-called second and third radials of a ten-armed crinoid. The other species of *Eudiocrinus* have these two primitively separate joints not united by syzygy but articulated, just as in *Thaumatocrinus*. The second one bears a pinnule both in *Thaumatocrinus* and in *Eudiocrinus varians*; but in *Eudiocrinus semperi* and *Eudiocrinus japonicus* the first pinnule is on the fourth joint after the radial. This would correspond to the second brachial of a ten-armed crinoid, but it is really the fourth brachial in *Eudiocrinus*. Lastly, in Perrier's *Eudiocrinus atlanticus*[c] the first pinnule is on the fifth brachial, which corresponds to the third brachial of an *Antedon*.

[a] On the genus *Actinometra*, Müll., with a morphological account of a new species (A.) *polymorpha* from the Philippine Islands, Trans. Linn. Soc. (Zool.), [2], II, pp. 1–122, pls. I–VIII, (1879).

[b] Report upon the Crinoidea collected during the voyage of H. M. S. Challenger during the years 1873–1876; Pt. 1, the Stalked Crinoids, Challenger Reports, vol. XI of Zoology, p. 47 (1884).

[c] In reality the first pinnule in *semperi, japonicus*, and *atlanticus* is on exactly the same joint; but Perrier considered syzygial pairs as two joints, Carpenter as a single joint "with a syzygy;" hence the confusion.

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While correct so far as *Eudiocrinus indivisus* goes, this construction is quite wrong for *semperi*, *japonicus*, and *atlanticus*, as will be shown later.

In regard to *Metacrinus*, Doctor Carpenter says that the first post-radial joint "is actually a syzygial joint with a pinnule on the epizygal, just as in the simpler *Eudiocrinus indivisus*, but an axillary appears a few joints farther on and the rays begin to divide." Now, although no definite statement is made, the inference is that he considers the two first post-radial joints in *Metacrinus* to be, as in the case of *Eudiocrinus indivisus*, homologous with the first two post-radial joints of a ten-armed crinoid. This is erroneous; but had he compared *Metacrinus* to "*Eudiocrinus*" *varians*, *semperi*, *japonicus*, or *atlanticus* it would have been correct, as will appear later.

Of the remaining recent genera (as then known) he says:

> In the other Pentacrinidæ, however, in *Bathycrinus*, *Holopus*, and in most Comatulæ, as well as in the fossil *Encrinus* and *Apiocrinidæ*, the second joints above the primary radials are axillaries, and it is not till the second (or rarely the first [a]) joints beyond these that the pinnules appear. In all these types, the axillary and the joint immediately below it are of the same width as the primary radials in the calyx. But in *Marsupites* and in many Palæocrinoids (*Platycrinus*, *Cyathocrinus*, etc.) they are very much smaller than the primary radials, just as the homologous joints are in *Hyocrinus*.

The first thing in discussing brachial homologies in the crinoids is to determine upon some method by which we may, with a fair degree of certainty, fix upon single joints, or a pair of joints, as being homologous in all the genera and species considered, no matter where we may find them; when this point is once decided it will be easy enough to work backward and forward from it, and to arrive at the homologies of the adjacent parts. Fortunately the determination of such a joint is comparatively simple, when we have a clear understanding of the types of articulation occurring among the recent crinoids of the families under consideration. These fall at once into two groups, *muscular articulations*, and *nonmuscular articulations*, differing, as their name implies, in the presence and absence of muscle bundles. The differences between them may be shortly summarized as follows:

MUSCULAR ARTICULATIONS (divided into (*a*) *straight*, and (*b*) *oblique*).	NONMUSCULAR ARTICULATIONS (divided into (*a*) *synarthries* or *bifascial articulations* and (*b*) *syzygies*).
Muscle bundles present.	Muscle bundles absent.
May bear pinnules, or may be doubled, thus forming an axillary with an additional arm.	Never bear pinnules, and are never doubled.
Whether pinnulate or not always affects the position of the next following pinnule, throwing it to the opposite side of the arm from the immediately preceding pinnule.	Have no effect on pinnulation; the succeeding pinnule occupies exactly the same position as it would were the nonmuscular articulation not there, but the two joints connected by it merely a single joint.

[a] See beyond, under *Comaster* and *Isocrinus*, and also *Metacrinus*.

It is evident that there is a very radical difference between these two types of articulation morphologically in their effect upon the arm structure as well as in their composition.

Muscular articulations fall naturally into two types, which, so far as I have seen, are always perfectly distinct, *and are not interchangeable in position:*[a]

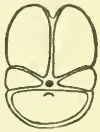

FIG. 1.—ARTICULAR FACE OF A "STRAIGHT MUSCULAR" ARTICULATION.

(*a*) *Straight muscular articulations* (fig. 1), which have the transverse ridge separating the large dorsal ligament fossa from the interarticular ligament fossæ perpendicular to the dorso-ventral axis of the joint face, and the two interarticular and muscular fossæ similar and equal in size.[b] This is the type of articulation by which the radial articulates with the next following joint, and it is *never* found beyond the distal faces of the last axillary in any arm, and sometimes does not occur even so far out as that. (See below under *Metacrinus*, *Isocrinus*, and *Comaster*.)

In an external dorsal view of an arm a *straight muscular articulation* may be distinguished by having the two points of contact of the two joints lateral and equidistant from the median dorsal line (figs. 10 and 11).

FIG. 2.—ARTICULAR FACE OF AN "OBLIQUE MUSCULAR" ARTICULATION.

(*b*) *Oblique muscular articulations* (fig. 2), which have the transverse ridge separating the large dorsal ligament fossa from the interarticular ligament fossæ strongly oblique (either to left or right) to the dorso-ventral axis of the joint face, accompanied by a corresponding distortion of the interarticular and muscular fossæ. This type of articulation is first found *at the second articulation beyond the last straight muscular articulation*, and *immediately succeeding the last synarthry* (see below), and continues thence throughout the arm, except for the occasional interpolation of *syzygies*.

FIG. 3.—AN AXILLARY WITH "STRAIGHT MUSCULAR" DISTAL FACES.

