

SEA-LILIES AND FEATHER-STARS

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(WITH 16 PLATES)

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PREFACE

Of all the animals living in the sea none have aroused more general interest than the sea-lilies and the feather-stars, the modern representatives of the Crinoidea. Their delicate, distinctive and beautiful form, their rarity in collections, and the abundance of similar types as fossils in the rocks combined to set the recent crinoids quite apart from the other creatures of the sea and to cause them to be generally regarded as among the greatest curiosities of the animal kingdom. They have usually been considered as the rare, curious and decadent remnants of an interesting animal type once important but now trembling on the verge of extinction, and it is from this melancholy viewpoint that they are discussed in practically all the text-books.

The discoveries of the last few years have shown that the living crinoids, far from being rare or few in numbers, are abundant both as individuals and as species, and that in all localities where the somewhat exacting conditions under which they can exist are met they occur, sometimes in enormous numbers. The requirements necessary for the maintenance of crinoidal life are unfortunately of such a nature that, though quite generally distributed in the deeper waters of the oceans, they become rare or very local in the littoral, which, together with the great difficulty of preserving them in anything approaching satisfactory form, has served to keep them enshrouded in mystery while animals of other types engaged the attention of investigators.

NUMBER AND SYSTEMATIC ARRANGEMENT OF THE RECENT CRINOIDS

There are known from the seas of the present day 576 described species of crinoids which are distributed in 142 genera and 28 families and subfamilies; of these, 76 species, included in 22 genera and 6 families, are stalked, while 500 species, included in 120 genera and 22 families and subfamilies, belong to the unstalked or comatulid type.

The systematic arrangement of the families and higher groups is as follows:

Order Inadunata.

Family Plicatocrinidæ (*Calamocrinus*, *Ptilocrinus* [fig. 42], *Thalassocrinus*, *Gephyrocrinus* and *Hyocrinus*).

Order Articulata.

Family Bourgueticrinidæ (*Rhizocrinus*, *Bythocrinus*, *Democrinus*, *Bathycrinus*, *Ilycrinus* and *Monachocrinus* [fig. 39]).

Family Phrynocrinidæ (*Phrynocrinus* and *Naumachocrinus*).

Family Apioocrinidæ (*Proisocrinus* [fig. 40] and *Carpenterocrinus*).

Family Pentacrinidæ.

Section I: Pentacrinites (*Metacrinus*, *Isocrinus*, *Endoxocrinus*, *Comastrocrinus* [fig. 41] and *Hypalocrinus*).

Section II: Comatulids (see below).

Family Holopodidæ (*Holopus*).

The comatulid section of the family Pentacrinidæ in the recent seas has become so numerous, so widely spread and so diversified that it alone has acquired all the characteristics of an order. It is thus subdivided:

Suborder Macrophreata.

Family Atelecrinidæ.

Family Pentametrocrinidæ (figs. 49, 50).

Family Antedonidæ (including the subfamilies Antedoninæ [figs. 47, 48].

Thysanometrinx, Perometrinx, Heliometrinx, Zenometrinx, Insometrinx and Bathymetrinx).

Suborder Oligophreata.

Family Charitometridæ.

Family Thalassometridæ (including the subfamilies Ptilometriniæ [fig. 46] and Thalassometriniæ).

Family Calometridæ (fig. 45).

Family Tropiometridæ.

Family Colobometridæ.

Family Mariametridæ.

Family Stephanometridæ.

Family Himerometridæ.

Family Zygometridæ.

Family Comasteridæ (including the subfamilies Capillasteriniæ, Comaciniiniæ [fig. 44] and Comasteriniæ).

THE INTERRELATIONSHIPS OF THE CRINOID SPECIES

The various crinoid species are of very different relative value. In some comatulid genera, especially those including species with many arms, if any one character whereby the species are commonly differentiated be plotted on a species curve the several species will be found to be indicated not by a series of separate triangles, but by a succession of more or less marked nodes which are united to the mass forming the adjacent nodes by coalesced bases in thickness equal to from 10 to 60 or more per cent of the maximum height of the neighboring nodes. Such variability and lack of absolute fixity in any one character is as a rule reflected in all the characters, and thus there results a species group or genus which may be compared to a small mountain system rising out of a plain each peak of which represents a recognized form. In such a genus every character varies between two extremes, but there is often no correlation whatever between the different characters. Thus every sort of combination is possible and a very large variety is found, though the tendency is for the characters to form more or less definitely correlated groupings and to crystallize into certain definite types.

This type of variability is not connected with the geographical origin of the specimens except in a very general way; it is chiefly seen in the multibrachiate species of the Oligophreata, and in specimens of these species from the East Indian region, though there are one or two good examples in the Caribbean Sea. In the Indo-Pacific many species which occur in numerous well-marked varieties in the Malayan region when extending their range outside of this region gradually become more and more fixed and definite in their characters so that individuals from, for example, Madagascar or southern Japan, are all found to be practically uniform in their various features and to represent the mean of the two extremes seen in a series from the central East Indian region.

Thus it is evident that in a number of crinoid genera, as in many groups among the fixed and arborescent marine organisms, we have to deal not only with the usual and well-recognized geographical variation and the formation of geographical "subspecies," but also with the formation of "varieties" which are strictly comparable to the accepted "varieties" among the plants. Such difficult and intricate genera as *Cratægus*, *Aster*, etc., have their representatives among the crinoids, though in the latter the number of included species is not by any means so large.

Many plants form marked local varieties correlated with the physical and chemical character of their immediate environment—the type of soil, amount of sunlight, average temperature, amount of moisture, etc.—and several of these varieties may often be found within a relatively limited area, as in certain species of *Aster*. Many crinoids do exactly the same thing as a result of local variations in the food supply, the amount and kind of illumination, and the temperature.

FORM AND STRUCTURE OF THE CRINOIDS

Typically a crinoid is rather abruptly divided into a slender and more or less flexible column which supports at its summit a pentaradiate head or crown (figs. 39-42) the five divisions of which each may bear anywhere from one (figs. 42, 50) to nearly forty (fig. 17, left), but most commonly two (figs. 39, 43, 46-48), flexible arms along the ventral side of which, giving off branches to the slender alternating lateral appendages or pinnules, runs a narrow ciliated groove (fig. 36, left), the grooves from all the arms of each division uniting and running in a single groove across the so-called ventral disc to the mouth (figs. 4, 5). The cilia in these grooves pick up and convey to the mouth the minute plankton organisms, both animal and vegetable, which serve the crinoid as food.

A single living crinoid (*Holopus*), lacking the column altogether, is attached directly by the crown, the basal portion of which becomes much elongated. In the Plicatocrinidæ the column continues throughout life to add new segments just beneath the crown and never, so to speak, matures. In the large group to which all the living crinoids except the Plicatocrinidæ belong the column increases to a definite size, the topmost columnal then enlarging and becoming permanently attached to the crown, forming a sort of apical plate. This is the general law which, like all of nature's laws, must be liberally interpreted, for it is subject to curious modifications. In some types, as in *Bathycrinus*, maturity comes slowly and several of these topmost

columnals, progressively increasing in width with the growth of the crown, are formed before a fixed attachment occurs. In the group including the pentacrinites (fig. 41) and the feather-stars (figs. 43-50) two widely different extremes are found. The pentacrinite column is extremely precocious. It reaches the mature stage and forms the definite topmost columnal when the crown is still extremely immature and, so to speak, as yet lacks the instinct to attach itself to the column. The column therefore continues to grow and forms a second topmost columnal as in *Bathycrinus*, though in this case the two are separated from each other by a number of intercalated columnals. The second, like the first, fails to become attached to the crown and, the rapidity of stem growth increasing, a continuous series of these topmost columnals is formed each of which immediately after its appearance is pushed away from the crown by the formation of another one above it, the column becoming so enormously overdeveloped that the animal cannot nourish it all and so it dies away at the distal end as rapidly as new segments are added beneath the crown. As they are pushed backwards the numerous elements which nature intended for topmost columnals become separated by a definite number of intercalated segments from which they are always to be distinguished by their larger size and the presence of a whorl of five long jointed processes ending in a strong hook, the so-called cirri. In the feather-stars the column is just as precocious as in the pentacrinites, reaching maturity and forming the definite topmost columnal at a very early stage (fig. 55). But in this group attachment occurs. The column, being mature, has ceased its development; the crown is as yet very small and young; the topmost columnal has become attached to the latter and now forms an integral part of it, and it continues to develop with it regardless of the conditions in the column of which it was once a part. The crown becoming too large and heavy for the column, the latter breaks away just beneath the enormously enlarged topmost columnal, now called the centrodorsal, and the animal becomes free. The further development of the soft structures of the column takes place entirely within the centrodorsal (fig. 7) from which the numerous cirri, here crowded together instead of spaced in whorls of five as in the pentacrinites, are extruded (fig. 10).

Feather-stars mostly attach themselves to foreign objects by means of their usually stout and hook-like cirri which are most commonly from one-fourth to one-third the length of the arms (figs. 33, 34), though in a few species they are longer than the arms (figs. 32, 46). In some the cirri are very numerous, long, slender and nearly straight, forming collectively a sort of disc which, on the principle of a snow-

shoe, supports the animal on soft ooze or mud (fig. 35), and in one family (Comasteridæ) they are frequently quite absent, the centrodorsal being atrophied and sunken in so that its now flat surface does not project beyond the dorsal surface of the crown (fig. 11). Pentacrinites attach themselves to arborescent marine animals by their cirri, like the comatulids, or lie upon the sea floor with the column more or less coiled and the crown raised high above it. The other crinoids, except *Holopus*, are either attached to solid objects by the expanded and encrusting basal columnal or terminal stem plate (Plicatocrinidæ, Apiocrinidæ, and Phrynocrinidæ), or send out from the distal portion of the column a mass of root-like processes by which, plant-like, they are able to maintain an erect position on muddy bottoms (Bourgueticrinidæ). It is curious that in some of these if the crown be lost before the stem dies a mass of roots is produced from the upper end of the column similar to those at the lower end.

The crown of a crinoid is composed primarily of three alternating circlets of five plates, excepting in the Plicatocrinidæ in which there are only two, calling to mind the bracts, sepals and petals of a flower. The plates of the lowest circlet (infrabasals) are small, often only three in number, and frequently, or perhaps usually, absent in mature animals; the plates of the second circlet (basals) are larger and more constant, though in the feather-stars they become transformed into an internal septum (fig. 7, shown cut across just above the cavity within the centrodorsal) with no hint of their original significance, and in the Plicatocrinidæ there are frequently only three of them; the plates of the third circlet (radials) are always highly developed, and are structurally the basal plates of the arms. In a few types each of these is doubled so that there are ten of them instead of only five (compare figs. 49 and 50).

Following the radials there is a linear series of ossicles which rarely remains undivided (figs. 42, 49, 50), almost invariably forking on the second (figs. 39, 46-48); this gives ten arms, the commonest number among the crinoids; but each of these may again divide on the second or fourth segment beyond the first division (very rarely on any other) (figs. 40, 41) and this process may be repeated in extreme cases as many as eight or nine times (fig. 17, left). Ordinarily all of the five groups of arms are alike and all of the arms are of the same length, but in the Comasteridæ the arms arising from the left posterior radial, sometimes from both posterior radials, are frequently shorter than the others, sometimes scarcely more than a third as long (fig. 44), and they are further peculiar in lacking the ambulacral groove (fig. 36), in bearing more numerous and more developed

gonads, and in ending in a terminal brachial bearing a pair of pinnules instead of in a growing tip as do normal arms.

From the second onward the arm segments bear on alternate sides long slender jointed processes called pinnules (figs. 1, 44, 48), which, in the comatulids, are of three types. At the base of the arms and on the second ossicle of division series composed of four elements are the so-called oral pinnules which lack the ambulacral groove and are variously modified into very sensitive tactile organs (figs. 47, 48, 51) or into stout spines (fig. 52) extending over and protecting the disc; following these and more or less abruptly differentiated from them are the shorter genital pinnules (figs. 1, 51, 52), with, or, more rarely, without (fig. 36, left) an ambulacral groove, on which the gonads are developed; there are usually between six and twenty of these on each side of the arm, and distally they pass gradually into the longer and usually very slender distal pinnules (figs. 1, 51, 52) which serve purely as food gatherers. In a few types one or more of the earlier pinnules are lacking (fig. 43), while in the Comasteridæ (figs. 15, 43) the oral pinnules bear curious comb-like structures recalling the pectinate antennæ of certain insects. In the crinoids other than the comatulids the pinnules are much more nearly uniform in structure and in function; in some types (*Metacrinus*, *Hypalocrinus*, *Comastrocrinus* [fig. 41] and *Proisocrinus* [fig. 40]) they are rudimentary or even quite lacking on the terminal portion of the arms. In one comatulid (*Comatulella brachiolata*) many of the pinnules are modified into stout organs resembling cirri which assist the animal in clinging to arborescent marine organisms.

The various ossicles which together form the crinoidal skeleton are tied together by more or less closely packed bundles of fibrillæ the ends of which take the form of loops within the calcareous substance. Between most of the brachials or ossicles of the arms there is found in addition to the ligaments a pair of ventral muscle bundles and between the ossicles of the pinnules there are sometimes a few muscle fibers or a small muscle bundle. Excepting in *Holopus* more or fewer of the brachials are united in pairs by ligament fibrillæ only; such unions, known as syzygies, are extremely close, at right angles to the axis of the arm, and with the joint faces marked with radiating ridges; two brachials so united usually appear as a single one with a thin dotted line across it (fig. 54). Crinoids seem to have the power of severing the syzygies at will, and arm fracture almost invariably takes place at these unions. As a rule syzygial pairs are regularly distributed throughout the crinoid arm, the first being composed of the third and fourth brachials; their number decreases with specialization and with increase in the number of arms.

In addition to the primary bony framework including the ossicles of the crown—calyx plates, brachials and pinnulars—and stem and cirri crinoids have two other skeletal systems; one, superficial, takes the form of very numerous spicules which may increase in size to definite plates sometimes mutually in contact protecting the soft ventral integument; along the ambulacral grooves, especially on the pinnules, these become more regular and better developed than elsewhere (figs. 18-26) and often form large and definite side and covering plates (figs. 27-31) the former lying in the perisomic wall and the latter, hinged to them by ligaments, in the lappets which line the ambulacral grooves and capable of being closed down over them; the other skeletal system is the internal, consisting of numerous spicules and networks occurring more or less plentifully in the bands of connective tissue traversing the body wall and in the walls of the digestive canal.

In a very large 10-armed feather-star in which side and covering plates are developed there are visible externally about 600,000 distinct skeletal elements each of which arises from a separate center of ossification; of these about 87,000 belong to the primary and about 513,000 to the secondary or perisomic skeletal series. In a large comasterid with no side and covering plates visible there may be as many as 700,000 primary skeletal elements, while in the very small antedonids the number probably never falls below 10,000. The greatest of the figures, however, is insignificant when compared with the number of ossicles in the larger pentacrinites where, in the recent species, nearly two and one-half millions are found. These figures, large as they are, must be approximately doubled when the internal skeleton is taken into consideration.

