Patrulius (1956) considered the thick-walled *Pseudosaccocoma* related to the Thiolliericrinidae, but Bachmayer (1958) found it related to *Saccocoma*.

ECOLOGY AND PALEOECOLOGY

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CONTENTS

ECOLOGY OF RECENT CRINOIDS

By Albert Breimer

GENERAL STATEMENT

In this chapter on ecology the crinoid's function and behavior is described as it reflects interrelations between the organism as a functional system on the one hand, and the surrounding medium on the other. Thereby, the organism is not considered as a "closed" functional system. From a point of view of physiology probably no such "closed" functional system exists. All metabolic processes (respiration, digestion, and excretion) require interchange of the animal with its environment. For this reason, not only the usual biological factors influencing the crinoid's mode of life are included, but also physiological factors are briefly dealt with in this chapter.

A detailed monographic treatment of the physiology of echinoderms has been published by a team of echinoderm zoologists under editorship of R. A. Boolootian (1966a). The book gives pertinent descriptions and compilations on the present stage of our knowledge on the subject. The result of this work again clearly demonstrates to the student of crinoids that virtually nothing is known about the basic physiological processes and mechanisms in crinoids. This lack of knowledge partly may be explained by the difficulties met with in finding and maintaining suitable crinoid material for physiological experiments.

Thus, a discussion of crinoid physiology is necessarily short. It should provide pertinent information at least on fundamental physiological processes which are vital to the crinoid organism as a functional system: the metabolic processes (respiration, digestion, and excretion) and their possible regulatory mechanisms, either nervous or glandular. The paucity of available observations is reflected in the brevity of descriptions given here, derived mainly from the above-cited book.

Fell (1966) has reviewed the ecology of recent crinoids, with attention given to several interesting aspects of the subject. The physicochemical interrelations of the crinoid and its environment, as well as its distributional patterns are described in separate sections of the chapter on Ecology.

PHYSIOLOGICAL FACTORS

RESPIRATION

No special respiratory organs are found in crinoids, for it is only the podia or tube feet that provide a respiratory surface as they do in echinoderms generally. All cells, however, are permeable to oxygen and it may be expected that oxygen penetrates both specialized and nonspecialized surfaces. Hence, the body wall presumably obtains oxygen directly from sea water. Probably about 60 percent of the oxygen intake of crinoids is utilized mainly by metabolism of the body wall.

The digestive tract is sometimes said to be involved in respiratory exchange inasmuch as water is frequently observed to be taken in by the anal cone and again ejected. This is undoubtedly a minor supply of oxygen, since histologically and physiologically the tissues of the digestive tract are not adapted to serve for respiration.

A specialized respiratory surface of crinoids is found in terminal branches of the water-vascular system (podia or tube feet). In other echinoderm classes it is known that oxygen is transported in the lumina of the podia by ciliary currents to the respective ampullae, where it diffuses across the ampullar membrane into the perivisceral coelomic fluid. Neither the water vessels nor the hemal lacunae are directly involved in a vascular transport of oxygen. The transmittal of oxygen to the internal organs is effected by the perivisceral coelomic fluids, which are kept in motion by flagellae of the coelomic endothelial cells.

Since crinoids have a primitive sort of water-vascular system, lacking ampullae and fully open to the external medium, the supply of ambient oxygen to the perivisceral coelomic fluid can be furnished only by direct intake of water through the hydropores and ciliated funnels, which for this purpose probably beat in one direction. In this way ambient oxygen is brought directly to the viscera. Supply of oxygen to the subambulacral coelomic fluid is inferred to be provided by diffusion through the horizontal membrane.

The fluid present in the hemal lacunae is often referred to as blood. However, any differences in the chemical constituents of perivisceral coelomic fluid and hemal lacunar fluid remain to be demonstrated. Probably it is the perivisceral rather than hemal fluid that transports the oxygen. In any case, a free exchange between the two fluid bodies is possible, since coelomocytes are present in both. The presence of specialized hemocytes containing pigments closely allied to the hemoglobins of vertebrates are unknown in crinoids. Such cells have been clearly demonstrated to function in transporting or storing oxygen, or both. They occur in some genera of holothuroids and in one species of ophiuroid.

Crinoids thus are devoid of effective respiratory organs, effective vascular circulation, and respiratory pigments. This probably makes them unable to maintain a constant consumption of oxygen. Rather, this is thought to vary with changes in oxygen of the environment.

DIGESTION

The nature of the food taken by the crinoids has been described previously. The processes and mechanisms of digestion in crinoids and the manner of transporting and storing nutrients required by them are little known. Normally in echinoderms digestive enzymes are secreted by secretory cells in the epithelia of digestive caeca dependent from the foregut. The functional nature of the diverticula in crinoids appears to be unknown, although supposedly it is digestive. The source and nature of digestive enzymes in crinoids remains to be investigated. Similarly, nothing now is known about the mechanisms of uptake and the transport and storage of nutrients. Generally in echinoderms coelomocytes play a role in ingesting sufficient nutrients to satisfy metabolic requirements. In crinoids the activity of certain cells is known to be phagocytic; some also may be adapted for transport and storage of nutrients. The perivisceral coelomic fluid, however, in many echinoderms has been proved to contain products of digestion, with traces of protein and amino nitrogen, as well as a small quantity of reducing sugar. The perivisceral coelomic fluid seems to be the most important medium of nutrient transport. An exchange of substances between the coelomic fluid and tissues of the body seems to be continuous in crinoids.

EXCRETION

Crinoids lack well-defined excretory organs. In older literature the sacculi and the globular brown bodies known to live in the digestive tract of *Antedon* (Fig. 1) have been interpreted from time to time as excretory bodies. The structure of the sacculi and brown bodies is well known. Each sacculus is a special spherical body enclosed within a thin membrane and containing a number of pyriform sacs filled with refractive spherules. The sacculi of the crinoid disc, arms, and pinnules periodically rupture and extrude their granular contents freely into the surrounding medium. Those in the wall of the gut (especially at its posterior end) mostly discharge into the gut. No mucus is associated with the extruded matter and the nature of excretory products and manner of their elimination is physiologically unknown.

Recent literature, however, takes into account the fact that phagocytic coelomocytes may convey ingested particles from the coelomic fluid to the exterior and it has been assumed that the coelomocytes could be responsible for the elimination of metabolic waste, at least partly. Excretory products, principally ammonia and urea, occur in the coelomic fluid. Crinoids have a special type of coelomocyte with short pseudopods possessing a large nucleus and a cytoplasm which commonly contains granules, some of which may be colored. The phagocytes with short pseudopods are known to be actively phagocytic, ingesting colored particles. No information is available as to whether ingested particles are conveyed to the exterior by the crinoid phagocytes or are deposited at definite sites in bodies of these animals. The coelomic epithelia could contribute in this way to excretion since they are supposed to have phagocytic powers and to be able to accumulate substances. In other echinoderms coelomocytes carrying ingested material may aggregate in the axial gland or may be eliminated through gills or respiratory trees, or through the stone canal and madreporite.

BIOLOGICAL FACTORS

In dealing with crinoid behavior and habits, most attention needs to be directed to feeding and reproducing, the two most essential functions of the organism. Recently the feeding behavior of extant crinoids in their natural habitats has received much attention. Magnus (1963, 1964, 1967), Fishelson (1974), and Rutman & Fishelson (1969) have reported on the feeding behavior of shallow-water comatulids from the Red Sea; Meyer (1973a,b) and Macurda (1973) on shallow-water comatulids from the Caribbean Sea; Pérès (1958, 1959) on deep-water comatulids from the Pacific; and Macurda & Meyer (1974) on deep-water isocrinids from the Caribbean. Less attention is given to the reproductive behavior. This subject lately has been excellently reviewed by Boolootian (1966b).

PERCEPTION

A key question in crinoid ecology relates to possibilities for the organism to perceive its environment, react to stimuli received from it, and to translate these into actions. Crinoids have only an unspecialized sensory system, mainly located in the sensory papillae of the podia and tube feet and in free nerve endings distributed over the body surface and connected to the subepidermal nerve plexus. Crinoids probably are capable of discriminating chemical, photic, tactile, and thermal stimuli—particularly their presence or absence and probably also changes in their intensity. The motor system is located in a well-developed aboral nerve system, which allows the animal to make and coordinate independent movements of arms and pinnules in respect to one another and to the tegmen. Among stalked crinoids both the stalk and cirri are capable of movement.

POSITION, RIGHTING, LOCOMOTION

The normal position of both stalked and stalkless crinoids is determined by fixation to the bottom or any substrate in such a way that the mouth is directed upward. Crinoids are the only surviving echinoderms that retain this primitive condition. Stalkless comatulids normally are attached by their cirri to a bottom object. They will not move about as long as ecological conditions at the spot of their attachment remain satisfactory. They move actively by swimming or creeping only in case environmental factors become unsatisfactory. Seemingly, the stemless crinoids have only gained the vagile capacity of active movement in order to gain efficiency as sedentary animals. Movements are aimed at finding better attachment sites. CLARK (1921) has described the desperate need of comatulids to attach themselves to suitable bottom objects. He wrote:

> If a dozen specimens of *Antedon* were thrown at night into a large basin of water and were left without any means of attachment they were all found dead in the morning, conglomerated at the bottom of the basin, clinging to each other with their cirri and having their arms intertwined in such a manner as to suggest the idea that they had died of the asphyxia produced by overcrowding after exhausting themselves in efforts to find a suitable attachment; while if, in a basin of the same size and containing the same quantity of water, there were placed with a like assemblage of specimens a sufficient number of rough stones to afford them all a basis for attachment, they would be all found in the morning in a state of full expansion, with every appearance of health and vigor!

Suitable objects for clinging and attachment are rock, coral, arborescent growths such as algae, coelenterates, seaweeds, and any object available which projects slightly above the bottom surface.

If comatulids happen to turn to an upside down position with the mouth below, they are able to right themselves by means of a pull and push mechanism operated by the arms.

Movements of comatulids are twofold. Antedontids are specialized for swimming and have a slender construction suited to this, whereas comasterids only creep around and have a more sluggish appearance. Both arms and cirri play an active role in locomotion.

The well-known swimming movements of *Antedon* begin by release from an attached position in which its five bifurcated arms are spread out horizontally. The arms then act as two groups of five, one comprising the left half-rays and the other the right half-rays. Arms of one group are first raised upward with the pinnules flexed inward against the arm. Next these arms lash rapidly downward but now with extended pinnules to give maximum strength to their stroke. The same movements are performed by the other group of arms repeated again and again. The crinoid can swim in any direction. A differential horizontal component is given to the motion in swimming by variation in the strength of strokes with arms in one position or another. The swimming of *Antedon* is graceful; however, it is induced by unfavorable conditions in the environment, such as oxygen deficiency, intense illumination, and thermal changes. Swimming is restricted to short distances, several meters at most.

Comasterid movements are best described as creeping in which they mostly utilize their cirri, although the arms may assist. These crinoids persistently decline to swim, even when diligently stimulated to do so in experiments. The creeping movements of comasterids are based on a pull-and-push mechanism carried out by the cirri. They may crawl about for hours, with arms aiding their movement. The anterior arms, extended forward during locomotion, serve as tactile organs and assist in pulling, while the posterior arms assist in pushing. Fell (1966) has stated that the longer arms lie on one side of the disc, to which the mouth is displaced, and these longer arms invariably occupy an anterior position during locomotion. He stressed the theoretical importance of this phenomenon for the relationship between mouth and anus as markers of the anteroposterior axis of echinoderms.

AUTOTOMY AND REGENERATION

It is well known that crinoids may shed their arms and then are able to regenerate them. Some authors have doubted whether the shedding of arms constitutes true autotomy, for a majority of regenerated arms are found to have originated from a syzygial contact or from another sort of nonmuscular contact. Autotomy may easily be brought about by degeneration of the very short and delicate ligament fibers connecting brachials in syzygial contacts. Of course, true autotomy has to be distinguished from the breaking of arms in response to mechanical external pressure. Arms of crinoids are indeed liable to break at syzygial contacts by reason of inflexibility at such contacts. Shedding of arms mostly takes place under unfavorable physical conditions in the environment (e.g., high temperature, oxygen deficiency, etc.).

Regenerative powers are very strong in crinoids. If arms are lost or shed, they are readily regenerated, and if two or more are lost at the same time, all are regenerated. Crinoids with all arms missing at the same time are reported to die, but the cast-off arms remain alive for a long time (up to several weeks) and continue to feed, without ability to regenerate an entire animal, however. The tegmen, if lost, regenerates, as do crinoids which have been eviscerated. Cirri, if all are removed at the same time, do not regenerate. Regeneration is only successful as long as the aboral nerve center remains intact. Therefore, any crinoid part containing the aboral nerve center plus one arm generally will regenerate an entire animal.

Minckert (1905a) has observed the connection between regeneration and growth of crinoids mainly in the later stages. Autotomy of arms occurs in juvenile ten-armed comatulids as a means of growing out to a multibrachiate condition. In such a case, each shed arm is not simply replaced but reduplicated, for two arms replace one that is lost. This is termed **augmentative regeneration.**

Fell (1966) has considered regeneration in connection with reproduction. He envisaged the possibility of dividing a crinoid in such manner as to regenerate two entire specimens from the original one. This would mean asexual reproduction. He concluded that spontaneous or induced division of the body does not lead to the production of two individuals from one. Crinoids lack asexual reproductive powers.

REPRODUCTION

Sexual reproduction is the only natural means of self-duplication among crinoids. Most have distinct reproductive periods (breeding seasons) which are marked by periodical outgrowth of the gonads and the spawning of gametes. The crinoid gonads are lodged in specialized pinnules which are interpreted to serve mainly as storage organs. Therefore, periodic growth of the gonads is inferred to succeed gametogenesis, growth being due to gamete accumulation.

The first, and probably only, report of crinoid gamete shedding behavior in its natural habitat is by Fishelson (1968) for *Lamprometra* from Eilat, Red Sea. The shedding behavior of this crinoid is described as follows:

> . . . at 17.45 h. individuals were observed climbing out of their daytime hiding places on an isolated coral block at a depth of 2 m. At 18.00 h. twelve were found attached by their cirri along a deep notch in this block with fully extended arms and swollen genital pinnules. One of these individuals started violent undulations of its arms, and after several seconds the remaining individuals were whipping their arms vigorously. Simultaneously, a dense greenish-coloured cloud of gametes arose around them, partly covering them. Arm-whipping continued for 25 s. and then stopped abruptly. Laboratory observations revealed that the individual which began the gamete shedding was a male, and that in this group there were females and males.

In spawning, all gonads in all genital pinnules of every arm release their gametes at the same time. Male individuals spawn first and their products probably stimulate females to release their eggs. This is a very effective mechanism for immediate fertilization of the just-shed eggs. Release of the gametes is by rupture of the pinnular body wall, either in preformed thin spots or elsewhere. In many cases and typically in *Antedon,* eggs are stuck to the pinnules by secretion of an adhesive from gland cells.

Boolootian (1966b) tabulated data supplied by Clark and Mortensen on the reproductive periods of 21 species of comatulids. A majority of these have distinct and mostly short reproductive periods of one or two months. The only species which seems to spawn the year round is *Antedon mediterranea.* Breeding seasons of the different species of crinoids are scattered throughout the year except in November and December. No data are available on the spawning and breeding behavior of stalked crinoids. Attention already has been given (see Morphogenesis) to the fact that several Antarctic species of comatulids breed their young in special brood-pouches or marsupia (Fig. 36).

No information can be given on the physiological mechanisms which regulate the course of events in reproductive cycles of crinoids. Crinoids are known to spawn at very specific moments of the day or night, and their spawning activities have been observed to correlate with several external factors such as presence of moonlight. *Comanthus japonicus* spawns on a single afternoon in October at 3 o'clock, the date depending on lunar periodicity (Dan & Dan, 1941; Dan & Kubota, 1960).

FEEDING

The importance of feeding for crinoids is indicated by the estimation that they probably spend at least half of their entire life time in obtaining food. They are exclusively suspension-feeders that depend on small planktonic and nektonic organisms such as algae, dinoflagellates, diatoms, radiolarians, foraminifers, small crustaceans (e.g., amphipods, copepods, larval stages of malacostracans), and larvae of other organisms.

Rutman & Fishelson (1969) have studied the food composition of comatulids in the Red Sea. Food selectivity concerns the size of the food organisms. Nearly 85 percent of the ingested organisms are within the size range of less than 1 micron to 300 microns. There seem to be two size-limiting factors; one is the width of the food-conveying ambulacral tract, and the other is the locomotory strength of the organisms captured in the mucus net. Larger organisms are capable of forcing their way out of the net. The food of these crinoids consists of organisms belonging mainly to the finer fractions of microplankton and to the nannoplankton. Also benthonic micro-organisms, such as brown algae, swept up from the bottom by currents, are ingested as food. The average diet of these crinoids contains about 10 percent phytoplankton, 50 percent protozoans and about 40 percent crustaceans and mollusks. Phytoplankton is always found to be the minor constituent in the food, the most frequent relation between phytoplankton and zooplankton being one to nine in favor of the latter.

The crinoid feeding mechanism has been studied by Gislén (1924) and Nichols (1960) on specimens in aquaria. The crinoid tube feet are adapted to collect food particles, for this is their main use besides respiration and subsidiary sensory functions. The tube feet possess papillae with muscle-operated glands which produce strings of mucus for trapping food particles. Holland (1969) found that the papillar muscle cell is actually filled with microtubules. The activities of the tube feet in a feeding *Antedon* have been described by Nichols (1960, p. 106, 107, 115) as follows:

> The largest tube feet of each group project laterally almost at right angles to the long axis of the pinnule. The medium-sized tube feet of each group project upwards and outwards at an angle of about 45°, while the smallest of each group projects almost straight upwards. Bordering the food grooves of arms and pinnules are the groove lids or lappets. When the animal is feeding these project upwards at an angle, and each long tube foot projects laterally through the valley between the two adjacent lappets. The other two tube feet of each group lie against the inside wall of each lappet with the outer side of the proximal part of the tube feet fused to this wall, so that when the tube feet bend in

> towards the mid-line of the food groove they move the lappets in this direction too. If these tube feet contract, the lappet closes over the groove, so that only the largest tube feet remain protruding, though usually they too bend inwards to lie across the oral surface of the pinnule.
>
> When the animal is feeding, the tube feet make sudden and rapid bending movements every few seconds. This apparently happens whenever food material touches the tube feet and stimulates the sensory cells, since crushed fragments of food dropped onto a pinnule cause the tube feet immediately to bend and flick in an attempt to throw the food into the groove. The rapid movement of the long tube feet is almost entirely at right angles and towards the food groove; that of the medium-sized tube feet is almost always at right angles to the groove, but both towards and away from it; the small tube feet can twitch in any direction. The tube feet of the arms can move in any direction, though most of their movements are at right angles to the food groove. After a twitch the tube feet return to the "waiting-position" more slowly. The main food-entrapping organs are the largest tube feet of the pinnules and the medium-sized ones of the arm. The middle and small tube feet undoubtedly act mainly to transfer the particles into the groove. The median tube feet are able to move outwards as well as inwards to pick up the food-laden mucus strands, and the small feet can twist in any direction to catch the strands from the medium-sized feet and drop them into the groove.

Gislén (1924, p. 274, 275) has described the activities of ambulacral grooves and the mouth in feeding as follows:

> . . . the margins [of the ambulacral furrows] . . . generally lie pressed tightly together. [The furrow] opens as soon as any grains fall upon it, with a wavy movement proceeding towards or away from the mouth. The mouth, only a narrow slit before, opens to its widest extent, and becomes rounded. . . . [Food grains] are cast into the ambulacral groove, where the ciliary current takes hold of them and carries them to the mouth. The ambulacral furrow itself is slightly concave and ciliates strongly towards the mouth. The mucus is secreted in the ambulacral groove . . . and the grains are glued together into larger lumps by it. These are transported to the mouth, the edges of which are often pressed together like a pair of lips, during movements similar to swallowing.

Systematic observations on the feeding behavior of crinoids in their natural environment have resulted in important new insights into their feeding habits and postures. Crinoids living in very shallow water tend to be very sensitive to illumination. During daylight they hide in shadowy places, resting with the arms rolled spirally inward over the tegmen. The start of feeding activities is regulated by the sunset, feeding continues during all of the night and stops shortly before sunrise. Such very shallow-water crinoids are truly nocturnal animals. Crinoids living in somewhat deeper water seem to lack such pronounced diurnal rhythms, and are sometimes supposed to feed almost continually.

Among reef-dwelling comatulids two feeding postures are known. The first posture has been called a **"brachial filtration fan"** by Magnus (1967) and Breimer (1969). This feeding posture is illustrated in Figure 210, and was described by Magnus (1967, p. 649-650) as follows:

> Feeding obviously takes place only by filtration from the current. To catch food the animals try to climb higher places such as the tips of seagrass-leaves or rock ledges, and at first unroll only few of their arms, but later unroll all of them. Each arm takes a position in which the aboral side faces the current. The pinnules, pressed against the oral side of the arm when inactive, become erect and bend towards the aboral side so that all of them form a grating on each arm, opened against the current. The tube feet bordering the pinnular food grooves are erected so far that they contact the neighbor pinnules. In this position they form a fine network. With the arms extended against the current they orient themselves in a single plane to form a filtration fan across the axis of the current. In order to do this the arms on the side of the body that is not facing the current have to turn up to 180° around their long axis. If two animals are found side by side, they together form a unique fan with 40 arms, because each arm tries to get into a position with undisturbed current. The filtration fan, thus built, is usually held vertically. It can be pressed down and finally be resolved by a stemming pressure of the current. Generally, however, the animals seem to settle down at those places where there is a more or less constant and slight current (2-5 cm. per sec.). In this current strength the fans could remain such. They could not withstand stronger currents of even brief duration. When the current direction changes, the fans are first untied and then the arms are held randomly upward or to the side, but they never form a cup or funnel. The arms turn against the new current direction and form a new uniform filtration fan.

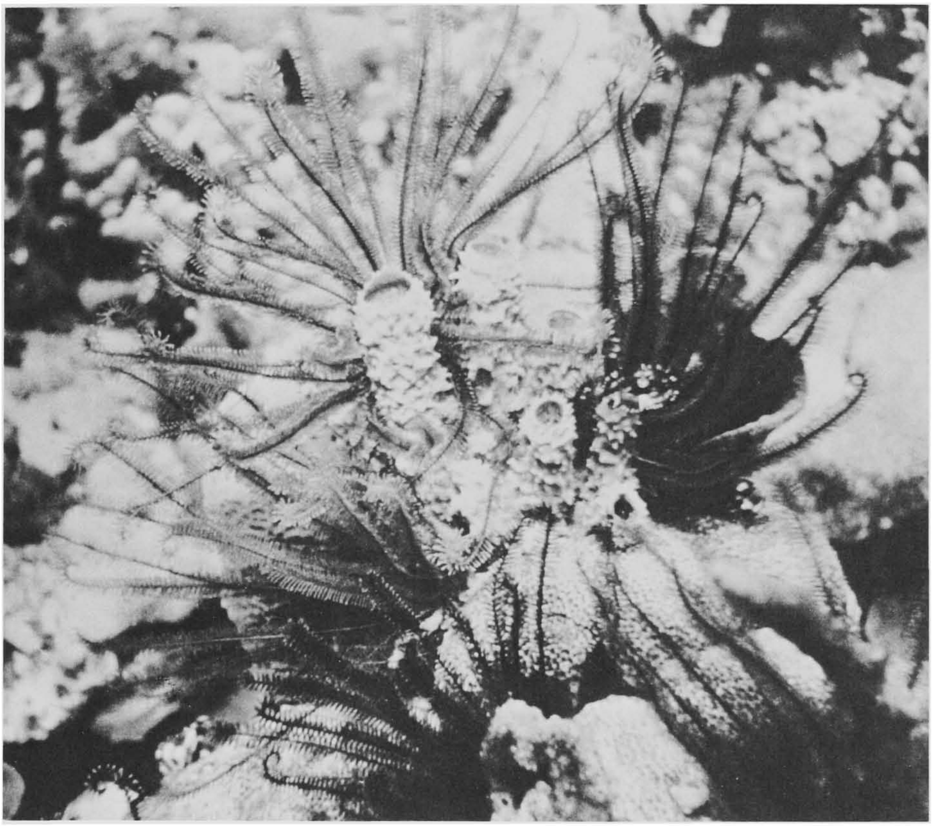


FIG. 210. Undetermined stalkless crinoid, probably comasteroid, on reef off Dominica (Caribbean), clinging to sponges with help of four arms; specimens form filtration fans and probably show their feeding posture (Breimer, n, by courtesy of Dr. Porter M. Kier, Washington).