Oblique muscular articulations are at once recognizable in an external dorsal view of an arm (figs. 10 and 11) by having the two points of contact, representing the ends of the transverse ridge, one dorso-lateral the other ventro-lateral; when occurring on the distal faces of axillaries (figs. 6 and 8) they may be distinguished from *straight muscular articulations* (figs. 3 and 4) by having the dorsal points of contact on either side of the anterior angle of the dorsal surface of the joint, instead of exactly at the anterior angle as is the case with *straight muscular articulations.*

[a] See footnote on p. 118.

[b] In the case of *straight muscular articulations* on the distal faces of axillaries, the outer elements of the joint faces are somewhat cut away.

Nonmuscular articulations fall also into two types; but, contrary to what we found to be the case in *muscular articulations*, the second type may partially or wholly replace the first in a given arm, though the reverse is not true:

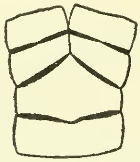

Fig. 4.—Dorsal view of an axillary united to the preceding joint by "synarthry," and to the two succeeding by "straight muscular" articulations; the two post-axillary joints are united by "synarthry."

(*a*) *Synarthries* or *bifascial articulations* (fig. 5); these are distinguished by having the joint faces with a pair of large shallow pits, separated by a ridge which traverses the joint face along its dorso-ventral axis; this is the type of articulation which is *always* found on the distal end of a joint the proximal end of which is united to the preceding by a *straight muscular articulation, and occurs nowhere else;* any, or all, *synarthries* in an arm may be replaced by *syzygies.* The most distal *synarthry* in an arm is always immediately followed by an *oblique muscular articulation*, as stated above.

Fig. 5.—Articular face of a "synarthry."

Synarthries are readily distinguishable in a dorsal external view of an arm by having the points of contact exactly in the median dorsal line (figs. 4, 10, and 11).

(*b*) *Syzygies* (fig. 7); the joint faces are unmarked, or are marked with striations radiating outward from the central canal, the articulation being extremely close, effected by numerous short ligament fibers which are not segregated into bundles. *Syzygies* may replace any or all *synarthries*, and occur at intervals throughout the arm.

Fig. 6.—An axillary with "oblique muscular" distal faces.

Syzygies are at once recognizable dorsally by the extreme closeness of the articulation, which appears as a very fine or dotted line. In drawings *syzygies* are always represented by dotted lines (figs. 10 and 11).

From the above discussion it is evident that there are two joints in each arm which, by their mode of articulation with each other and their neighbors, are sharply differentiated from all the other joints; I refer to the joints on either side of the last *synarthry;* these joints have articulating faces as follows: a *straight muscular articulation*, binding the first to the preceding joint, a *synarthry*, by which the joints are bound together, and an *oblique muscular articulation*, which binds the more distal of the two to the succeeding joint. Of course, as has been mentioned, the *synarthry* may be replaced by a *syzygy;* but there is no difficulty in distinguishing the pair even in that case, for it is the only *syzygial* pair united to the preceding

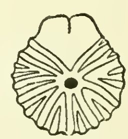

Fig. 7.—Articular face of a "syzygy" (adapted from Chadwick).

joint by a *straight muscular*, and to the succeeding by an *oblique muscular articulation*. Having now discovered a pair of joints, which we may for convenience call Z_1 and Z_2, which are, no matter where they may be, always readily identifiable, we are now ready to enter into a detailed discussion of the brachial homologies.

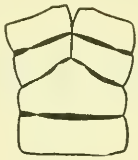

FIG. 8.—DORSAL VIEW OF AN AXILLARY, ALL THREE OF WHOSE FACES ARE "OBLIQUE MUSCULAR;" THE ARTICULATION BETWEEN THE TWO POST-AXILLARY JOINTS IS ALSO "OBLIQUE MUSCULAR."

NOTE.—In the illustrations Z_1 is in all cases dotted, and Z_2 is solid black.

FIG. 9.—PENTAMETROCRINIDÆ; PENTAMETROCRINUS (ADAPTED FROM P. H. CARPENTER.)

Pentametrocrinidæ (figs. 9, 10, 12, and 13).—I recently[a] separated under the name of Pentametrocrinus (figs. 9 and 10) the species *atlanticus*, *japonicus*, *semperi*, *tuberculatus*, and *varians*, which had previously been confused, because of their undivided arms, under the generic name of *Eudiocrinus*, with *Eudiocrinus indivisus* and *granulatus*, on account of the simplicity of their arm structure, which agrees with that of the species *Decametrocrinus* (fig. 13) and with *Thaumatocrinus* (fig. 12) which also have undivided arms, with which I united them under the family name of Pentametrocrinidæ.

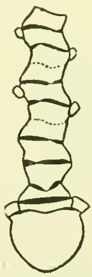

FIG. 10.—PROXIMAL PART OF ARM OF PENTAMETROCRINUS TUBERCULATUS, SHOWING THE EXTERNAL APPEARANCE OF THE ARTICULATIONS.

In this family, Pentametrocrinidæ, we find the following sequence of articulations: *straight muscular* between the radials and the following joints; *synarthrial* between the first and second post-radial joints; *oblique muscular* between the second and third post-radial joints; we at once recognize, therefore, the joints Z_1 and Z_2, for all the succeeding articulations, as is always the case after the first *oblique muscular articulation*, are also *oblique muscular*, or more rarely, *syzygies*. Thus the family Pentametrocrinidæ exhibits the

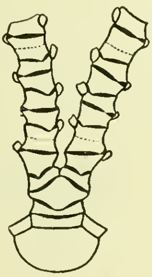

FIG. 11.—PROXIMAL PART OF ARMS OF THAUMATOMETRA TENUIS, SHOWING THE EXTERNAL APPEARANCE OF THE ARTICULATIONS.

[a] New Genera of Unstalked Crinoids, Proc. Biol. Soc. Washington, XXI, pp. 125–136 (April 11, 1908).

simplest type of arm structure possible, Z_1 and Z_2, followed by brachials of the type common to the distal part of the arm in all the other types.

FIG. 12.—PENTAMETROCRINIDÆ; THAUMATOCRINUS (ADAPTED FROM P. H. CARPENTER).