The internal structure of all the crinoids which have been studied is very similar. The mouth, at the point of convergence of the ambulacral grooves coming onto the disc from the arms (figs. 4, 5), usually central or subcentral but often excentric or even marginal in the Comasteridæ (fig. 12), leads downward through the gullet into the digestive tube (fig. 13) which, turning to the right, makes somewhat more than one complete coil (four in some of the Comasteridæ), the posterior portion bending upward and slightly forward to end at the summit of the so-called anal cone situated on the disc between two of the ambulacral groove trunks. Except for its canal-like prolongations into the arms the body cavity is filled with a mass of mesenteries, bands and septa so that it is reduced to a minimum, and in some cases, as in *Isocrinus*, has entirely disappeared.

Within the centrodorsal in the comatulids (fig. 7) and just over the summit of the column in the other types lies the chambered organ;

its central axis from which the partitions dividing it into five sections arise is continued irregularly upward to the vicinity of the mouth as the so-called axial organ, a cord of connective tissue including a number of open spaces or lacunæ. Five slender prolongations, one from each of the chambers of the chambered organ, accompany the axial organ for some distance, ending blindly, and each cirrus includes a median vessel from the same organ.

Except at the point where the axial organ leaves it the chambered organ is completely encased in a mass of nerve fibrillæ from which the large dorsal nerves of the arms and pinnules and their various derivatives as well as the cirrus nerves arise (fig. 9); while over this nervous envelope and along the nerve cords lie multitudes of wandering cells which play an important part in the regeneration of lost members. The envelope of the chambered organ and its derivatives, including also a closely associated nerve ring about the mouth which sends off very numerous branches including two cords running along the ventral surface of each arm, form the chief nervous system of the crinoids, but beneath the ambulacral grooves of the disc, arms and pinnules there is second quite independent nervous system consisting of a continuous thin layer of nerve fibrillæ.

The water vascular system of the crinoids consists of a ring canal about the mouth and vessels radiating out from it under each of the ambulacral grooves which they follow in their course to the pinnule tips, sending off branches into the delicate tentacles. Attached to the ring canal is a row of little tubes which open into the body cavity, and communication between the body cavity and the sea water outside the body is maintained by a number of calyx pores (5 in *Rhizocrinus*, 1500 in *Antedon mediterranea*, and still more in larger species) which pierce the body wall.

The blood vascular system of the crinoids is very highly developed, though the blood vessels are nothing more than intercommunicating cavities or gaps in the connective tissue of the mesenteries, bands and cords which in all directions traverse the body wall, the walls of the digestive tube, the axial organ, etc.

The so-called genital cord forms an irregular pentagon about the mouth from which five branches are given off, these running beneath the water tubes into the arms and pinnules; but it is only in certain of the lower pinnules in most comatulids or at the pinnule bases and rarely in the arms in the stalked types that the sexual products are developed. It has already been mentioned that in the short posterior arms of certain of the Comasteridæ the ambulacral grooves are absent; when this occurs the ambulacral nerves, water vessels and tentacles are also absent, but the genital cord is here especially developed.

Along the ambulacral grooves, except in most of the Comasteridæ, and usually also internally along the digestive tube, is a usually regular row of little round bodies, conspicuously colored in preserved specimens though usually colorless in life, called sacculi (fig. 4) which remind one strongly of the glandular dots on the leaves and petals of certain plants such as the species of Hypericaceæ. They are assumed to be excretory organs.

VIVIPAROUS CRINOIDS, AND SEXUAL DIFFERENTIATION

Three antarctic comatulids are viviparous, the young developing in special pouches or marsupia formed on the pinnules in two, but on the arms themselves in one. In all three of these the two sexes are easily distinguished by superficial external examination. Besides these three comatulids only six echinoderms are known to exhibit sexual dimorphism, four irregular echinoids, one holothurian, and one ophiuran. Excepting for one of the echinoids (*Anochanus*) all are from antarctic or subantarctic regions.

THE DEVELOPMENT OF THE COMATULIDS

The early stages of the comatulid larvæ are passed within the egg membrane and the developing eggs usually hang from the bases of the genital pinnules like little bunches of grapes. It is only after the formation of the elements of the skeleton—the rudiments of the terminal stem plate, a number of columnals, the infrabasals, basals and orals—that the larva emerges as a small barrel or bean-shaped creature with five transverse ciliated bands, an anterior tuft of long cilia, and a deep ventral groove (fig. 56).

In the best-known species (*Antedon adriatica*) the length of the free-swimming life varies very greatly, even in different individuals of the same brood; some attach themselves after a few hours and immediately proceed to further development, while others are to be found still swimming about after a lapse of as much as four and a half days. As a rule the free-swimming existence terminates after a few hours and is rarely as long as two or three days; larvæ still swimming at the end of that time are abnormal and incapable of fixation.

After attachment the larva soon assumes the form of a curious little stalked creature composed of a delicate column attached by a spreading base and supporting a calyx consisting of three or five, or often no, infrabasals which are very small, delicate, and difficult of detection, five large united basals forming a cup in which the visceral mass is enclosed, and five equally large orals superposed upon them

which may be opened outward or closed together over the mouth. The plates of the radial series appear first as minute spicules in the angles between the basals and orals, one in each of these angles, or sometimes two in the right posterior angle. These grow very rapidly and two additional plates appear beyond them, the outer giving rise to two plates each of which forms the base of a rapidly growing arm. The additional plate in the right posterior area, known as the radianal, is always present, often appearing before any of the radials, but sometimes, as in *Antedon*, not being formed until a relatively advanced stage has been reached; it grows very slowly and by the growth of the radial just to the right of it it is shoved gradually upward and to the left, so that when the radials have come into lateral contact and have united into a ring it occupies a position at the edge of the disc where it is soon resorbed. Though small and soon disappearing in the young comatulid this is a very important plate in many fossil types. The arms at first are very different from the arms of the adults; they are composed of a series of exactly similar brachials without pinnules and with all the articulations between them the same, without muscles, and crossing the arm at right angles. Pinnules first appear at the tip of the growing arm after from nine to fourteen brachials have been formed, these being followed by the pinnule on the second brachial and considerably later by the pinnules on the intervening brachials (fig. 55). The first cirri appear on the now enlarged topmost columnal just before, simultaneously with, or just after, the first formation of the pinnules. Just before the appearance of the pinnules and cirri and before the disappearance of the radianal the larval comatulid is a remarkably perfect replica of a fairly typical representative of the *Flexibilia Impinnata*, but after the appearance of the pinnules and the cirri the crown undergoes a most extraordinary transformation and rapidly assumes all the characters of the adult comatulid, at various periods between five or six months and two and one-half years breaking away from the column and becoming a free-living feather-star.

The fully grown pentacrinoid young of different species show great variation, and range between 15 mm. and 65 mm. in total length; in some the column is very short and relatively stout, not more than one-third of the total length, and composed of as few as 10 segments, while in others it is very slender and much elongated, reaching four-fifths of the total length and being composed of more than 65 segments.

In the comatulids and in the pentacrinites (possibly excepting *Metacrinus*) with more than 10 arms the young always have 10 arms

only until a considerable size is reached; increase in the number of arms is accomplished by breaking off each of the original 10 arms at the articulation between the first and second (more rarely between the third and fourth) brachials and forming on the stump an axillary ossicle from which two arms arise, one or both of which may still further divide.

REGENERATION

In the crinoids, especially in the feather-stars, the replacement of lost parts by regeneration reaches an unusual extreme. It is most highly developed in the comatulids, pentacrinites and bourguetiacrinites, and least in the Plicatocrinidæ and, so far as we know, in *Holopus*.

In the pentacrinites it is very common in *Metacrinus*, nearly as common in *Isocrinus*, less noticeable in *Endoxocrinus*, and relatively rare in *Comastrocrinus* and in *Hypalocrinus*. This is not necessarily the result of a greater inherent ability to regenerate on the part of *Metacrinus* and *Isocrinus*, but is correlated with the fact that they run up into the shallowest water where the wave action makes itself felt, for the proportion of regenerated individuals decreases rapidly with depth regardless of species.

Although inhabitants of deep water the species of *Ilycrinus* and *Bathycrinus* lose the radials, arms and visceral mass very readily and specimens are frequently found regenerating from the basal ring. Similarly the species of *Bythocrinus*, *Rhizocrinus* and *Democrinus* lose their arms so easily that it is very difficult to secure individuals with the arms still attached to the basiradial cone.

The family Apiocrinidæ as represented in the recent seas is known from two specimens, each representing a different genus. One of these (the type of *Proisocrinus ruberrimus*) is perfect, the other (the type of *Carpenterocrinus mollis*) is only a fragment. Similarly the family Phrynocrinidæ is known only from two specimens each representing a different genus. One of these (the type of *Phrynocrinus nudus*) is perfect, though the arms were broken during capture, while the other (the type of *Naumachocrinus hawaiiensis*) lacks the arms beyond the radials and the terminal stem plate.

Among the comatulids regeneration is very common in all littoral species, but with increasing depth it becomes less and less frequent. Broadly speaking it appears to occur to a much greater extent in the Macrophreata than in the Oligophreata, though partially regenerated cirri have been mostly recorded in the latter. It is quite possible that this is connected with the large chambered organ of the Macrophreata; and it is also possible that it is the small size of the chambered organ

which to a large degree limits the extension of the pentacrinites and such comatulids as the *Thalassometrinæ* and the *Charitometridæ* toward the surface, since as a result of wave action breakage is most common in the littoral and without a large chambered organ a crinoid, unless unusually tough, could not repair its injuries with sufficient rapidity to survive.

The most common mutilations are the loss of the visceral mass and of more or less important portions of the arms, the fracture in the latter case almost invariably occurring at a syzygy. Loss of the visceral mass appears to cause the animal no inconvenience whatever, and it is entirely replaced in a little more than three weeks.

ASYMMETRY

There are four types of deviation from the normal pentamerous symmetry of the crinoids. These follow the following lines:

1. A rearrangement of the five primary groove trunks upon the disc whereby (a) the left posterior increases in size and gives off more branches than any of the others; (b) as a result of the anterior migration of the mouth the two posterior become much longer and the anterior much shorter than the others and a condition of bilateral symmetry is attained; (c) correlated with the anterior migration of the mouth, all of the primary groove trunks become merged into a horseshoe-shaped ring which skirts the lateral and anterior borders of the disc, giving off branches to the arms, the mouth being in the right center of the ring so that the ambulacra on the left are more developed than those on the right, or the ambulacra leading to the left posterior ray disappear altogether so that the ambulacra on the right are more developed than those on the left.

2. A dwarfing, or an overdevelopment, of the left posterior, more rarely of both posterior, radial with the accompanying post-radial series.

3. The intercalation of additional radials and post-radial series which alternate with the original five, and the associated dropping out of one of the five radials.

4. The suppression of two of the primarily five basals.

Asymmetry is almost universal in the comatulid family *Comasteridæ*, which includes the most specialized of all the recent types; in this family the first and second types occur, though the latter is much less common.

Asymmetry is characteristic of the genus *Promachocrinus*, which is probably rightly considered as the most specialized genus in the subfamily *Heliometrinæ*; here the first and third types occur.

Asymmetry is equally characteristic of the genus *Thaumatrocrinus*, the most specialized genus of the family Pentametrocrinidæ; in this genus the third type is found.

Asymmetry exists in all of the recent genera of the Plicatocrinidæ, the first, second and fourth types being represented; the third also occurs in the fossil representatives of this family.

Asymmetry is characteristic of both of the recent genera of Apiocrinidæ, which are the most highly specialized genera in the family; in these the second type occurs.

Asymmetry of the second type is characteristic of *Holopus*.

Asymmetry characterizes both of the species of *Rhizocrinus* existing in the present seas, and one of the species of *Monachocrinus*; in these the third type is found.

It appears that, no matter in what form it may manifest itself, in the recent crinoids asymmetry is an attribute of the most specialized types in the groups in which it occurs. From the conditions in the Plicatocrinidæ, the last remnants of the once abundant Inadunata, it would appear that asymmetry is an attribute of phylogenetically decadent types—types in which type senescence has so far advanced as to inhibit the normal course of development.

Although occurring everywhere except in the Arctic Ocean and in the Mediterranean, Bering, Okhotsk and Japanese seas, asymmetrical types are most frequent and most highly developed (1) in warm and shallow water from southern Japan southward throughout the Malayan archipelago to northern Australia and thence westward to Ceylon, and (2) in the Antarctic and in the cold abysses.

Though present among species inhabiting the western Atlantic from North Carolina to Brazil, and characteristic of many forms living at intermediate depths in the western Pacific and in the Indian Ocean, in these it is never more than slightly developed, even though they may be very closely related to types in which it is, in other situations, carried to an extreme.

Briefly stated among the recent crinoids any wide departure from the normal close approximation to true pentamerous symmetry indicates unfavorable conditions of one or other of two main types which are not mutually exclusive; these two types are:

1. *Internal unfavorable conditions*, induced by incipient phylogenetical degeneration through type senescence, as in the Plicatocrinidæ which in the recent seas represent the otherwise almost exclusively palæozoic Inadunata; and

2. *External unfavorable conditions*, taking the form of

- a. *Phylogenetically excessive cold*, and

- b. *Phylogenetically excessive warmth*.

THE COMPOSITION OF THE CRINOID SKELETON

The skeleton of the crinoids has the composition of a moderately magnesian limestone, the proportion of magnesium carbonate to calcium carbonate appearing to be a function of temperature and rising from 7.26 per cent in the coldest water to as high as 13.74 per cent in the tropical littoral. A trace of phosphate of lime appears always to be present, but whether or not it is an essential constituent is uncertain.

THE DISTRIBUTION OF THE CRINOIDS

The modern distribution of the crinoids has been chiefly the result of the gradual differentiation in the conditions of different sections of a once uniform sea area resulting in the evolution of more or less distinct faunal units through the selective extirpation of different types in different regions; combined with this there has been under the changing conditions the evolution of a few new types and the further specialization of others, some of which, efficient and aggressive, have apparently extirpated the previous crinoidal inhabitants from all the regions into which they have been able to extend their range.

Changing geological and meteorological conditions affect chiefly the shallow water of the littoral and sublittoral regions; the intermediate depths are but slightly affected, and the abysses not at all. Thus faunal differentiation is most marked in shallow water, much less marked in water of intermediate depth, and but vaguely indicated in the abysses.

One of the results of the gradual change in conditions in a once nearly uniform ocean has been the discontinuous distribution of many marine types occurring in two or more widely separated localities which have been subjected to less modification than the intermediate regions but which are now separated by impassable thermal or other barriers. This is well brought out in many marine types and in the crinoids is illustrated by the curious correspondence between the fauna of Australia and that of the Caribbean Sea.

After the differentiation of a fauna land barriers sometimes appear isolating a certain section from the main range. It is thus that we account for the reappearance of Arctic types in the Okhotsk and Japanese seas.

Geographically the littoral crinoids are divisible into a number of more or less well-marked faunas corresponding in the main to those indicated by other marine types. In those regions where the temperature of the water is more or less uniform from the surface to

great depths, as in the Arctic, the Antarctic, the Mediterranean, etc., the littoral crinoids descend with it and there is then a uniformity in the crinoid fauna from the surface almost or quite to the abysses; but where the temperature decreases rapidly with depth, as along the tropical shores, the bathymetric extension of the littoral types is very limited and the littoral fauna is underlain by an intermediate fauna consisting for the most part of more ancient and more conservative types which is fairly uniform the world over, though it reflects the broader divisions of the local overlying faunas. It is from this intermediate fauna that the littoral faunas on the one hand and the abyssal faunas on the other appear to have been derived.