Comatulids employing a brachial filtration fan actively search for favorable places to feed. Such places are mostly on top of the reef structure. They extend the arms above the surrounding topography so that the arms are exposed to horizontal or unidirectional currents and wave oscillation. The filtration fan is typically held normal to the direction of water movement, which ensures a maximum exposure of the tube feet to food-carrying currents. The arms of such crinoids are featherlike, with the pinnules placed in two rows, but lying in a single plane.

The brachial filtration fan probably is widely in use by current-seeking or rheophilic crinoids. It is now known to occur in reef-dwelling comatulids from the Mediterranean (MAGNUS, 1963, 1964, 1967; FISHELSON, 1974; RUTMAN & FISHELSON, 1969), from the Caribbean (MEYER, 1973a,b; MACURDA, 1973), and also from the Indian and Pacific Oceans (MACURDA & MEYER, pers. commun.).

The second feeding posture among reef-dwelling comatulids is called **radial feeding posture** by MEYER (1973a,b). Crinoids employing this feeding posture live in crevices and other restricted places deeper within the reef infrastructure. Their arms do not extend above the surrounding topography. Water movement within the reef infrastructure is more turbulent and of reduced velocity compared to that just above the irregular reef topography. In response to the complex flow regime of the

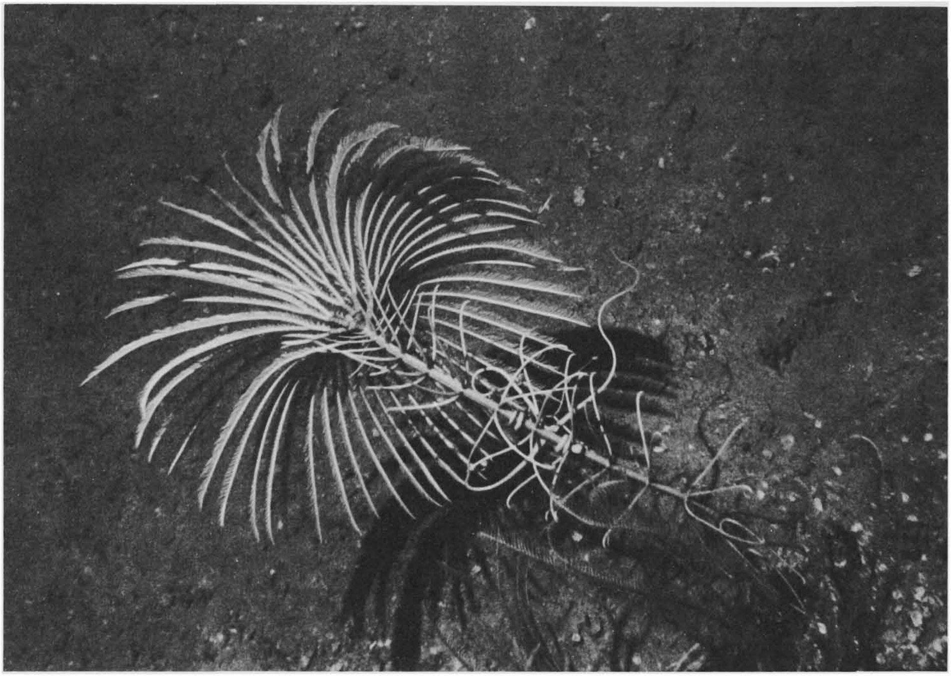


FIG. 211. *Cenocrinus asterias* (LAMARCK), 180-240 meters, off Discovery Bay, Jamaica. (Photograph by W. K. Sacco; Breimer, n, through courtesy of D. L. Meyer.)

reef infrastructure, these crinoids utilize the radial feeding posture. In this posture, the arms are extended in many directions and the pinnules are held in a four-row, radial arrangement, providing maximum exposure of the tube feet to multidirectional water movement prevailing in their microhabitats.

The radial feeding posture also seems to be in general use. Although it is not yet known from the Mediterranean, it seems to occur also in Indian and Pacific reef crinoids (MACURDA & MEYER, pers. commun.).

Deep-water comatulids (PÉRÈS, 1958, 1959) use still another feeding posture, known as the **collecting bowl.** These crinoids seem to feed on the settling plankton falling upon them from the "plankton rain," and passively await the arrival of food. The mouth in such crinoids is directed upward, and the arms are spread out so as to form a collecting bowl or funnel to capture food. This feeding posture may be interpreted as being in use by current-avoiding or rheophobic crinoids, relying for their food on plankton rains, rather than water currents.

Traditionally (HYMAN, 1955; NICHOLS, 1960), all crinoids were believed to form a "collecting bowl or funnel" with the mouth at the center. This opinion was based on observation of *Antedon* held in aquaria and fed by means of artificial plankton rains, produced by grinding plankton samples and dropping them in aquaria with motionless water. This traditional opinion has now been abandoned. *Antedon*'s feeding habit in aquaria must be held to represent a special adaptation to living under artificial aquarium conditions in motionless water.

The feeding posture of deep-water isocrinids from the Caribbean has recently been described by MACURDA & MEYER (1974). Isocrinids also seem to use a brachial filtration fan (Fig. 211). During feeding the stalk is slightly bent over, and the crown is held in a more or less vertical position, with arms and pinnules all stretched out.

The arms are held with the aboral side facing the current, and the tips of the arms are recurved. In this posture a parabolic filtration fan is built. In some multibrachiate forms this may form an almost continuous filter. Caribbean isocrinids are moderately rheophilic crinoids, relying for their food on slight water movements.

Recent investigation has shown that many crinoids prefer to live in areas with sufficient water currents so that they can rely on these currents for feeding. Such crinoids are **rheophilic.** Their preferred feeding posture seems to be the brachial filtration fan, either planar (as in comatulids) or parabolic (as in isocrinids). The widespread use of this feeding posture in modern rheophilic crinoids has led Breimer (1969) to infer that many stalked Paleozoic crinoids may be interpreted as using a brachial filtration fan for feeding, and thus be rheophilic crinoids. (See also section on Autecology of fossil crinoids, this *Treatise* volume.)

Feeding postures discussed so far occur in adult crinoids. Lane & Breimer (1974) have distinguished a sequence of feeding habits during ontogeny of modern crinoids. For crinoids in the armless cystid growth-stage they inferred that they relied on epidermal feeding, utilizing dissolved exogenous nutrients. Crinoids in the pentacrinid growth-stage use their long, tentacular oral podia for capture of smaller planktonic particles, a mechanism called tentacular feeding. The juvenile, nonpinnulate crinoid growth-stage would use tube feet and ciliary feeding, whereas the mucus net feeding is only to be expected in adult crinoids with pinnulated arms.

PREDATION, PARASITISM, AND COMMENSALISM

No animals are known to feed regularly upon crinoids. Some authors believe that the supposed toxic excretions in mucus produced by the crinoids is unattractive to other animals. Crinoids thus are judged to lack enemies. Many animals, however, live in association with crinoids either as casual or permanent commensals or parasites. Clark (1921) and Fishelson (1974) have listed many such organisms, among which are crustaceans (mostly casual commensals), ophiuroids (semiparasitic commensals), gastropods (ectoparasites), and especially polychaete worms (mostly permanent semiparasitic commensals). The polychaetes all belong to different species of *Myzostomum,* which are highly specialized and aberrant. They mostly live on the outer side of the crinoids, arms or pinnules or make burrows, which induce malformations such as cysts, etc. Myzostomes have adopted the habit of sucking up food from the mucus streams coming down along the ambulacral grooves of their crinoid host. Crustacean commensals are interesting in that their color patterns provide camouflage for their life among crinoid arms and pinnules. These have been described by Potts (1915).

Magnus (1963) has observed fishes feeding on the food-laden mucus strands in the ambulacra of *Heterometra savignyi.* Clark (1921) has discussed the apparent immunity of crinoids to attack by fishes.

An ectoparasitic gastropod and commensal gorgonian octocorals on bourgueticrinids are illustrated in Figure 212. Both are rare and little known cases of parasitism and commensalism in stalked crinoids.

PHYSICAL FACTORS

Attention here is drawn to physiochemical interrelations between crinoids and their environment. It is evident that such physical factors as light, salinity, bottom conditions, water movements, temperature and pressure influence the acceptability of various habitats to crinoids. Some factors may influence or even govern both bathymetrical and geographical distribution of these echinoderms.

LIGHT

The diurnal rhythm of crinoids may depend entirely on environmental light conditions. Very shallow-water reef-dwelling comatulids are known to be night-active, whereas some other tropical reef-inhabiting comatulids are inferred to be day-active. Night- and day-active crinoids are supposed to have quite different reactions to light conditions in their environment.

Few precise data on light responses of crinoids are known, and these only for a small number of species. Generally crinoids

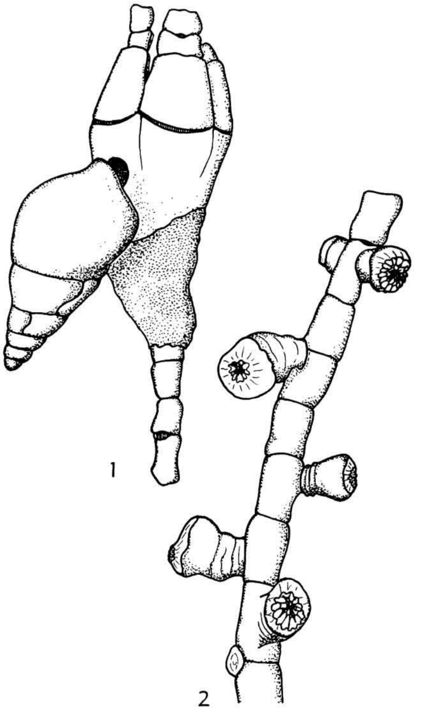


FIG. 212. Parasitic and commensal organisms associated with recent crinoids (Breimer, n).——*1.* Ectoparasitic gastropod attached to calyx of specimen of *Rhizocrinus lofotensis* next to hole drilled in its side.——*2.* Commensal gorgonian octocorals attached to column of specimen of *Democrinus rawsoni.*

appear to avoid direct sunlight and withdraw into shady places. This behavior is also known to characterize littoral species of *Antedon.* Another littoral species, *Tropiometra picta,* which lives in tropical waters, is reported to show no response to intense illumination for it does not avoid direct sunlight and will not seek it when in shadowy places.

The spawning activity of *Comanthus japonicus* is known to be correlated with occurrence of moonlight. Other crinoids have also shown an attraction to weak light during darkness.

The nature of the protoreceptive ability of crinoid sensory systems needs further investigation. Holland (1967) proposed that each crinoid saccule constitutes a photoreceptive lens.

SALINITY

Some crinoids of littoral tropical habitats have shown relative indifference to experimental changes in salinity, including both increase and decrease. Probably they can withstand temporary changes in salinity that might occur in their natural environment. On the whole, crinoids are not markedly tolerant to a definite decrease of salinity, in view of the fact that they are absent from brackish and freshwater environments.

SUBSTRATE

Soft sandy or muddy bottoms are inhabited by stalked crinoids attached by radicular cirri. The radices may penetrate the bottom to provide a holdfast. A majority of stalked crinoids use this mode of attachment. A small minority of comatulids also live on sandy or muddy bottoms, for temporary anchorage to which they have developed very long, slender and straight cirri. These spread out radially to prevent the animal from sinking into the mud.

Most crinoids living on firm substrates such as rocky and shelly bottoms and on arborescent growths such as coelenterates, weeds, and other available substrates commonly possess holdfasts formed by the excretion of lime carbonate. Cementation in exceptional cases is effected by the base (e.g., *Holopus*), or by radicular cirri (e.g., *Democrinus rawsoni*), but usually by an attachment disc that in some stalked crinoids is permanent or that in all comatulid pentacrinoid juvenile stages is transitory. Therefore, pentacrinoids or comatulids may live on substrates other than those adopted in adult stages. Adult comatulids living on rocky or shelly substrates have developed long, but stout and rigid curved cirri. Those which adhere to arborescent growths have short, stout, curved cirri for grasping such means of anchorage.

WATER MOVEMENT

Fell (1966) has noted the relation between crinoids and movements of water masses surrounding them. In this context crinoids may be classed either as rheophobes (current avoiders) or rheophiles (current seekers). Fell concluded that most crinoids are moderate rheophiles. Several good rea-

TABLE 4. *Chemical Composition of Crinoid Skeletal Parts in Relation to Temperature of Environment.*

[Compiled by A. BREIMER from data by F. W. CLARKE in A. H. CLARK, 1921 (*A Monograph of the Existing Crinoids,* v. 1, pt. 2, p. 296-301).]

	Latitude Longitude	Depth (in m.)	Temperature (degrees C.)	$MgCO_3$ (percent)	$CaCO_3$ (percent)
Promachocrinus kerguelensis Antarctic	67°S., 90°E.	375	–1.85	7.86	91.55
Anthometra adriani Antarctic	67°S., 90°E.	375	–1.85	8.23	91.05
Psathyrometra fragilis Japan	44°N., 145°E.	750	1.61	9.25	87.77
Florometra asperrima Washington Coast	47°N., 125°W.	1,145	3.28	9.44	89.45
Pentametrocrinus japonicus Japan	34°N., 137°E.	1,123	3.39	10.15	87.34
Hypalocrinus naresianus Philippines	9°N., 121°E.	612	10.22	10.16	89.66
Parametra granulata Philippines	9°N., 123°E.	502	11.95	11.08	87.86
Crinometra concinna Cuba	23°N., 82°W.	59	26.17	11.69	87.96
Zygometra microdiscus Aru Arch.	6°S., 134°E.	13	–	13.37	85.48
Tropiometra picta Tobago	12°N., 61°W.	littoral	28.–	13.74	83.13

sons favor such an interpretation. Many recent observations on feeding habits of crinoids have shown that these animals rely at least partly on water currents for their supply of food particles. Also for respiration the animals need well-aerated water movements. Excessive currents and other turbulence, however, could be disadvantageous to crinoids since they may disturb bottom sediments, with danger of fouling the minute hydropores, if ciliary movements of their funnels are unable to keep polluted water out of the animal. Too strong water movements have been known to prevent individuals of *Heterometra savignyi* from erecting their filtration fans for feeding. Crinoids are also liable to break in strong currents.

TEMPERATURE

Crinoids inhabit waters of temperatures ranging from those of warm tropical littoral seas to cold polar seas and frigid waters of oceanic depths.

Crinoids show several interesting morphological features that are probably correlated with temperature. First, it appears that multibrachiate comatulids (with more than ten arms) preferably inhabit the warmer shallow waters of tropical and subtropical seas, whereas forms living in cold waters of polar seas and abyssal depths predominantly have five arms or ten arms. Notable exceptions are found, but the overall simplification holds true. Next, a correlation between temperature and chemical composition of the crinoid skeleton seems discernible, for the proportion of magnesium carbonate in crinoid hard parts appears to be a function of temperature. Crinoids living in warmer habitats tend to be richer in $MgCO_3$ than cold-water forms (Table 4).

The literature provides some indications that the length of crinoid arms varies with temperature. Representatives of one species living in colder waters tend to have longer arms than those of the same species living in relatively warmer waters.

The nature of response in crinoids to

temperature changes in their habitat, either natural or experimental, is not well known. It is to be expected that warm-water crinoids of littoral tropical seas should be able to tolerate temperature fluctuations. CLARK (1921) has reported that *Tropiometra picta* at Tobago can tolerate temperature fluctuations of at least 15 degrees C., but probably this is an extreme case of temperature tolerance.

On the whole, crinoids probably include both eurythermal and stenothermal types.

POPULATION DENSITY, SPECIES DIVERSITY, COMMUNITY FORMATION

Long known is the fact that crinoids may occur together in very large assemblages. A classic example of such an occurrence is found in a littoral community near Roscoff, France, where multitudinous individuals of *Antedon bifida* cling to laminarians. The crinoid population at this place reportedly is not stable, for specimens vary greatly in number from year to year. *Antedon* may be the dominant member in the community, which otherwise is composed of sponges, bryozoans, and some other benthonic invertebrates. Other dense littoral communities in which crinoids are subdominant have been described by MAGNUS (1963) from the vicinity of Ghardaqa on the Red Sea, and by FISHELSON (1974) from near Eilat, Red Sea.

Trawl samples taken by zoological expeditions have sometimes yielded such massive numbers of crinoids that one can only explain them by postulating the existence of dense crinoid populations on the sea bottom. The record for one such haul is some 10,000 specimens of *Hathrometra tenella* from a depth of 240 meters off Massachusetts.

In recent years sea-floor photography has contributed to our knowledge on this topic. The preliminary results published seem to confirm that crinoids occur in aggregations, although FELL (1966), who has been especially interested in the matter, doubts that crinoids may figure as dominant or even subdominant members of benthonic communities.

Exact figures for crinoid population densities are scarce. The number of specimens of *Heterometra savignyi* near Ghardaqa, estimated from data given by MAGNUS (1963), is about two or three specimens per square meter over an area of 250 to 300 square meters. FELL has reported the density of an undetermined, probably antedontid species, living at a depth of 650 meters on Galicia Bank off northern Spain, as 65 individuals per square meter over an area of about 100 square meters.

FISHELSON (1974) estimated the total number of crinoid specimens counted during one night along a 200 meters long coral table near Eilat as 12,000. In this crinoid community *Lamprometra klunzingeri* constituted about 70 percent, *Heterometra savignii* about 25 percent, and *Capillaster multiradiatus* about 5 percent. The population density of *L. klunzingeri* may be as high as 50 to 75 specimens per square meter.

Dense populations of crinoids seem to be restricted to areas with optimum ecological conditions. The formation of crinoid aggregations is interpreted by HYMAN to reflect the slight amount of dispersal afforded by the feeble swimming powers of larvae. If these settle close to parent animals and if the conditions are favorable they will grow to maturity near the latter, and a large population may result, especially as adults are not much inclined to leave a good environment.

MEYER (1973a,b) found species diversity and abundance of shallow-water comatulids in Colombia and Panama to be greater than in the islands of the Caribbean Sea. He tentatively proposed that this may be related to more favorable food conditions provided by increased or more diversified primary productivity close to the larger, nutrient-shedding land masses.

DISTRIBUTION

The overall distribution of crinoids is governed by several ecological factors, among which temperature and pressure presumably are the most influential in determining large-scale bathymetric and geographic distributions. As a class, crinoids inhabit every part of the marine environment, having adapted themselves to all natural temperatures and pressures and living at all latitudes and depths. On a smaller scale, however, ecologic parameters importantly influence the acceptability of a given habitat for the crinoids. FELL (1966) has defined as two principal parameters 1) clearness of surrounding sea water resulting from absence of turbulence which might introduce sediment into suspension and 2) availability of suitable microplankton and micronekton. To these should be added 3) presence of proper bottom requirements.

For the purpose of clarity, the large-scale bathymetric and geographic distributions of crinoids are discussed below in separate sections. Some emphasis is placed on the distributional patterns of the separate higher systematic crinoid categories.

BATHYMETRIC DISTRIBUTION

The bathymetric distribution of crinoids is mainly governed by the ecologic parameters of temperature and pressure. At the specific level, however, crinoids include stenobathic or eurybathic and stenothermic or eurythermic forms, with every possible interrelation and intergradation between them. Generalizing, crinoid species are prevailingly stenobathic rather than eurybathic. Following observations by ZENKEVITCH (1959), FELL (1966) has listed 12 eurybathic crinoid species, some of which may even tolerate differences in depth up to about 1,000 meters and a factorial pressure increase of up to 100 times. ZENKEVITCH has analyzed the known bathymetric ranges of all extant crinoid species known to him (615 in number). As a result one may state that comatulids generally are stenobathic, showing less tolerance to difference in depth and pressure than stalked crinoids. Eurybathic forms are found chiefly among the isocrinids.

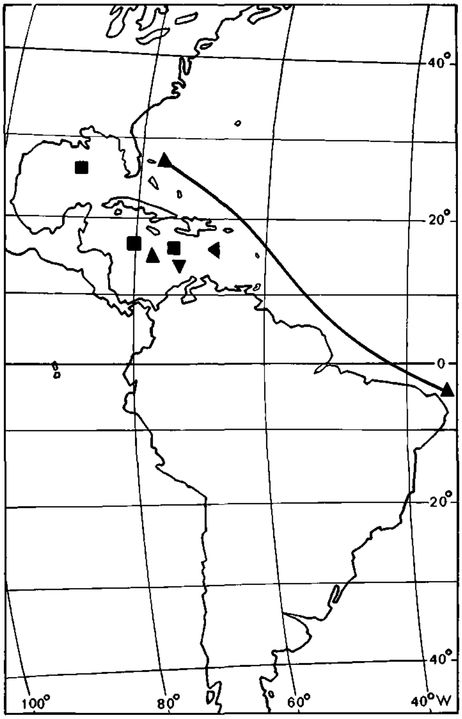
Also generalizing, it is possible to say that the vast majority of comatulids inhabit shallow waters (to 200 m.) in such environments as found on continental shelves, surrounding reefs, and on fringes of island archipelagos. Only a minority of forms occur on the continental slopes. The isocrinids are moderately deep-water forms, mostly occurring between 200 and 1,000 meters in depth, thus being typical inhabitants of upper parts of the continental slopes. Only a few *(Neocrinus decorus, Cenocrinus asteria)* are known to occur in the shallow shelf waters and adjacent to island archipelagos. Their known maximum depth is at about 2,500 meters. Bourgueticrinids are also relatively deep-water forms, entirely absent from waters shallower than 200 meters. They typically inhabit the full bathymetric range of the continental slope and even descend to abyssal depths on the ocean floor, their known maximum depth being 6,000 meters. The few species of cyrtocrinids, like those of the isocrinids and bourgueticrinids again are deep-water crinoids, known to occur between 500 and 5,000 meters. *Holopus* is the only stalked crinoid restricted to shallow waters (10 to 250 m.). As a reef-dweller it is very specialized in its way of direct cementation to the bottom.

GEOGRAPHIC DISTRIBUTION

When geographic distribution of crinoids as a class is studied, it is found that they are cosmopolitan, inhabiting every marine environment of the globe. However, if the distribution of the several different crinoid orders is studied separately, the influence of restrictive ecological factors becomes evident.

The crinoid orders of millericrinids, bourgueticrinids, and cyrtocrinids are worldwide in distribution. This is not surprising, inasmuch as they thrive in deep-water habitats of the lower continental slopes and the oceanic floor where conditions of pressure and temperature vary little and thus do not act as limiting factors on distribution of these crinoids.