Eudiocrinus (restricted) (fig. 14).—In this genus, in which the five arms are undivided, the sequence of articulations is as follows: *straight muscular* between the radials and next following joints; *syzygy* between the first two post-radial joints (therefore occupying the position of a *synarthry*); *straight muscular* again, a pinnule being developed on the proximally adjacent joints; *synarthry* (with, of course, no pinnule); *oblique muscular*, a pinnule being developed on the proximally adjacent joint on the opposite side to the first pinnule, as pinnules always alternate in position at succeeding articulations, unless the articulation is a primarily nonpinnulate *synarthry* or *syzygy*, which has no effect on pinnulation. In the third and fourth post-radial joints we can again immediately recognize our Z_1 and Z_2; therefore, the first two post-radial joints in the Pentametrocrinidæ are homologous with the third and fourth post-radial joints in *Eudiocrinus*. But what are the two joints between the radials and Z_1? It is evident that the first post-radial joint agrees with Z_1 in the manner of its proximal and distal articulations, except that the normally present synarthry is replaced by a syzygy, which, as it is morphologically the same thing, is a point of interest, but not of importance; Z_2 agrees with the second post-radial joint in having proximally a *synarthrial* articulation, distally a *muscular* (but *straight* instead of *oblique* muscular); thus we find that the arms of *Eudiocrinus* resemble those of the Pentametrocrinidæ, *except that Z_1 and Z_2 are repeated, the additional pair being interpolated between Z_1 and the radials.*[a]

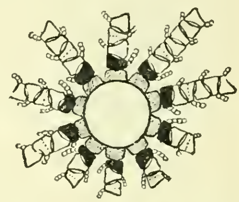

FIG. 13.—PENTAMETROCRINIDÆ: DECAMETROCRINUS (ADAPTED FROM P. H. CARPENTER).

FIG. 14.—ZYGOMETRIDÆ; EUDIOCRINUS.

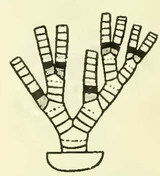

FIG. 15.—ZYGOMETRIDÆ; ZYGOMETRA.

[a] In cases like this where Z_1 and Z_2 are repeated, the primarily *oblique muscular articulation* on the distal face of Z_2 is, on the interpolated repetitions, transformed into a *straight muscular articulation.* This articulation would normally be *oblique muscular* when considered as the distal articulation of a Z_2; but, considered as the proximal articulation of the following Z_1, it is, of course, *straight muscular;* whenever an articulation is morphologically both *straight* and *oblique muscular*, the former, being dominant over the latter, is always found.

Atelecrinidæ (fig. 18) and *Antedonidæ* [a] (fig. 17).—In these families the arms, instead of remaining single throughout, fork at the second post-radial joint; this is a matter of no real importance so far as the arm structure goes, for it must be remembered that any *muscular* articulation, whether *straight* or *oblique*, occurring at the distal end of a joint may divide and form two, from which two similar arms arise; the important thing is not the forking of the arms, but *the determination to what type of muscular articulation belong the articular faces on the distal end of the axillary.*

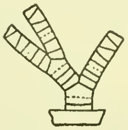

FIG. 16.—ZYGOMETRIDÆ; CATOPTOMETRA.

Bearing this in mind it will be found that the sequence of articulations of these two families is as follows: *straight muscular* between the radials and first post-radial joints; *synarthrial* between the first two post-radial joints; *straight muscular* between the second post-radial (axillary) and third post-radial (first post-axillary) joints; *synarthrial* between the third post-radial (first post-axillary) and fourth (second post-axillary) joints, and *oblique muscular* between the fourth and fifth post-radial (second and third post-axillary) joints. The first and second post-axillary, or third and fourth post-radial joints, therefore, are our Z_1 and Z_2, while the first and second post-radial joints (the second an axillary) correspond to the first and second post-radial joints in *Eudiocrinus* (in which the second is not an axillary, bearing merely a pinnule instead of an additional arm), and are really an interpolated reduplication of the first and second post-axillary joints interpolated between them and the radials.

FIG. 17.—ANTEDONIDÆ; HELIOMETRA.

Now in the Atelecrinidæ and Antedonidæ, and in ten-armed species belonging to genera in other families (which are constructed upon the same plan as the universally ten-armed genera and species of Atelecrinidæ, and the primarily such of Antedonidæ) we are so fortunate as to find additional proof of the correctness of this analysis of the proximal arm structure. In certain species, such as *Perometra diomedeæ*, enormous tubercles are developed at the *synarthry* between Z_1 and Z_2; these are always repeated on the *synarthry* between the first and sec-

FIG. 18.—ATELECRINIDÆ; ATELECRINUS.

[a] *Adelometra angustiradia* and occasionally specimens of *Antedon bifida* have more than ten arms, their structure being then similar to that of the Himerometridæ, and multibrachiate comatulids in general, except *Comaster* (see below); *Antedon* (restricted), considered by Doctor Carpenter as a primitive type, is in reality one of the most specialized genera in the family, approaching the Himerometridæ in many ways.

ond (axillary) post-radial joints, *but nowhere else;* in *Tropiometra* Z_1 and Z_2 are disproportionately large and broad, and we find the first and second (axillary) post-radial joints similarly enlarged; any ornamentation or carination of Z_1 and Z_2 is always duplicated on the two preceding joints.

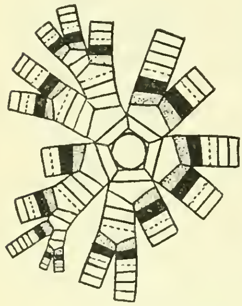

FIG. 19.—THALASSOMETRIDÆ; CHARITOMETRA.