The distribution of the crinoids appears to be governed entirely by temperature, pressure playing no part whatever.

There seems to be a close correlation between the bathymetric (or thermal) range and the geographical range of the same type, a form with a restricted bathymetrical range having a similarly restricted geographical range and the reverse.

THE PALEONTOLOGICAL HISTORY OF THE LIVING CRINOIDS

Of the four great divisions of the crinoids, the Camerata, the Flexibilia, the Inadunata and the Articulata, two, the Inadunata and the Articulata, are represented in the present seas.

The Inadunata are almost entirely confined to the Paleozoic, ranging from the Ordovician to the Carboniferous, with one of the 18 families (Poteriocrinidæ) represented in the Trias and another (Plicatocrinidæ) known only from the Upper Jurassic and from the recent seas.

The Plicatocrinidæ (including the living genera *Calamocrinus*, *Ptilocrinus*, *Thalassocrinus*, *Gephyrocrinus* and *Hyocrinus* and the fossil genus *Plicatocrinus*) are at present entirely confined to the deep and cold abysses; all of the species are very rare, most of them having only been dredged once and none of them more than twice. The Jurassic representative of this family is also very rare, and its remains are commonly associated with those of hexactinellid and lithistid sponges so that it also probably lived at considerable depths. No representatives of the Plicatocrinidæ are known from the Cretaceous or from the Tertiary.

The Articulata are entirely post-paleozoic, all from the Jurassic or later except the pentacrinites, which are also represented in the Trias.

The Phrynocrinidæ are not represented as fossils; the ranges of the other families and of the genera including both recent and fossil species are as follows:

Bourgueticrinidæ: Upper Jurassic to Recent.

Rhizocrinus: Cretaceous (New Jersey); Eocene (Europe); Recent.

Democrinus: In a recent breccia at Guadeloupe which also contained a human skeleton; Recent.

Apiocrinidæ: Jurassic, Cretaceous and Recent.

Pentacrinidæ: Trias to Recent.

Isocrinus: Triassic and Jurassic; Recent.

Zygométridæ: Jurassic to Recent.

Catoptomtra: Jurassic to Recent.

Eudiocrinus: Jurassic to Recent.

Holopodidæ: Jurassic to Recent.

Holopus: Tertiary to Recent.

THE FOSSIL REPRESENTATIVES OF THE RECENT CRINOID GENERA

Only a very few crinoid genera include both recent and fossil species, and these are divided into two groups, (1) those occurring only in the western Pacific (*Eudiocrinus*, *Catoptomtra*, *Proisocrinus* and *Carpenterocrinus*, the species of the two last being apparently congeneric with certain species of *Millericrinus*) and (2) those confined to the western, or western and boreal, Atlantic (*Isocrinus*, *Rhizocrinus* and *Holopus*). The recent distribution of these types is thus seen to be the same as that of the living king or horseshoe crabs (Xiphosuridæ).

Excepting only *Proisocrinus ruberrimus* and *Carpenterocrinus mollis*, all of the species of these genera are chiefly represented in shallow water, and these two are the only ones which do not occur within 100 fathoms of the surface; indeed the species of three of the five other genera are entirely confined to water of less than 155 fathoms depth.

The maximum representation is between the shore line and 200 fathoms, especially between 50 and 150 fathoms; as, taking the ocean as a whole, we find at a depth of 200 fathoms a temperature of 50.1° F. and at 100 fathoms a temperature of 60.7° F. it is evident that these genera are most abundantly represented within the optimum temperature for crinoid life, which is between 50° and 65° F. It is interesting to observe that (excepting for *Proisocrinus* and *Carpenterocrinus*, each only known from a single dredge haul at temperatures of 36° and 40° F.) the only increase in the numbers falls between 50° and 64°, that is, within the optimum temperature for crinoids, and is particularly emphasized between 56° and 64°, the emphasis within the optimum temperature range being between 60° and 65°.

THE COURSE TAKEN BY SPECIALIZATION AMONG THE
CRINOIDS

The dominant feature of the progressive specialization among the crinoids from the earliest times to the present day has always been a process of progressive simplification in structure, the result of a process of progressive atrophy or suppression affecting some part or other of the organism. Thus the more specialized types differ from the more generalized through the atrophy or suppression of some important structural element, while the later groups are differentiated among themselves according to the lines which this atrophy or suppression has followed.

The (recent) Articulata are distinguished from the Inadunata by the sudden cessation of stem growth (with an apparent, though not real, exception in the pentacrinites) after the stem has attained a definite and fixed length, and by the extreme atrophy of the calyx involving in most cases the complete disappearance of certain essential elements; the comatulids are differentiated from all the other (recent) types by the suppression of the column excepting for the proximal or topmost columnal which becomes permanently attached to the calyx; *Holopus* is differentiated from all other (recent) genera by the suppression of the column, the infrabasals and the basals, the stalk being formed by the coalesced and elongated radials; the Phrynocrinidæ differ from the Bourgueticrinidæ in the complete suppression of the radicular cirri, and the Bourgueticrinidæ differ from the Phrynocrinidæ in the suppression of the terminal stem plate.

THE OCCURRENCE OF LITTORAL CRINOIDS

Except on sandy and exposed muddy shores littoral crinoids occur in all possible situations. Their one essential requirement is pure, well-aërated water having a relatively high minimum salt content and well provided with minute plankton organisms, and wherever this condition is met within the range of the littoral species they may be looked for in the water just below the low-tide mark or in protected situations; sometimes they even occur in regions left bare at low tide.

Along the shores of the Indian Ocean from southeastern Africa, Madagascar and Mauritius to Suez, India and the Malay archipelago, along the coasts of Australia, especially in the north, and thence northward to Fokien and southern Japan, littoral comatulids of many species are abundant—about 30 are known from Singapore alone—particularly on reefs and rocky shores, less commonly in sheltered situations and in eelgrass, though their occurrence is commonly more or less local and they are frequently not to be found in apparently

ideal places. A few species have been found by shore collectors in New Caledonia, Lord Howe Island, Fiji, Samoa, the Marshall, Gilbert (Kingsmill), Pelew, Caroline, Society and Hawaiian Islands, but throughout Oceania they appear to be relatively rare. None are known from the Japanese coasts north of Tokyo Bay, from the Asiatic coasts north of Fokien, from the northern or eastern shores of the Pacific, or from New Zealand.

In the Atlantic basin littoral crinoids occur from Scandinavia and Great Britain to the Gulf of Guinea, including the Mediterranean area (but not the Black Sea) and the islands of the European and African coasts, and in the region of Cape Town, and in the west from the Bahamas and Florida to southern Brazil; but in the west they are extraordinarily rare, there being, except in the case of *Tropiometra*, but six records, one from the Bahamas (*Nemaster*), one from the Tortugas, Florida (*Nemaster*), one from St. Thomas (*Antedon*), one from Dominica (*Nemaster*) and two from Brazil (*Nemaster* and *Antedon*).

Of all the comatulids the preëminently littoral genus is *Tropiometra*, and wherever this genus occurs, from South Africa to Australia, Oceania and southern Japan, and from the southern Caribbean to south Brazil and St. Helena, it is commonly found along the shores, often in great abundance. In the western Atlantic, from Tobago, Trinidad and Venezuela to southern Brazil, it is the only really common littoral form.

A close second to *Tropiometra* is found in the genus *Antedon*, ranging from Scandinavia and Great Britain to the Gulf of Guinea, including the offshore islands and the entire Mediterranean basin, and also found from St. Thomas to Brazil, all the species of which occur along the shores, where they are often locally abundant. Only two specimens of the American species are known, one from shore collections at Rio de Janeiro, the other from shore collections at St. Thomas.

The species which have actually been captured along the shore number no less than 152, representing 38 genera and 12 families and subfamilies, while 93 more undoubtedly occur there, making a grand total of 245 shore-living types already known. Of these 227 are from the Indo-Pacific region (including two from South Africa), eight are from the region between the Bahamas and Florida and Brazil, six are from the northeastern Atlantic north of the Gulf of Guinea, and four are from southern Australia.

The favorite localities for shore-living comatulids are more or less shaded situations, holes and crevices in reefs, beneath stones, in half-

submerged caves, on piling beneath wharves, and in the irregularities on the outer side of breakwaters; but they are sometimes found among gorgonians or eelgrass, on mangrove roots, and occasionally on mud.

THE RELATION OF THE COMATULIDS TO TEMPERATURE

In the recent seas the comatulids range from the very warm water of the tropical littoral to water with a temperature of only 28.7° F., considerably below the freezing point of fresh water.

The species of the genera of the Oligophreata are especially developed in the warm waters of the present seas, and they are peculiarly characteristic of the warm waters of the tropical coasts. The species which occur in this warm water are almost without exception highly specialized, and they are especially remarkable for a great reduplication in the number of their arms, of which they may have as many as 150 or even more, and also for their large size.

A study of the ontogeny of the most extreme of these types shows that the essential characters of the adults appear at an extraordinarily early age, and also suggests that these characters do not indicate a true phylogenetic progress which will eventually lead to the evolution of new types, but rather a more or less pathological hyperdevelopment, an abnormal exaggeration of the normal phylogenetical tendencies, which will lead nowhere, but will terminate simply in the extinction of the species in which it appears. The fundamentally aberrant or unbalanced nature of these types is strongly indicated by the invariable conservation of some primitive character, for example spiny borders on the brachials, a regular distribution of the syzygies in the arms, a very primitive type of cirri or of pinnules, etc.

The species of the genera of the Macrophreata are mostly developed in the colder waters of the recent seas, and this suborder includes all the comatulids of the polar regions and of the abysses. The species which are found in very cold water are almost without exception very primitive, and they are especially remarkable for a reduplication of the radials, a conservation of the carination of the ossicles of the division series and of the arms, a conservation and an exaggeration of the spines which ordinarily are found only among the young, an abnormal shortness of the brachials and of the segments of the pinnules and of the cirri, as well as for their very large and very primitive pentacrinoids in which the radial plate approaches its original position beneath the right posterior radial; the greater part of these species are remarkable for their very large size, and they include among their number the largest living crinoids known; their

arms are never more than 10 in number except in the forms with 10 radials, which may have 10 or 20.

A careful study of these types, together with a detailed comparison between their characters and the characters shown by other species found in water abnormally cold for their immediate phylogenetic stock shows that the apparently primitive characters are without doubt the result of a repression or an inhibition of the normal phylogenetic development; furthermore, in combination with these characters we always find other characters which indicate a condition of very marked specialization, as for example a large number of proximal pinnules which are provided at their tips with more or less developed terminal combs, both of which characters are otherwise only found in the comatulids of very warm water at the opposite end of the temperature scale, and a great specialization of the centro-dorsal.

The species of very cold water thus resemble the species of very warm water in the possession of a fundamentally aberrant structure, for they preserve and exaggerate certain very primitive characters while at the same time they show a high degree of specialization along other lines.

However extraordinary it may appear, in their unbalanced type of specialization the comatulids of the coldest water agree more nearly with the species inhabiting very warm water—nearly all of which belong to the other suborder—than with any of the species of the intermediate waters, and the largest species, the smallest species, and the species with the greatest number of segments in the arms, pinnules and cirri are found equally at both extremes of temperature.

The Oligophreata and the Macrophreata are both represented by six families between the temperatures of 50° and 55° F., but the Oligophreata predominate at all temperatures above this, while the Macrophreata predominate at all temperatures below.

In the Oligophreata the greatest number of families is found between 60° and 65°, and in the Macrophreata between 50° and 66°. For all the comatulids the greatest representation is between 55° and 65°, with the emphasis on 60°-65°.

It would therefore appear that the temperature range included between 55° and 65° represents the temperature phylogenetically most suitable for the recent crinoids. It is a very curious fact that the comatulids found between 55° and 65° are all of medium size, none very large and none very small, and that they all show well-balanced and conservative characters.

So far as we can see it is with the recent species which are found within these temperature limits that the fossil crinoids best agree, and one might hazard the guess that it was principally, if not entirely, within these temperatures that the crinoids of the post-palæozoic faunas, characterized by a very great development of the Articulata, were developed.

FOOD

Duchassaing records that the stomach contents of a specimen of *Isocrinus decorus* which he fished up in relatively very shallow water at Guadeloupe consisted only of the remains of small crustaceans.

Bronn, summarizing previous accounts, wrote that the stomach contents of *Isocrinus* were made up of the remains of small crustaceans, while those of the comatulids consisted of diatoms such as *Navicula*, *Bacillaria*, *Actinocyclus* and *Coscinodiscus*, of *Tethya*, and of many types of entomostraca.

W. B. Carpenter said in 1866 that in the very numerous specimens of *Antedon bifida* from Arran of which he examined the contents of the digestive cavity he never found anything other than microscopic organisms, and the abundance of the horny rays of *Peridinium tripos* made it evident that in this locality that organism is one of the principal articles of food. But in specimens from other localities he found a more miscellaneous assemblage of alimentary particles, the most commonly recognizable forms being the horny casings of entomostraca or of the larvæ of higher crustaceans.

In his account of *Hyponome sarsii* (the visceral mass of *Zygometa microdiscus*) Lovén states that in the ambulacral grooves he found masses consisting of minute crustaceans, larval bivalves, and other remains of food.

In 1876 W. B. Carpenter wrote that the contents of the alimentary canal of *Antedon bifida* both in the pentacrinoid stage and in the adult consists of minute entomostraca, diatoms, spores of algæ, etc., but in his Lamnash specimens especially of *Peridinium tripos*, which was usually very abundant in that locality. He also notes that the contents of the alimentary canals of the various types of pentacrinites examined by him are of the same nature.

P. H. Carpenter says that the food of a crinoid is considerably varied in its nature according to the character of the sea bottom on which it lives. The horny casings of entomostraca and the larvæ of larger crustacea are frequently to be found in the digestive tube together with the frustules of diatoms, spores of algæ, etc. In sections of *Bathycrinus*, *Rhizocrinus*, *Isocrinus* and *Endoxocrinus* from deep water the silicious skeletons of radiolarians may be found in

considerable abundance and variety. Foraminifera also form a staple article of food for these deep-sea species, for he frequently found *Globigerina*, *Biloculina* and other types beneath the covering plates of the food grooves on the arms and pinnules, while the remains of their soft parts occur in the intestines of decalcified specimens.

Seeliger believes that he recognized in the earliest food of the larvæ of *Antedon adriatica* half-digested infusorians and different pelagic larvæ. Bury found the stomach of the very young pentacrinoids of *Antedon mediterranea* so filled with diatoms that the cutting of sections was rendered very difficult.

Dr. Edwin Kirk states that in the case of a number of specimens of *Comanthus japonica* which he examined the contents of the intestine were almost wholly comminuted animal matter.