The crinoid order Isocrinida and to a lesser degree that of the Comatulida show the influence of restrictive ecologic factors in governing their geographical distribution. It is believed that temperature acts as the principal limiting factor. This, too, is not surprising, taking account of the facts that comatulids predominantly inhabit the shallow waters of shelf seas and that isocrinids flourish on the upper parts of continental slopes. In these upper regions the conditions of water pressure and temperature are far more variable than in lower regions. This is particularly true of temperature conditions, which are subject to far more environmental changes (wave and current actions, seasonal changes, etc.) than



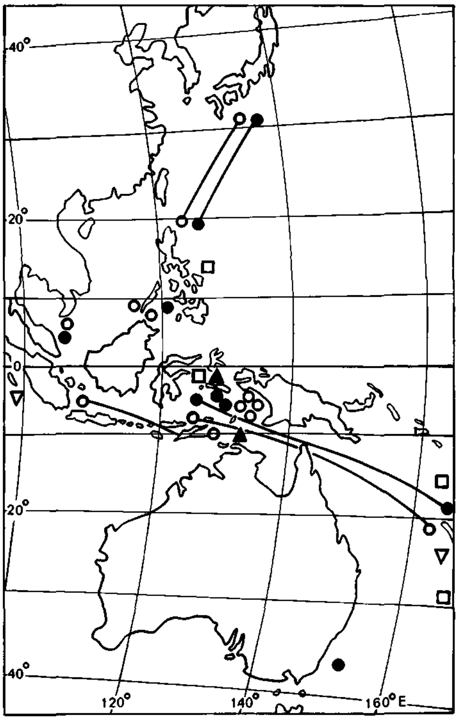
▼ Endoxocrinus
◀ Cenocrinus
■ Neocrinus
▲ Diplocrinus

Fig. 213. Distribution of isocrinid species in central West Atlantic region (Breimer, n). [Each symbol represents one species. A full drawn line between two symbols indicates the total geographic range of one species.]

pressure. Therefore, it is logical to suppose that temperature rather than pressure influences the geographic distribution of crinoids.

Temperature influence is probably to be introduced as a factor to explain the distributional pattern of isocrinids, as given in Figures 213 and 214. They do not occur beyond 40 degrees North and South latitudes. Geographically, the isocrinids have their dominant occurrence in two areas: 1) the central West Atlantic, mainly the Caribbean Sea (Fig. 213), and 2) the Indo-Pacific and West Pacific, dominantly in Banda, Sulu, and Moluccan Seas (Fig. 214). These areas are curiously equivalent in being situated between two larger continental blocks in geologically unstable belts which provide much bottom relief of island archipelagos and deeper trenches; both areas receive water currents from main oceanic streams coming in from the East.

The bulk of comatulids has the same two principal areas of geographic distribution as isocrinids, although they inhabit shallower habitats. Also as an order they are not restricted to these areas, but are worldwide. Their maximum occurrence is in the shallow tropical zones just mentioned, and from there they spread to the polar regions, even reaching the Northern Ice Sea and the Antarctic shelf (Marr, 1963). Probably their number of species and even more so their number of specimens per species decreases in poleward directions.



● Metacrinus
○ Saracrinus
▽ Teliocrinus
☐ Hypalocrinus
▲ Diplocrinus

Fig. 214. Distribution of isocrinid species in Indo-West Pacific region (Breimer, n). [Symbols and explanations as in Fig. 213.]

PALEOECOLOGY

By Albert Breimer and N. Gary Lane

The morphological diversity of fossil crinoids, expressed taxonomically by the fact that more than 800 genera and 5,500 species have been described, indicates that they have been highly successful animals, especially during the Paleozoic Era. More genera and species of fossil crinoids have been described than of all other fossil echinoderms taken together, a clear indication of their prominent role in ancient marine habitats. The great variety of form that extinct crinoids exhibit surely reflects their presence in many different shallow-water marine environments and is evidence that different forms had somewhat different life styles. These two aspects of study of fossil crinoids, their communal relations and the adaptive significance of their morphology, together constitute the paleoecology of fossil crinoids and provide the content of this chapter. The autecological aspects of crinoids will be discussed first, followed by considerations of the synecology.

AUTECOLOGY

By Albert Breimer

PREVIOUS LITERATURE

The literature on autecology of fossil crinoids, based either on direct analogy with recent forms, or on a functional interpretation of their morphology, is scattered among papers of a predominantly morphologic and systematic nature, and is mostly limited to remarks concerning single crinoid species. In many such cases the crinoids involved are unusual or specialized forms. Such special life histories are dealt with further in this chapter.

Some data on autecology of fossil crinoids may be found in works of a more general ecological nature, e.g., by Bather (1928), Dacqué (1921), and Yakovlev (1964). Older, more specific papers on autecology of fossil crinoids are scarce (Wachsmuth, 1868; Kirk, 1911; Ehrenberg, 1922c, 1928b, 1929, 1930a,b, 1954). Much of the work of Kirk and Ehrenberg was centered on whether fossil crinoids were sessile or vagile animals. Their deductions were almost exclusively based on morphological comparisons, data on ecology of recent crinoids as observed in their own habitat being extremely scarce, if not absent, in their day. Kirk claimed a free-living existence for many fossil crinoid species. Ehrenberg was also strongly attracted to potential free-living forms, some of which (mostly Myelodactylidae) he considered very specialized *"Nebenformen"* or crinoid heteromorphs. One suspects, however, that these crinoids attracted so much attention because of their being curiosities. No attempts were made as yet to explain the mode of life of the more normal or usual crinoid species in relation to important ecological parameters.

More recent literature on autecology of fossil crinoids has been greatly stimulated by two sources. One source is the strongly increased wealth of data and progress in the general fields of ecology and paleoecology. Resultant from this trend are papers (Brower, 1973; Dubatolova, 1973; Halleck, 1973; Lowenstam, 1957; Manten, 1970) seeking to connect the mode of life of fossil crinoids with major physical parameters in the environment (mostly bottom conditions), with special habitats (mostly reefs), and with important ecological factors such as ecological succession. From this type of research many new data are to be expected in the future.

Another stimulus has come from new studies on ecological conditions of modern crinoids in their natural habitats (Fishelson, 1968, 1974; Macurda, 1973; Macurda & Meyer, 1974; Magnus, 1963, 1964, 1967; Meyer, 1973a,b; Pérès, 1958, 1959; Pérès & Picard, 1955; Rutman & Fishelson, 1969). These studies have made possible for the first time more accurate and more valid actualistic deductions for the mode of life of fossil crinoids in relation to major ecological parameters in their environment. Such actualistic deductions were recently made by Breimer (1969), Breimer & Webster (1975), Lane (1968), Lane & Breimer (1974), and Meyer & Lane

(1976). Their papers tried to combine results from actualistic deduction with interpretation from functional morphology. Their work was done in an effort to find paleoecological conditions under which the more "normal" or usual crinoid species could have lived, and to develop a model for their mode of life. A summary of their results is presented below.

GENERAL REMARKS

Autecology of fossil crinoids necessarily is based to a large extent on actualistic extrapolations made by analogy to known habits of recent crinoids. To a certain extent conclusions as to the ecology of fossil crinoids may also be derived from an interpretation of their functional morphology.

The possibility of actualistic interpretations of mode of life and behavior depends to a large extent on direct morphological and anatomical comparability of the major organ systems in crinoids. Key questions are whether organ systems in recent crinoids are organized in a similar manner as in fossil crinoids, to what extent they might differ from one another, and to what the difference in structure might imply for differences in functions of the organs or organ systems. Characteristic differences may indeed be suspected to exist, especially for the fully extinct subclasses Camerata and Flexibilia. Direct comparability of fossil and recent structures indeed determines the degree of accuracy of our actualistic extrapolations. Therefore, the several organ systems of the crinoids will be briefly reviewed.

The ambulacral system, as associated with the water-vascular system (NICHOLS, 1972), is held to be very uniform and homologous throughout the class Crinoidea. DELPEY (1942) and HAUGH (1973, 1975a) have described characteristic differences in the arrangement of the digestive tract (including proximal ambulacral tracts) in the theca of the camerates, as compared to recent articulates. Nevertheless, the means for food gathering by arms and pinnules is established to be very similar throughout the entire class. The available evidence suggests that typical crinoids (leaving aberrant armless forms and microcrinoids apart) were always suspension feeders, feeding on planktonic and detrital matter.

The reproductory system is poorly known in fossil crinoids. The genital systems of the several subclasses may have known differences. For instance, the genital system in the non-pinnule-bearing flexible crinoids could have been different from the one known in recent pinnule-bearing articulates, which store the ripe gametes in special genital pinnules. Such differences could have implied differences in reproductory behavior, and even in reproductory advantages or disadvantages influencing their taxonomic diversity. Neotenic, armless crinoids, such as known from the Permian of the Soviet Union and Timor, certainly had a primitive genital system and almost certainly a modified reproductory behavior.

The mode of life of crinoids, and especially the functioning of their arms, depends to a large extent on the organization of the nervous system. This may be specifically true for the main motor system. Throughout the crinoids the aboral nervous system may be considered to be the motor system (see BATHER, 1917b; HAUGH, 1975b; PAUL, 1970; SPRENG & PARKS, 1953; YAKOVLEV, 1954b; ŽÍTT, 1973). Any direct indication of the sensory system is lacking, but it is reasonable to suppose that the tube feet exercised a sensory function.

Respiration in crinoids is essentially a function of the entire body wall, but may be located more specifically in specialized respiratory tissues, such as the tube feet, or in specialized respiratory organs. YAKOVLEV (1944) interpreted the inadunate anal sac as a respiratory organ, by analogy of anal respiration in some recent crinoids. SPRINGER (1900a) has described specialized pores in inadunate crinoids, which LANE (1957) supposed were either respiratory or modified madreporic structures. Among others, KESLING & PAUL (1971) have described specialized respiratory structures in the aboral cup of fossil crinoids, which are unknown in recent crinoids.

As the main organ serving the crinoid for support, the skeleton deserves attention here. The microstructure of fossil crinoids has not been studied comprehensively as yet, but from scattered data in the literature it is not expected to differ significantly from that of recent crinoids (see MACURDA

& Roux, this *Treatise* volume). The porosity of the skeleton may have been variable (Strimple, 1972a). Also, the microstructure of fossil crinoids may have been adapted to special functions it might have had in relation to associated mesodermal tissues. This is known to be the case for ligaments and muscles in articular surfaces in the arms (Lane & Macurda, 1975).

The chemical composition of the skeleton in fossil crinoids (Bethune & Martin, 1969; Weber, 1968) is known to be comparable to that of recent crinoids, although actually few data are available as yet. Also, the chemical composition may be expected to vary strongly with ecological parameters in the environment, perhaps especially with temperature.

The growth of fossil skeletons is accretionary throughout their forms. The growth of plates characteristically produces growth lines on the internal sides of the plates (Meyer, 1965). Regeneration in fossil crinoids must have been very much the same as it is now (see Hattin, 1958; Strimple & Beane, 1966; Yakovlev, 1952; and many sources scattered in literature). The reactions of fossil crinoids to mechanical influences during growth have been studied by Ehrenberg (1922b) and Yakovlev (1947c,d; 1949a). The functional interpretation of sculpture patterns in fossil skeletons (Yakovlev, 1950) is in need of rethinking, protection being their prominent function postulated so far.

Many authors have described aberrant and anomalous growth phenomena, even leading to deformed growth-structures (Etheridge, 1879; von Graff, 1885; Sieverts-Doreck, 1963; Springer, 1926b; Strimple, 1957; Wanner, 1949a, 1954). Such structures are either related to pathological or mechanical causes, or are to be seen as a response to activities of parasites or commensals. These phenomena seem to be directly comparable to facts known from recent crinoids. A special case of aberrant growth may be represented by the phenomenon of gigantism (Yakovlev, 1954a). The most important deviations from normal growth patterns are to be found in fossil crinoids that underwent regressive trends during their evolution and have developed rudimentary organs (see Arendt, 1968, 1971, 1972; Wanner, 1920; Yakovlev, 1946, 1951).

The evidence available so far seems to indicate that deductions on behavior of fossil crinoids are indeed valid, even within the limitations discussed above.

FUNCTIONAL MORPHOLOGY AND ACTUALISTIC INTERPRETATION

General remarks. Consideration of the mode of life of stalked crinoids has proven to be more fruitful if water movements in the environment which they inhabit are taken into account. Crinoids may be classed either as current-seekers or rheophiles, or current-avoiders or rheophobes. Their way of life was probably strongly influenced by this important ecological parameter.

With regard to water movement in the environment, two different feeding postures are postulated for fossil crinoids as adaptations to either a rheophilic or a rheophobic mode of life. Rheophilic crinoids probably employed a mode of feeding known in recent crinoids as brachial filtration fan feeding (see section on Ecology). In such a feeding posture the arms and pinnules are spread out, so as to form a brachial filtration fan, which is held with the aboral side facing the water current. In this posture crinoids are thought to have fed by means of filtering plankton from a horizontal water current employing a mucus net formed by the erect tube feet in order to intercept planktonic and detrital food particles. Rheophobic crinoids probably employed a mode of feeding described as collecting-bowl feeding. Arms are spread out horizontally, and food is collected from the settling planktonic and detrital matter.

More detailed information on the mode of life of any particular crinoid species may be obtained from an interpretation of their functional morphology. From the point of view of functional morphology, the living position of the stalked crinoids as elevated benthic animals is deeply influenced and even dependent upon 1) the mechanical and functional properties of the stalk; 2) the position of the center of gravity in relation to the bottom; 3) the mobility of the arms and probably also their cirri; and 4) their ability to form an effective food-gathering apparatus.

Most Paleozoic stalked crinoids have the essential part of the body (the food-gathering and food-digesting crown) elevated to a level well above the bottom. Most sessile benthic invertebrates rest directly on the bottom. By elevating themselves many crinoids have given up all the direct advantages that the bottom affords as a supporting surface, and they have had to solve all the mechanical and hydrodynamical problems connected with their elevation from the bottom. Their main problem lies in the fact that by elevating their weighty crown, they have also elevated their center of gravity to a position well above the bottom. Commonly the center of gravity is in the crown or just below it, in the proximal part of the stalk. By elevating themselves from the bottom, crinoids have made themselves top-heavy. Nevertheless, this elevation may be explained as a meaningful adaptation, clearly advantageous to the animals and working to their benefit.

Four basic mechanisms of elevating the crinoid crown from the bottom may be distinguished. The crown is kept elevated 1) on a vertical stalk, serving as a direct support for the crown; 2) by adjusting movements of arms, probably aided by righting movements of the cirri; 3) by obtaining lift from horizontal water currents; and 4) by decreasing its specific gravity, that might result in neutral buoyancy.

Benthic forms elevated on rigid stalks; specialized arm structures; rheophobic adaptations. Elevation of the crown by direct support of a vertical stalk is best performed by a stout and rigid stalk. Any stalk with little or no inherent flexibility and with good dimensions and weight serves this purpose best. A stalk of this nature could bear the functional name column. It is evident that a crinoid in the possession of such a rigid column would have to feed on the settling plankton, because in the absence of flexibility in the stalk its crown would be unable to bend over to form a filtration fan. If it had to rely on settling plankton, forming a collecting bowl with its arms to catch food particles, it is also evident that, theoretically at least, there is no need for the crinoid to be elevated from the bottom, other than avoiding some crowding on the bottom. Feeding in this way can as well be performed by animals directly resting on the bottom.

These considerations may explain why stalks of this columnar type are relatively rare among crinoids. *Euspirocrinus,* a Silurian inadunate crinoid from Gotland; *Calpiocrinus,* a Mississippian flexible crinoid from North America, and *Apiocrinites,* a Jurassic articulate from Western Europe, may be examples. It may also explain why some benthic crinoids are devoid of a stem, or have only rudiments of the stem left, or are even cemented to the bottom.

Reduction of the stalk, leaving only a rudimentary stump, occurs in some species of *Millericrinus,* a Jurassic articulate crinoid from Europe. These forms rested directly on the bottom. Some genera have completely given up the stalk, at least during their adult life stages. A much cited example is to be found in the genus *Agassizocrinus,* a Mississippian inadunate crinoid from North America (see ETTENSOHN, 1975). Such genera have added much weight to the aboral cup, bringing the center of gravity down. They are constructed like "roly-poly" dolls. They rest freely on the bottom and employ collecting bowl feeding. Similar phenomena are known from species of *Edriocrinus,* a Devonian camerate crinoid, and some species of *Pterotocrinus,* a Mississippian camerate crinoid, all from North America. This trend is most pronounced, however, in the genus *Timorocidaris,* a crinoid from the Permian of Timor (LAKEMAN, 1950; WANNER, 1951).

Some forms, apparently also resting directly on the bottom during adult life, have modified their base. Such is known in the genus *Calceolispongea,* a Permian inadunate crinoid from Australia, Timor, and India (TEICHERT, 1949). In this form the basals underwent excessive growth so as to become bulbous or spatulate, to allow the crown to rest directly on the bottom.

Still other genera became cemented to hard bottoms, or hard substrates or objects. This is known to occur in some species of *Edriocrinus,* but also in *Palaeoholopus, Calycocrinus,* and *Permobrachypus,* flexible crinoids from the Permian of Timor, in the Jurassic genus *Cotylederma,* and the Cretaceous genus *Cyathidium* (see JAEKEL, 1907).

It is increasingly evident that crinoids in possession of rigid, columnar stalks, or without stalks, must be looked at as adapted to a rheophobic mode of life. Further evidence to support this view comes from a functional interpretation of the structure and mobility of their arms. Examples may be drawn from both the flexible and camerate crinoids.

As far as flexible crinoids are concerned, it is probably highly significant that their arms do not bear pinnules. Moreover, in some of these forms the free arm endings may be very short, making the surface area of the arms comparatively low if compared to the surface area of the theca. Such short, non-pinnule-bearing arms are not well adapted to filtering plankton from a current. For this reason the crowns of many flexible crinoids could never have functioned as filtration fans. Rather, they are to be regarded as collecting bowls. Theoretically, extreme adaptations could exist in which the whole crown is cup or beaker shaped for better performance of its function. Indeed, such forms did exist among the flexible crinoids. Forms like *Icthyocrinus,* with its expanded theca and relatively short arm endings, may be taken here as an example.

As far as camerate crinoids are concerned, it becomes evident that elevation of the crown on a fully rigid, columnar type stalk is to be found in very specialized forms, probably living in special habitats. The genus *Trybliocrinus,* a camerate crinoid from the Lower Devonian of Spain is a typical example (Breimer, 1962). In this form the columnar stalk serves to elevate a very weighty, almost gigantic theca, with strongly modified, and nearly immovable arm structures.

The camerate genera *Barrandeocrinus* and *Polypeltes* from the Silurian reefs of Gotland may provide even more extreme examples (Ubaghs, 1956). These crinoids are interpreted as rheophobic crinoids, probably living in the infrastructure of the reef, where currents are absent or non-directional (turbulent). The crown of *Barrandeocrinus* is highly specialized, with arms recurving and forming special arm chambers by close juxtaposition of adjoining pinnules.

Barrandeocrinus is interpreted by Ubaghs as a crinoid creating its own water currents for feeding and respiration. This current is created by ciliary actions on the ambulacral tracts of the arm chambers, thus drawing water into the chambers. Other examples of rheophobic crinoids creating their own currents for feeding may be found. *Eucalyptocrinites,* a camerate genus from the Silurian of North America and Europe, has a very specialized adoral body wall, which together with the pinnulated arms could have formed suction chambers for creating its own feeding currents (C. E. Brett, pers. commun.), in a way more or less analogous to *Barrandeocrinus.*

The highly specialized genus *Crotalocrinites,* a Silurian inadunate crinoid from Europe and North America, and probably also a reef dweller, may be taken as an extreme example of a collecting bowl feeder. Arm groups are joined laterally in each ray, and spread out horizontally to collect food. The stalk is of the rigid, columnar type, but very short. Perhaps this genus also may be seen as creating its own water currents.

Also, flexible crinoids adapted to a rheophobic mode of life may be expected to have created, at least partly, their own feeding currents. Such currents could have been produced by pulsatory movements due to contractions and expansions of the crown, brought about by inward and outward movements of the arms.

Crinoids, like the ones discussed above, are adapted to living under conditions of slack water or slight water movement (probably mostly nondirectional or "turbulent"). As such they are interpreted as rheophobic crinoids. These crinoids may be active rheophobes, which are not actively current avoiding crinoids, but actively creating their own water currents for feeding and respiration. As such they are contrasted to passive rheophobes, which do not create their own currents.

Benthic forms elevated on partly flexible stalks; nonmuscular arm structures; rheophobic trends. Usually, however, the crinoid stalk is not fully rigid, but partly flexible. This is probably the most common situation found in fossil crinoids. Such stalks are found in all three Paleozoic subclasses of crinoids. The flexible part of the stalk is generally the upper or proximal part of the stalk, the lower or distal part being rigid. Generally, there is in the stalk a gradual decrease of flexibility away from the cup. This gradual change of flexibility is inherent to the way many crinoid stalks are formed during ontogeny.

When the stalk is not entirely rigid, a certain slight amount of water pressure exercised by horizontal water movements tends to displace laterally the heavy, elevated crown, and with it the elevated center of gravity. If a crinoid wanted to keep its stalk vertical so as to support directly the weight of the crown, keeping its center of gravity in a vertical position above the point of attachment of the stalk, the crinoid should be able to achieve certain functions, either separately, or in any combination of them: 1) control of rigidity in the proximal part of the stalk, 2) righting movements with the cirri, and 3) adjusting movements with the arms.

Rigidity control could be effectuated by stiffening the upper, or proximal, part of the stalk through tightening of the ligaments in between the stem segments. It is completely feasible to think that somewhat delicate and partly flexible stalks could have functioned as columns lending direct support to the crown.

It is believed that arms would be needed to make occasional adjusting movements in order to assist in maintaining balance. Lane (1968) first suggested such actions for the arms. Also, it is feasible that righting movements of the cirri would produce the same effect of elevating, righting, and balancing the crown in slightly flowing water. It certainly would be correct to think that a combination of these three possibilities has the best effect under conditions of slight, horizontal water pressure. Righting and balancing the crown probably was a combined action of the stalk and the arms. It would perhaps be advantageous if most of the efforts were extended by the stalk and its cirri, thus not disrupting the feeding of the arms.

Camerates probably did not have the right sort of arms (biserial arrangement of brachials, absence of articular brachial surfaces) to be used for exercising adjusting movements. In such a case righting movements were probably made by long and flexible cirri at the proximal part of the stalk, as in the genera *Clarkeocrinus* and *Cordylocrinus,* Devonian camerate crinoids from North America. Such movements would create water currents from which the arms could profit in feeding.

Adjusting movements of the arms could be very efficient in case of specially modified arm structures such as the brachial petals of *Petalocrinus,* a Silurian inadunate crinoid from Europe and North America, probably also a reef dweller.

If arms are not specifically modified for such a function, adjusting movements of the arms in general would be possible only for Paleozoic flexible and inadunate crinoids, and in all Mesozoic and Cenozoic articulate crinoids, which have the proper articular connections in the arms.

As an overall conclusion, it seems valid to state that elevation of the crinoid crown by direct support of a rigid, columnar stalk, or by a partly flexible stalk capable of rigidity control, is probably useful only in the presence of slack water or slight, mostly nondirectional, water currents. In such cases there is evidence of modified, or specialized, brachial and cirral structures, further testifying to the probable rheophobic nature of their adaptations.