Passing now to the Comatulida with more than ten arms (excepting *Comaster mariæ*, *C. fimbriata*, *C. coppingeri*, *C. borneensis*, *C. multiradiata*, *C. iowensis*, *C. sentosa*, *C. lineata*, *and C. discoidea*) (figs. 15, 16, 19, 20, 22, and 23); these multibrachiate forms are always ten armed until of considerable size, when, by a process of autotomy, the arm is cast off at the *synarthry* (or *syzygy*) between the third and fourth post-radial (first and second post-axillary) joints, or at the syzygy between the fifth and sixth post-radial (third and fourth post-axillary) joints, and from the stump an axillary grows replacing the cast-off arm by two or more. This process of arm reduplication by autotomy was described by Minckert in 1905, but was independently discovered by the present author through observations made on quite different material before Minckert's paper was consulted. In the Comatulida, as is well known, the various "division series" of the arm or ray between the first post-radial axillary (second post-radial joint) and the free undivided arm are composed of either two or four joints. If of two, they are united either by *synarthry* or *syzygy;* if of four, the third and fourth are always united by *syzygy*, while the first and second are almost always united by *synarthry*, but occasionally are united by *syzygy;* the two pairs, the first and the second, and the third and the fourth, are united by a *straight muscular articulation* between the second and third. No matter how many axillaries may intervene between the radials and the free undivided arm, we are always able to recognize Z_1 and Z_2 as the first and second joints beyond the last axillary; and when the division series

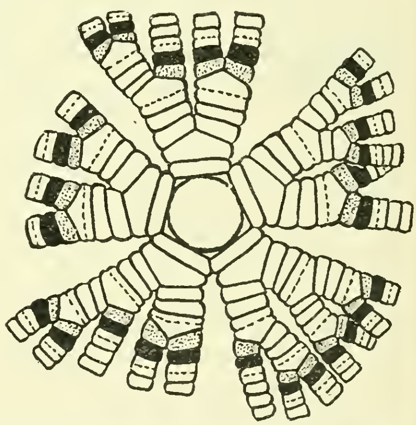

FIG. 20.—HIMEROMETRIDÆ; HIMEROMETRA; ALSO, COMASTERIDÆ; PHANOGENIA.

FIG. 21.—COMASTERIDÆ; COMATULA.

are all of two joints, joined by *synarthry* (or, more rarely, *syzygy*), the distal faces of the axillary are always *straight muscular articulations*. Thus we see that, whereas in the Antedonidæ and ten-armed genera and species of other families (except the Pentametrocrinidæ and Uintacrinidæ) the first post-radial joint and the axillary are merely repetitions of Z_1 and Z_2 interpolated between Z_1 and the radials, so we find that *all* the division series, no matter how many there are, are all additional repetitions of Z_1 and Z_2, interposed between the true Z_1 and Z_2 and the first post-radial reduplication of those joints. When the division series consist of four instead of two joints, it is merely a case of a doubling of the more common primary two, so that, instead of single division series of two joints the division series are double, the two component pairs being united by a *straight muscular articulation* like that on the distal face or faces of the second joint of a division series of two joints only. It is interesting to note that in *Thalassometra gigantea*, in which species Z_2 bears a very sharp median keel, quite lacking on all the other joints of the free undivided arm, this keel is repeated on the second post-radial joint (first axillary), the second and fourth (the latter an axillary) joints of

FIG. 22.—COMASTERIDÆ; COMATULA.

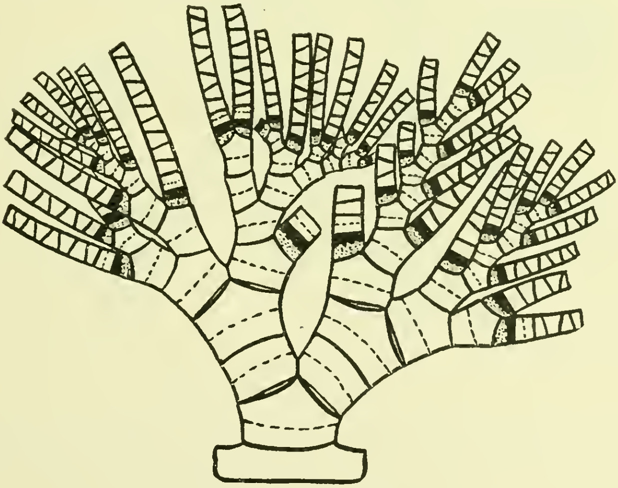

FIG. 23.—COMASTERIDÆ; COMATULA.

division series of four joints (the remaining first and third joints being quite without it), and the second joint of division series consisting of two joints.

In the young ten-armed stage of all comatulids, so far as I have been able to find out, Z_1 is always the first post-axillary (third post-radial) joint, and Z_2 the next following; succeeding Z_2 are two joints united by *syzygy;* now Z_2 always has distally an *oblique muscular articulation;* but a 4 (3+4) or 4 (1+2; 3+4) second post-radial division series always has the two component parts separated by a *straight muscular articulation;* the explanation appears to be that when an *oblique muscular articulation* on the distal face of Z_2, through autotomy taking place beyond it, comes to occupy the position of a *straight muscular articulation*, the dominance of the latter asserts itself, and the *oblique muscular articulation* of the young gradually transforms into the *straight muscular articulation* of the adult.

Now, since the second (and following) post-radial division series of the comatulid arm are frequently doubled, appearing as 4 (3+4)

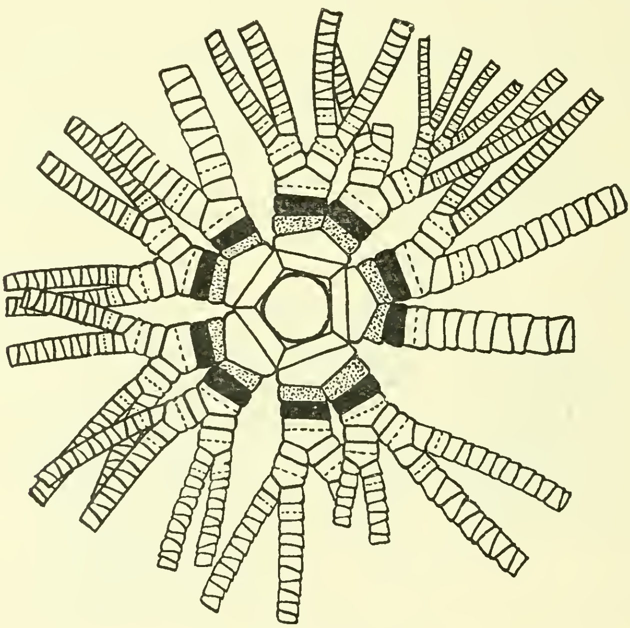

FIG. 24.—COMASTERIDÆ; COMASTER.

(figs. 15, 16, 19, and 20) or 4 (1+2; 3+4) (fig. 23) instead of 2 (fig. 22), we should expect that the first post-radial division series would occasionally be doubled, since it is morphologically comparable to the more distal division series, and we find that such, though rarely, is the case; for Carpenter[a] records that in one "*Antedon*" that passed through his hands "one of the rays consists of five joints, the axillary being a syzygy."