At Maër Island, Torres Strait, Dr. H. L. Clark examined the stomach contents of four comatulids (species undetermined). He found that in each case the greater part of the food material was green algæ, chiefly unicellular though some linear forms (thread algæ) were also noted; a few diatoms were detected, and some foraminifera. In one of the stomachs several radiolarians were seen, in another a piece of a red alga, and in a third some fragments of minute crustaceans. Dr. Clark also examined the stomach contents of *Tropiometra picta* at Tobago which he found to consist of a mixture of vegetable and animal food, the former predominating. The plants were diatoms and unicellular green algæ, with occasional fragments of seaweeds; of animals, crustaceans were most frequently noted, but a few foraminifera were also seen; the crustaceans were minute amphipods, copepods and crab zoæas.

Dr. Th. Mortensen found that a relatively large percentage of the pentacrinoids of *Isometra vivipara* have in their stomachs the half-digested, but still perfectly recognizable, remnants of the larvæ of the same species; he even found very young pentacrinoids with the vestibule recently ruptured and the arms not yet developed with embryos almost as large as themselves in their mouths. He remarks that on account of the large number of pentacrinoids found attached in clusters to the tips of the upturned cirri—as many as 99 in one specimen—this danger to the embryos is very real, and probably quite a large number of them perish in that way.

LOCOMOTION

Excepting for the pentacrinites all of the stalked crinoids are firmly attached to foreign objects or rooted in the mud and therefore incapable of locomotion. The pentacrinites have such long and heavy

stems which are usually so entangled with the objects on the sea floor and with the stems of other individuals that they are to all intents and purposes as firmly fixed as are the other stalked types. But the comatulids, attached by their highly mobile dorsal cirri, are able to detach themselves and move about, though as a rule they remain pretty constantly in one place and rarely change their position except as a result of some unusual stimulation.

Among the comatulids locomotion is of two types, swimming and crawling; swimming is the more usual, and apparently all littoral comatulids can swim. In swimming the arms of each pair beat the water alternately and at first quite rapidly, as much as 100 times a minute, but the animal soon tires and the longest distance recorded as covered by a swimming comatulid is less than 3 meters. The swimming of the feather-stars has been likened to the flitting of small birds in shrubbery as contrasted with sustained flight.

The young of two species, *Dorometra nana* and *Comanthus parvicirra* (twice) have been captured while swimming at the surface from ships at anchor or in plankton hauls.

Crawling is accomplished by a combined pulling and pushing, and in the comasterids the long anterior arms are extended forward and used for pulling while the short and stout posterior arms are used for pushing. The rate of progress has been calculated as 85 mm. a minute, or 5 m. an hour.

COLOR

Of all the animals in the sea there are none that exceed in beauty and variety of coloration the shallow water crinoids. Flower-like in form and almost flower-like in the fixity of their habit, they are also flower-like in the variety and distribution of their pigments. But with depth the diversity of hue diminishes so that we find the color range of the species of the deeper water relatively restricted while the individuals themselves, losing the almost universal spottings and bandings of the littoral types, become comparatively plain.

Though crinoids resemble flowers in the diversity and brilliance of their colors, their color types are quite the reverse of flower-like. In a particolored flower the center or eye is more or less abruptly lighter or darker than the remaining portions, or the petals are longitudinally striped; cross-banding of the petals is very rare. Among the crinoids particolored specimens are usually cross-banded, regularly or irregularly, and though the tips of the pinnules may be of a different color from that of their bases a true longitudinal striping of the arms is very rare and a conspicuous eye is never developed.

The published records show in the feather-stars the following frequency for the various colors; the numbers in parentheses show the individuals entirely of the color given, the others all the records for that color both in unicolor and in variegated types:

Yellow	194 (47)	Black	43 (3)
Brown	138 (24)	Orange	39 (5)
White	126 (1)	Gray	22 (1)
Red	80 (8)	Violet	15 (6)
Green	74 (7)	Blue	15 (0)
Purple	70 (10)		

While white and yellow occur in all possible combinations, orange does not occur with violet, black or green; red does not occur with black; purple does not occur with black, gray or green; violet does not occur with orange, black, gray or brown; black does not occur with orange, red, purple, violet, gray, green, or brown; gray does not occur with purple, violet, black, green or brown; green does not occur with purple, black or gray; and brown does not occur with red, violet, black or gray.

It is of course true that this apparent incompatibility of colors is partly due to a lack of observations and to a misinterpretation of the colors as recorded, and the foregoing list must therefore be accepted with considerable reservation.

In particolored comatulids the distribution of the colors on the arms and pinnules falls into several well-marked types, which may be arranged as follows:

I. Arms and pinnules uniform in color.

- a. Arms and pinnules uniform in color, but differing in color from the cirri.
- b. Arms and pinnules uniform in color, but the ventral and dorsal surface of different colors.

II. Pinnules of a different color from that of the arms.

- a. The distal portion of the pinnules (and usually also the arm tips) is of a different color from that of the proximal portion and the arms.
- b. All of the pinnules are of a color different from that of the arms.

III. Arms and pinnules irregularly spotted, mottled and blotched.

IV. Arms with more or less regular and uniform spots.

- a. Spots confined to the division series and arm bases.
- b. Numerous small spots generally distributed.

- V. Arms with a median dorsal stripe.
- a.* A broad median stripe, lighter or darker than the color on either side of it.
 - b.* A narrow median stripe, always very dark.
- VI. Arms conspicuously and regularly cross-banded.
- a.* With several more or less irregular broad bands.
 - b.* With a broad approximately central band.
 - c.* With broad alternating bands of equal width.
 - d.* With narrow alternating bands of equal width.
 - e.* With narrow well-spaced bands.

As a general rule the coloration of the pinnules follows that of arms, but in a few types they are banded on each segment and in at least one case this is a good specific character.

The cirri are usually unicolor, less commonly dull at the base, becoming gradually or abruptly brighter distally, and rarely show distinctive color types; when this occurs the color types are usually a reflection of the color types of the division series and arm bases and very rarely distinctive.

Particolored cirri, except those which are merely brighter distally, fall into the following classes:

- I. Each cirrus segment with a transverse band.
- II. Cirri unicolor, but of a color not found in the calyx or arms.
- III. Cirri blotched or spotted.
 - a.* Cirri with irregular blotches or irregular bands.
 - b.* Cirri with small spots.
- IV. Cirri longitudinally striped.

A study of the development of the colors seems to indicate that all colors except gray and black may arise directly from white, and that yellow, red and brown usually arise directly from white, while violet arises as often from white as from any other color. All colors may develop from yellow; gray and black are developed only from yellow, and purple and green arise more frequently from yellow than from any other color. Red frequently develops into purple, and occasionally into yellow, violet and green. Brown develops into green and, less frequently, into violet. Orange develops into brown.

At a depth of 55 fathoms in the sea the relative proportion of the red rays is considerably diminished, and at 300 fathoms they have almost completely disappeared. In a discussion of colors, color combinations and color types and their relation to depth, therefore, it would seem that bathymetric divisions of 0-55 fathoms, 55-300 fathoms, 300-600 fathoms and 600 fathoms and over would be as satisfactory as any.

A tabulation of the colors according to depth shows that black does not occur below 55 fathoms; red, violet, gray and white do not occur below 300 fathoms; purple, green and orange do not occur below 600 fathoms; yellow and brown occur at all depths.

Yellow and brown are relatively much more frequent below 300 fathoms than above; purple, green, orange, gray and white occur in about the same relative proportions down to 300 fathoms, at that point decreasing abruptly or disappearing altogether; red, violet and black decrease abruptly below 55 fathoms.

No colors are more frequent between 55 and 300 fathoms than elsewhere. The proportion of uniformly colored species increases markedly with depth, while the corresponding decrease in variegated species is even more abrupt. All of the color types given occur only above 300 fathoms. The median dorsal stripe is most common between 55 and 300 fathoms. Distinctively colored pinnules and regular crossbands occur in about the same proportion down to 300 fathoms. Distinctively colored cirri and irregular spotting or mottling are much more common above 55 fathoms than below. Regular spotting occurs only above 55 fathoms.

Whereas the development of color in the crinoids seems to have a more or less definite relation to illumination, it appears to have no relation whatever to the temperature of the water in which the crinoids live. The various color types are almost entirely confined to water of high or intermediate temperature; but this is undoubtedly due to the fact that the crinoids of the colder parts of the oceans belong to groups in which color patterns are not developed even in their tropical representatives. This supposition is emphasized by the occurrence of several well-marked and beautiful color types in the species of the genus *Antedon* which are quite as well developed in the Scandinavian species as in those inhabiting the shores of northwestern Africa and the Mediterranean.

From the evidence at hand the following conclusions seem justified:

White, which is the original color of the pentacrinoid young and occurs frequently in the adults, denotes the more or less complete absence of pigment.

Yellow is the color of practically all of the more primitive forms, and of many of the more specialized, throughout life, and with very few exceptions (occurring in the brilliantly illuminated littoral) of small specimens and of advanced pentacrinoids. Orange or red, in reality an intensification of the yellow, is the color of a few primitive forms, and of nearly all the young which are not yellow.

After the full size has been reached a dusky factor makes its appearance which may be generally diffused or more or less localized, and deepens, alters, or obscures the original colors.

Illumination of the habitat results in an intensification of the natural colors and the very early appearance of the dusky age factor, as well as in the appearance of a blue factor resulting in the formation of bright greens, purples and violet, which may deepen to black.

All the comatulids living below the limit of light penetration exhibit the basic colors, white, orange or red, only, which, though they may become more intense toward the calyx and arm bases, are never otherwise diversified. Each of these colors, however, may be modified by the dusky age factor, resulting in "dusky purple," greenish or brownish yellow, brown, orange brown, crimson, or red brown. The blue factor is absent in these species, but in the group as a whole it gradually increases from the limit of light penetration to the surface, causing the appearance of greens, purples and violets of increasing intensity.

Geographically the maximum development of color diversity appears to be in the Malayan and north Australian region, and thence westward to Ceylon; but it is here also that the maximum development of littoral types is found. The whole littoral and intermediate fauna from east Africa to Oceania and southern Japan is notable for the diversity in the coloration of the endemic forms.

On the other hand, throughout the vast extent of the east and north Pacific we find the minimum diversity of crinoid coloration; all of the comatulids are unicolor, most of them yellow, becoming yellow brown, a few purplish brown or red; all of the stalked forms are yellow.

The crinoids of the Caribbean Sea as we know them to-day are much less highly colored than those of the Indo-Pacific region, and this holds good for stalked as well as for unstalked types. But here the groups which furnish the majority of the most variegated species are absent. In the remaining portions of the Atlantic, outside of the region of the Cape of Good Hope where the Indo-Pacific fauna intrudes for a short distance, we note especially the presence of the highly colored species of *Antedon*, which range collectively from Rio de Janeiro to St. Thomas and from the Gulf of Guinea to Norway, including the Mediterranean basin; of the green or white species of *Leptometra* which occur from Madeira to Scotland, including the Mediterranean basin; and of the small green or gray species of *Hathrometra* which are found from Chesapeake Bay and Portugal northward.

The coloring matter of crinoids is freely soluble in fresh water and in alcohol. It is possible to keep certain species for some time in water fresh enough to dissolve out a considerable amount of pigment without apparent injury, while many may be partially decolorized in a stream of fresh water while still alive.

As a general rule comatulids preserved in alcohol, no matter what their original colors may have been, become brown, usually a yellowish, more rarely a purplish, reddish or greenish brown, later slowly fading out to grayish white. The bands and spots often persist for some time, though with entirely changed color values, but they eventually disappear. On account of the wonderful diversity of the colors in life and of the altogether extraordinary alteration of the colors by preservation the greatest care is necessary in identifying living specimens, especially from descriptions based upon preserved material, for the color may or may not be a good specific index; it usually is not.

THE SIMILARITY BETWEEN CRINOIDS AND PLANTS

Although they are animals possessing a relatively high type of organization the crinoids are so plant-like in their outward form that it seems worth while to explain briefly the extent of and the reasons for this curious and striking similarity.

The roots of the stalked crinoids are of several different types varying from a large encrusting mass with digitiform processes about its borders to a long slender taproot buried in the mud from which very numerous delicate lateral roots are given off. Every type of crinoid root can be matched among the plants, though the crinoid root performs only one of the functions of the plant root, and that is to hold the organism in place.

The stem of some of the stalked crinoids, such as *Proisocrinus*, is long, smooth, slender, and enlarged toward the base, and thus strikingly similar to the stems of many of the commonest palms, this similarity being heightened by the numerous pinnate arms like palm leaves at the summit. The pentacrinite stems with their whorls of five cirri at regular intervals call to mind the stems of many plants with narrow whorled leaves, in combination with their lily-like crowns, especially such lilies as *Lilium philadelphicum*. From their resemblance to palms the stalked crinoids are commonly called "sea-palms" in French and Spanish, while their usual appellation in English is "sea-lilies."

The food of the crinoids consists of the minute plankton organisms suspended or moving slowly about in the surrounding water. In

order to obtain an adequate supply of these organisms they must intercept the maximum amount of water without, however, impeding its flow, for it must pass by them constantly and continuously in order to furnish them with a supply of oxygen without which they would soon perish, as well as to deliver to them the requisite amount of food. As the maximum area is included within a circle the crinoids have developed a circular food-collecting apparatus consisting of slender pinnules which, spread out in the form of a circular net, filter the maximum amount of water while at the same time they interrupt the flow of water to the minimum degree. In this circular food-collecting apparatus composed of a vast number of slender filaments we see at once the influence of the same factors which have determined the development of the submerged filiform-dissected leaves among the water plants; and the similarity becomes more striking still when we call to mind such carnivorous plants as the species of *Utricularia*.

The crinoid crown is almost entirely a food-collecting apparatus; the essential organisms of the animal are reduced to a minimum and subordinated to the development of a structure offering a maximum area for the interception of food particles. This is not by any means a peculiarity only of the crinoids, for all of the other fixed and arborescent animals, the sponges, coelenterates, polyzoans, tunicates, protochordates, etc., have similarly subordinated, as it were, their whole being to the specialization of the mechanism for collecting mobile food to such a degree that they may be differentiated often down to genera, and sometimes even down to species, by the characters found in the food-collecting apparatus alone without consideration of their other structures. The polyp or polypoid individual more or less flower-like in form or else capable of maintaining a strong inflowing current of water is a physical necessity correlated with a fixed existence, and the contrast between the requirements of a fixed and an active life are nowhere better illustrated than in the echinoderms through the comparison between the crinoids on the one hand and the echinoids, asteroids and ophiuroids on the other.

Terrestrial plants live rooted in the earth from which and from the surrounding atmosphere they derive all the substances necessary for their existence. But the medium about them is so light that some special provision must be made for the fertilization of their ova. Thus while the crinoids, and all the other fixed marine animals, have had to specialize, so to speak, on the development of an adequate apparatus for food collection, the plants have had to devote their energies to the problem of securing cross fertilization. This is largely

accomplished through the intermediary of insects of various types, more rarely by small birds, which transport the pollen through the air, and the plants have developed all sorts of artifices by which they make their flowers attractive to these creatures. The result of this necessity has been to localize in the flowers the chief differential characters of the plants just as the same characters have in the crinoids and in the other plant-like animals been chiefly segregated in the commonly flower-like food-collecting mechanism.