Benthic forms elevated on partly flexible stalks; pinnulate nonmuscular arm structures; rheophilic trends. It is believed that a vertical position of the crinoid stalk, particularly if its upper part is flexible, is of no use in case of stronger currents, especially not if these currents were unidirectional, or periodically unidirectional (bidirectional, such as tidal currents). It would be unrealistic to think of a crinoid actively fighting any stronger current action in efforts to maintain its balance in a vertical position. Rather, it is believed that the prime reaction of a crinoid toward a persistent horizontal water current is to form a subvertical brachial filtration fan and to initiate feeding from the current. This is known to greatly increase its feeding efficiency.

There is a potential action-reaction system between a crinoid and a persistent, horizontal current in its environment. The hydrodynamic effect of such a current on a crinoid whose stalk is flexible in its upper portion is to passively orient it. A passive orientation of the crown can be obtained without any positive reaction of the crinoid toward the current. The crinoid will lean over with the crown downcurrent from the stem attachment. The stalk is required to support the crown; it has to be partly rigid, at least in its lower or distal half, in order to ensure the elevation of the crown. The stalk typically stands with its convex side facing the current. It must be firmly and definitely anchored in order to prevent the crinoid from breaking or becoming uprooted and being carried away by the current. Anchoring would be either by cementation to hard objects or by rooting in soft bottoms. Passive orientation of the crown by persistent water currents is probably connected with definite anchoring of the crinoid in one place. This may have had unfavorable consequences for the crinoid in case of deterioration of environmental conditions in its habitat.

If the crinoid spreads out its arms and pinnules, a brachial filtration fan is built in essentially the same way as is known in recent crinoids. The brachial fan is oriented perpendicular to the current, the aboral sides of the arms and pinnules facing the current. Filtration fans thus built could be either planar, conical or parabolic, depending on the brachial and thecal structures of the crinoid. In case the crinoid is unable to make active, discriminate, muscular movements with the arms, the crown remains passively oriented, perpendicular to the current. The current will exercise upon it as much upward as downward pressure. As a consequence, no lift is derived from the current to help elevate the weighty crown.

The biological effect of the rheophilic mode of life, outlined above, is considerable. Not only is an enormous body of water being filtered during each active period of the crinoid, but also, the capturing of food is greatly aided. The brachial fan has a baffling effect, and at the lee side of the fan a turbulence may be created, which greatly facilitates the capture of food by the tube feet. Food transport in ambulacral tracts occurs at the sheltered sides of the arms. Fecal wastes are carried away hygienically by the current.

The ecological requirements for a rheophilic mode of life was passive orientation of the crown in the current, but without receiving lift from it, seem to be almost perfectly filled by the batocrinid camerates. The essential morphological characters of camerate crinoids seem further to indicate the rheophilic nature of their adaptations. In this feeding posture the arms are not required to make complicated movements. Arms of camerates lack muscular contacts between brachials. Also, feeding would be greatly aided by the presence of as many pinnules as possible. Camerates have provided for this by making the arms biserial, increasing the number of pinnules per arm two or more times.

Passively oriented crinoids, such as the ones discussed above, may be able to regulate the pressure exercised on their extended brachial fans. This pressure is a function of the total surface area exposed to the current. By folding pinnules in and out, a pressure regulation system may be developed. The advantage of it evidently would be to provide for an equilibrium between the pressure exercised by the current, and the strength of the anchoring device. Such a regulatory system, again, may save the crinoid from being uprooted or carried away by the current.

Some camerate crinoids, like the rhodocrinitids and dimerocrinitids, have the distal parts of the stalk coiled around objects. A well-known example of it is *Acanthocrinus rex* from the Devonian of Europe (JAEKEL, 1895). This type of attachment was a definite one, judging from the wedge-shaped columnals in the coiled part of the stalk. Perhaps such type of attachment also was profitable from a point of view of pressure regulation, the anchoring being less rigid and able to give somewhat if necessary in order to prevent too much longitudinal stress in the stalk. Some slip at the attachment site would have prevented the stalk from breaking. This type of crinoid is typically devoid of cirri and has many nodal plates in the stalk (see also BATHER, 1912; BRETT, 1978; EHRENBERG, 1928b, 1929).

Passive orientation of crinoids in currents may have had a disadvantage. Partial or differential movements of different arm groups may have caused the crown to rotate about a horizontal axis, thus causing torsion in the flexible, upper part of the stalk. It is believed that many crinoid stalks could have coped with a certain amount of torsion, but this may be doubtful for some others.

Pterotocrinus, a camerate crinoid from the Mississippian of North America, probably was not able to cope with such a situation. In some of its species (e.g., *P. spatulus*) there are large, bladelike processes on the adoral body wall, which could well have functioned as stabilizing fins, in order to prevent the crown from rotating. Other species (e.g., *P. coronarius*) probably gave up the stalk in adult life, adding much weight to the crown, and rested directly on the bottom. Another mechanism preventing the crown from rotating on the stalk, which would resist torsion, could perhaps be found in the spirally coiled stalks of some platycrinitid crinoids. Spirally coiled stalks are supposed to resist torsion.

A rheophilic mode of life is also possible for some flexible crinoids, especially those with densely ramulate arms, like taxocrinids. These flexibles are interpreted by MEYER & LANE (1976) as forming a filtration fan similar to the modern basket star, *Astrophyton muricatum* (LAMARCK), which forms the fan at low current speeds.

Benthic forms; elevation involving lift; pinnulated, muscular arm structures; strong rheophilic trends. Rheophilic adaptations for the crinoid's mode of life could be still more advanced. The situation in a persistent current could be entirely different if the crinoid were able to exert some sort of active orientation of its crown in relation to the direction of the current. If the crinoid were able to actively orient its filtration fan at a proper oblique angle to the current direction the current would exercise an upward pressure on the crown. The crinoid crown then receives a certain amount of lift, which helps it to be elevated, and partly compensates for negative buoyancy which it might have.

Active orientation of the crown in the current direction, so as to derive some degree of lift from it, is of great consequence for the mode of life of the crinoid. Because the crown is elevated from the bottom partly because of the lift, the stalk may provide less support, and become more delicate and flexible, and even much longer. Also, the type of attachment of the stalk is influenced. Attachment may be either definite or not, a less definite anchoring affording many advantages.

If lift were about equal to the negative buoyancy of the crown, or even slightly higher, the crown would be suspended in the water, or even have a tendency to ascend. The stalk no longer would be required to support the crown. On the contrary, the crown would be supporting the weight of the stalk, which could merely serve for anchoring. The total organism would then act as a kite on a line. Extreme flexibility of very long crinoid stalks would be in agreement with mechanical requirements for kite lines.

Crinoids also would be able to regulate the degree of lift. The degree of lift is determined by the total surface area of the crown exposed to the current. Regulation of the degree of lift would be possible, 1) as a response to current direction by changing the angle between the current direction and the plane in which the brachial fan is formed, 2) as a response to current strength, by changing the total surface area by flexing pinnules in and out, thus letting water slip freely through the fan if necessary.

Active orientation, understood as an activity of the crinoid itself in response to current direction, is thought to have been possible mostly in rheophilic inadunates and articulates. This type of orientation requires the arms to be pinnulate and to be movable by muscular control. Muscular actions are clearly impossible for the arms of camerates, but advanced Carboniferous and Permian inadunates and all articulates developed the necessary muscular articulations in their arms to allow for active orientation of the crown, and derivation of lift from a current, as an auxiliary device for elevating their crowns from the bottom. The efficiency of active orientation is probably dependent on the number of muscular articulations in the arms. Clearly, the ar-

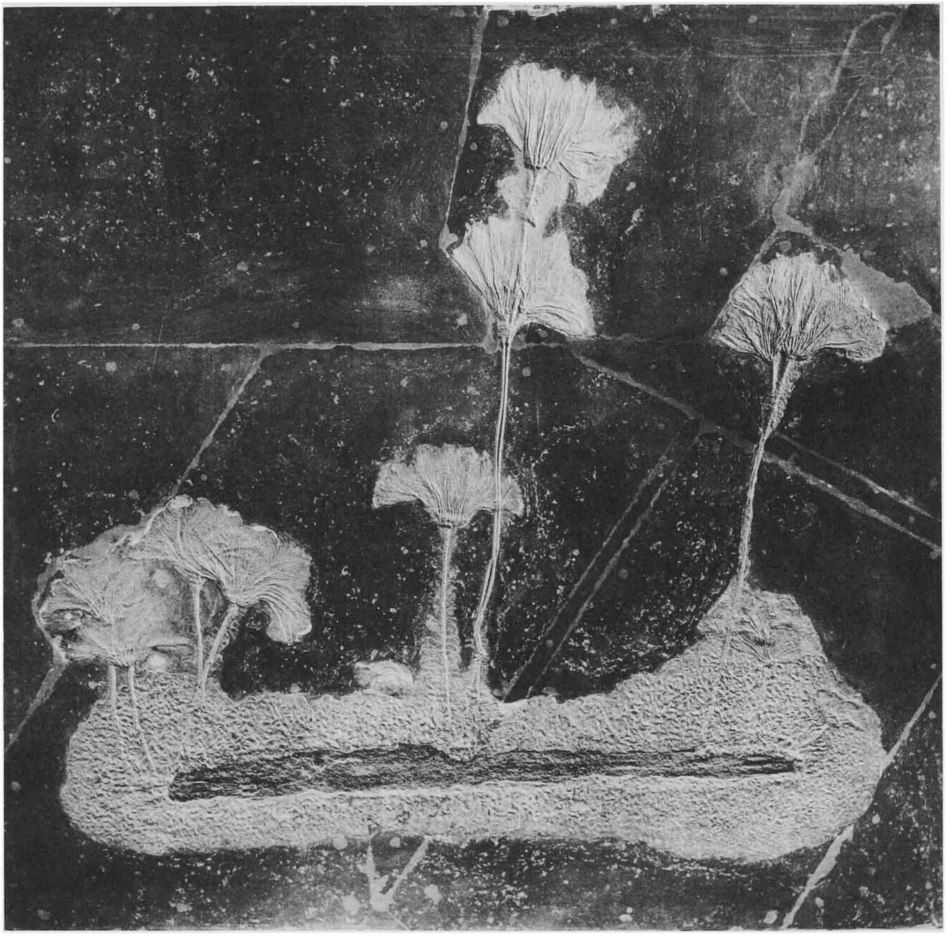


FIG. 215. Several specimens of *Seirocrinus fasciculosus* (VON SCHLOTHEIM), Lower Jurassic (upper Liassic), Holzmaden, Germany; attached to driftwood heavily encrusted with shells of *Pseudomytiloides dubius* (SOWERBY), ×0.04 (SMF XXIII/115a, Natur-Museum Senckenberg, Frankfurt; photograph by courtesy of Forschungsinstitut Senckenberg).

ticulates could be much more efficient than the advanced inadunates.

Some Jurassic isocrinids, as *Seirocrinus* and *Pentacrinites,* have exceedingly long stalks (up to 15-20 m.), which are flexible throughout. Juvenile stages of some of their species are known to be pseudopelagic and attached to driftwood (Fig. 215). Mature specimens of some species could have lived as benthic species, deriving lift from the current in order to remain elevated, the stalk acting as a kite-line. It is not considered likely that such crinoids actually stood vertically on a stalk that long. Neither is it realistic to think that such heavy crinoids were hanging down from driftwood in all their life stages. [For an alternative interpretation see this volume, p. *T*865—Eds.]

Among flexible and inadunate crinoids with rheophilic life habits special adaptations for active orientation may exist. They are probably to be found in the pivot-joint in the proximal part of the stalk of some taxocrinid flexible crinoids, such as in *Nevadacrinus,* a Permian flexible crinoid from North America (see Fig. 542,*1*); and in the muscular thecal hinge, developed between the triangular basal circlet and the compound *E*-radial of the calceocrinid inadunates. These special adaptations could be interpreted as allowing the crinoid to rest on the bottom, and to obtain an elevated feeding position, deriving lift from the current in order to ascend. Such special adaptations apply only if they were definitely anchored in one place, and if the arm density of the crown is high enough, as in the genera *Chiropinna* and *Chirocrinus.*

Many rheophilic crinoids must be interpreted as no longer being definitely attached to one and the same spot, but to have achieved a less definite type of attachment, allowing the crinoid to be moved about by the current, to establish itself only temporarily in one place or another. Such temporary attachments would be greatly advantageous for the crinoid, in case of deterioration of ecological conditions on one particular spot.

Many adaptations are known in crinoid stalks that may best be interpreted as being structures for temporary anchoring. This may be found in stalks with cirri placed at one side only, and such stalks should be interpreted as recumbent, and only loosely anchored by the cirri. There are tapering stalks with pointed ends, coiled around objects, which could be interpreted as prehensile stalks, such as found in the genus *Eifelocrinus,* a Devonian inadunate crinoid from Germany. Also, special organs have developed such as the anchor in *Ancyrocrinus,* a Devonian inadunate crinoid from North America (GOLDRING, 1942; LOWENSTAM, 1942; MCINTOSH & SCHREIBER, 1971) (see Fig. 396,*4*). This heavy anchor-like organ apparently served the crinoid as a drag, allowing it to settle temporarily in one place or another.

Another, very interesting case of specialization of the stalk for a limited free-living mode of life is presented by the inadunate genus *Myelodactylus* (Sil., Dev.; N.Am.,Eu.) and its younger camerate homeomorph *Camptocrinus* (Carb., Perm.; N.Am., Eu., Asia). These genera are essentially benthic crinoids, frequently inhabiting reef environments (EHRENBERG, 1922a,b, 1926a, 1930a,b, 1954; WOLBURG, 1938). In both genera the distal part of the stalk is greatly developed, and provided with two rows of cirri. The proximal part of the stalk is delicate, as is the entire crown. These crinoids could spirally coil, so as to enclose the crown within the coiled distal part of the stalk, the cirri radially covering the crown at both sides, thus providing protection. The coiled living position is interpreted to be the resting and hiding position, the crinoid lying on the bottom. During activity the crinoid would uncoil, the bulky distal part of the stalk lying flat on the bottom, serving as a drag, and eventually the cirri could grasp some neighboring parts of the bottom to afford some additional, but temporary fixation. The proximal part of the stalk would stand subvertically during feeding. Movement would be achieved by actions of the cirri, either for crawling over the bottom, or for short swims slightly above the bottom, using the cirri for rowing.

A somewhat similar situation may be found in the genus *Ammonicrinus,* a Devonian inadunate crinoid from Europe (EHRENBERG, 1939; KRAUSE, 1927; UBAGHS, 1952; WANNER, 1954; WOLBERG, 1937). In this benthic genus the modified stalk is also spirally coiled around the delicate crown, but is devoid of cirri. One of the two known species was free-living. In its coiled resting position it had a globular shape, which allowed it to be rolled passively along over the bottom by current actions.

Considering benthic stalked crinoids as potential rheophiles has brought us to the subject of vagility versus sessility in crinoids. As we have seen, definite attachment, and thus sessility, is thought to be related to rheophobic life conditions or, at most, to be related to rheophilic crinoids only capable of being passively oriented in a current for brachial filtration fan feeding. Vagility in stalked, benthic crinoids is probably connected, and caused by current action of the waters they inhabit.

Elevation involving density-control; free-living forms. An excellent means for elevating the crown of a stalked crinoid above the bottom would be to lower the overall specific gravity (density) of the crown, so as to approach that of the surrounding seawater. Such a crown would be suspended in seawater, or even have slight buoyancy. A stalk would not have to serve for support, but could merely act as a buoy line.

Lowering the specific gravity of the crown could be achieved by modification of 1) the body wall, 2) the body cavity, and 3) specialized organs. Compensation for the heavy weight of the crinoid skeleton, should, in theory at least, come from light materials, such as gases or light oils, stored either within the body wall, within the body cavity, or within organs specially developed for that purpose. The body wall is known to be very porous, in some cases even very much so, but actually gases never have been proved to be stored in skeletal pore volumes. The body cavity, though small in many cases, could have had special compartments to store light materials, as do special organs.

Not much is known about benthic crinoids employing this type of elevation from the bottom. Perhaps the only case in which this ought to be considered is the prominent, thin-plated anal sac of some dendrocrinid and poteriocrinitid inadunate crinoids, which could have stored light materials. This would not conflict too much with a presumed respiratory function of that organ. If the anal sac were not slightly buoyant, these inadunates are among the more top-heavy crinoids known.

Once achieved, the full benefit of a suspended crinoid crown seems to come from a pelagic mode of life. Probably, the only crinoids who ever evolved a pelagic life by modification of the body wall, making the skeleton delicate and porous, and maybe even by employing light materials, are the roveacrinids (e.g., *Saccocoma,* an articulate crinoid from the Jurassic and Cretaceous of Europe). Some uintacrinids, such as *Uintacrinus,* and perhaps also *Marsupites,* articulate crinoids from the Cretaceous of North America and Europe (SIEVERTS-DORECK, 1927; SPRINGER, 1901) (Fig. 216), might have modified the body cavity by developing special oil or gas compartments in their expanded, thin-walled theca. Both roveacrinids, and uintacrinids are stalkless crinoids. The best example of modification of a special organ for buoyancy is the gas-filled lobolith at the distal extremity of the stalk in the genus *Scyphocrinites,* a Silurian and Devonian camerate genus from North America and Europe (EHRENBERG, 1926; HAUDE, 1972; JAEKEL, 1904b; SARDESON, 1908; SCHUCHERT, 1904; SPRINGER, 1917a; YAKOVLEV, 1953). This form is considered to be epipelagic.

A pseudopelagic mode of life may be obtained by crinoids settling on floating or drifting objects, or by settling on planktonic or nektonic organisms. Settling on driftwood is known with certainty to be the case in juvenile growth stages of the camerate *Melocrinites* from the Devonian of Ohio (WELLS, 1941), and of certain isocrinids, e.g., *Seirocrinus* and *Pentacrinites,* from the Jurassic of Europe (SEILACHER *et al.,* 1968). Settlement on the float of a *Scyphocrinites* is known from a species of *Edriocrinus,* a Devonian crinoid from North America (KIRK, 1911, p. 114). Settlement on orthoconic nautiloids (endocerids and orthocerids) is known from an unidentified Ordovician crinoid genus (GANSS, 1937). Settlement on ammonoids is known from the genus *Cyrtocrinus,* a Jurassic articulate crinoid from Europe (GANSS, 1936; KUSS, 1963).

The most efficient, and least vulnerable, crinoids ever developed, are the stalkless comatulid crinoids. During adult life stages they are free-living. They have developed the ability to crawl over the bottom with the help of cirri, and to swim with the help of their arms. They are able to actively select their living sites, can escape from them if necessary, and can hide away whenever necessary for whatever reason. From the point of view of evolution in crinoids, they seem to be in full bloom at the present time, having colonized many different habitats, from extremely shallow water to the deeper parts of the continental slope.

MODIFICATION OF MODE OF FEEDING

Suspension feeding in crinoids must have been diverse with regard to type. LANE & BREIMER (1974) have distinguished several modes of suspension feeding in crinoids, based on an interpretation of the different arm structures, and by analogy with the

FIG. 216. Specimens of free-swimming crinoid *Uintacrinus* clustered on a slab of thin limestone found interbedded with chalk of Cretaceous age in western Kansas (about two-fifths natural size) (from *Historical Geology,* by R. C. Moore, copyright 1933, McGraw-Hill Book Company; used with permission of McGraw-Hill Book Company and University of Kansas Museum of Natural History). [For detailed discussion of this occurrence see STRUVE, 1957.—Eds.]

mode of feeding employed in successive growth stages by recent crinoids.

Full mucus-net feeding, with potential rheophilic adaptations using brachial filtration fans, would be possible for pinnulate crinoids, such as camerates, advanced inadunates, and articulates. Many nonpinnulate inadunate and flexible crinoids could have employed only a limited mucus-net feeding. Crinoids with undivided, nonpinnulate arms, such as gasterocomids and pisocrinids, could have used only tube-foot and ciliary feeding.

A strong reduction of number of arms

is known in neotenic crinoids from the Permian of Timor and Ural Mountains (Arendt, 1968, 1971, 1972; Wanner, 1920; Yakovlev, 1946, 1951), and also from many microcrinoids with arm facets. These crinoids must have relied on a type of feeding called tentacular feeding, employed by recent crinoids, shortly after heterotrophic feeding was initiated. These crinoids could have employed epidermal feeding, in part, by absorbing dissolved nutrients from the environment. Certainly, the armless crinoids must have relied entirely on such type of feeding.

SYNECOLOGY

By N. Gary Lane

The single most conspicuous feature of fossil occurrences of crinoids is a strong tendency for specimens to occur in close proximity to each other. This clustering habit is evidenced by numerous slabs that have several to many crinoid crowns preserved on them (Fig. 216). Common references in the literature are to nests, clumps, patches, or colonies. Examples include the well-known occurrences of Mississippian crinoids at LeGrand, Iowa, and Crawfordsville, Indiana, as well as Pennsylvanian crinoids from LaSalle, Illinois (Strimple & Moore, 1971a), and Devonian occurrences of *Clarkeocrinus* figured by Goldring (1923). In some instances the specimens on a slab all may be of a single species, a condition called a "stand" by Lane (1973); in other cases, several different species may be found in proximity. This clustering habit is still evident in living crinoids as well as in many other shallow water marine invertebrates. Fossil crinoids were mainly sessile attached dioecious animals with external fertilization. Thus, an adaptation that would result in mature males and females living close together would be advantageous in helping insure that a reasonable number of released ova would be fertilized. Although some living crinoids retain the fertilized eggs in special brood pouches, there is little evidence that ancient crinoids did so, but, in any event, close proximity of males and females would still be advantageous. Clusters of mature adults could have resulted from sensing of adults by free-swimming larvae and settling of the larvae nearby, or by free-swimming larvae that did not move far from their parents. Alternatively, passive recruitment near adults may have been enhanced by selective survival of the young in suitable microhabitats where adults already lived. The adults of a few fossil crinoids may have been able to swim or crawl close to other individuals of the opposite sex. The great hindrance to study of these aspects of the clustering habit is that the skeletons of fossil and living crinoids do not allow us to distinguish males from females.

There is little evidence that Ordovician and Silurian crinoids had yet specialized into distinctive communities occupying different habitats. The principal exception to this generalization are the distinctive assemblages of reef-dwelling crinoids of the Middle Silurian, found both in western Europe and North America. The structure of crinoid communities that lived during different phases of Silurian reef growth has been documented by Lowenstam (1957), who recognized that a variety of specialized camerate crinoids were conspicuous reef dwellers during rough water stages. During quiet water phases crinoids were not prominent and camerates and inadunates were about equally represented. Some Silurian crinoids are conspicuous in the ubiquity of their distribution. Both *Eucalyptocrinites* and *Pisocrinus* are reef dwellers, but also occur in many areas of nonreef rocks. Other Silurian crinoids, such as the camerate *Siphonocrinus,* are known only from reefal habitats. Although reefs are found throughout the Paleozoic, specialized crinoids that were confined to reef habitats do not reappear again after the Middle Silurian until the Late Permian, when a variety of small, unusual inadunates are found exclusively on or near reefs in West Texas and Timor. Crinoids are found on or near many Devonian through Pennsylvanian reefs but the genera found in these habitats are also known from nonreefal areas.