[a] Challenger Reports, XI, Zoology, p. 51.

In *Comaster mariæ*, *C. fimbriata*, *C. coppingeri*, *C. borneensis*, *C. multiradiata*, *C. iowensis*, *C. sentosa*, *C. lineata*, and *C. discoidea* (fig. 24), and in a number of undescribed species from the West Indies, we find a somewhat anomalous condition; the second post-radial division consists of four joints, 4 (3+4); but the next joint succeeding the second post-radial axillary bears a pinnule, whether it be the first joint of another division series or the first joint of an undivided arm; in other words, all the joints following the second post-radial axillary are pinnulate, except of course, the axillaries. It is at once evident, then, that the first joint in the free undivided arm can not be Z_1, for it bears a (*oblique*) *muscular articulation* instead of a *nonmuscular articulation* distally. Where, then, is Z_1? The articulations subsequent to the first post-radial axillary are, *straight muscular articulation*, by which the first post-radial axillary articulates with the next succeeding joint, *synarthry* connecting that joint with the next; *oblique muscular articulation*, *syzygy*, and, on the distal faces of the axillary, *oblique muscular articulations*. By the application of our definition, we find that Z_1 and Z_2 are the *first and second joints following the first post-radial axillary*, instead of the first and second joints of the free undivided arm, as we found in all cases heretofore. The axillaries and division series subsequent to the first post-radial axillary are, therefore, not morphologically homologous with the first division series, and the division series in all the other forms which we have considered, although, of course, they are physiologically analogous. We may designate the division series formed by the presence of repetitions of Z_1 and Z_2 interposed between the primitive Z_1 and Z_2 and the radials as *interpolated division series*, while division series formed by a splitting of the arm at a certain joint, which therefore becomes an axillary, may be called *extraneous*[a] *division series*.

It seems to me that such a radical departure from the ordinary comatulid type of *interpolated* arm division occurring in a group of species entitles them to recognition as a valid genus, more especially as *Metacrinus* has been separated from *Isocrinus* along exactly similar lines; and, since a generic name has been based on a species in each group of the genus *Comaster*, I propose to reinstate Lovén's name *Phanogenia*, and to consider the family Comasteridæ to be naturally divisible as follows:

a^1. Synarthries all replaced by syzygies........COMATULA (figs. 21, 22, and 23)
a^2. Synarthries present between the first two post-radial joints.
  b^1. *interpolated* arm divisions throughout............PHANOGENIA (fig. 20)
  b^2. first arm division *interpolated*, all following *extraneous*..COMASTER (fig. 24)

[a] From *extraneus*, external (in reference to Z_1 and Z_2) as opposed to *interpolated* (between the radials and Z_1).

The described species would therefore arrange themselves as follows:

COMATULA Lamarck, 1816.

Genotype.—Comatula solaris Lamarck, 1816.

Comatula distincta (P. H. Carpenter).
Comatula multibrachiata (P. H. Carpenter).
Comatula notata (P. H. Carpenter).
Comatula paucicirra (Bell).
Comatula pectinata (Linnæus).
Comatula solaris Lamarck.

PHANOGENIA Lovén, 1866.

Genotype.—Phanogenia typica Lovén, 1866.

Phanogenia alata (Pourtalès).
Phanogenia alternans (P. H. Carpenter).
Phanogenia belli (P. H. Carpenter).
Phanogenia bennetti (J. Müller).
Phanogenia briareus (Bell).
Phanogenia carpenteri (A. H. Clark).
Phanogenia divaricata (P. H. Carpenter).
Phanogenia duplex (P. H. Carpenter).
Phanogenia echinoptera (J. Müller).
Phanogenia elongata (P. H. Carpenter).
Phanogenia gracilis (Hartlaub).
Phanogenia grandicalyx (P. H. Carpenter).
Phanogenia japonica (J. Müller).
Phanogenia meridionalis (Agassiz and Agassiz).
Phanogenia littoralis (P. H. Carpenter).
Phanogenia macrobrachius (Hartlaub).
Phanogenia maculata (P. H. Carpenter).
Phanogenia magnifica (P. H. Carpenter).
Phanogenia nobilis (P. H. Carpenter).
Phanogenia novæ-guineæ (J. Müller).
Phanogenia orientalis (A. H. Clark).
Phanogenia parvicirra (J. Müller).
Phanogenia peronii (P. H. Carpenter).
Phanogenia quadrata (P. H. Carpenter).
Phanogenia regalis (P. H. Carpenter).
Phanogenia robustipinna (P. H. Carpenter).
Phanogenia rotalaria (Lamarck).
Phanogenia rubiginosa (Pourtalès).
Phanogenia schlegelii (P. H. Carpenter).
Phanogenia serrata (A. H. Clark).
Phanogenia solaster (A. H. Clark).
Phanogenia stelligera (P. H. Carpenter).
Phanogenia trichoptera (J. Müller).
Phanogenia typica Lovén.
Phanogenia valida (P. H. Carpenter).
Phanogenia variabilis (Bell).

COMASTER L. Agassiz, 1836.

Genotype.—Comatula multiradiata Lamarck, 1816=*Asterias multiradiata* Linnæus, 1758.

Comaster borneensis (Grube).
Comaster coppingeri (Bell).
Comaster discoidea (P. H. Carpenter).
Comaster fimbriata (Lamarck).
Comaster iowensis (Springer).
Comaster mariæ (A. H. Clark).
Comaster multiradiata (Linnæus).
Comaster scutosa (P. H. Carpenter).
Comaster lineata (P. H. Carpenter).