The polyps of the plant-like animals cover the maximum area with their arms or tentacles in order to collect the maximum amount of food, while the flowers cover the maximum area with their petals in order to attain maximum visibility, with the common result of a circular expanse of symmetrically arranged parts in both cases. To increase their efficiency by mass effect the polyps of plant-like animals are often spiked, sometimes spirally arranged on the axis, and occasionally grouped in umbels or in imperfect racemes like flowers, while to counteract unusual external stresses of waves or wind both flowers (*Raoulia*, etc.) and polyps (brain-corals, etc.) are sometimes in the same way gathered together in great more or less globular and highly resistant masses.

A very large proportion of the conspicuous flowers are pentapartite, with five sepals and five petals alternating with them, and commonly bracts beneath the sepals; crinoids are also pentapartite, with five basals and five arm-bearing radials alternating with them, and commonly infrabasals beneath the basals. Some flowers are tetrapartite, like the crucifers; some crinoids are the same, like *Tetracrinus*. Many flowers are hexapartite, as are also some crinoids, like *Hexacrinus*. The reason for the most common occurrence of five in both cases is probably that in the pentapartite division there lies the maximum strength.

The basals of the crinoids normally enclose the visceral mass much as in many flowers the sepals enclose the ovary, and sometimes (*Isocrinus*, etc.) they imbricate over the bases of the radials as the sepals imbricate over the bases of the petals.

In many crinoids the arm bases are firmly united by interbrachial plates or so closely pressed against each other that they may almost be said to possess a gamopetalous corolla.

In a few fossil crinoids (*Petalocrinus* and *Crotalocrinus*) all the arms borne by each radial are united into a single, broad, flat plate which may be highly flexible, and the crowns of these crinoids resemble flowers to a most astonishing degree.

At the base of the petals in the flowers are the stamens, while at the bases of the arms in the comatulids are the elongated oral pinnules which are usually bent inward over the sometimes central high anal tube which in many cases looks very much like a pistil.

The essential part of the plant is the flower; roots, stem and leaves may be dispensed with in the parasitic types, but the flower must be developed. In the crinoids the great essential is the food-collecting apparatus; everything else may be reduced to a minimum, but that must remain at an irreducible maximum. In the family Rafflesiaceæ the whole plant is reduced to nothing but a flower, which may be very large, as much as three feet in diameter; in the comatulids the animal is little else than arms and pinnules, and the diameter of the expanded animals in one species is about three feet.

Since the spermatozoa of the crinoids escape into the sea while the ova remain attached to the pinnules of the female it is evident that in this group conditions exist in a way comparable to those found in wind-pollinated plants, and it is interesting to note that the crinoids possess many scores of entirely separate and distinct gonads arranged in a series along both sides of each arm on the pinnules or at the bases of the pinnules remotely suggesting the arrangement of many wind-pollinated flowers in catkins.

The ciliation of the crinoid larvæ may be compared with the development of the fibers on the seeds of such plants as the cotton, and the development of the long anterior tuft of cilia with the coma on such seeds as those of the milkweed (*Asclepias*) or fireweed (*Epilobium*).

The color of the crinoids has already been discussed, but there are one or two points regarding color which are of interest in this connection.

Many of the species of Comasteridæ are asymmetrical, one or two of the arm clusters being more or less, sometimes very much, shorter than the others, the animal developing a secondary bilateral symmetry from an original pentamerous symmetry. Many flowers also develop a bilateral symmetry from an original pentamerous symmetry, as is well seen in our species of Orchidaceæ, Scrophulariaceæ, Menthaceæ, etc., and in all intermediate stages comparable to those seen in the Comasteridæ, in the Campanulariaceæ and Solanaceæ. Because of the coiled digestive tube the visceral mass in the center of a crinoid never shares the pentamerous symmetry of the rest of the animal, and in the pentapartite flowers the similarly placed ovary, excepting only in the Crassulaceæ, is out of harmony with the radial symmetry of the other structures.

Flowers facing directly upward or directly downward are always regular, insuring maximum visibility from all directions; irregular flowers always are directed more or less laterally. Crinoids which rest on muddy bottoms and therefore face directly upward (as *Pentametrocrinus*) or which have pendent crowns (as *Ptilocrinus*) are also symmetrical since this means maximum efficiency in combing the water which may pass across them in any direction.

Among our native flowers (in eastern North America) the various colors represented fall into three distinct groups on the basis of the proportion of irregular to regular flowers included, as follows:

GROUP I: ABOUT ONE-QUARTER OF THE FLOWERS IRREGULAR

	Red	White	Green
Per cent of regular flowers.....	78	73	72
Per cent of irregular flowers.....	22	27	28

GROUP II: NEARLY ONE-HALF OF THE FLOWERS IRREGULAR

	Brown	Yellow	Orange
Per cent of regular flowers.....	57	56	56
Per cent of irregular flowers.....	43	44	44

GROUP III: MORE THAN THREE-QUARTERS OF THE FLOWERS IRREGULAR

	Blue	Purple
Per cent of regular flowers.....	24	21
Per cent of irregular flowers.....	76	79

The proportion of variegated flowers is much higher in irregular than in regular types since in the irregular types every artifice which will increase the visibility must be adopted. The proportion of variegated crinoids is very much higher in the irregular than in the regular species because they are all from shallow water and it is in the shallow water that the colors of crinoids are best developed. From a minimum in the coldest regions the proportion of irregular flowers increases to a maximum in the tropics; from a minimum in the coldest water the irregular crinoids increase to a maximum in the tropical littoral.

About three-quarters of all our blue, violet and purple flowers are irregular; since blue, violet and purple seem to be the most conspicuous colors so far as insects are concerned a flower loses less in visibility by being of these colors than it would by being of other colors. Blue is only recorded from irregular crinoids, and violet and purple are much more common in irregular than in regular types, as a result of the occurrence of the former only in shallow water.

In the crinoids the pigment is not confined to the exterior of the animal as in most active types, including the other echinoderms, but

occurs more or less generally distributed throughout the body just as pigment is distributed throughout the interior of many plants. The coloring matter of the crinoids is, in part at least, a lipochrome, and other lipochromes occur in a number of flowers just as indigo, occurring in many different plants, is also found in the Polyzoa and other animals, and just as cellulose or a very closely allied substance is found in the tunicates.

Many flowers have a sweet and attractive odor, and certain crinoids (*Tropiometra* and others) also exhale a pleasant plum-like aroma, though this is not so marked as in the case of certain polyzoans (*Flustra*); as this pervades the whole animal it is perhaps better to compare these types with such plants as those of the families Menthaceæ or Myricaceæ, most of which are aromatic. But among the fixed animals these plants more nearly parallel the sponges in this respect, while the sharp principle pervading the cruciferous plants calls to mind the very acrid secretions found in the coelenterates.

Many plants, like nettles, have stinging hairs; in the crinoids the secretion from the glands connected with the hair-like papillæ on the tentacles appears to possess stinging qualities. Just as cattle will not eat nettles, so the fishes carefully avoid the crinoids.

The petals of certain flowers, as in the Hypericaceæ, are dotted with so-called glands containing excretory products and often arranged in regular rows. Along the ambulacral grooves in the crinoids is a row of minute glandular bodies also containing excretory products.

Similarity of habit and the resultant similarity or at least parallelism in the problems to be met have given rise to a very close correspondence in many features between the fixed and sessile animals and the plants, though the means by which this close correspondence has been attained differ very widely in the two classes of organisms.

PARASITES AND COMMENSALS

A very large number of organisms belonging to very diverse groups are found more or less associated with the crinoids. The relation between these types and the crinoid hosts runs by imperceptible gradations all the way from true parasitism, in which the organism feeds directly upon the body tissues or fluids of the host, to the most casual or even accidental association.

The animals associated with the crinoids may be grouped as follows:

I. *True parasites*.—Animals which (1) live upon the tissues or body fluids of the crinoids and occur either (a) internally or (b) externally; (2) occur internally, though not feeding directly upon

the tissues of the host; or (3) while living externally upon the surface of the body and not feeding directly upon the tissues or fluids of the host are more or less permanently fixed in position and cause more or less extensive malformations, sometimes becoming encysted.

This class includes a few "worms," a number of myzostomes, a few crustaceans, and the parasitic gasteropods.

II. *Semiparasitic commensals*.—Animals which feed upon minute organisms and have to a greater or lesser extent adopted the habit of sucking up the food particles from the streams flowing down the ambulacral grooves of the crinoid to the mouth, or of temporarily entering the digestive tube and feeding upon the contained matter.

This class includes the polynoid and ophiuran parasites, most of the crustacea, and most of the myzostomes.

III. *Nonparasitic commensals*.—Animals which, while usually, or commonly, found living upon or among the crinoids lead an entirely independent existence and for the most part are found living under similar relations with other organisms.

Here are included the foraminifera, sponges, corals, hydroids, polyzoa, barnacles, tunicates and *Rhabdopleura*, as well as certain shrimps.

IV. *Casual associates*.—Animals which normally occur hiding among, crawling over, or attached to other usually arborescent organisms (fig. 62) from which they may or may not derive nourishment, or which normally occur attached to any available support, and which occasionally stray among or upon, or attach themselves to, the crinoids, but remain otherwise entirely independent of them.

This class includes a vast number of organisms of very diverse types.

As in the case of the other arborescent marine types, and in general among the animals that live by filtering the smaller plankton from the sea water, the crinoids are chiefly subject to indirect parasitism, that is to say, the creatures depending upon them for their existence appropriate the food particles which the crinoids have collected in the ambulacral grooves, or even which they have swallowed, instead of consuming the tissues or body fluids directly. Of the animals which derive a part or all of their nutriment from the body or from the efforts of the crinoids about 10 per cent are directly parasitic, and about 90 per cent are indirectly parasitic in varying degrees.

Of the animals which are parasitic on the crinoids nearly all may be described as casual parasites, for they belong to genera or families other representatives of which are nonparasitic; that is to say, they are merely particular species which have found an easy existence in

preying upon the crinoids, though this mode of life has not induced any special modification of their structure.

There is a curious and interesting correspondence between the relations of the fixed marine organisms (including the crinoids) and their parasites and commensals and those between parasitic and epiphytic flowering plants and their hosts. The barnacles, most hydroids, polyzoans, etc., correspond very closely to the epiphytic plants, especially those of the families Orchidaceæ and Bromeliaceæ. *Rhabdopleura* and certain hydroids are quite vine-like in habit, ascending crinoid stems as vines do the trunks of trees. Most parasitic plants appropriate the unelaborated sap of the host and convert it to their own ends; most parasites of the fixed marine organisms in the same way appropriate the concentrated but undigested microplankton in or approaching the stomach of the host. On land most animals are parasitized by animals of an inferior organization; but among the fixed marine animals the parasites for the most part belong to a phylum with a superior organization and sometimes even to the same phylum (cœlenterates parasitic on cœlenterates, crustaceans parasitic on crustaceans, ophiurans parasitic on crinoids, etc.). The relations between the fixed marine animals and their parasites are thus more nearly the same as those between parasitic flowering plants and their hosts. On land the various animal groups are definitely parasitic or nonparasitic; but many plant families, such as the Scrophulariaceæ, Santalaceæ, etc., and even many single genera, such as *Pedicularis*, *Melampyrum*, *Gerardia*, etc., include both parasitic and nonparasitic species, just as do many families and genera, such as *Synalpheus*, *Periclimenes*, etc., occurring with the fixed marine animals.

The three types of parasites which are of especial interest are the gasteropods (*Stilifer*, *Stylina*, *Sabinella* and *Melanella*), *Enterognathus* and the myzostomes (figs. 57, 58).

The family Melanellidæ to which *Stilifer*, *Stylina*, *Sabinella* and *Melanella* belong includes species showing all gradations between free-living nonparasitic types and shell-less parasites living entirely within the body of the host. As parasites the Melanellidæ occur only upon the echinoderms, in which group, however, they are found on species of all the classes. Most of the parasitic forms, including all of those occurring on the crinoids, are characterized by extraordinarily delicate shells. Some of the species are permanently fixed in one position on the body of the host, but others, including all those found upon the crinoids, appear to move about and to bore into different parts of the host. It is not a little curious that, apart from *Melanella capensis* and *Stylina comatulicola*, all the species parasitic on the

crinoids are always attached to the calyx plates, or to the cirrals, brachials and pinnulars instead of to the soft ventral integument.

The curious copepod *Enterognathus* occurs only in crinoids, but the family to which it belongs is well known as a parasite (or commensal) of the tunicates, most of the species living in the branchial chamber of these animals.

The myzostomes form a group of very highly specialized polychæte annelids and are the chief parasites of the crinoids, to which animals they are almost exclusively confined. On the crinoids they are, with one possible exception, always ectoparasitic, though they may form soft or calcified cysts within which they are almost completely isolated from the outer world. An organism, possibly a myzostome, has been reported in the ovarian cavity of *Notocrinus virilis*. If this really is a myzostome, which is not unlikely as similar endoparasitic species occur in starfishes (*Asterias*, *Stolasterias* and *Ceramaster*) and astrophytons (*Gorgonocephalus eucnemis* and *G. arcticus*), we find in the crinoids the five following groups of myzostome species:

1. Wandering species which move about freely and actively over the body of the host, as *Myzostomum cirriferum*.
2. Sedentary species which rarely, if ever, leave the spot where they have settled, as *M. parasiticum*.
3. Cyst-producing species which cause the formation of galls or swellings on the arms or disc, as *M. cysticum*.
4. Entoparasitic species inhabiting the digestive tract, as *M. pulvinar*.
5. Entoparasitic species living in the ovaries, as *Protomyzostoma polynephris* does in the astrophytons.

Thus in the crinoids we find a single group of animals which, broadly speaking, play the part of the fleas, lice, jiggers and bots, intestinal worms and flukes combined as we know them among the land vertebrates.

A comparison between the myzostomes and the species of *Thrips*, occurring only on flowers, is also interesting.

In the vertebrates the blood with its multitudes of red corpuscles which when destroyed are promptly and continuously renewed is the logical food of practically all the parasites which do not inhabit the intestinal canal. The dilute blood of the crinoids, without structures corresponding to the red corpuscles, has none of the features which make the blood of the vertebrates such a reservoir of concentrated food. But the uncountable myriads of minute organisms flowing continuously downward along the ambulacral grooves and into the mouth form a stream of nutrient fluid in many ways analogous to the

vertebrate blood stream, and it is from this source that the myzostomes as well as most of the other parasites derive their subsistence.

The species in each group parasitic on the crinoids in those cases in which our information is sufficient to permit us to speak with a reasonable amount of certainty follow bathymetrically and geographically the distribution of the classes to which they belong quite regardless of that of their hosts, and apparently, excepting possibly in the case of *Stelechopus*, the most primitive of the myzostomes parasitic on the most ancient of the living crinoids, there is not the slightest correlation between the systematic position of the parasite and that of the crinoid.

An undetermined internal worm, a parasitic ostracod, *Laphystiopsis*, *Anilocra*, *Cirolana* (fig. 60), *Cyclotelson* (fig. 61), *Synalpheus*, *Periclimenes*, *Pontoniopsis*, *Galathea* (fig. 59), *Ophiactis*, *Ophiomaza*, *Ophioæthiops*, *Ophiophthirius*, *Ophiosphæra*, *Sabinella* and *Polynoë* are known as parasites on crinoids only in the Indo-Pacific region, though *Laphystiopsis*, a parasitic ostracod (on fish), *Sabinella*, *Synalpheus*, *Periclimenes*, *Galathea*, *Anilocra*, *Cirolana*, *Ophiactis* and *Polynoë* also occur in the Atlantic.