During the lower and middle Paleozoic, crinoids probably did compete indirectly with other stalked echinoderms, principally blastoids and cystoids, for suitable life sites. Partitioning of microhabitats among cystoids and crinoids has not yet been demonstrated but may well be shown by careful studies in the future. Crinoids and cystoids are found together in many rocks of Ordovician through Devonian age, and crinoids and blastoids occupied similar habitats in Silurian through Mississippian time, after which blastoids became much more restricted in distribution. Throughout the Paleozoic after the Cambrian crinoids were more widely distributed than either cystoids or blastoids. Many localities have yielded specimens of crinoids without a trace of other stemmed echinoderms, whereas there are few cystoid or blastoid localities at which at least a few crinoids have not been found. This difference in availability of habitats has not been worked out in detail, nor have explanations for this gross aspect of Paleozoic echinoderm distribution been forthcoming. The great diversity of Paleozoic crinoids, compared to other stalked echinoderms, is surely related to their ability to occupy habitats not available to these other echinoderms. One possible explanation for this phenomenon may be that crinoids early in their history developed much longer stems than any of the other stalked echinoderms. As adults, crinoids were farther from the sea floor and not in such direct competition with benthonic dwellers as were cystoids and blastoids, most of which were raised only a few centimeters above the bottom. If this explanation has merit, still it poses another problem concerning crinoid paleoecology that has also not been solved. If crinoids were so successful in their "high-rise" life style, as they surely were, they also had to be successful animals during all of their growth stages, before they attained their lofty position above the bottom. Thus, they had to compete with brachiopods, bivalves, and other bottom-dwelling animals during very early growth stages, and with bryozoans, sponges, corals, and short-stalked echinoderms during intermediate growth stages. The adaptive strategies utilized by crinoids to grow up through the lower levels of stratified communities, of which they were the upper level as adults, have not yet been elucidated.

By Devonian time crinoids began to show a clear division into major groups with respect to gross habitat (LANE, 1971). Camerate crinoids predominated in areas of carbonate sedimentation and continued to do so until the Late Mississippian, when they dwindled so much in diversity and abundance that they were no longer a conspicuous element in any marine community. Camerates reached their apogee during Early Mississippian time, when their remains are primarily responsible for the very widespread, thick crinoidal limestones of this time interval. Inadunate crinoids of the Devonian are found in greatest abundance and diversity in rocks composed of fine, terrigenous clastics. They lived on muddy bottoms and in turbid waters from which most, though not all, camerates were presumably excluded. Inadunate crinoids were present on carbonate sea floors, where they tended to be relatively diverse but sparse compared to the great numbers of camerates that contributed much bioclastic debris in these areas. Inadunates, especially the most advanced ones belonging to the suborder Poteriocrinina, continued to be dominant in areas of terrigenous sedimentation until Late Mississippian time when, for reasons still not clear, the camerates underwent an abrupt decline. By Early Pennsylvanian time, the poteriocrinids had taken over virtually all marine environments and occupied carbonate habitats left vacant by camerates. Whether camerates were eventually "forced out" of these areas by the direct competition of inadunates, or whether the latter simply occupied the niches left vacant by camerates is still an unsolved problem of Mississippian paleoecology.

Flexible crinoids, from their origin from dicyclic inadunates in the Ordovician until they became extinct in the Permian, were always a minor component of Paleozoic marine communities. Although specimens of flexibles may be common at some localities, and in a few instances outnumber specimens of other crinoids, they seemingly were limited by a lack of diversity. One or two genera of flexibles are all that are generally found at most good crinoid localities, whereas at the same sites many genera and species of camerates or inadunates, or both, may be known. The flexibles apparently had a distinctive set of adaptive features that allowed them to consistently occupy specific niches. Although they presumably were quite successful in these niches, for very long periods of time, they were unable to radiate out from them. The main exception is found in the lecanocrinid and homalocrinid flexibles that became homeomorphs of inadunates and that are the most diverse of any flexible groups, especially in the late Paleozoic.

Studies of fossil crinoid communities to date have concentrated on localities where reasonably complete crowns or calyces have been collected. Such sites are widely separated stratigraphically and geographically and do not permit evaluation of important paleoecological problems in areas where crinoids are represented mainly by disarticulated ossicles. Future research on the synecology of fossil crinoids may have as one important facet the study of individual crinoid ossicles, especially those of the calyx and arms, obtained from bulk samples. Many such plates can, by reference to more complete specimens, be assigned to nominal genera or at least to a suborder. In this way the gross composition of fossil crinoid communities could be ascertained from many sites where complete calyces or crowns have never been found. Such studies would undoubtedly lead to new hypotheses concerning the evolution and structure of ancient crinoid communities.

MUTUALISTIC RELATIONS OF FOSSIL CRINOIDS

By N. Gary Lane

Many fossil crinoids had quite close and long-lasting relationships with other kinds of invertebrate animals. The exact nature of some of these relationships is still uncertain, hence use of the general term mutualism in the heading for this section, rather than more explicit terms like commensalism, symbiosis, parasitism, or predator-prey relations. Even the disarticulated ossicles of dead crinoids that lay on the sea floor were favorite settling sites for the free-swimming larvae of brachiopods, bryozoans, worms, acrothoracic barnacles, corals, and other animals.

The most enduring and best-known mutualistic relationship of crinoids with other animals is with members of the gastropod family Platyceratidae (Clarke, 1908, 1921; Bowsher, 1955). This association began in the Ordovician and continued into the Permian when both these gastropods and the crinoids on which they lived became extinct. Early in this relationship, especially in the Ordovician, the gastropod is commonly found among the arms of crinoids but not in a specific position, as if the gastropod may have simply used the crinoid tegmen as a firm living site and nothing more (Fig. 217,*3*).

By Devonian time the relationship was much more explicit, the snail being invariably found in the posterior interray of the crinoid tegmen, with the aperture over the anal opening of the crinoid (Fig. 217, *2,4;* also see Fig. 40,*2b-d*). These platyceratids are thus interpreted as having been coprophagous, feeding at least partly on the excrement of the host crinoid. Whether this relationship was mutually beneficial to each animal, beneficial for the snail and neutral for the crinoid, or at least slightly harmful for the crinoid, is not known. That the snail lived on the crinoid for most of its life is certain. The growth lines of numerous gastropod conchs match in detail irregular nodes or other ornament on the tegmen of the host crinoid. Lane (1973) has shown that different subgenera of platyceratids were species specific as to the crinoid on which they settled. Thus, either their free-swimming larvae could sense appropriate species on which to settle or an immature snail was able to crawl to a suitable individual. If the life spans of the crinoid and snail were approximately equal, then the snail may have settled as a larva or young adult on the crinoid when the latter was quite young and elevated only a centimeter or so above the sea floor. As the crinoid grew, the snail would have been raised higher and higher above the sea floor as the crinoid stem lengthened. Platyceratids are most commonly found on crinoids that have a solid tegmen with firmly fused plates on which the anal opening is flush with the surrounding surface of the tegmen. A few specimens are known from camerate crinoids with a long anal tube, like *Actinocrinites,* but in these instances the tube is typically broken or the distal end is plugged with small plates and a secondary anal opening was resorbed through the tegminal plates.

An ophiuroid, *Onychaster,* is found among the arms of some Mississippian crinoids (Fig. 217,*1*). It is not known to be associated with the anal vent and is commonly found on specimens with a long, functional anal tube. In such individuals the brittle star is commonly wrapped around the base of the tube. Whether the ophiuroid fed from excrement, from the food tracts of the crinoid, or preyed on the crinoid, or simply used the crinoid as an angling perch, from which to capture its own food supply from passing currents, is not certainly known. Some living ophiuroids live on the stem of stalked crinoids and exhibit close mimicry to the long slender cirri of the stem, in this case surely using the crinoid mainly as a perch.

A variety of organisms caused holes, pits, burrows, or cysts to be developed on various parts of the crinoid skeleton (WARN, 1974; WELCH, 1976). Some of these are cysts caused by peculiar ectoparasitic annelids called myzostomes that today infest the arms and pinnules of living crinoids. Insofar as known, myzostome cysts are confined to brachial and pinnular plates in both fossil and living crinoids. Swollen cystlike structures on the stems of Ordovician through Permian crinoids that have been referred to the myzostomes are now known to have been a response on the part of the host crinoid to attached animals with a small, golf tee-shaped, phosphatic skeleton (Fig. 218,*2-4*). The affinities of the attaching animals is not known, but they have been most recently assigned to the Hyolithelminthes (WELCH, 1976).

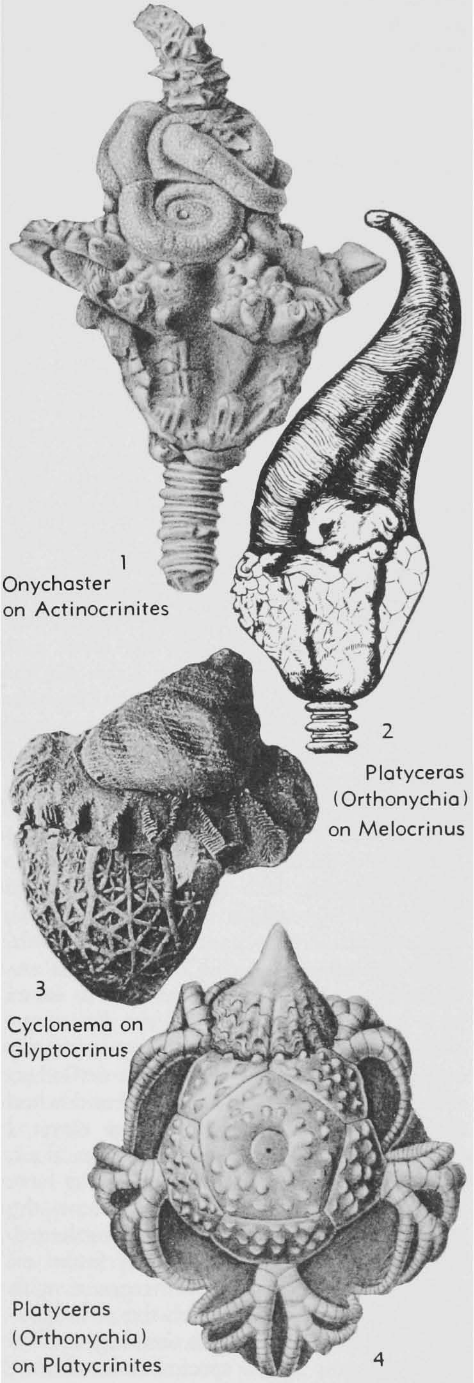


FIG. 217. Mutualistic relationships of fossil crinoids (*1,4,* Wachsmuth & Springer, 1897; *2,* Clarke, 1921; *3,* Bowsher, 1955a).——*1. Actinocrinites multiramosus* WACHSMUTH & SPRINGER, with an ophiuroid *Onychaster* fastened to the anal tube; Lower Mississippian (Keokuk), Indiana.——*2. Melocrinites micmac* CLARKE with attached shell of *Platyceras (Orthonychia),* Lower Devonian, Gaspé Peninsula.——*3.* Shell of *Cyclonema* sp. attached to tegmen of *Glyptocrinus dyeri* MEEK, from Upper Ordovician (Cincinnatian) of Ohio, ×1——*4. Platycrinites hemisphericus* MEEK & WORTHEN, dorsal view, with a *Platyceras (Orthonychia) infundibulum* covering anal opening, from Lower Mississippian (Keokuk), Indiana.

Other induced structures on stem and calyx plates are circular depressions that resemble holes drilled in shells by carnivorous gastropods (Fig. 218,*1*). The great majority of these holes fail to penetrate the plate in which they were started. Whether these are abortive preying attempts on the part of a carnivorous animal or depressions excavated by an organism as a dwelling site is not known.

Very little is known about the predator-prey relationships of fossil crinoids. Several authors have stated that living crinoids apparently have no enemies in the sense that no other animal is known to feed on them (Hyman, 1955). Laudon (1957) has suggested that late Paleozoic bradyodont or hybodont sharks with batteries of flat crushing teeth may have fed on the crowns of crinoids. He envisioned these fishes grazing over extensive crinoid meadows that formed the Burlington Limestone, which also contains numerous shark teeth of this type. The closest living relative to the hybodonts, the Port Jackson shark, does today feed on echinoids *(Strongylocentrous)* and starfishes, which does lend some tenuous support to this hypothesis. Predation of crinoids by sharks would help explain why so many stems and so few heads are found in some rock units, although alternate hypotheses have been proposed (Lane, 1971).

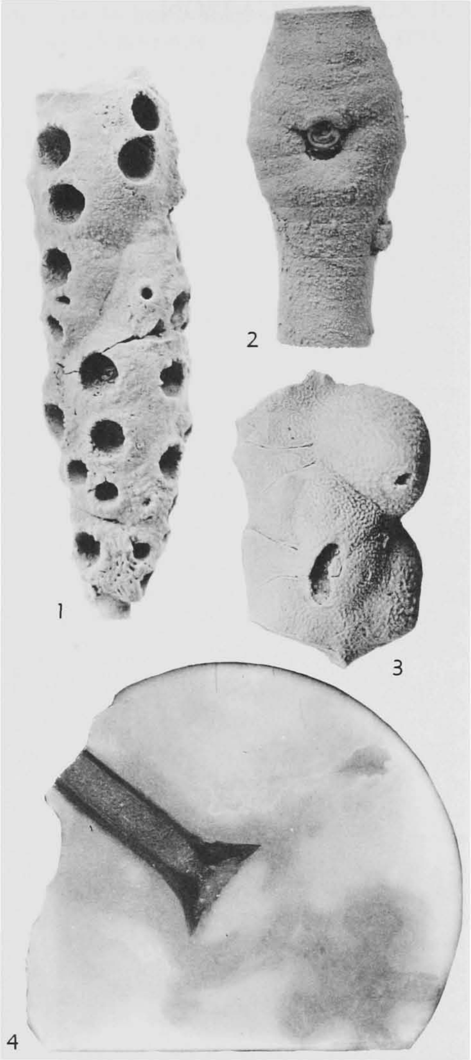


Fig. 218. Mutualistic relationships of fossil crinoids: cysts and other structures (Lane, n; photographs by James R. Welch).——*1*. Crinoid stem that has been penetrated numerous times by borings of unknown affinity, from Upper Pennsylvanian (Seminole F.), Tulsa County, Oklahoma; ×3.2.——*2*. Broken base of a *Phosphannulus* funnel within a cavity in a swollen stem, from Upper Mississippian (Haney Formation), Crawford County, Indiana; ×3.——*3*. Myzostome gall of an arm of an pper Pennsylvanian crinoid from the Seminole rmation, Tulsa County, Oklahoma; ×3.7.——*4*. Transverse section of a crinoid stem with a parasitic *Phosphannulus* on a plug of stereom; cavity surrounding funnel is open to the axial canal of the crinoid stem; from Haney Formation, Crawford County, Indiana; ×10.

HISTORICAL REVIEW OF CLASSIFICATION OF CRINOIDEA

By N. Gary Lane

The earliest written account of crinoids was by Agricola in 1546, who proposed four names for the stems of fossil crinoids. *Entrochus* referred to individual round columnals and *Trochites* to a series of such columnals joined together. *Encrinus* was the name given to isolated columnals of pentagonal outline, and *Pentacrinus* to a series of united ossicles of this shape. These four names continued to be used for virtually all known fossil crinoids until J. S. Miller (1821) introduced several generic names that provided the foundation for modern studies of fossil crinoids. Some of the most important advances in knowledge concerning crinoids—such as the conclusion that their fossil remains were really skeletal parts of organisms, that the fossils were of animal rather than of plant origin, that the stem and crown really belonged together and were part of a single individual, that the fossils were related to living echinoderms—were accomplished long before first attempts at classification and hence will not be elaborated here.

Prior to J. S. Miller's clear distinction between stalked crinoids and starfishes, all living and fossil crinoids were commonly associated with the starfishes as one major group of the echinoderms, which were in turn placed within the zoophytes or radiate animals. A distinctive group name for crinoids was lacking until William Martin in 1809 proposed the family Stylastritae for Lower Carboniferous crinoids from Derbyshire. Martin's name was specifically rejected by J. S. Miller because it referred to an assemblage and could not be combined readily with prefixes to form new generic names. Miller therefore replaced Martin's group name with Crinoidea, or lily-shaped animals.

Miller restricted the term Crinoidea to those living and fossil crinoids that had a stem or column, and specifically did not include living stalkless crinoids, called *Comatula,* or the fossil *Marsupites.* He considered these stemless forms to be transitional between starfishes and crinoids. Miller divided the Crinoidea into four divisions:

Classification of Crinoids by Miller (1821)

Division Articulata. Plates of cup loosely articulated: *Apiocrinites, Pentacrinites, Encrinites.*
Division Semi-articulata. Plates of cup articulating imperfectly with each other: *Poteriocrinites.*
Division Inarticulata. Plates of cup adhering by sutures lined by muscular integument: *Cyathocrinites, Actinocrinites, Rhodocrinites, Platycrinites.*
Division Coadunata. Plates of cup fused to first columnal: *Eugeniacrinites.*

Miller's classification and new group name for these animals were slow to be accepted by other paleontologists. Several German authors continued to use Martin's older name, as Stilastritidae or Stylastritae, rather than Crinoidea, for several decades, and French authors commonly used *Encrinidés* or *Encrines,* based on Agricola's old name, *Encrinus.* A new family-level name, Asterencrinidae, was proposed by de Blainville in 1834 as a synonym of Crinoidea. English authors also did not accept Crinoidea readily. In 1842, Austin and Austin proposed Pinnastella as a replacement name for Crinoidea without attempting to justify the change. They also rejected Forbes' Pinnigrada which was proposed in 1841 as a substitute name for Crinoidea. Neither of these latter names was accepted by subsequent authors. Of Miller's four division names, only Articulata has survived to the present-day classification, where it is used as a subclass for all Mesozoic and Cenozoic crinoids except for the Triassic genus *Encrinus.*

Münster, in 1833, placed the crinoids within the Stellerides or sea-stars. He recognized two major groups of starfishes, the stalked sea-stars or Stilasteritae, using Martin's name for this group, and the Asterites liberi or free sea-stars, within which he placed *Comatula* and *Ophiura.* Within the Stilasteritae, Münster recognized two of Miller's four divisions, distinguishing the articulated crinoids from the nonarticulated ones, which he called Crinoidea inarticulata. He included *Eugeniacrinites, Solanocrinites, Pentacrinites, Encrinites* and *Apiocrinites* in the first group and *Platycrinites, Cyathocrinites, Actinocrinites, Melocrinus* [=*Melocrinites*], *Rhodocrinus* [=*Rhodocrinites*], *Cupressocrinus* [=*Cupressocrinites*], and *Eucalyptocrinus* [=*Eucalyptocrinites*] in the latter group.

The classification of crinoids by F. A. ROEMER (1836) was closely similar to that of MÜNSTER. ROEMER used Stylastritae as a group name equal in rank to the Stellerides, in which he placed *Comatula* with *Ophiura* and *Asterias*. ROEMER accepted three of MILLER's subdivisions based on articulation of cup plates, but included, for the first time, *Marsupites* with the articulated Stylastriten, separated *Poteriocrinus* [=*Poteriocrinites*] as the one genus in the Semi-articulata *(halbeingelenkte Stylastriten),* and included the newly named genera *Caryocrinus* [=*Caryocrinites*] and *Scyphocrinus* [=*Scyphocrinites*] with the inarticulate genera that had been listed by MÜNSTER.

AUSTIN and AUSTIN (1842) proposed a classification of crinoids in which all but one of the then-known genera were placed in the class Pinnastella of the section Echinodermata, substituting this new class name for MILLER's Crinoidea. The class Pinnastella was divided into two orders: Cionacineti for crinoids with a jointed, flexible column, and order Liberidae for crinoids that lacked a stem or were capable of free motion. The latter group included *Marsupites* and *Comatula,* thus placing the living stalkless crinoids with fossil relatives. The stalked crinoids were divided into nine families that contained 25 genera as well as the cystoid *Caryocrinites*. One crinoid, *Sycocrinites,* was placed in the class Adelostella, which was divided into two orders, the first containing the echinoids; the second, order Columnidae, consisting of stem-bearing forms that supposedly lacked arms and included cystoids, blastoids, and *Sycocrinites.*

Most of the aforementioned early workers on fossil crinoids coined new generic names that ended in *crinites*. This procedure was in accord with an early informal practice that generic names of fossils ended in *ites*. This tradition ended abruptly as far as fossil crinoids are concerned when LOUIS AGASSIZ, in 1836, changed the names of all crinoid genera known to him from a *crinites* to a *crinus* ending, for the sake of uniformity. AGASSIZ' authority was accepted tacitly by virtually all later crinoid workers until 1938, when BASSLER published the *Fossilium Catalogus* volume on Paleozoic pelmatozoans. BASSLER returned to the original spellings for these oldest generic names of fossil crinoids, and, in accordance with the rules of nomenclature now in effect, these names are now used with their original, correct endings.

As various groups of stalked, extinct Paleozoic echinoderms, especially cystoids and blastoids, came to be better known and new genera were described, these forms were placed in the Crinoidea. At first, only a few genera were involved (e.g., *Caryocrinites* and *Pentremites*), but the concept of crinoids was expanded gradually until it included all known Paleozoic echinoderms except echinoids and starfishes. This broadening of the idea of crinoids led to an increasingly diverse and morphologically dissimilar group of fossils being included together under this name. For a long time, the tendency was to retain Crinoidea in this broad sense and to propose other new names for crinoids in a strict sense.

In his pioneering studies of the morphology of living stalked crinoids, MÜLLER (1843) divided the Crinoidea into two major groups, *Crinoiden mit Arme* for crinoids, and *Crinoiden ohne Arme* for blastoids and cystoids. The crinoids proper were split into four divisions of very different content. The two large, inclusive groups were the Articulata and Tessellata. The former name was used in the sense of MILLER (1821), but included both stalked and unstalked Mesozoic and recent forms. The latter group of tessellate (plated) crinoids included most Paleozoic genera, as well as *Marsupites*. MÜLLER defined the Articulata as including crinoids with radii free down to the base of the calyx, implying a flexible ventral integument and lack of solid interradials binding the ray plates together. The tessellate crinoids were characterized by a solid plated calyx. The division Costata was named solely for *Saccocoma,* principally because this crinoid was supposed to have opposed "pinnules," and Testacea was erected for *Haplocrinus* [= *Haplocrinites*]. *Holopus* was included but without placement in any of the four groups.

LEUCKART (1848) established a class Pelmatozoa for (transl.) "echinoderms that throughout life, or at least for some period during their youth, are stalked and attached." He divided the class into two orders, which he called *Cystideen* and *Crinoideen*.

BURMEISTER (1856) included in the Crinoidea the Brachiata, formalizing MÜLLER's term, and the Anthodiata, for blastoids and cystoids. ROEMER (1855 in BRONN & ROEMER, 1851-56) included three suborders in the so-called order Crinoidea: Actinoidea for true crinoids, Blastoidea for blastoids, and Cystidea for cystoids. This broad usage of Crinoidea continued until the 1880's (ZITTEL, DE LORIOL), but after that the cystoids and blastoids were generally separated as classes or orders of echinoderms equivalent in rank to the Crinoidea.

D'ORBIGNY (1852) contributed little to the classification of crinoids, simply listing under Order Crinoidea families that included cystoids and blastoids. He informally divided the order into fixed and free crinoids *(crinoïdes fixés et libres)*.