Having discussed all the types of arm division commonly found in the Comatulida, I now pass on to the stalked crinoids, after calling attention to two points of interest. In *Uintacrinus* (fig. 25), which is most nearly related to the Comasteridæ, the peculiarities of the pinnulation[a] are at once explained if we consider Z_1 and Z_2 to be the third and fourth joints after the axillary, instead of the first and second, as would be expected; moreover, the size and the shape of the joints and the examination of the external lines of contact of the articulations lead us to the same conclusion, while I have already shown[b] that the abnormalities recorded by Mr. Springer in his monograph of the genus again favor this interpretation. The arms of *Uintacrinus*, therefore, after the costal axillary, resemble those of *Eudiocrinus* in having a repeated Z_1 and Z_2 series of which the second is not an axillary. I have already[c] called attention to a similar state of affairs occurring abnormally in a specimen of *Heliometra tanneri*. It was stated that muscular articulations were occasionally divided, so that an axillary was formed giving rise to a pair of arms instead of to a single arm. The thought naturally arises, does the *straight muscular articulation* on the distal face of the radial ever divide; and do the *oblique muscular articulations* of the distal part of the arm ever divide? In answer to the first ques-

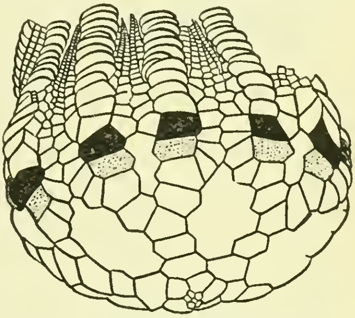

FIG. 25.—UINTACRINIDÆ; UINTACRINUS (ADAPTED FROM SPRINGER); THE "INTERRADIAL" AND INTERBRACHIAL PLATES ARE OMITTED SO AS TO MORE CLEARLY BRING OUT THE ARMS AND PINNULES.

[a] In *Uintacrinus* the first pinnule is on the second post-axillary joint, the next on the fourth, and *on the opposite side of the arm*. Now, these pinnules are separated by two articulations. Were they both *muscular*, they would, so far as the position of the pinnule is concerned, counteract each other, and the second pinnule would be on the same side as the first; were they both *nonmuscular* neither would have any effect on the pinnulation, and the second pinnule would again be on the same side as the first; but it is on the opposite side; therefore, one of the articulations must be *muscular*, and the other *nonmuscular*. A pinnule can not be developed at a *nonmuscular* articulation; therefore, the articulation at the distal end of the second post-axillary joint is *muscular;* hence the articulation between the third and fourth post-axillary joints must be *nonmuscular*, either a *synarthry* or a *syzygy*. In the comatulids, the pinnule on Z_2 is almost universally different from that on all succeeding brachials, but resembles those on all the interpolated repetitions of Z_2. In *Uintacrinus* the second pinnule resembles the first, and not those following (in size): hence, the conclusion is reached that the joint which bears the second pinnule is homologous with that which bears the first, and that the first and second post-axillary joints in *Uintacrinus* are an interpolated Z_1 Z_2 series, of which the second is not, as is usually the case, an axillary.

[b] Proc. U. S. Nat. Mus., XXXIV, p. 269.

[c] Idem., XXXIV, p. 267.

tion, Carpenter[a] mentions a specimen of *Phanogenia alata* ("*Actinometra pulchella*") in which one of the radials is an axillary, supporting two post-radial series, and I have recently recorded a specimen of *Heliometra maxima* which presents the same condition; moreover it is probable that *Promachocrinus* and *Decametrocrinus* originally came into existence through a division of the muscular articulation on the distal end of the radial, which later became more and more firmly fixed, finally resulting in a division of the radials themselves, so that the two genera now have ten radials instead of the original five. If this were true we should expect reversions to occur, and *Promachocrinus* to sometimes be found with one or more radials single instead of double, and bearing a post-radial series comparable to those in *Heliometra*, the most closely allied genus; and *Decametrocrinus* to occasionally occur with fewer than ten rays, thus approximating the most nearly related genus, *Pentametrocrinus;* and it is somewhat remarkable that, considering the small number of specimens representing species of these two genera which has been discovered, one, the type of *Decametrocrinus rugosus*, should be only nine armed, through the persistence of one entire radial (the right posterior), and the division of the remaining four.

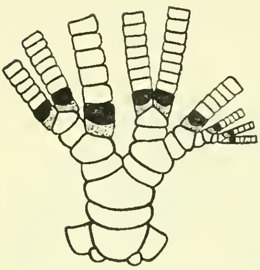

Fig. 26.—Pentacrinitidæ; Endoxocrinus.

Isocrinus (fig. 27).—In *Isocrinus naresianus* we find a condition exactly similar to that described for the Atelecrinidæ and Antedonidæ; Z_1 and Z_2 are the third and fourth post-radial joints, or the first two joints following the axillary. In *Isocrinus wyville-thomsoni*, *I. parræ* (= *Pentacrinus mülleri* + *P. maclearanus*), *I. alternicirrus*, and *I. sibogæ* (fig. 26) Z_1 and Z_2 are the first and second joints of the free undivided arm. The arm structure is therefore similar to that described for the comatulids with more than ten arms, excepting those in the genus *Comaster;* in these species

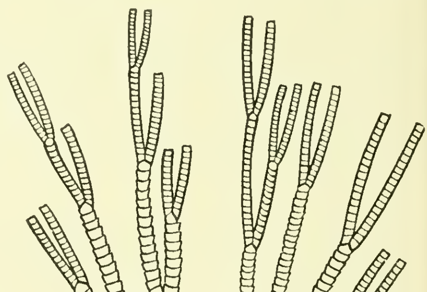

Fig. 27.—Pentacrinitidæ; Isocrinus.

[a] Challenger Reports, XXVI, Zoology, p. 27.

of *Isocrinus* all the synarthries are replaced by syzygies, and all the divisions are interpolated, consisting of two joints. *Isocrinus decorus* and *I. blakei*, in the ten-armed immature state, are exactly similar in arm structure to *Isocrinus naresianus* and the ten-armed comatulids, excepting *Uintacrinus* and *Decametrocrinus*. In the adult multibrachiate condition, however, instead of adding interpolated joint pairs as in the comatulids and in the species of *Isocrinus* just considered (*parræ, wyville-thomsoni, alternicirrus, and sibogæ*), the arm branching, as in *I. asteria* (fig. 27), is of the *extraneous* type, as in *Comaster* (as restricted), Z_1 and Z_2 remaining *always* the first and second joints after the first axillary, or the third and fourth after the radial, as was found to be the case in *Comaster;* and, as in *Comaster*, the syzygy between the two joints following Z_2 is morphologically the syzygy between the third and fourth joints of the undivided arm in the ten-armed young, and comparable to the similarly situated syzygy in all ten-armed comatulids, while in *Phanogenia* and other forms in which the second division series is of four joints, the two outer united by syzygy, the syzygy is morphologically homologous with the *synarthry* between the first two joints in the free undivided arm, and all other syzygies and synarthries proximal to it. In other words, the syzygy between the third and fourth joints after the first axillary in *Comaster, Isocrinus blakei, I. decorus*, and *I. asteria*, is homologous with the first syzygy in the free undivided arm in all other forms (except in cases where the first syzygy replaces a synarthry) *and with no other*, no matter how many syzygies may intervene between that syzygy and the radials.