Collocheres, *Enterognathus*, *Stylina* and *Hemispeiropsis* are known as parasites on crinoids only from the Atlantic; but all of these are small and must be especially searched for; probably all occur in the Indo-Pacific.

Mortensen's parasitic worm of doubtful affinities is only known from the Antarctic; but only *Notocrinus virilis* offers a suitable habitat for it.

Thus while the myzostomes occur wherever crinoids are found the majority of the other parasites and commensals on crinoids are confined to the Indo-Pacific region, though many are very closely related to nonparasitic Atlantic species. The chief reasons for this are probably the absence of a richly developed littoral crinoid fauna in the tropical Atlantic comparable to that in the Indo-Pacific region, and the plating of the ambulacra in most of the tropical Atlantic types, including the littoral species, which renders them unavailable as a source of food to most of the parasitic forms.

It is interesting to note that, with the exception of the myzostomes and the gasteropods, the great majority of the organisms which are directly or indirectly parasitic upon the crinoids are confined to the littoral zone. The reason for this is probably to be found in the development of side and covering plates along the ambulacral grooves of the pinnules, arms and disc of the crinoids from intermediate and great depths which enables the animals to convert the ambulacral

grooves into closed tubes and prevents the appropriation of food particles by the ectoparasitic crustaceans, the ophiurans, and the polynoid worms.

The larger commensals living on the crinoids are usually striped or banded, and resemble them more or less closely in color, though in many cases the closely related noncommensal species are quite plain. This may or may not be the case with the myzostomes.

In regard to the parasites and commensals of the comatulids there is one curious feature which stands out very prominently—the majority of the records, especially of the larger and more vigorous types, are based upon species of the family Comasteridæ, probably the most specialized of all the comatulid types.

COMMENSALISM OF THE CRINOIDS

A number of small comatulids and the young of certain others may be considered as truly commensal, living as they do in the cavities of large sponges and gathering the minute organisms brought to them by the currents flowing into the afferent openings of the host. Many others habitually cling to gorgonians or withdraw into crevices in corals where they live symbiotically, but quite independently of the supporting organism.

ECONOMIC VALUE OF THE LIVING CRINOIDS

Economically the crinoids serve no useful purpose—at least up to now they have been put to none. They cannot be eaten, and they are not, so far as we know, eaten by any fish or other animal that serves as human food.

As a result of their ordinarily fixed mode of life it is possible that they might be used to furnish an index of the density of the finer plankton content of the water in which they live, though it is probable that other more generally distributed animals with more or less similar feeding habits would serve the purpose better.

Because of their beauty and delicacy of form as well as on account of their rarity they are frequently preserved and offered for sale as curios in Japan and China and, less frequently, in India, Oceania, Australia and the West Indies.

In southern Japan crinoids are frequently brought up on the long lines used for fishing in deep water in Sagami Bay. The comatulids, because of their beauty and delicacy of form, are called “komachi”—a name originally borne by an exceptionally well-favored lady of the court upwards of a thousand years ago—while the local stalked crinoid (*Metacrinus rotundus*) is known as the “bird’s foot.” The

former when well preserved are sometimes sold as curios, while the latter always meet with a ready sale at extraordinarily high prices on account of their rarity combined with their paleontological interest.

In China comatulids are sometimes offered for sale which have been brought from a considerable distance.

At Barbados the local species of *Isocrinus*, especially *I. asteria*, and *Holopus rangii*, are occasionally to be found in the curio shops.

Among the Slavic peoples red is the color about which all their abstract ideas of beauty, and hence of idealism, revolve. The delicate and often gorgeously colored red Adriatic Feather-Star (*Antedon adriatica*) occurs more or less abundantly along the coasts of the largely Slavic provinces of Istria and Dalmatia where it is frequently found in the fishermen's nets and is sometimes brought up on their hooks. Its beauty of form, and particularly its red color, especially commend it to the local fishermen, who commonly take it to market and exhibit it along with the fish offered for sale.

EXPLANATION OF PLATES

PLATE I

- FIG. 1. A Feather-Star (*Antedon adriatica*) with the terminology of its parts explained.
2. Lateral view of the centrodorsal and articular faces of the radials of a Feather-Star (*Himerometra martensi*) with the terminology of its parts explained. Fossil Feather-Stars usually consist of this portion of the animal only.
 3. The same, in ventral view.
 4. The naked incised disc of *Cenometra bella* with the terminology of its parts explained.
 5. The plated entire disc of *Neometra multicolor* with the terminology of its parts explained.
 6. Lateral view of the centrodorsal and articular faces of the radials of *Pentametrocrinus japonicus*.
 7. Longitudinal section of the same.
 8. Ventral view of the same (compare with fig. 3).
 9. The dorsal nervous system of *Tropiometra macrodiscus*.
 10. The proximal portion of *Nanometra bowersi* showing the difference between the large cirri about the periphery of the centrodorsal and the small one near its apex.
 11. Dorsal view of the centrodorsal, radials and arm bases of a specimen of *Comatula rotalaria* showing the centrodorsal reduced to a stellate plate.
 12. The disc of a specimen of *Comatula micraster* with four grooved and six ungrooved arms.
 13. The ambulacral grooves and the digestive tube of *Antedon bifida* (adapted from P. H. Carpenter).
 14. The arm tip of *Pterometra trichopoda*.

- FIG. 15. The terminal comb on the oral pinnules of *Leptonemaster venustus* in external, internal and ventral view.
16. The tip of an outer pinnule of *Capillaster multiradiata* in lateral and dorsal view, showing the long spines.
17. The division series and arm bases of *Comanthus bennetti* with, on the right, homologous ossicles shown similarly shaded.

PLATE 2

- FIG. 18. The calcareous deposits in the perisome bordering the ambulacral grooves and in the tentacles of the pinnules of *Dorometra parvicirra*.
19. The same in *Leptonemaster venustus*.
20. The same in *Eudiocrinus junceus*.
21. The same in *Heterometra bengalensis*.
22. The same in *Amphimetra discoidea*.
23. The calcareous deposits in the perisome bordering the ambulacral grooves in *Psathyrometra antarctica*.
24. The same in *Pentametrocrinus varians*.
25. The same in *Eumorphometra concinna*.
26. The same in *Sarametra triserialis*.
27. The side and covering plates of *Glyptometra tuberosa*; the latter (above) are hinged to the former and can be closed down over the ambulacral grooves.
28. A side plate of *Strotometra hepburniana* in (upper) interior and (lower) dorsal view.
29. Interior view of two side plates of *Pachylometra distincta*.
30. Ventral view of a portion of a pinnule of *Pachylometra distincta* showing the side and covering plates, the latter closed down over the ambulacral groove.
31. Lateral view of the side and covering plates of *Pachylometra distincta*, the latter partially closed down.

PLATE 3

- FIG. 32. Diagram showing the relative proportions of the arms and cirri in *Asterometra macropoda*; the cirri are adapted to clinging to very rough bottom.
33. Diagram showing the relative proportions of the arms and cirri in *Comactinia echinoptera*; the short, strong and stout cirri are well fitted to hold the animal securely.
34. Diagram showing the relative proportions of the arms and cirri in *Pentametrocrinus tuberculatus*; the animal is very different in every way from the preceding, but the cirri are of the same type.
35. Diagram showing the relative proportions of the arms and cirri in *Pentametrocrinus varians*; the cirri collectively form a sort of circular mat supporting the animal on soft ooze.
36. The grooved anterior (left) and ungrooved posterior (right) arms of a specimen of *Comatula pectinata*, drawn to the same scale.
37. A cirrus of *Capillaster multiradiata* in dorsal (upper) and lateral (lower) view, showing the dorsal spines.
38. A smooth cirrus in dorsal (upper) and lateral (lower) view.

PLATE 4

- FIG. 39. Crown and upper part of the column of *Monachocrinus sexradiatus*.

PLATE 5

- FIG. 40. Crown and upper part of the column of *Proisocrinus ruberrimus*.

PLATE 6

- FIG. 41. Crown and upper part of the column (above) and central portion of the column (below) of a pentacrinite, *Comastrocrinus springeri*.

PLATE 7

- FIG. 42. Crown and upper part of the column (*a*), and middle (*b*) and lower (*c*) part of the column of *Ptilocrinus pinnatus*; in life the upper part of the column is recurved so that the crown points directly downward.
43. *Comatilia iridometriformis*, a species of Comasteridæ with some of the pinnules at the base of the arm lacking.

PLATE 8

- FIG. 44. A specimen of *Comatula pectinata* from Singapore showing long anterior and short posterior arms (compare with fig. 36).

PLATE 9

- FIG. 45. *Neometra acanthaster*, one of the Calometridæ.

PLATE 10

- FIG. 46. *Asterometra macropoda*, one of the Ptilometrinæ.

PLATE 11

- FIG. 47. *Antedon adriatica*, one of the Antedoninæ.

PLATE 12

- FIG. 48. *Compsometra incommoda*, one of the Antedoninæ.

PLATE 13

- FIG. 49. *Thaumatoocrinus jungerseni*, a ten armed species of Pentametrocrinidæ.

PLATE 14

- FIG. 50. *Pentametrocrinus diomedææ*, a five armed species of Pentametrocrinidæ.

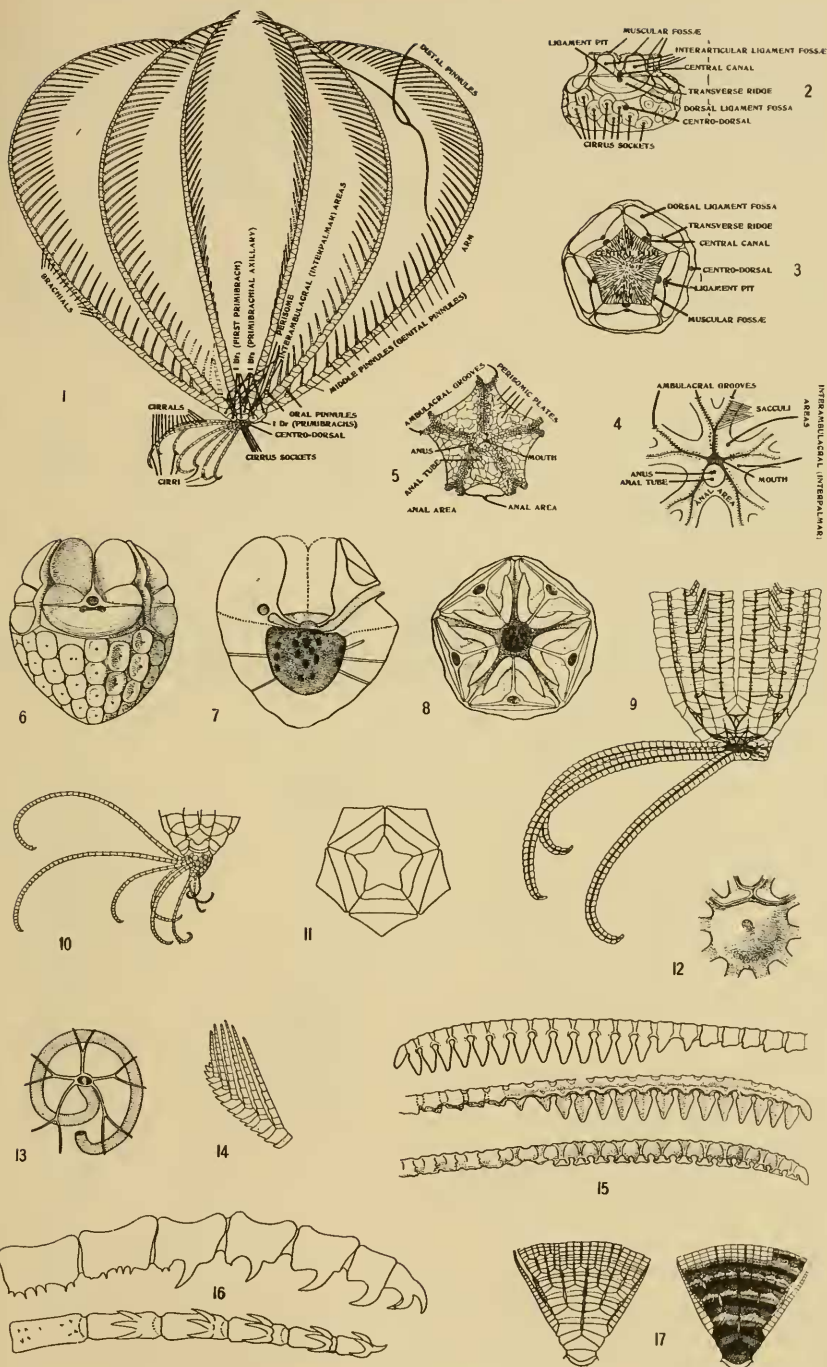
PLATE 15

- FIG. 51. An arm of *Heterometra compta*, showing the difference between the oral, genital and distal pinnules.

- FIG. 52. An arm of *Stephanometra echinus*, showing the stout and spine-like oral pinnules.
53. An arm of *Stylometra spinifera*, showing the mid-dorsal overlapping spines.
54. Four syzygial pairs from the arm of *Stylometra spinifera*, showing the progressive increase in the individuality of the two elements distally.
55. Pentacrinoid larva of a large Feather-Star, *Heliometra glacialis* (after Levinsen).
56. Ventral view of a larva of *Antedon mediterranea* early on the eighth day (adapted from Bury).
57. *Myzostomum costatum*, dorsal view (after Boulanger).
58. The same, ventral view (after Boulanger).
59. *Galathea elegans* (after Potts).
60. *Cirolana lineata* (after Potts).
61. *Cyclotelson purpureum* (after Potts).
62. *Scalpellum pentacrinarum* (after Pilsbry).

PLATE 16

A specimen of *Nemaster iozvensis* captured in shallow water in the Bahamas (Cat. No. 36164 U. S. N. M.).



(For explanation see page 40.)



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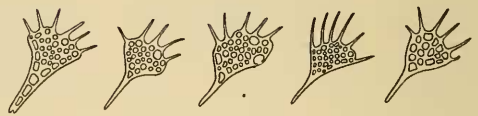
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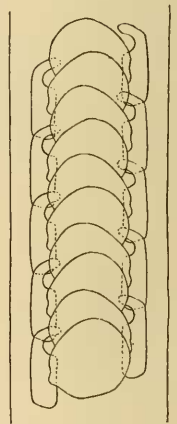
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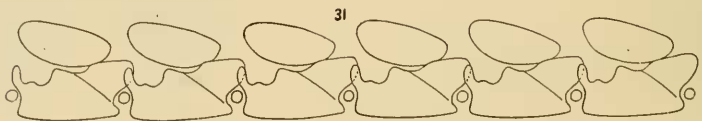
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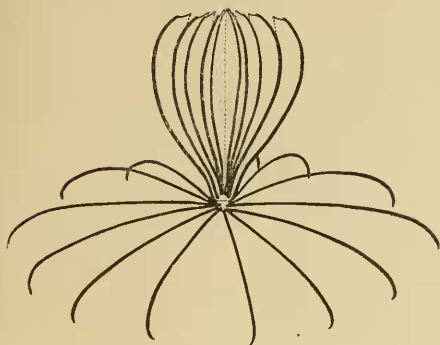


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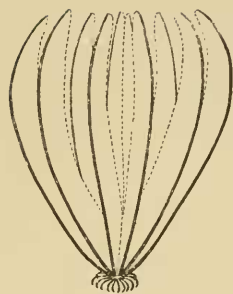


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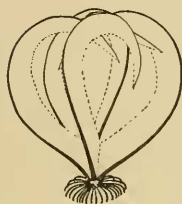
(For explanation see page 41.)