ROEMER (1855 in BRONN & ROEMER, 1851-56) attempted the most detailed arrangement of the known kinds of crinoids into hierarchial groups. Within his suborder Actinoidea he devised a dichotomous key based on important morphological features, including presence or absence of a column, and especially on various features of arm development. Only the two primary branches of the key were given names—the Astylida, crinoids without an articulated column, and Stylida, crinoids possessing such a column. The key of ROEMER was formulated as follows:

Classification of Crinoids by Roemer (1855)

Suborder Actinoidea. Crinoids with large pinnule-bearing arms.
  A. Astylida. Crinoids without articulated column.
    a. Cup adnate: Halopocrinidae. Cyathidiocrinidae.
    b. Cup free: Astylocrinidae, Marsupitidae, Saccocomidae, Comatulidae.
  B. Stylida. Crinoids with articulated column.
    a. Arms strongly developed.
      1. Ventral side a leathery integument.
        aa. Arms not normally folded over tegmen: Pentacrinidae.
        bb. Arms folded into regular pyramid over tegmen: Apiocrinidae [= Apiocrinitidae], Eugeniacrinidae [= Eugeniacrinitidae], Encrinidae, Cyathocrinidae [= Cyathocrinitidae].
      2. Ventral side composed of immovable flat plates.
        aa. Tegmen diffuse between arm bases; arms folded over tegmen.
          aaa. Arm branches separate:
            Poteriocrinidae
              [= Poteriocrinitidae],
            Rhodocrinidae
              [= Rhodocrinitidae],
            Platycrinidae
              [= Platycrinitidae],
            Actinocrinidae
              [= Actinocrinitidae],
            Melocrinidae
              [= Melocrinitidae],
            Ctenocrinidae, Sagenocrinidae
              [= Sagenocrinitidae].
          bbb. Arms coalesced into five petal-shaped, reticulate laminae: Anthocrinidae.
        bb. Tegmen forming apex of crown; arms in resting position embedded into sides of tegmen: Eucalyptocrinidae [= Eucalyptocrinitidae].
    b. Arms incompletely developed. Haplocrinidae [= Haplocrinitidae], Gasterocomidae.

PICTET (1857) retained the scheme formulated by D'ORBIGNY, merely listing families of crinoids, cystoids, and blastoids under the order Crinoides. GOLDFUSS (1862) continued to use an antiquated classification, placing the crinoids in the Stellerites and dividing them into the Stilasteritae, or stalked sea stars, and the Asterites liberi, or free sea stars. He recognized two divisions of stalked crinoids (Articulata and Inarticulata), retaining these groups in the sense of MILLER (1821). QUENSTEDT (1852) simply listed crinoid genera under the order Crinoideae.

The next important step forward in classification was by WACHSMUTH (1877) who proposed that all Paleozoic crinoids be grouped together in the Paleocrinoidea. He based this grouping primarily on a distinction between the heavily plated tegmen of Paleozoic crinoids, with subtegminal ambulacral tracts, and the flexible tegmen of

Mesozoic and younger crinoids that had an exposed mouth and ambulacral grooves. WACHSMUTH believed that the "visceral disc" of younger, post-Paleozoic crinoids is not homologous with the solidly plated oral part of the theca of Paleozoic crinoids, which he called the "vault." This division into two major groups based on the nature of the oral side of the theca was similar to that of ROEMER (1855, in BRONN & ROEMER, 1851-56) who had recognized a similar, unnamed division of stalked crinoids with well-developed arms. ROEMER, however, placed the Cyathocrinidae [= Cyathocrinitidae] in the group with flexible integuments, whereas WACHSMUTH demonstrated that these Paleozoic crinoids had a solid "vault" similar to that of other Paleozoic crinoids. Within the Paleocrinoidea WACHSMUTH recognized three basic kinds of thecae, which he did not name but informally called the taxocrinid, cyathocrinid, and spheroidea plans. The third name applied to crinoids now called Camerata, and WACHSMUTH set the stage for the eventual recognition of three prime groups of Paleozoic crinoids—camerates, flexibles, and inadunates.

In 1880, WACHSMUTH and SPRINGER elaborated on the Paleocrinoidea, when they changed the spelling to Palaeocrinoidea and named the remaining, exclusively younger, crinoids the Stomatocrinoidea, in reference to an external mouth. They recognized three so-called families within the order Palaeocrinoidea, each corresponding to one of WACHSMUTH's original three plans of organization: the Ichthyocrinidae and Cyathocrinidae, discussed in 1880, and the Sphaeroidocrinidae, named in 1881. They thus formalized the distinctions discussed earlier by WACHSMUTH, while making some changes such as substitution of Ichthyocrinidae [= Icthyocrinidae] for the taxocrinid plan and changing the informal name spheroidea to Sphaeroidocrinidae.

Between these important publications by WACHSMUTH and SPRINGER, the posthumous work of ANGELIN (1878) was issued. The classification adopted there was an extremely artificial grouping of families into four sections based on the number of plates in the proximal circlet of the theca: Trimera, Tetramera, Pentamera, and Polymera. This classification was not used by subsequent workers. Another contemporaneous work was ZITTEL's *Handbuch der Palaeontologie,* which appeared in 1879. Within the class Crinoidea, ZITTEL designated three orders: Eucrinoidea, or true crinoids, Cystoidea, and Blastoidea. Among the Eucrinoidea ZITTEL recognized three suborders: the Tessellata, Articulata, and Costata of MÜLLER.

Beginning with the publications by WACHSMUTH and SPRINGER, one of the most intense periods of discussion concerning the study of both fossil and living crinoids began. This period of several decades was characterized by the description of diverse and well-preserved Paleozoic crinoid faunas from the central United States, and by a substantial increase in knowledge of living, especially stalked, crinoids. Sharp differences of opinion arose as to which morphological features constituted reliable criteria for subdivision of crinoids into major groups. Especially characteristic of this period were the published arguments and rebuttals between English paleontologists, especially P. H. CARPENTER and, later, F. A. BATHER, on the one hand, and WACHSMUTH and SPRINGER, on the other. Each side in these controversies had certain strengths and weaknesses. The American paleontologists generally had much larger, better-preserved collections of Paleozoic crinoids on which to base their arguments than did the British workers. On the other hand, CARPENTER, especially, was a trained biologist and had much experience with living stalked and unstalked crinoids, whereas most of the American scientists had little biological training.

CARPENTER and ETHERIDGE (1881) promptly objected to calling all Mesozoic and younger crinoids the Stomatocrinoidea, principally because they were not convinced that all Paleozoic crinoids had a subtegminal mouth and they predicted that open ambulacral tracts would be found on the tegmen of the Ichthyocrinidae, a discovery that was announced by WACHSMUTH and SPRINGER in 1889. ETHERIDGE and CARPENTER proposed Neocrinoidea as a substitute name and considered other morphological features diagnostic of the neocrinoids, especially lack of anal or interradial plates and perfect five-fold symmetry of the cup as well as consistent division of the arms on the "third radial" (in modern terms, the second primibrach).

De Loriol (1882-84) used Crinoidea in the broad sense of Zittel and others, and under the Eucrinoidea accepted Etheridge and Carpenter's divisions named Palaeocrinoidea and Neocrinoidea. In 1882, S. A. Miller named two new orders of crinoids, each containing a single family, the Lichenocrinoidea and the Myelodactyloidea. The first name applied to plated holdfasts for which the crown was unknown, and the second partly to coiled crinoid stems that Miller believed represented an echinoderm body related to the cyclocystoids, which he also described and placed in the same order.

In 1885 and 1886 the first and second sections of Part 3 of Wachsmuth and Springer's *Revision of the Palaeocrinoidea* were published. Although these authors continued to disagree with the reasons for Etheridge and Carpenter's substitution of Neocrinoidea for Stomatocrinoidea, they accepted the former name, principally because it was euphonious. Wachsmuth and Springer accepted the principle implicit in Zittel's (1879) classification that a relatively large number of families of palaeocrinoids should be recognized, and they both elevated in rank and changed the names of their earlier three subdivisions of the Palaeocrinoidea. The Sphaeroidocrinoidea was changed to suborder Camarata, which was later corrected to Camerata; the Cyathocrinidae was changed to suborder Inadunata, based on the arms being free above the radial plates; the taxocrinid plan or Ichthyocrinidae was changed to Articulata. Wachsmuth and Springer recognized that they were not using this name in the sense of Miller (1821) or Johannes Müller (1843) but considered it such an appropriate name for Paleozoic crinoids referred to the group that no misunderstanding would arise. The use of Articulata in this new sense was not acceptable to many paleontologists, and Zittel in 1895 proposed Flexibilia for these crinoids, Articulata in its original sense applicable to Mesozoic and younger crinoids. Thus, with the completion of Wachsmuth and Springer's *Revision,* the main outlines had been drawn of our present classification of crinoids.

Within the Camerata, Wachsmuth and Springer included both monocyclic and dicyclic crinoids characterized by a boxlike theca of solidly united plates. The Articulata included known crinoids now placed in the Flexibilia, as well as the Crotalocrinitidae. The Inadunata were divided into two branches named Larviformia and Fistulata. The first of these included both monocyclic and dicyclic inadunates characterized by a very simple theca, commonly consisting of only basals, radials, and orals. The simplest genera, *Haplocrinites* and *Allagecrinus,* were regarded as representing true crinoid larvae, "not only of the Inadunata, but of the Palaeocrinoidea generally." The Fistulata were defined as inadunate crinoids in which the visceral disc was partly or completely exposed as a ventral or anal sac that had pores along sutures between some or all of the plates. They divided the suborder into ten families, some monocyclic, others dicyclic, that included, as youngest representatives, the Triassic Encrinidae.

A new classification of echinoderms with several new names for higher categories was published by Neumayr in 1889, who divided the class Crinoidea into two new subclasses, named (in German) the *Hypascocrinen* and the *Epascocrinen.* These were distinguished mainly on the location of ambulacral tracts beneath or upon the tegmen. Thus, these units correspond reasonably closely in definition to Wachsmuth's Paleocrinoidea and Etheridge and Carpenter's Neocrinoidea, although the content of Neumayr's subclasses is quite different. He used three superfamily names within the *Hypascocrinen:* Sphaeroidocrinacea (equivalent to Wachsmuth and Springer's old name for the camerates); Haplocrinacea, corresponding approximately to the larviform crinoids; and Ichthyocrinacea, which included the flexibles, Crotalocrinidae, and Uintacrinidae. The *Epascocrinen* included superfamilies named Cyathocrinacea and Pentacrinacea, thus bearing close resemblance to Roemer's old grouping together of these crinoids. Neumayr's classification, which was far removed from the gradually developing arrangements by British and American workers, did not gain acceptance.

In CARPENTER's (1884a) important work on recent stalked crinoids published in the *Challenger* reports, the long-neglected name Pelmatozoa, introduced by LEUCKART in 1848, was revived. CARPENTER defined the pelmatozoans as a "branch" or subphylum of the phylum Echinodermata, assigning to it all stalked echinoderms. LEUCKART (1848) had proposed two other major divisions of the echinoderms in addition to the Pelmatozoa: Scytodermata for holothurians, and Echinozoa for starfishes and echinoids. CARPENTER's classification was used by WACHSMUTH and SPRINGER in 1885, who published their recommendations based on proofs of the *Challenger* report supplied by CARPENTER. They recognized Pelmatozoa as a class containing two subclasses, BURMEISTER's Anthodiata (for cystoids and blastoids) and Crinoidea (or Brachiata).

In 1886 the final classification adopted by WACHSMUTH and SPRINGER in the last part of their *Revision,* was briefly as follows:

Classification of Crinoids
by Wachsmuth & Springer (1886)

Phylum Echinodermata
  Class Pelmatozoa
    Subclass Crinoidea (Brachiata)
      Order Palaeocrinoidea
        Suborder Inadunata
          Branch Larviformia
          Branch Fistulata
        Suborder Camarata
        Suborder Articulata (or "Articulosa")
      Order Neocrinoidea

In 1890, these authors again revised the major divisions of crinoids and abandoned the two main groups, palaeocrinoids and neocrinoids. Instead they recognized three groups, the Camerata; the Inadunata, still divided into larviform and fistulate types; and the Articulata, which they now expanded to include the Ichthyocrinidae, or all flexible crinoids, as well as post-Paleozoic forms. Thus, they returned to a usage of Articulata that was modified and expanded, but more in keeping with the original concepts of MILLER (1821) and MÜLLER (1843). This three-fold division was also used by them in their camerate monograph of 1897, where the following classification was used:

Classification of Crinoids
by Wachsmuth & Springer (1897)

Class Crinoidea
  Order Inadunata
    Suborder Larviformia
    Suborder Fistulata
  Order Camerata
  Order Articulata
    Suborder Impinnata
    Suborder Pinnata

They recognized division of their broad group Articulata into two suborders, the Impinnata referring to Paleozoic flexible crinoids, and Pinnata to Mesozoic and younger crinoids. These two divisions furnished the basis for BATHER's (1899b) separation of the order Flexibilia into two grades with the same names, although his grade Pinnata was very different in scope from WACHSMUTH and SPRINGER's suborder, including only about one-half of the recognized families of post-Paleozoic crinoids, the remainder being included in dicyclic and monocyclic Inadunata.

In 1890, BATHER published a detailed classification of the fistulate inadunates that foreshadowed his gradually developing ideas concerning the phylogeny and classification of crinoids. BATHER followed WACHSMUTH and SPRINGER's definition of the Inadunata and of the Fistulata, within which he attempted to arrange genera and families of crinoids on a phylogenetic basis. Although no formal names were applied between the suborder Fistulata and the family level, BATHER recognized two divisions which he called group A and group B, and a secondary subdivision of group B, into what he called divisions in the text but omitted from a tabular summary of his classification. Divisions were viewed by BATHER as categories that differed in kind, whereas series represented differences in degree and were stages in evolutionary lineages. He used series for subdivisions of families, equivalent to subfamily rank. Within the Fistulata the family Hybocrinidae was set aside as a separate entity without close relationship to any of the other groups. Group A of Bather included three families of monocyclic fistulates, the heterocrinids, calceocrinids, and catillocrinids. Group B included all dicyclic forms except for the monocyclic Belemnocrinidae. Within group B, Bather recognized three main groupings of families, which he informally called divisions in text, but did not name. The first division consisted of the families Dendrocrinidae, ?Carabocrinidae, and Euspirocrinidae. This group was characterized by having three anal plates in the cup and dichotomously branching arms. The Dendrocrinidae contained genera which he judged to be direct progenitors of the other two main groups, *Homocrinus* to the Decadocrinidae, and *Ottawacrinus* to the Cyathocrinidae. The second group, the Decadocrinidae, was characterized especially by having ten arms. Within this later assemblage anal plates were early added to the cup, with a later, secondary loss of anal plates. In addition, there was an evolutionary trend toward development of pinnules. The third group consisted of the Cyathocrinidae, divided into three series.

Implicit in this classification was Bather's judgment that advanced fistulate crinoids of the late Paleozoic were derived from two different ancestral stocks, genera such as *Poteriocrinites, Scaphiocrinus,* and *Zeacrinites* evolving from a *Dendrocrinus*-type ancestor, whereas scytalocrinids, graphiocrinids, erisocrinids, and cromyocrinids evolved from a *Botryocrinus*-type ancestor. Bather completely abandoned this scheme three years later in 1893, when, in revising the Silurian inadunates of Gotland, he discarded Larviformia and Fistulata and instead proposed two new suborders: Inadunata Monocyclica and Inadunata Dicyclica, with strict separation based on the presence or absence of infrabasals. Bather emphasized that in monocyclic inadunates three of the radials were commonly bisected transversely, or two of the radials were conspicuously larger than the other three radials, whereas neither of these conditions was seen in dicyclic inadunates. Monocyclica and Dicyclica were thus initially proposed as subdivisions of the Inadunata.

Six years later, in 1899, Bather again proposed substantial changes in crinoid classification, but he had so altered his views that the Monocyclica and Dicyclica took on a completely different content. By this time, he had become convinced that crinoids were biphyletic in origin and that monocyclic forms had not evolved into dicyclic crinoids, or vice versa. He thus proposed two subclasses, Monocyclica and Dicyclica, each of which contained different grades of increasing morphologic complexity followed by secondary simplification. These levels of complexity were basically the inadunate, camerate, flexible, and articulate plans distinguished by other crinoid workers. Within each subclass he regarded the inadunate conditions as the ancestral stem from which other major groups arose. The monocyclic inadunates included the larviform crinoids of Wachsmuth and Springer, as well as monocyclic inadunates (mainly the Hybocrinidae) which previously had been placed in the Fistulata. The Monocyclica Inadunata were supposed to continue to the present, represented by the Hyocrinidae, and to have given rise to two additional Paleozoic orders; the Adunata and the Camerata. The Adunata are composed of three monocyclic families which previously had been classified as camerates: the Platycrinidae [=Platycrinitidae], Hexacrinidae [=Hexacrinitidae], and Acrocrinidae. The Camerata included all other monocyclic "camerates" and were divided into three suborders, named Melocrinoidea, Batocrinoidea, and Actinocrinoidea.

The dicyclic crinoids were also divided into three orders, the Inadunata, Flexibilia, and Camerata. Two informal grades were recognized within the dicyclic inadunates: grade Distincta comprising crinoids with all brachials free above the radials, and grade Articulata characterized by proximal brachials flexibly incorporated into the cup and provided with suprategminal ambulacral tracts. Bather did not indicate what families or genera should be assigned to these two grades and, instead, divided the dicyclic inadunates into two suborders called Cyathocrinoidea and Dendrocrinoidea. The former included Paleozoic families exclusively, whereas the latter (including *Bathycrinus*) ranged from Paleozoic to recent.

The order Flexibilia was derived from the Dicyclica Inadunata Distincta and encompassed two grades, Impinnata for nonpinnulate forms, and Pinnata for crinoids with pinnules. The Impinnata consisted of all crinoids now called flexibles, and the Pinnata of the great majority of Mesozoic and younger crinoids. The Dicyclica Camerata were crinoids usually classed as camerates that possess an infrabasal circlet.

BATHER's classification was a serious attempt to relate all crinoids within a comprehensive phylogenetic scheme, most earlier classifications being based on morphological similarities and dissimilarities, without discussion of implied origins or relationships. His scheme suffered from two principal defects. There was substantial evidence available that BATHER's basic premise was in error—that monocyclic and dicyclic forms could be more closely related to each other than to other crinoids with the same number of circlets. In addition, the categories proposed by BATHER were awkward and unnecessarily confusing. In order to specify several major groups at the order and suborder level, it was necessary to use binomial or even trinomial terms, such as Dicyclica Inadunata and Dicyclica Inadunata Distincta. BATHER adopted this same classification in LANKESTER's *Treatise on Zoology*, published in 1900. His classification was never used by SPRINGER in numerous subsequent publications on fossil crinoids, or by other American crinoid workers, but was utilized by British paleontologists.

Beginning in 1894, OTTO JAEKEL began a series of papers on fossil crinoids which expressed his views on classification. His initial proposal, in connection with a study of crinoids of the Devonian Hunsrückschiefer, was to divide the Crinoidea into three main groups, Blastoidea, Cladocrinoidea, and Pentacrinoidea; the latter two names were new but were not defined. Only camerate genera were assigned to the Cladocrinoidea and he arranged the Pentacrinoidea in three divisions of unstated rank, but approximately at suborder level, because he named superfamilies within one of these divisions. All pentacrinoid genera were inadunates. JAEKEL proposed the Larvata (a variant of Larviformia), Fistulata, and Costata, the latter used solely for Hapalocrinidae. He divided the Fistulata into two superfamilies named Cyathocrinacea [= Cyathocrinitacea] and Dendrocrinacea, both shortly raised to suborder rank by BATHER (1899b).

JAEKEL gradually defined and expanded his ideas on classification of crinoids and other echinoderms in a series of papers that culminated in his important summation issued in 1918 on the *Phylogenie und System der Pelmatozoen*. The class Crinoidea was divided into three subclasses named Eocrinoidea, Cladocrinoidea, and Pentacrinoidea. He considered the eocrinoids to be the ancestral stock from which the other two groups were derived, the cladocrinoids corresponding to camerates, and the pentacrinoids to all other crinoids. Within the subclass Cladocrinoidea, two orders were recognized, the Monocyclica and Dicyclica, respectively equivalent to BATHER's Monocyclica Camerata and Dicyclica Camerata and to the currently used Monobathrida and Diplobathrida. Within each of these orders several suborders were proposed, each based primarily, but not exclusively, on number of plates in the lowest circlet of plates in the theca.

Within the Pentacrinoidea six orders were recognized, Fistulata, Articulata, Articulosa, Reducta, Turbata, and Costata. The fistulate crinoids included six suborders of Paleozoic, primarily dicyclic, crinoids and correspond approximately to the Cladida of present classification. The Articulosa, which JAEKEL adopted from WACHSMUTH and SPRINGER's provisional name, were the flexible crinoids, which JAEKEL divided into four suborders.

The Articulata were composed of Mesozoic to recent crinoids, including the Triassic Encrinidae, as well as most but not all stalked and stemless crinoids currently assigned to the Articulata. Three suborders were recognized: suborder Typica, stemmed crinoids with basals; suborder Libera, stemless crinoids; and suborder Compacta, comprising crinoids with only radials in the cup. A small group, order Reducta, was composed of secondarily simplified, dicyclic Paleozoic reef-dwellers with fused infrabasals, now placed in the Cyathocrinina. Order Turbata consisted of monocyclic crinoids having radials of unequal size and shape, arranged in five suborders. The Costata, used by JAEKEL in a very different sense from that of MÜLLER, or of JAEKEL's early papers, was also composed of monocyclic forms and included two suborders, Hybocrinites, now considered disparid inadunates, and suborder Hyocrinites, for living and fossil stalked crinoids as well as the stemless Saccocomidae. These were separated from the Articulata because they have large oral plates and, according to JAEKEL, ramules rather than pinnules. A summary of his classification of 1918, above the family level, is as follows:

Classification of Crinoids by Jaekel (1918)

- Class Crinoidea
  - Subclass Eocrinoidea
  - Subclass Cladocrinoidea
    - Order Monocyclica
      - Suborder Tetramera
      - Suborder Disjuncta
      - Suborder Pentamera
      - Suborder Miomera
    - Order Dicyclica
      - Suborder Tetramera
      - Suborder Pentamera
  - Subclass Pentacrinoidea
    - Order Fistulata
      - Suborder Cyathocrinites
      - Suborder Dendrocrinites
      - Suborder Merocrinites
      - Suborder Barycrinites
      - Suborder Rhenocrinites
      - Suborder Poteriocrinites
    - Order Articulata
      - Suborder Typica
      - Suborder Libera
      - Suborder Compacta
    - Order Articulosa
      - Suborder Taxocrinites
      - Suborder Calpiocrinites
      - Suborder Lecanocrinites
      - Suborder Ichthyocrinites
    - Order Reducta
    - Order Turbata
      - Suborder Heterocrinites
      - Suborder Calceocrinites
      - Suborder Triacrinites
      - Suborder Symbathocrinites
    - Order Costata
      - Suborder Hybocrinites
      - Suborder Hyocrinites

Several aspects of JAEKEL's classification deserve amplification. The primary reason for dividing crinoids into two main groups, cladocrinoids and pentacrinoids, was JAEKEL's premise that the arms of these two groups were not homologous. He judged the biserial pinnulate arms of cladocrinoids, which appear very early in the fossil record, to be an intermediate stage between the brachioles of eocrinoids, blastoids, and other primitive echinoderms, and the true arms of pentacrinoids which only gradually developed ramules and later pinnules. He also thought that the arm-bearing calyx plates of the cladocrinoids were not homologous to the radials of pentacrinoids, and he called the former costalia. Another important difference was that the ambulacral tracts branched within the theca of cladocrinoids, hence the name Cladocrinoidea. JAEKEL disagreed vigorously with BATHER's separation of crinoids into two primary divisions, Dicyclica and Monocyclica, maintaining that many monocyclic crinoids represent secondary simplification from a dicyclic condition, hence are not part of a single phylogenetic lineage.