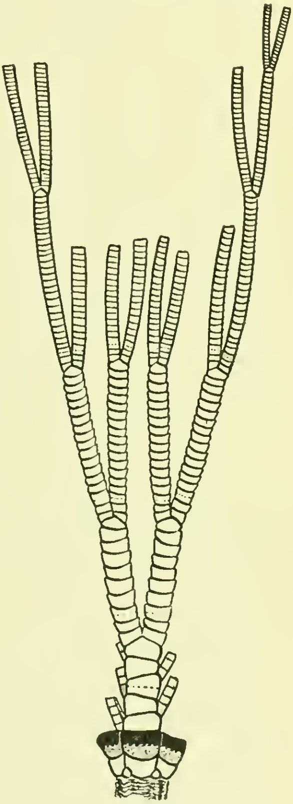

Fig. 28.—Pentacrinitidæ; Metacrinus.

An *extraneous division*, arising as it does from a division of the arm at an *oblique muscular articulation*, might reasonably be supposed to be of somewhat uncertain nature in the position of the succeeding axillaries, because of the fact that all the arm joints after Z_2, except occasional syzygies, are thus articulated, and, of course, every such articulation is a potential axillary; and, as a matter of fact, this is the case; while in the type of *Comaster* considered the division was regular in the number of joints between successive axillaries, in

Comaster maria and in a species mentioned, but not named, by Carpenter[a] (of which I have been able to examine specimens), it is very irregular, and in *Isocrinus blakei*, *decorus*, and *asteria* it is usually more or less, and sometimes very, irregular, especially in the last named. In all the species in which *extraneous division* occurs, the irregularity increases with each successive arm division, so that, in *Metacrinus* and in *Isocrinus asteria*, with their numerous division series, the later division series are of very numerous joints, and much more variable than the division series of *I. blakei* and *I. decorus*, whose most distal series correspond to one of the more proximal series of *I. asteria* and *Metacrinus*.

Metacrinus (fig. 28).—The species of *Metacrinus* are remarkable in possessing a type of arm structure different from any we have considered. There are no synarthries in the *Metacrinus* arm; the first two post-radial joints are always united by *syzygy* (the second bearing a pinnule), the second and third by an *oblique muscular articulation;* all the subsequent articulations are *oblique muscular*, with the exception of occasional syzygies. Therefore Z_1 and Z_2 are recognized as the *first two post-radial joints*, occupying the same position in which we found them in *Pentametrocrinus*, *Decametrocrinus*, and the peculiar *Thaumatocrinus;* but while in these genera the arms are undivided, in *Metacrinus*, *extraneous* division *always* occurs, often as many as five times. All the axillaries in *Metacrinus*, therefore, always have the proximal and both distal faces *oblique muscular*, while in *Isocrinus blakei*, *decorus*, and *asteria*, the first post-radial axillary has *straight muscular* faces, distally, synarthrial proximally, the remainder all *oblique muscular;* and in *I. wyville-thomsoni*, *I. parræ*, *I. alternicirrus*, and *I. sibogæ* all the axillaries have distal faces with *straight muscular articulations* and proximal with *syzygial*. Now, in the young stages of most of the comatulids and in the genus *Isocrinus* where the adults are multibrachiate, the young have only ten arms, Z_1 being separated from the radials by a single interpolated series, representing an additional Z_1 and Z_2; in adult life, Z_1 is, in most multibrachiate comatulids, and in *Isocrinus wyville-thomsoni*, *I. parræ*, *I. alternicirrus*, and *I. sibogæ*, separated from the radials by a number of *interpolated* division series; in *Comaster* (as restricted) and in *Isocrinus blakei*, *decorus*, and *asteria*, Z_1 remains in its primitive position, while *extraneous division* occurs beyond it; but in *Metacrinus* Z_1 is *always* the first post-radial joint, and is *never* separated from the radial by an interpolated series. This is interesting; for the ten-armed young stage of multibrachiate forms depends on the presence of a single interpolated series, and, as this series (which invariably persists in after life) is absent in *Metacrinus*, the natural inference is that *Meta-*

[a] Challenger Reports, XXVI, Zoology, p. 328.

crinus, in its young stage corresponding to the ten-armed condition of *Isocrinus*, *has but five arms;* consequently we await with more than usual interest the discovery of the very young of *Metacrinus*.

This result of the analysis of the arms in *Isocrinus* and *Metacrinus* raises the question, are they really so different as is commonly supposed? Is the separation of *Isocrinus* and *Metacrinus* as at present understood natural? Both these questions must be answered in the negative. *Metacrinus* was separated from *Isocrinus* because of its more numerous "radials," the homologies of the joints not being considered. Thus it appears that *Isocrinus blakei*, *I. decorus*, and *I. asteria* (to which must be added *I. naresianus*) are intermediate in structure between *Isocrinus wyville-thomsoni*, *I. parræ*, *I. alternicirrus*, and *I. sibogæ*, and the numerous species of the genus *Metacrinus*. The *I. asteria* group has Z_1 and Z_2 united by synarthry, and separated from the radials by a single interpolated series; *extraneous division* occurs distal to Z_2; the *I. parræ* group always have the *synarthries* replaced by *syzygies*, and Z_1 and Z_2 always in the free undivided arm, separated from the radials by a series of *interpolated divisions; extraneous divisions* never occur. *Metacrinus* has Z_1 the first post-radial joint, no *interpolated* series, but all the arm divisions *extraneous;* the single possible *synarthry* is replaced by a syzygy. The interrelations of *Metacrinus*, the *Isocrinus asteria*, and the *I. parræ* groups, may be summarized as follows:

Metacrinus (fig. 28).	*I. asteria* (fig. 27).	*I. parræ* (fig. 26).
No synarthries.	Synarthries present.	No synarthries.
Z_1 first post-radial joint.	Z_1 third post-radial joint.	Z_1 separated from the radials by numerous *interpolated* series.
Extraneous division only.	One *interpolated* series only; distal divisions *extraneous*.	All *interpolated* divisions.