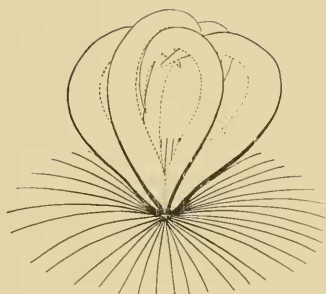
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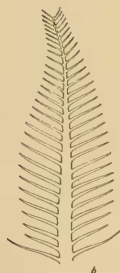
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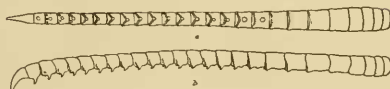
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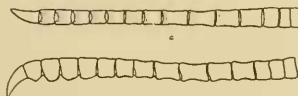
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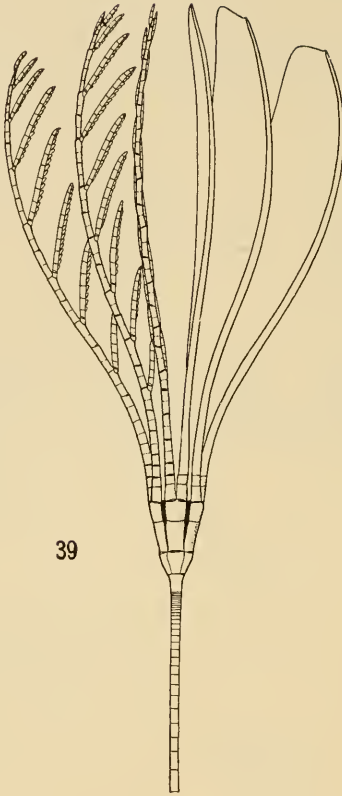
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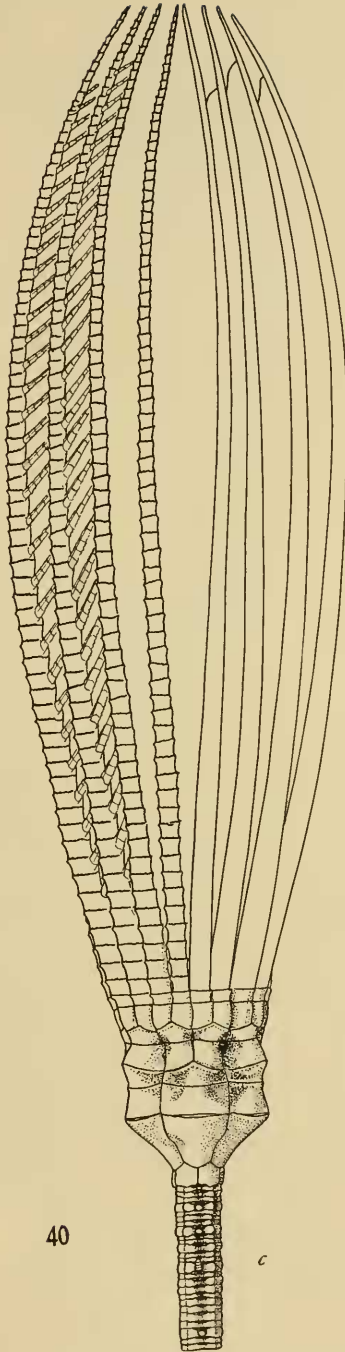


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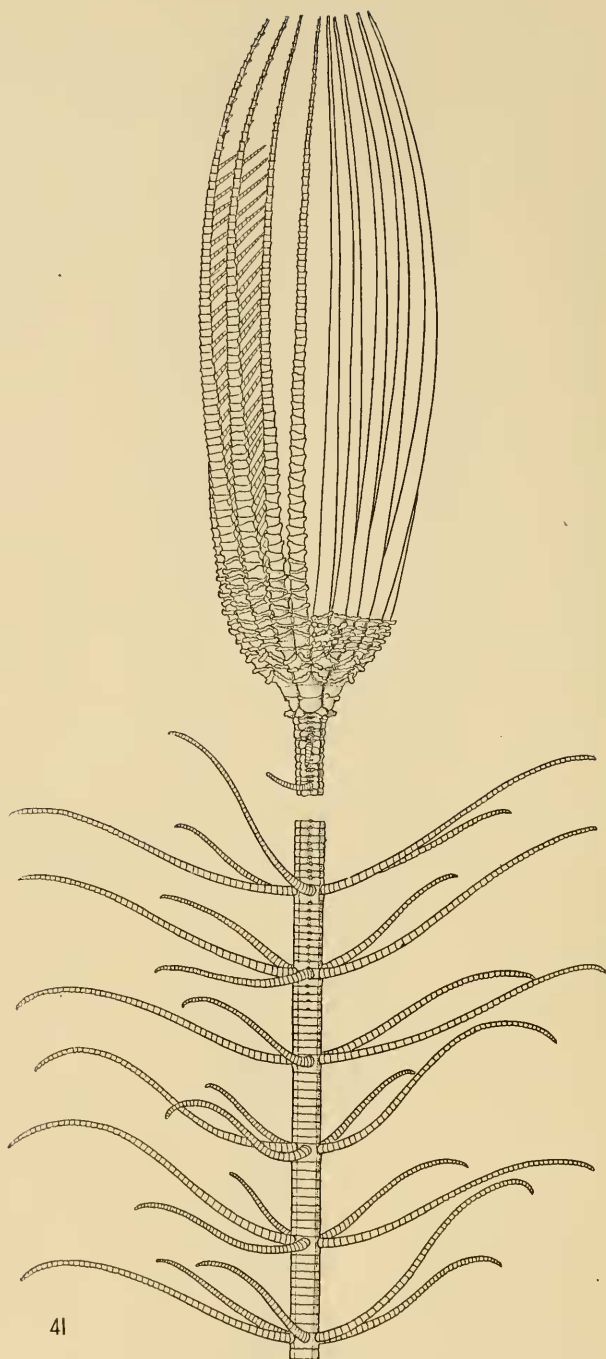


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(For explanation see page 42.)

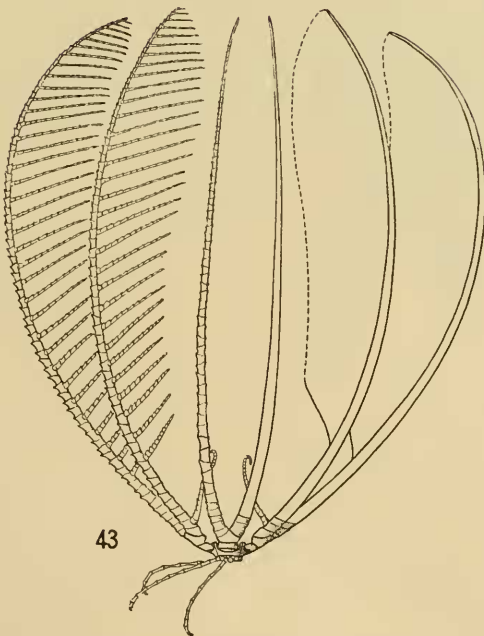
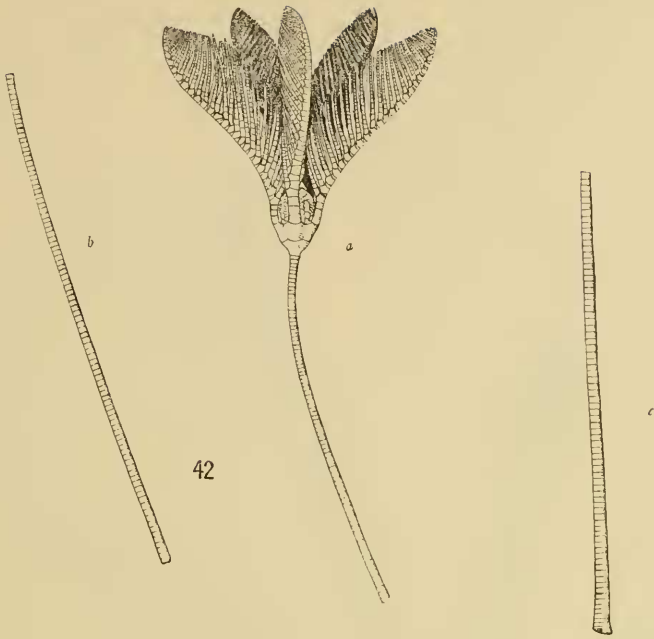


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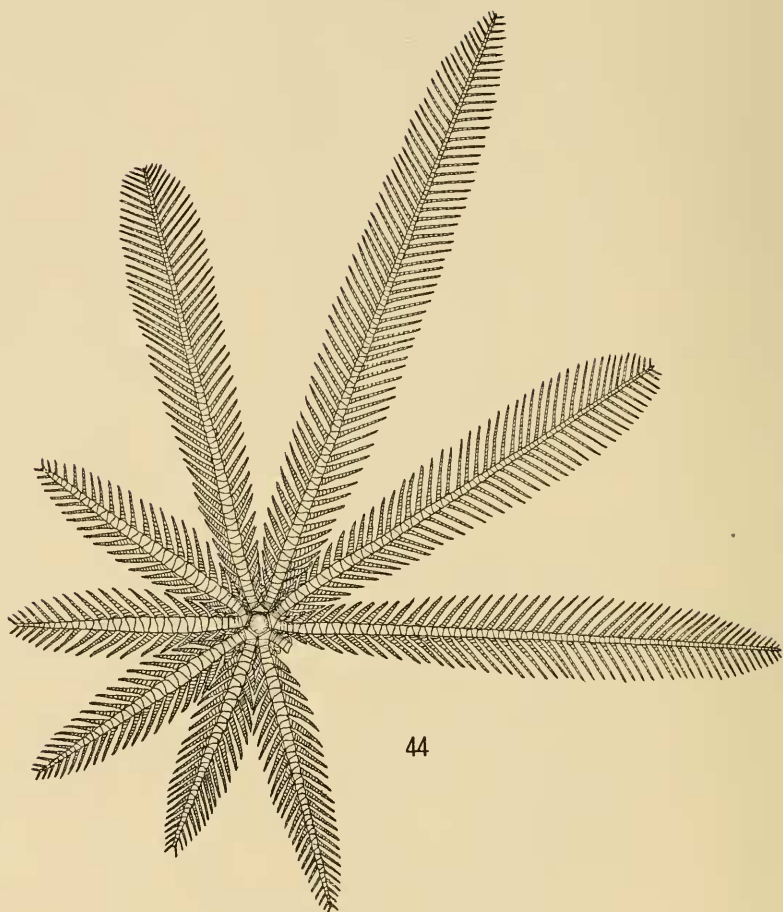


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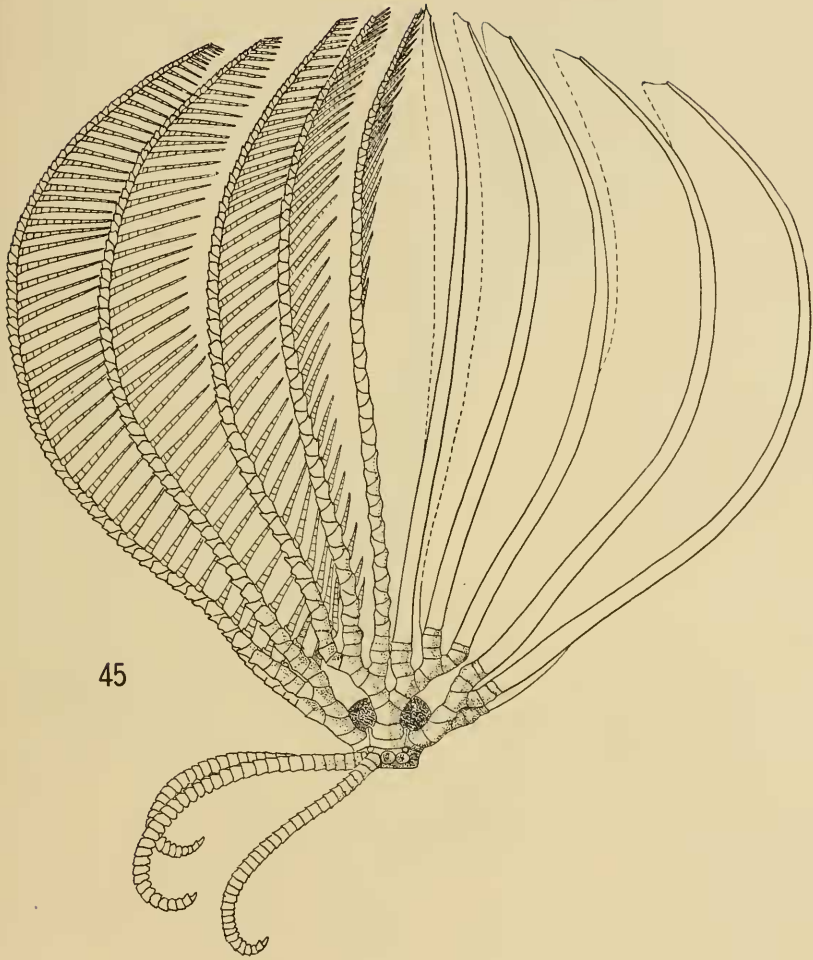