Thus, upon publication of JAEKEL's classification (1918) three very different arrangements of crinoids were offered, each developed more or less independently over a period of years, and each presenting divergent views concerning relationships and phylogeny within the Crinoidea. WACHSMUTH and SPRINGER's (1886) classification, later modified (WACHSMUTH & SPRINGER, 1897) recognized four major groups of crinoids, three major Paleozoic groups, the camerates, flexibles, and inadunates, and one post-Paleozoic group, the articulates. BATHER recognized two throughgoing lineages from early Paleozoic to the present day, based on presence or absence of an infrabasal circlet. JAEKEL set apart camerate crinoids as a distinctive Paleozoic group rather far removed from all other crinoids. Like BATHER, he judged that some crinoids, at the ordinal level, at least, had persisted from Paleozoic to recent time and that living crinoids are polyphyletic.

By 1920, SPRINGER had abandoned Articulata for any Paleozoic crinoids and adopted ZITTEL's (1895) name, Flexibilia, but restricted it to Paleozoic forms, whereas ZITTEL had initially proposed the name to include the Ichthyocrinidae as well as *Marsupites* and *Uintacrinus*. SPRINGER recognized four major groups of crinoids, the Paleozoic Inadunata, Camerata, and Flexibilia, and the post-Paleozoic Articulata.

Since publication of SPRINGER's chapter on crinoids in the ZITTEL-EASTMAN *Textbook of Palaeontology* (VON ZITTEL, 1913) and his monograph on flexible crinoids (1920), virtually all students of fossil and living crinoids have accepted this arrangement, although there has been considerable revision within each of these four groups.

In the English adaptation of VON ZITTEL's textbook, SPRINGER (in VON ZITTEL, 1913) restated the basic classification of crinoids proposed earlier by him and WACHSMUTH, recognizing four main divisions: camerates, flexibles, inadunates, and articulates. He thus accepted VON ZITTEL's name for the Flexibilia and returned to the long-standing usage of Articulata for all post-Paleozoic crinoids, except the Encrinidae. The main new feature of this classification (1920) was division of the Flexibilia into two suborders, named Taxocrinoidea and Sagenocrinoidea. The order Articulata was revised jointly by SPRINGER and A. H. CLARK, who was responsible for treatment of living crinoids in the classification. No divisions between the order Articulata and the family level were recognized, CLARK's earlier order Comatulida, for instance, but the family Pentacrinidae was divided into several sections, tribes, and subtribes to take account of most of the stalked articulates, as well as all known stemless forms except *Saccocoma.*

The classification of living comatulid crinoids was considered by A. H. CLARK in several papers in 1908 and 1909. He proposed the order Comatulida in 1908, and also proposed, in another paper that year, division of living stemless crinoids into two main groups, the Thalassometroida and Antedonoida. The first group comprises crinoids with pinnules of triangular cross section and small eggs; the Antedonoida have round pinnules and large eggs. The two groups were re-named in 1909 as Oligophreata and Macrophreata, respectively, in reference to size of the visceral cavity within the centrodorsal. The two groups also correspond generally to comatulids bearing multibrachiate arms and those having ten or fewer arms, although other important morphological differences are observed. A similar subdivision of the comatulids into ten-armed forms and those with more than ten arms had been proposed as long ago as 1849 by MÜLLER, who recognized two species groups within the broadly defined genus *Comatula.* The concept of comatulids was broadened by SPRINGER and CLARK (in VON ZITTEL & EASTMAN, 1913) to include the fossil *Marsupites* and *Uintacrinus,* classed as tribe Innatantes equivalent in rank to the Oligophreata and Macrophreata.

These major divisions of living comatulids were recognized by CLARK in his exhaustive monograph of the existing crinoids, the comatulid portion of which was started in 1915 but not completed until after CLARK's death. This two-fold division was not accepted by GISLÉN (1924), who proposed four groups of comatulids, splitting the Oligophreata into three tribes. This change was rejected by CLARK in subsequent parts of his monograph. However, GISLÉN's divisions have been accepted by other workers, notably SIEVERTS-DORECK, who utilized GISLÉN's four groups as suborders within the Order Comatulida in UBAGHS' (1953) chapter on Crinoidea in PIVETEAU's *Traité de Paléontologie.* In this classification of comatulids, the Macrophreata stand apart. Living members of the group include the most active crinoids which are characterized by the presence of ten arms, prominent muscular articulations, and a centrodorsal with a large internal cavity. The suborder Comasterina includes comatulids in which cirri are absent or rudimentary and an exocyclic tegmen is developed. The suborder Mariametrina include multibrachiate crawling crinoids with a discoid centrodorsal and the suborder Thallassometrina comprise crinoids which generally bear a pentagonal impression on the base of the centrodorsal.

The remainder of the Articulata, exclusive of comatulids, were classified for many years as miscellaneous families. CLARK (1910b) proposed three orders of living articulates: the Holopodida, containing *Holopus;* the Ptilocrinida, comprising four families of stalked crinoids; and the Comatulida, including stalkless forms and the living pentacrinites. The fossil Articulata were not revised comprehensively until SIEVERTS-DORECK, in MOORE, LALICKER & FISCHER (1952), proposed division of these crinoids into six orders: the Isocrinida, Millericrinida, Cyrtocrinida, Uintacrinida, Roveacrinida, and Comatulida. Her isocrinids encompassed living representatives of the Pentacrinidae as well as several fossil groups. The Millericrinida included CLARK's Ptilocrinida and several exclusively fossil families. The Uintacrinida are Cretaceous stemless forms, and the Roveacrinida are small stalkless Mesozoic crinoids. The Cyrtocrinida include a variety of fossils as well as the living *Holopus*. This classification was repeated by SIEVERTS-DORECK in the *Traité de Paléontologie* (UBAGHS, 1953), with addition of two new suborders within the Millericrinida. This provides the latest authoritative statement on classification of the Articulata.

Between 1920 and 1943 there were few changes in definition of the principal groups of crinoids. Major emphasis in studies was directed toward discovery and description of many late Paleozoic crinoids from the Midcontinent of the United States, especially by MOORE and STRIMPLE, from Russia by YAKOVLEV, and from Timor by WANNER. Prior to this research few crinoids of Pennsylvanian or Permian age were known, and those mainly from western Europe. MOORE and PLUMMER (1940) described many new genera of advanced inadunates and placed them all in the family Poteriocrinitidae.

A comprehensive survey of the classification and evolution of all known Paleozoic crinoids was undertaken by MOORE and LAUDON in 1943. They reviewed the different bases for classification used by WACHSMUTH and SPRINGER, BATHER, and JAEKEL, and concluded that the primary divisions utilized by WACHSMUTH and SPRINGER were in closest accord with the evolution of Paleozoic crinoids as interpreted by them. Therefore, they recognized three subclasses, the Camerata, Flexibilia, and Inadunata, in which they included Triassic Encrinidae. Within the flexibles, they accepted SPRINGER's division into two major groups, the orders Taxocrinoidea and Sagenocrinoidea, but rejected the group called Adunata by BATHER, placing these advanced crinoids with a secondarily simplified cup among the Camerata. They divided the camerates into two major groups, orders Monobathra and Diplobathra, based on presence or absence of infrabasals. WACHSMUTH and SPRINGER had never recognized a primary division within their Camerata, although JAEKEL had divided his Cladocrinoidea into two orders, Monocyclica and Dicyclica, similar in content to MOORE and LAUDON's two orders.

The most significant revisions in classification made by MOORE and LAUDON were within the Inadunata by grouping all monocyclic inadunates in the order Disparata, and within this group recognizing two informal groups called the homo-synbathocrinid stock and the hybocrinid stock. This order was equivalent to BATHER's awkward and potentially confusing Inadunata Monocyclica, and was very different in concept from JAEKEL's separation of these crinoids into two orders, one of which included living crinoids. The dicyclic inadunates were assigned to the new order Cladoidea divided into two suborders, the more primitive Cyathocrinoidea, and the advanced Dendrocrinoidea, terms adopted from BATHER. The coining of new names at the order and suborder level within the camerates and inadunates by MOORE and LAUDON fulfilled several purposes. It effectively set apart their classification from earlier ones, and prevented confusion with earlier concepts of phylogeny and interpretation of morphology which had caused long-established names to be utilized in quite divergent ways by different authors; Larviformia, for instance. They abandoned the old Monocyclica and Dicyclica, substituting for them Monobathra and Diplobathra in the Camerata and Disparata and Cladoidea in the Inadunata. The name Disparata referred to the very unequal size of cup plates, especially radials, in this group of crinoids, Cladoidea was chosen in reference to the richly branched and eventually pinnulate arms of the dicyclic inadunates.

This classification of Paleozoic crinoids has been used with little modification to the present day, and with some elaboration, but without substantive change, is accepted in the present *Treatise* volume. MOORE, in MOORE, LALICKER & FISCHER (1952), changed the endings of some of the new names established in 1943—Disparata altered to Disparida, Cladoidea to Cladida, Monobathra to Monobathrida, and Diplobathra to Diplobathrida. These modifications were made in order to conform with general adoption of the ending -ida for orders and -ina for suborders. MOORE also separated the hybocrinids from the disparids as a new order, the Hybocrinida, based on JAEKEL's (1918) suborder Hybocrinites. The suborders Cyathocrinoidea and Dendrocrinoidea were changed to Cyathocrinina and Dendrocrinina, and the endings for the two flexible suborders were altered in similar manner. The monobathrid camerates were divided into two new suborders, named Tanaocrinina [= Compsocrinina] and Glyptocrinina, thus formalizing the two stocks recognized within this group by MOORE and LAUDON in 1943. Within the cladid inadunates the crinoids that had all been classed in the Dendrocrinoidea in 1943 were divided between the more primitive suborder Dendrocrinina and the more adanced, pinnulate, forms, suborder Poteriocrinina.

The classification of MOORE and LAUDON (1943a) and MOORE (1952a) was adopted by UBAGHS (1953) with some amplification. The principal features of the arrangement by UBAGHS are a number of new categories, especially superfamilies, within established suborders and some new ones. Within the diplobathrid camerates he introduced new suborders named Eudiplobathrina and Zygodiplobathrina, the former divided into three new superfamilies. Each of the two monobathrid suborders was divided into several superfamilies. The disparid inadunates, exclusive of the hybocrinoids, which were recognized as a separate order, were divided into three superfamilies based on different symmetry plans of the theca. No new higher categories were established for the cladid inadunates or flexibles.

The Russian treatise volume on crinoids by GEKKER (1964) adopted UBAGHS' classification, except that superfamilies were not utilized.

CLASSIFICATION OF THE ECHINODERMS

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In Parts S (1968) and U (1966) of the *Treatise* the classical division of the phylum Echinodermata into usually attached forms (Pelmatozoa) and free-living forms (Eleutherozoa) was replaced by a division into four subphyla (Homalozoa, Crinozoa, Asterozoa, and Echinozoa), which had been used for the first time by FELL in 1962. Since the publication of these volumes, the classification of the echinoderms has been the object of varying criticisms, additions, and modifications, of which a short resumé is given below.

Haplozoa. This subphylum, which was not recognized in the *Treatise* (Part S, 1968, p. S364), had been established by WHITEHOUSE (1941) for two enigmatic forms, *Cymbionites* and *Peridionites,* from the Middle Cambrian of Australia. DURHAM (1971), however, believed that the subphylum Haplozoa should be preserved because its two genera appear to be sufficiently distinct from other echinoderms to occupy a place of their own in the classification. The fact remains, nevertheless, that these fossils, which resemble each other only in their apparent simplicity, do not furnish any information as to the organization of the organisms to which they belong. It therefore seems preferable at the present not to assign to them a definite systematic position.

Homalozoa. In 1941 WHITEHOUSE united the classes Machaeridia WITHERS, 1926, and Carpoidea JAEKEL, 1901, in a separate subphylum which he called Homalozoa.

The affinities of the Machaeridia to the echinoderms had first been suggested by BATHER (in WITHERS, 1926), because of the fact that the plates of the genus *Lepidocoleus* show cleavage surfaces judged to be similar to those seen in the plates of fossil echinoderms. In reality, however, as S. BENGSTON (personal communication, 1976) is about to prove, these plates possess a microstructure completely different from that of echinoderm plates. On the contrary, they seem to be of exoskeletal origin, and to have been formed as successive deposits secreted by an epithelium. If this is so, there would be no reason to retain the Machaeridia in the echinoderms, and one can reject with confidence the hypothesis of POPE (1975), according to which *Lepidocoleus* is supposed to be the skeletal envelope of the posterior spines of the stylophoran *Enoploura*.

The carpoids, whose skeleton is typically echinodermal, then remain the only group within the subphylum Homalozoa. They differ from almost all other echinoderms in the complete absence of radial symmetry (at least their skeleton reveals no trace of such) and they deserve to be distinguished taxonomically. Their diversity is such that it was judged necessary by UBAGHS and CASTER (1968) to abandon the name Carpoidea and to divide these forms into three classes known as Stylophora, Homostelea, and Homoiostelea. To these a fourth class, Ctenocystoidea, was added by ROBISON and SPRINKLE (1969).

In a series of papers, JEFFERIES (1967, 1968a, 1968b, 1969, 1973, 1975; JEFFERIES & PROKOP, 1972) has stated the opinion that the Stylophora are not echinoderms but chordates with affinities to the echinoderms, for which he proposed the subphylum Calcichordata JEFFERIES, 1967, within the phylum Chordata. This thesis, which had already been suggested by MATSUMOTO (1929) and GISLÉN (1930), was accepted by EATON (1970) and favorably considered by BONE (1972). On the other hand, it has been the object of criticism and even rejection by numerous authors (DENISSON, 1971; NICHOLS, 1969; REGNÉLL, 1975; UBAGHS, 1970, 1971b, 1975; see also discussion in JEFFERIES, 1967, 1968a). It is true that this theory meets with many difficulties, particularly in view of the fact that the skeleton of the Stylophora is in every way comparable to that of the echinoderms. It is in fact inconceivable that such a skeleton whose characters are unique in the animal kingdom should have been associated with such soft parts as a notochord, muscle blocks, a dorsal nerve cord, a brain and cranial nerves more or less like those of fishes, that is, all features which belong to another phylum, namely that of Chordata. In general, it does not seem to be advisable to substitute for the simplest and most direct interpretation of the observed facts, a construction perhaps ingenious, but nevertheless with a basis whose elements are essentially hypothetical.

Crinozoa. This subphylum was introduced by MATSUMOTO in 1929. In proposing it for the cystoids, blastoids, and crinoids, MATSUMOTO only came back to the concept of LEUCKART (1848) who, 81 years earlier, had united two of these classes, the cystoids and crinoids, under the name of Pelmatozoa, literally signifying animals possessed of a stalk. The term "Crinozoa," therefore, was unnecessary; however, at the time of MATSUMOTO's writing the term Pelmatozoa had gradually lost its original meaning, because under this name in addition to the three above-mentioned classes, the edrioasteroids and the carpoids had also been included. It was undoubtedly because of a reaction to such usage that MATSUMOTO believed that it was necessary to replace the term Pelmatozoa with the new term Crinozoa.

This latter term is found in the classification of FELL (1962) and it was adopted in Parts S and U of the *Treatise* to include the Eocrinoidea, Lepidocystoidea, Paracrinoidea, Cystoidea, Edrioblastoidea, Blastoidea, Parablastoidea and Crinoidea. In other words, all echinoderms with radial symmetry, a stalk, a generally globular theca, and possessing feeding appendages called arms or brachioles were included.

During the last few years, several changes in this classification have been proposed. In 1968, PAUL suggested abandoning the class Cystoidea and elevated to class rank the two orders Rhombifera and Diploporita of which the class Cystoidea was usually composed. DURHAM (1971), on the other hand, retained the class Cystoidea, but added, in addition to the above-mentioned classes, the Edrioasteroidea and the Cyclocystoidea, although these forms have neither stalk, nor arms, nor brachioles. Although he didn't use the term, he thus returned to the older enlarged concept of Pelmatozoa. SPRINKLE (1973a), on the other hand, restricted the term Crinozoa solely to the Crinoidea and Paracrinoidea (the latter with some reservation) and proposed a new subphylum, Blastozoa, which comprises the Eocrinoidea, Parablastoidea, Blastoidea, and Rhombifera, that is, all groups whose representatives possess brachioles (not arms like the crinoids). In the absence of sufficient knowledge of their feeding appendages, he did not assign the Diploporita to any subphylum, he assigned Lepidocystoidea to the Eocrinoidea, and he incorporated the Edrioblastoidea in the Echinozoa.

BREIMER & UBAGHS (1974) proposed to retain all stalked echinoderms in a single subphylum and to return to the original concept and term "Pelmatozoa"; however, they recognized the necessity to separate the forms with brachioles or appendices which are morphologically equivalent from those which possess true arms. Inspired by a dualistic classification proposed by BURMEISTER (1856), they distinguished a superclass Cystoidea containing the classes Eocrinoidea, Rhombifera, Diploporita, and Blastoidea (including the Parablastoidea), and a superclass Brachiatoidea which contains only the class Crinoidea, and perhaps the enigmatic Middle Cambrian genus *Echmatocrinus*. The Paracrinoidea, whose origin and phylogenetic relationships are unknown, were left in an indeterminate position.

This classification has been criticized by SPRINKLE (1976), who considers that there is probably no fundamental unity in stalked echinoderms. For him, the known differences between arm-bearing and brachiole-bearing groups greatly outweigh the features in common, which could have arisen through parallel evolution. Therefore, he still favors his former division (1973) into a subphylum Blastozoa and a subphylum Crinozoa. He admits, however, that the class Diploporita probably belongs in the subphylum Blastozoa.

Finally, PARSLEY & MINTZ (1975), in the face of the difficulties of classifying the Paracrinoidea, created a subphylum Paracrinozoa, to be added to the two subphyla proposed by SPRINKLE (1973).

These modifications resulted no doubt from considerable progress made during the last few years in the knowledge of Paleozoic echinoderms and also from a better appreciation of the differences which distinguish the crinoids from other stalked echinoderms. But they also have their drawbacks. With so many and frequent changes, there is a risk of introducing instability into the classification. The term Crinozoa is used with different meanings. The terms Pelmatozoa and Cystoidea, which have a long tradition, have been abandoned without visible advantage. Finally, and most important, the multiplication of major units of equal rank has the consequence of obscuring the degrees of similarity that exist between the different classes of echinoderms, for obviously the stalked echinoderms are more similar to each other than to the echinoids or the asteroids.

Asterozoa. No important modifications have been introduced into the composition of this subphylum since the publication of Parts S and U of the *Treatise.*

Echinozoa. The classification adopted in Part U of the *Treatise* divided the subphylum Echinozoa into seven classes, named Helicoplacoidea, Holothuroidea, Ophiocistioidea, Cyclocystoidea, Edrioasteroidea, Camptostromatoidea, and Echinoidea. WEBBY (1968) and SPRINKLE (1973a) have added the class Edrioblastoidea (not recognized by BREIMER & UBAGHS, 1974), but this addition has been contested by MINTZ (1970), who regarded *Astrocystites* (the only representative of this group presently known) as a probable descendant of the eocrinoids and a member of the subphylum Blastozoa SPRINKLE. On the other hand, the assignment of some of these classes to the Echinozoa has been put in doubt. This applies particularly to the Helicoplacoidea (UBAGHS, 1971b, 1975) and the Edrioasteroidea (BELL, 1976).

As this brief review shows, no consensus exists in regard to the general classification of the echinoderms. On the contrary, profound differences are apparent, but this is only to be expected in matters which are so subjective. For this reason, the present writer, conscious of the necessity to stabilize the classification and not wanting to impose his personal preferences on a collective work such as the *Treatise,* has chosen to maintain in the following synopsis the four subphyla recognized in Parts S and U; however, some minor modifications and additions have been made in the contents of some of the subphyla.

Synopsis of Classification of Echinodermata

Subphylum Homalozoa Whitehouse, 1941.

Echinoderms without trace of radial symmetry; theca depressed, asymmetrical but showing varying degree of secondary bilateralization. *M.Cam.-M.Dev.*

Class Ctenocystoidea Robison & Sprinkle, 1969.

Body composed of a theca, without appendages; thecal outline nearly symmetrical; marginal and central plates usually differentiated; marginal frame two-layered, distinct; mouth in medial inferior face near anterior margin, with highly distinctive ctenoid (probably feeding) apparatus; anus near middle of posterior margin. *M. Cam.*

Class Stylophora Gill & Caster, 1960.

Body composed of a theca, and an armlike appendage (aulacophore), without peduncle (stele); mouth probably intrathecal, at or near proximal end of aulacophore; anus at opposite thecal extremity; aulacophore divided into 3 distinct regions. *M.Cam.-M.Dev.*

Order Cornuta Jaekel, 1901.

Theca with (generally strongly) asymmetrical outline; marginal thecal frame ordinarily well differentiated, commonly braced by a skeletal bar (zygal) on lower face; pores of various types generally present in upper right anterior area; aulacophore typically devoid of aboral spines. *M.Cam.-U.Ord.*

Order Mitrata Jaekel, 1918.

Theca with moderately asymmetrical to bilaterally symmetrical outline; marginal thecal frame slightly distinct from other thecal plates; no zygal; 1 or 2 pairs of pores may be present on lower or anterior thecal face; aulacophore typically with aboral spines or knobs. *L.Ord.-M.Dev.*

Class Homostelea Gill & Caster, 1960.

Body composed of a theca and a stele, without armlike appendage; thecal outline moderately asymmetrical; marginal frame one-layered, strongly differentiated; one large and one small orifice on margin opposite stele insertion; 1 or 2 epithecal marginal (?ambulacral) grooves leading to small orifice; stele not divided into several regions. *M.Cam.*

Class Homoiostelea Gill & Caster, 1960.

Body composed of a theca, a stele and an armlike appendage; theca moderately asymmetrical to almost bilaterally symmetrical; marginal frame usually not differentiated; mouth intrathecal, probably near proximal end of arm; anus commonly near left posterolateral margin; stele differentiated into 3 regions. *U.Cam.-L.Dev.*

Subphylum Crinozoa Matsumoto, 1929[1] (= Pelmatozoa Leuckart, 1848).

Radiate echinoderm typically attached throughout life or in young stage by a stalk inserted on aboral surface; viscera enclosed in a more or less globoid plated test or theca; mouth located at or near free pole of theca, exposed or covered by tegument; anus usually in adoral part of theca, never aboral; ambulacra acting as food grooves, extended distally onto projecting appendages (arms or brachioles). *L.Cam.-Holo.*

Class Eocrinoidea Jaekel, 1918.[2]

Crinozoa with biserial brachioles; theca globular, pyriform or flattened, generally made of numerous irregularly arranged plates, which may imbricate; sutural pores or epispires present or lacking; 2 to 5 ambulacral grooves confined to adoral end of theca and leading to erect brachioles; stem columnal bearing or irregularly multiplated, rarely absent. *L.Cam.-M.Ord., ?Sil.*

[Six orders have been recognized by Sprinkle (1973), but only one has been named.]

Order Imbricata Sprinkle, 1973 (= Class Lepidocystoidea Durham, 1967).

Aboral part of conical theca and holdfast composed of imbricate plates lacking epispires; adoral part composed of adjacent plates with numerous epispires. *L.Cam.*

Class Rhombifera Zittel, 1879.[2]

Crinozoa with biserial brachioles; globular pyriform or oval theca; exothecal or endothecal pore structures which consist of rhombic sets of thecal canals. *L.Ord.-U.Dev.*

Order Dichoporita Jaekel, 1899.

Rhombifera with endothecal pore structures composed of dichopores and only developed across certain plate sutures; theca comprising a small number of plates arranged in 3 to 5 circlets; well-developed stem throughout life. *L.Ord.-U.Dev.*

Order Fistuliporita Paul, 1968.

Rhombifera with exothecal pore structures composed of fistulipores and developed across all possible plate sutures; theca comprising a large number of randomly arranged plates; stem lost in adult or possibly totally absent in rare examples. *L.Ord.-U.Ord.*

Class Diploporita Müller, 1854.