It is plain that the *Isocrinus parræ* and *I. asteria* groups are as different from each other as *Metacrinus* is from the latter; and if *Metacrinus* is to be recognized as a valid genus, the *Isocrinus parræ* and *I. asteria* groups should also be kept separate. Treating these three divisions as of equal value generically, it is interesting to find that they fall into definite faunal areas, and occupy characteristic bathymetric altitudes. The three divisions, with the species in each as now understood, are as follows:

a^1. Z_1 and Z_2 the first two post-radial joints, not repeated; all arm division *extraneous;* second post-radial joint not an axillary, but bearing a pinnule; basals very broad, forming, when viewed dorsally, a rounded pentagonal figure; infrabasals large and prominent [a]___________METACRINUS (fig. 28)

a^2. Z_1 and Z_2 repeated at least once; the second post-radial joint an axillary.

b^1. Z_1 and Z_2 the third and fourth post-radial joints; infrabasals present?

c^1. One *interpolated* series only; basals broad, forming, when viewed dorsally, a rounded pentagonal figure; infrabasals?

HYPALOCRINUS (*cf.* figs. 11 and 17)

[a] Infrabasals have been found in *M. serratus* by Döderlein, and in *M. superbus* and in several specimens (all dissected) of *M. rotundus* by Clark.

c^2. One *interpolated* series, followed by one or more *extraneous* series; basals narrow, forming, in dorsal view, a rounded stellate figure; infrabasals large and prominent [a]________________ISOCRINUS (fig. 27)

d^1. First two post-radial joints united by syzygy; lower pinnules serrate; reentrant angles of stellate figure formed by basals shallow. [subgenus *Cenocrinus*]

d^2. First two post-radial joints united by synarthry; lower pinnules smooth; reentrant angles of stellate figure formed by basals deep. [subgenus *Isocrinus*]

b^2. Z_1 and Z_2 the first and second joints of the free undivided arm, separated from the radials by two or more *interpolated* series; infrabasals always (?) absent [b]__________________________ENDOXOCRINUS (fig. 26)

Genus METACRINUS P. H. Carpenter, 1882.

Genotype.—*Metacrinus wyvillii* P. H. Carpenter, 1884.

Geographical distribution.—Northern Australia and East Indies northward to Japan.

Depth.—60 to 630 fathoms:

Included species:

Metacrinus acutus Döderlein.
Metacrinus angulatus P. H. Carpenter.
Metacrinus cingulatus P. H. Carpenter.
Metacrinus costatus P. H. Carpenter.
Metacrinus moseleyi P. H. Carpenter.
Metacrinus murrayi P. H. Carpenter.
M. murrayi, var. *nobilis* P. H. Carpenter.
M. murrayi, var. *timorensis* Döderlein.
Metacrinus nodosus P. H. Carpenter.
Metacrinus rotundus P. H. Carpenter.
M. rotundus, var. *interruptus* P. H. Carpenter.
Metacrinus serratus Döderlein.
Metacrinus stewarti P. H. Carpenter.
Metacrinus sulucnsis Döderlein.
Metacrinus superbus P. H. Carpenter.
M. superbus, var. *borealis* [c] A. H. Clark.
M. superbus, var. *tuberculatus* [d] A. H. Clark.
Metacrinus tuberosus P. H. Carpenter.
Metacrinus varians P. H. Carpenter.
Metacrinus wyvillii P. H. Carpenter.

Genus HYPALOCRINUS, new.

Genotype.—*Pentacrinus naresianus* P. H. Carpenter, 1882.

Geographical distribution.—Kermadec Islands, Meangis Islands, Fiji, Celebes, and Philippines.

Depth.—500 to 1,350 fathoms.

[a] In fifteen specimens of *I. decorus*, including a very small ten-armed specimen with arms 25 mm. long the infrabasals are large and prominent, showing no trace of resorption; material of other species was not available.

[b] Infrabasals are absent in all specimens dissected, including one with arms only 25 mm. long.

[c] This variety differs from the typical form mainly in having the division series and arm bases smooth instead of very rough.

[d] This form has the division series with strong tubercles, but otherwise resembles the preceding.

Included species:

Hypalocrinus naresianus (P. H. Carpenter).

Genus ISOCRINUS, L. Agassiz, 1836.

Genotype.—Isocrinus pendulus von Meyer, 1837.

Subgenus CENOCRINUS Wyville Thomson, 1864.

Genotype.—Encrinus caput-medusæ Lamarck, 1816 (=*Isis asteria* Linnæus, 1766).

Geographical distribution.—Caribbean Sea and Gulf of Mexico.

Depth.—30 (?) to 320 fathoms.

Included species:

Isocrinus (*Cenocrinus*) *asteria* (Linnæus).

Subgenus ISOCRINUS L. Agassiz.

Geographical distribution.—Caribbean Sea and Gulf of Mexico.

Depth.—67 to 667 fathoms.

Included species:

Isocrinus (*Isocrinus*) *blakei* (P. H. Carpenter).
Isocrinus (*Isocrinus*) *decorus* (Wyville Thomson).[a]

Genus ENDOXOCRINUS, new genus.

Genotype.—Encrinus parræ Gervais, 1835 (=*Pentacrinus mülleri* Örsted, 1856).

Geographical distribution.—West Indies and Gulf of Mexico, Atlantic coasts of southern Europe and northwest Africa (including the outlying islands), and East Indies to Timor, the Philippines, the Kermadec, and the Meangis Islands.

Depth.—20 to 1,095 fathoms.

Included species:

Endoxocrinus alternicirrus (P. H. Carpenter).
Endoxocrinus parræ (Gervais).[b]
Endoxocrinus sibogæ (Döderlein).
Endoxocrinus wyville-thomsoni (Wyville-Thomson).

[a] Also many fossil species.

[b] *Pentacrinus mülleri* Örsted is a synonym of this species; *P. maclearanus* Wyville Thomson is merely a rather strongly marked variety.