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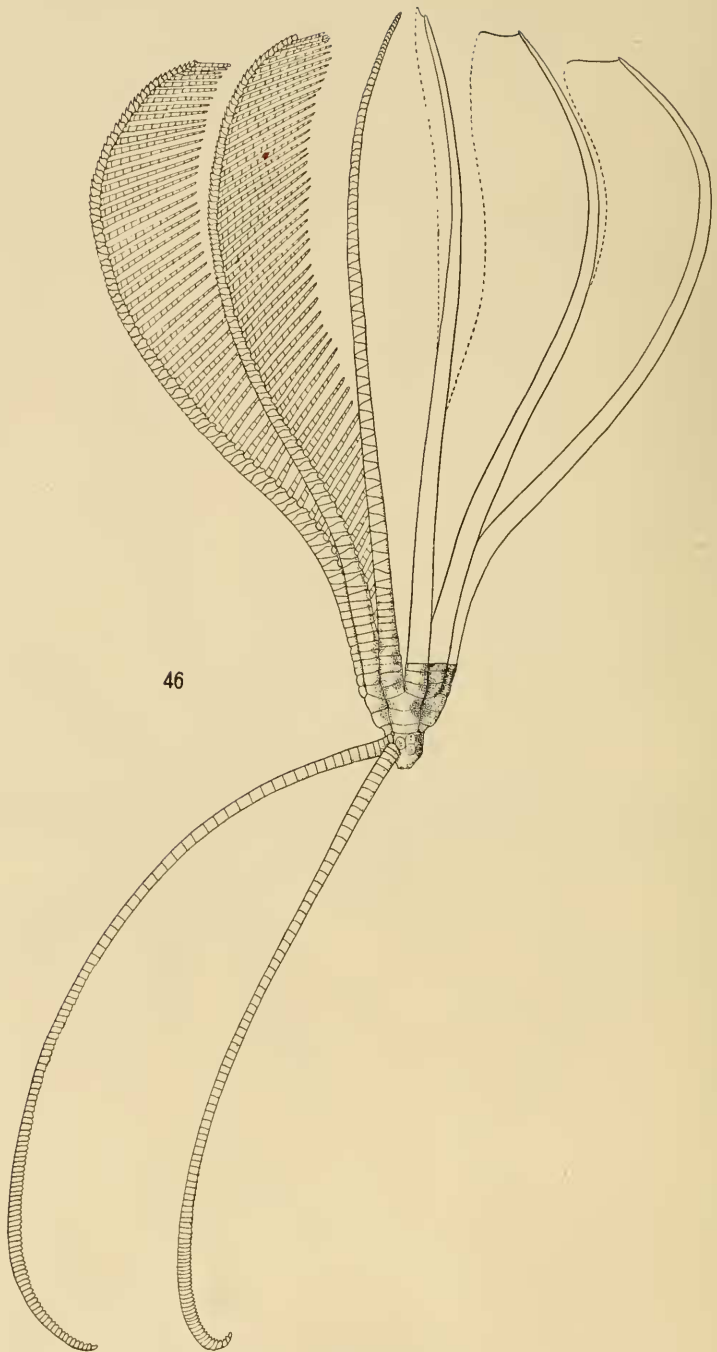
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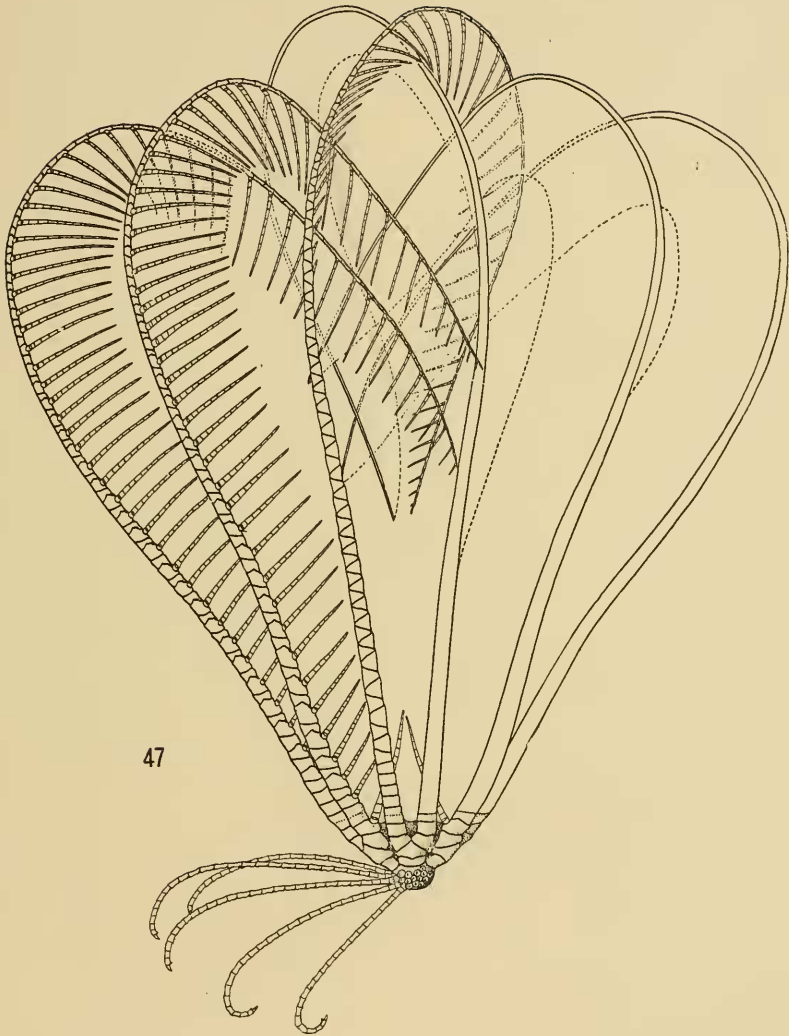


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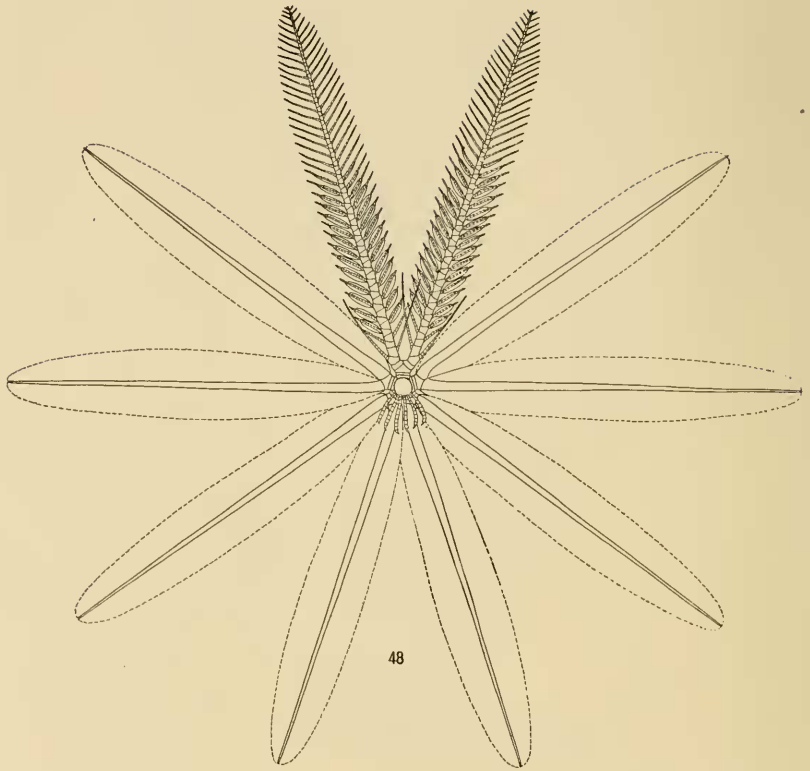


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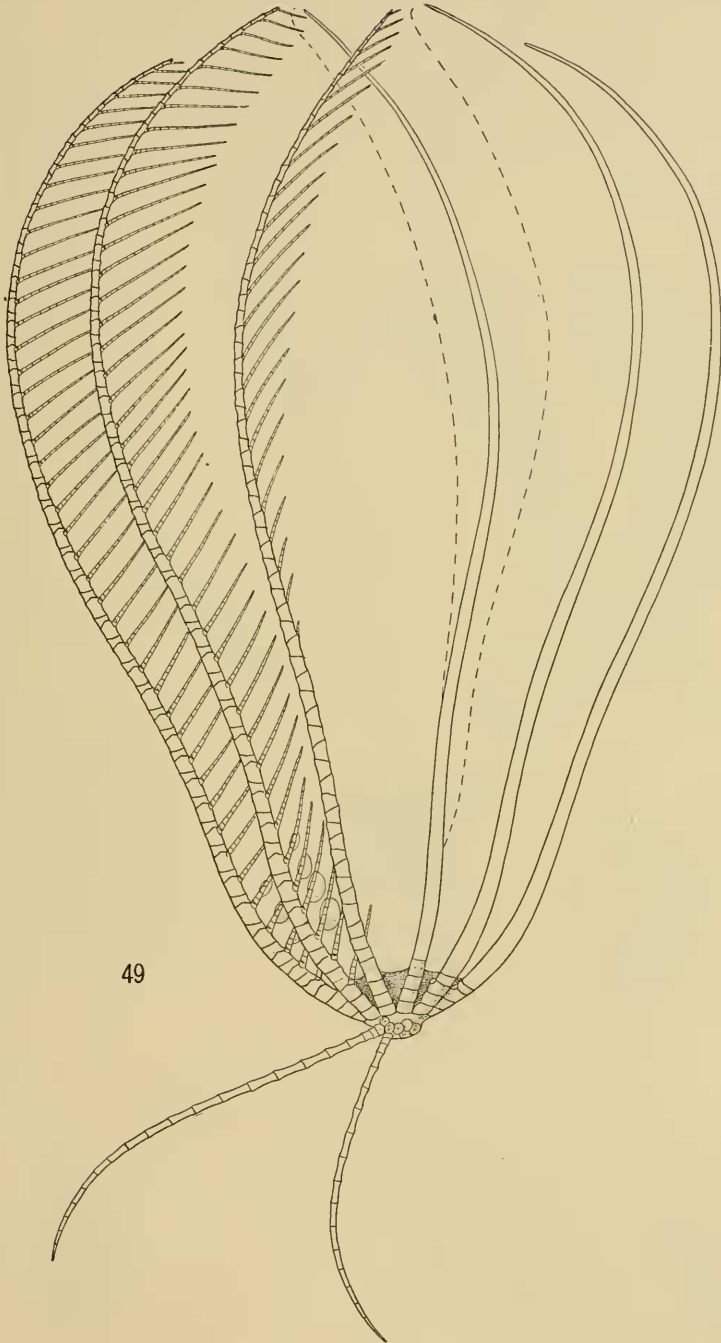
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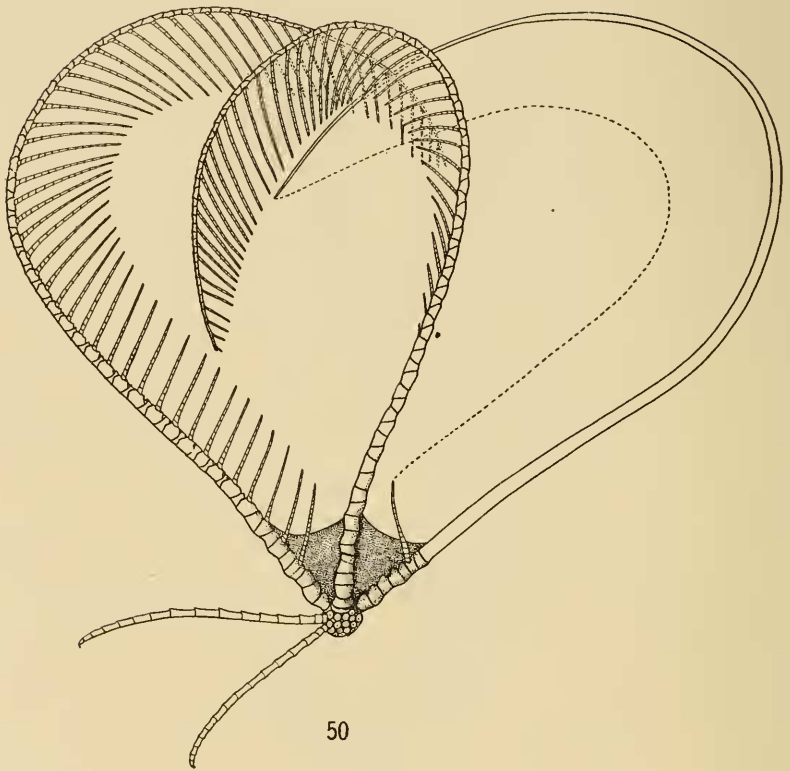
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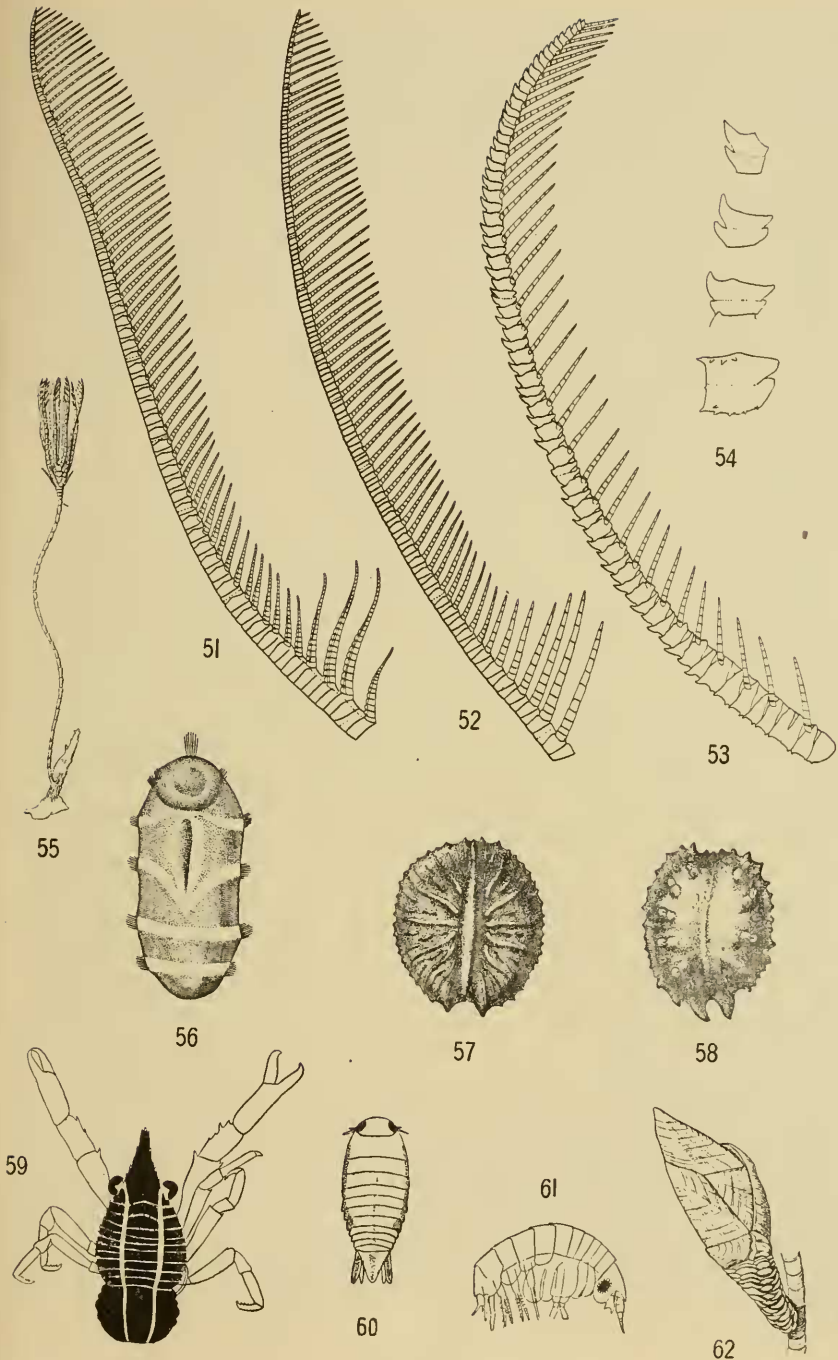


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(For explanation see page 42.)



(For explanation see page 42.)



(For explanation see page 42.)