Crinozoa with uniserial appendages (probably brachioles) very rarely preserved; globular or pyriform theca generally composed of a large

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[1] Breimer and Ubaghs (1974) have shown that the name Crinozoa Matsumoto, 1929, is a synonym of Pelmatozoa Leuckart, 1848, and thus superfluous. However, in order to preserve continuity with usage adopted in *Treatise* Part S, Dr. Ubaghs has agreed to give preference to the junior name in the present volume.—Curt Teichert.

[2] Sprinkle (1973) has erected a subphylum Blastozoa containing the classes Eocrinoidea, Rhombifera, Blastoidea, and Parablastoidea. Dr. Ubaghs feels that the validity of this concept is in need of further testing.—Curt Teichert.

number of randomly arranged plates; exothecal pore structures (diplopores) consist of single thecal canal; usually present on all thecal plates; stem present or lost in adult. *L.Ord.-M.Dev.*

Class Blastoidea Say, 1825.[1]

Crinozoa with biserial brachioles bordering ambulacral areas; well-developed pentameral symmetry; 17 major plates arranged in 3 circlets, in addition with 1 to 6 anal deltoids in *CD* interray; ambulacral system with underlying lancet plate; infolded thin-walled calcareous linear structures (hydrospires) on either side of each ambulacrum crossing plate suture. *Sil.-Perm.*

Order Fissiculata Jaekel, 1918.

Theca with exposed hydrospire slits or elongated spiracle (spiracular slit). *Sil.-Perm.*

Order Spiraculata Jaekel, 1918.

Theca with hidden hydrospire slits, spiracles, and hydrospire pores. *Sil.-Perm.*

Class Parablastoidea Hudson, 1907.[1]

Crinozoa with biserial brachioles bordering ambulacral areas; well-developed pentameral symmetry; theca blastoid-like with many regularly arranged plates; ambulacral areas composed of biserially arranged plates, without lancet plates; deltoids particularly prominent; external cataspire slits developed only through deltoids (not across plate suture). *L.Ord.-M.Ord.*

Class Paracrinoidea Regnéll, 1945.[2]

Crinozoa with typically uniserial, free or recumbent food-gathering appendages bearing uniserial side branches arranged in single row; theca boxlike, many-plated, asymmetrical, but tending to become bilaterally (rather than radially) symmetrical; peristome and column offset; with or without internally opening transverse sutural slits that variously extend through thickness of plates but do not open to exterior or connect with neighboring slits. *M.Ord.-U.Ord., ?Sil.*

Class Crinoidea Miller, 1821.

Crinozoa provided with true arms; pentameral symmetry well developed; theca divided into aboral cup and adoral tegmen, comprising 5 radial plates from which invariably the aboral skeleton of the arms starts; radial growth pattern concentrated on arms, which are directed away from theca; column ordinarily well developed, lost in postlarval stage in some forms. *M.Cam.; L.Ord.-Holo.*

Subclass Echmatocrinea Sprinkle & Moore, new subclass.[3]

Primitive Crinoidea with irregularly plated cup; no stem, cup attached to substrate by irregularly plated holdfast; 8 to 10 short, uniserial arms, 10 to 12 heavily plated brachials per arm bearing short, soft appendages; tegmen not known. *M.Cam.*

Order Echmatocrinida Sprinkle & Moore, new order.

Characters of subclass. *M.Cam.*

Subclass Camerata Wachsmuth & Springer, 1885.

Crinoidea with thecal plates typically united by rigid sutures; aboral cup generally including fixed brachials, interbrachials, and anal plates; tegmen usually strong, concealing mouth; arms typically pinnulate. *L.Ord.-U.Perm.*

Order Diplobathrida Moore & Laudon, 1943.

Camerata with dicyclic base. *M.Ord.-U.Ord.; M.Sil.-L.Carb.*

Order Monobathrida Moore & Laudon, 1943.

Camerata with monocyclic base. *?L.Ord.; M.Ord.-U.Perm.*

Subclass Inadunata Wachsmuth & Springer, 1885.

Crinoidea with aboral cup composed of close-sutured plates; fixed brachials and interbrachials lacking (exception in a few primitive forms); anal plates commonly present in aboral cup; mouth subtegminal; arms pinnulate or nonpinnulate. *L.Ord.-U.Perm.; M.Trias.*

Order Disparida Moore & Laudon, 1943.

Monocyclic inadunates with weak to very prominent bilateral symmetry developed in planes other than through *A* ray and *CD* interray; radials commonly compound; arms typically nonpinnulate. *L.Ord.-U.Perm.*

Order Hybocrinida Jaekel, 1918.

Monocyclic inadunates, with undivided radials; radianal present; arms 5, uniserial, atomous, nonpinnulate, that may be lacking in *B* and *E* rays, or are recumbent or reduced to ambulacral grooves on cup plates. *L.Ord.-U.Ord.*

Order Coronata Jaekel, 1918.

Monocyclic inadunates, with highly pentamerous theca; tegmen composed of 5 peristomials, 5 interradially located large plates (?orals), and 10 elongated plates covering ambulacrum; no anal plates; radials and tegminal interradially located plates prolonged adorally into high coronal processes; arms attached to adoral end of each radial plate, with fixed small primaxil. *M.Ord.-U.Ord.; M.Sil.-U.Sil.*

Order Cladida Moore & Laudon, 1943.

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[1] See footnote 2 on p. *T362.*

[2] Parsley & Mintz (1975) set aside this class as a new subphylum, Paracrinozoa.

[3] Although, according to Sprinkle (1973), these forms may possibly be related to the original stocks of crinoids, in my view the structure of the only known single genus and species of this subclass does not correspond to the definition of a crinoid.—G. Ubaghs.

Dicyclic inadunates, having mostly 3, 2, or 1 anal plate in cup, rarely none; anal sac generally prominent; arms branched or unbranched, nonpinnulate or pinnulate. *L. Ord.-U.Perm.; M.Trias.*

Subclass Flexibilia Zittel, 1895.

Crinoidea with cup plates mostly not rigidly united; aboral cup ordinarily including fixed brachials, interbrachials, and anal plates; tegmen flexible, with exposed mouth and food grooves; arms uniserial, nonpinnulate. *M.Ord.; L.Sil.-U.Perm.*

Order Taxocrinida Springer, 1913.

Flexibilia with elongate crown and relatively weak calyx; anal *X* not closely united to adjacent plates, and followed by series of anals bordered by many-plated tegument. *M.Ord.; L.Sil.-U.Penn.*

Order Sagenocrinida Springer, 1913.

Flexibilia with crown generally subglobular; calycal plates rather firmly united; anal *X* joined by close suture to adjacent plates; no series of anals bordered by many-plated tegument. *L.Sil.-U.Perm.*

Subclass Articulata Zittel, 1879.

Crinoidea with dicyclic or generally cryptodicyclic cup; basals generally small, reduced or even missing in some cases; no anal plates or compound radials in postlarval stage; tegmen flexible, with exposed mouth and ambulacral grooves; arms uniserial and pinnulate; articulations between radial and arm and between some or all brachials muscular; radials and brachials perforate. *L.Trias.-Holo.*

Order Millericrinida Sieverts-Doreck, in Moore, Lalicker, & Fischer, 1952.

Cup large, with 5 basals and 5 radials; infrabasals generally missing; fixed brachials and interbrachials may be present; column without nodals and cirri; articular face of columnals entirely covered with crenulae; proximal part of column commonly modified, 5 sided, or circular and forming a conical transition to cup; proximale incorporated in cup ordinarily present. *M. Trias.; L.Jur.-L.Cret.; L.Paleoc.; Holo.*

Order Cyrtocrinida Sieverts-Doreck, in Moore, Lalicker, & Fischer, 1952.

Cup composed of stout radials, with or without aboral part interpreted as fused basals or as proximale, and articulated to short column or directly to attachment disc; no cirri; arms short, commonly protected by interradial projections from cup or by stout proximal brachials. *L.Jur.-Mio.; Holo.*

Order Bourgueticrinida Sieverts-Doreck, 1953.

Cup small, lacking infrabasals; basals and radials united by closed sutures or fused. Columnals circular or elliptical in cross section, with synarthrial articulations; variable number of proximal columnals united by synostosis or fused to a proximale incorporated in cup; no cirri. *U.Cret.-L.Paleoc., ?M.Paleoc.; Eoc.-Mio.; Holo.*

Order Isocrinida Sieverts-Doreck, in Moore, Lalicker, & Fischer, 1952.

Cup rather small, dicyclic, cryptodicyclic, or lacking infrabasals; radial facet wide; column generally long, pentalobate, pentagonal or circular in cross section; nodals and cirri invariably present; no proximale. *L.Trias.-Mio.; Holo.*

Order Comatulida A. H. Clark, 1908.

Larval column typically obliterated except for cirriferous uppermost columnal or fused uppermost columnals enlarging and forming centrodorsal incorporated in cup. *L.Jur.-L.Paleoc.; Eoc.-Holo.*

Order Uintacrinida Broili in von Zittel, 1921.

Cup stemless, very large, spheroidal, composed of thin plates including centrale; no cirri or attachment organ; infrabasals may be present; proximal brachials and interbrachials incorporated in cup; arms very long. *U.Cret.*

Order Roveacrinida Sieverts-Doreck, in Moore, Lalicker, & Fischer, 1952.

Cup stemless, very small, composed of radials, small discrete or fused basals, and in some specimens, a centrale; arms well developed or absent. *M.Trias.-U.Trias.; U.Jur.-U.Cret.*

Subphylum Asterozoa Haeckel in Zittel, 1895.

Free-living radiate echinoderms in which a radially divergent pattern of growth produces projecting rays and star-shaped body; mouth on underside. *L.Ord.-Holo.*

Class Stelleroidea Lamarck, 1816.

Characters of subphylum. *L.Ord.-Rec.*

Subclass Somasteroidea Spencer, 1951.

Asterozoans with shallow ambulacral channel formed by double series of ambulacrals, each of which typically gives rise to transverse series (metapinnules) of rodlike ossicles (virgalia); radial water vessel enclosed to varying extent between ambulacrals. *L.Ord.-Holo.*

Order Goniactinida Spencer, 1951.

Characters of subclass. *L.Ord.-Rec.*

Subclass Asteroidea de Blainville, 1830.

Asterozoans with relatively broad, hollow arms which contain large lobes of body cavity and enclosed organs; arms normally not separated from central disc; radial water vessel on outside of ambulacral skeleton. *L.Ord.-Holo.*

Order Platyasterida Spencer, 1951.

Ambulacrals, adambulacrals and inferomarginals in regular transverse series recalling metapinnules. *M.Ord.-Holo.*

Order Paxillosida Perrier, 1884.

Mouth frame of adambulacral type; mouth-angle prominent; marginal frame (when present) separated from mouth frame by interradial areas with small ossicles; dorsal side usually covered with paxillae. *L.Ord.-Holo.*

Order Valvatida Perrier, 1884.

Mouth frame of adambulacral type; mouth-angle plate relatively inconspicuous; infero- and superomarginals (if present) normally equal in number and without intermarginal channels. *L.Ord.-Holo.*

Order Spinulosida Perrier, 1884.

Mouth frame of adambulacral type; mouth-angle plate prominent, not keeled; marginal frame ordinarily wanting; aboral skeleton reticulate, imbricate or absent; dorsal and oral sides with spines, mostly in groups on prominences from plates; simple pedicellariae may be present. *M.Ord.-Holo.*

Order Forcipulatida Perrier, 1884.

Mouth frame of ambulacral type; marginal plates generally inconspicuous; typical pedicellariae, when present, straight or crossed; disc generally small; arms ordinarily elongated, with rounded sides. *L.Ord.-Holo.*

Subclass Ophiuroidea Gray, 1840.

Asterozoans with slender, simple or branched arms sharply separated from disc, and typically supported by internal row of ambulacral ossicles; generally without open ambulacral groove; respiration by means of gills typically located in interrays. *L.Ord.-Holo.*

Order Stenurida Spencer, 1951.

Basins for tube feet shared, usually subequally, by 2 ambulacrals; buccal slits commonly present. *L.Ord.-U.Dev.*

Order Oegophiurida Matsumoto, 1915.

No oral or radial shields, dorsal or ventral arm plates, genital plates or bursae; disc covered by skin or imbricating scales; narrow frame at disc margin may be present; gastric coeca entering arms. *L.Ord.-Holo.*

Order Phrynophiurida Matsumoto, 1915.

Disc and arms covered with skin; radial shields and genital plates articulating by simple facet or transverse ridge; peristomial plates large; oral frame entire, without well-developed lateral wings; dorsal and ventral arm plates absent or rudimentary; lateral arm plates small, occupying only lower side edge of arms; ambulacrals with hourglass-shaped articulations. *L.Dev.-Holo.*

Order Ophiurida Müller & Troschel, 1840.

Radial shields, genital plates, and buccal shields generally present; ambulacral groove closed by growth of lateral arm plates on ventral side toward midline of arms; ambulacrals opposite and fused in pairs; dorsal and ventral arm plates typically present; ambulacrals with zygospondylous articulations. *Sil.-Holo.*

Subphylum Echinozoa Haeckel in Zittel, 1895.

Echinoderms mostly radiate, with globoid, cylindroid, or discoid body that typically lacks arms, brachioles, or outspread rays. *L.Cam.-Holo.*

Class Helicoplacoidea Durham & Caster, 1963.

Free-living nonradiate echinoderms with helically organized fusiform to pyriform test; mouth at one end of body. *L.Cam.*

Subclass Helicoplacida Durham & Caster, 1963.

Test built of columns of plates. *L.Cam.*

Subclass Polyplacida Durham, 1967.

Test built of mosaic of small plates. *L.Cam.*

Class Camptostromatoidea Durham, 1966.

Apparently medusaeform, radially symmetrical echinoderms with plated appendages attached to periphery of test; mouth and anus at opposite poles; sutural pores abundant except on region of aboral pole. *L.Cam.*

Class Edrioasteroidea Billings, 1858.

Sedentary radiate (generally quinqueradiate) echinoderms, with domal, clavate, or globose polyplated theca that lacks stalk; ambulacra endothecal, formed by floor plates and cover plates; anus on adoral surface. *L.Cam.-U.Penn.*

Order Stromatocystitoidea Termier & Termier, 1969.

Domal or semiconvex theca; aboral surface plated (at least in some genera); adoral surface ordinarily with frame of submarginal or (?) marginal plates; skirt of small plates forming margin may be present; ambulacra limited to adoral surface, with biserial floor plates and sutural passageways; interambulacral plates small, numerous, stellate with many sutural pores. *L.Cam.-M.Cam., ?U.Dev.*

Order Isophorida Bell, 1976.

Domal or clavate theca; aboral surface nonplated; ambulacra ordinarily limited to adoral surface, with uniserial floor plates, without sutural passageways; oral frame formed by proximal floor plates; cover plates with intraambulacral and/or intrathecal extensions. *M.Ord.-U.Penn.*

Order Edrioasterida Bell, 1976.

Edrioasteroidea with semigloboid theca; plated adoral surface extending below ambitus onto aboral side of theca; ambulacra passing onto aboral surface; ambulacral floor plates biserial with sutural passageways; cover plates without intraambulacral or intrathecal extensions. *M.Ord.*

Class Edrioblastoidea Fay, 1962.

Calyx made of numerous plates arranged into circlets, provided with a 5-part stem; quinqueradiate symmetry well developed; most large calycal plates with sutural indentations apparently penetrating to calyx interior; ambulacra 5, long, composed of halves representing deltoid limbs; food groove flanked by rows of pores and covered by biserial set of cover plates. *M.Ord.*

Class Cyclocystoidea Miller & Gurley, 1895.

Disk-shaped body with submarginal frame of thick, ornamented plates, enclosing central areas covered by thinly plated membranes, and with skirt of small plates around margin; sutural pores present on one central area; submarginal plates provided with large cuplike pores and small inner canals leading to interior of body. *M.Cam.-M.Dev.*

Class Ophiocistioidea Sollas, 1899.

Free-living quinqueradiate echinoderms with plated aboral face and plated or nonplated adoral face; peristome central, with 5 jaws; ambulacra confined to adoral face, composed of 3 plate columns; interambulacra with single plate column; appendages (? gigantic podia) located on adoral face, covered by imbricated scales; periproct aboral, not opposite peristome. *L.Ord.-L.Carb.*

Class Echinoidea Leske, 1778.

Free-living quinqueradiate echinoderms with plated test, bearing movable appendages (spines, pedicellariae, spheridia) externally; mouth directed toward substrate, primarily with, secondarily without masticatory apparatus; 2 principal systems of plates, 1) an apical system invariably including 5 ocular plates and 5 or fewer genital plates; 2) a coronal system composed of 5 ambulacral and 5 interambulacral areas, each one composed of 1, 2, or more meridional columns; ambulacral plates perforated for passage of tube feet. *Ord.-Holo.*

Subclass Perischoechinoidea M'Coy, 1849.

Ambulacrum composed of 2 to many columns; interambulacrum with 1 to many columns; ambulacral plates not compound; anus within apical system (endocyclic); perignathic girdle absent or composed of apophyses only. *M.Ord.-Holo.*

Order Bothriocidaroida Zittel, 1879.

Test rigid, plates not imbricating; ambulacrum of 2 columns, interambulacrum with single column; no genital plates. *Ord.*

Order Echinocystitoida Jackson, 1912.

Test flexible, plates strongly imbricating; ambulacral plates bevel under interambulacra; ambulacrum of 2 or more columns; interambulacrum of more than 2 columns. *U.Ord.-Perm.*

Order Palaechinoida Haeckel, 1866.

Test rigid, plates slightly imbricating; ambulacral plates bevel over interambulacrum; interambulacrum of 1 or more than 2 columns. *Sil.-Perm.*

Order Cidaroida Claus, 1880.

Test rigid or flexible; ambulacra conspicuously narrower than interambulacra; primary interambulacral tubercles conspicuous; ambulacrum of 2 columns, interambulacrum of 2 or more columns. *?Sil., U.Dev.-Holo.*

Subclass Euechinoidea Bronn, 1860.

External gills present or lost; ambulacrum and interambulacrum of 2 columns each; anus within apical system (endocyclic) or outside apical system (exocyclic); complete perignathic girdle present or lost. *?Carb., U.Trias.-Holo.*

Superorder Diadematacea Duncan, 1889.

Primary tubercles perforate; lantern with unkeeled teeth; perignathic girdle complete; gill slits present. *?Carb., U.Trias.-Holo.*

Order Echinothurioida Claus, 1880.

Test flexible; anus endocyclic; spines with hollow axis; ambulacral plates simple on peristome, compound in test; *U.Jur.-Rec.*

Order Diadematoida Duncan, 1889.

Test rigid or flexible; anus endocyclic; spines with axis; peristomial membrane with 10 buccal plates; ambulacrals simple or compound. *?L.Carb., U.Trias.-Holo.*

Order Pedinoida Mortensen, 1939.

Test rigid; anus endocyclic; spines with solid axis; peristomial membrane with 10 buccal plates; ambulacrals simple to compound. *U.Trias.-Holo.*

Order Pygasteroida Durham & Melville, 1957.

Similar to Pedinoida, but with anus exocyclic and consistently simple ambulacral plates. *L.Jur.-U.Cret.*

Superorder Echinacea Claus, 1876.

Test rigid; anus endocyclic; spines with solid axis; teeth keeled; perignathic girdle complete; gill slits present. *U.Trias.-Rec.*

Order Salenioida Delage & Hérouard, 1903.

Lantern stirodont; ambulacral plates simple or compound in diadematoid manner; apical system with one or more suranal plates; each interambulacral plate with single, large, usually crenulate, primary tubercle. *?U.Trias., L.Jur.-Holo.*

Order Hemicidaroida Beurlen, 1937.

Lantern stirodont; ambulacral plate diadematoid, simple adapically in some; primary tubercles perforate, mostly crenulate. *U.Trias.-U.Cret.*

Order Phymosomatoida Mortensen, 1904.

Lantern stirodont; ambulacral plates simple throughout or more usually diadematoid; primary tubercles inperforate. *L.Jur.-Holo.*

Order Arbacioida Gregory, 1900.

Lantern stirodont; test commonly with prominences simulating tubercles; ambulacral plates simple or arbacioid; primary tubercles imperforate, noncrenulate; periproct with conspicuous anal valves. *M.Jur.-Holo.*

Order Temnopleurida Mortensen, 1942.

Lantern camarodont; test usually sculptured, if not, gill slits deep; ambulacral plates compound, diadematoid or echinoid. *L.Jur.-Holo.*

Order Echinoida Claus, 1876.

Lantern camarodont; test not sculptured; ambulacral plates echinoid; gill slits shallow. *?U.Cret., Paleoc.-Holo.*

Order Plesiocidaroida Duncan, 1889.

Lantern unknown; apical system very large; gill slits absent (or indistinct); tubercles small, noncrenulate. *U.Trias.*

Superorder Gnathostomata Zittel, 1879.

Test rigid; anus exocyclic; lantern and girdle usually present in adult, with keeled teeth; apical system and peristome approximately opposite; spines hollow; primary tubercles usually perforate and crenulate. *L.Jur.-Holo.*

Order Holectypoida Duncan, 1889.

Ambulacra petaloid or not; narrower than interambulacra; apical system with genital plates fused or distinct; teeth with lateral flanges; anus supramarginal to inframarginal. *L.Jur.-Holo.*

Order Clypeasteroida A. Agassiz, 1872.

Ambulacra petaloid, as wide or wider than interambulacra on adoral surface; apical system with genital plates fused; lantern without compass; teeth without lateral flanges; small accessory tube feet outside of petals. *U.Cret.-Holo.*

Superorder Atelostomata Zittel, 1879.

Test rigid; anus exocyclic; lantern, girdle and gill slits absent in adult; apical system and peristome rarely opposite; primary spines hollow. *L.Jur.-Holo.*

Order Cassiduloida Claus, 1880.

Ambulacra petaloid adapically; phyllodes and bourrelet usually present; fascioles absent. *L.Jur.-Holo.*

Order Holasteroida Durham & Melville, 1957.

Apical system typically elongate or disjunct; no genitals; paired petals not impressed; plastron lacking to meridosternous; no floscelle. *L.Jur.-Holo.*

Order Spatangoida Claus, 1876.

Apical system compact; plastron amphisternous; phyllodes present, but no bourrelets; fascioles generally present. *L.Cret.-Holo.*

Order Neolampadoida Philip, 1963.

Apical system mono- or tetrabasal; ambulacra nonpetaloid, with pores simple or lacking adapically; floscelle absent or weakly developed. *U.Eoc.-Holo.*

Superorder Uncertain.

Order Orthopsida Mortensen, 1942.

Lantern camarodont; test rigid; ambulacral plates simple or with a few triads; tubercles perforate, noncrenulate. *L.Jur.-U.Cret.*

Class Holothuroidea de Blainville, 1834.

Echinoderms mostly free-living, usually with body elongated in oral-aboral axis and secondary bilateral symmetry; mouth encircled by tentacles; pharynx surrounded by calcareous ring; ambulacral grooves lacking; skeleton ordinarily consisting of microscopic sclerites embedded in body wall; gonad single. *Ord.-Holo.*

Subclass Dendrochirotacea Brandt, 1835.

Tentacles without ampullae; pharyngeal retractor muscles present; podia and respiratory trees usually present; madreporite free in body cavity. *Ord.-Holo.*

Order Dendrochirotida Brandt, 1835.

Tentacles richly branched, 10 to 30 in number. *Ord.-Holo.*

Order Dactylochirotida Pawson & Fell, 1965.

Tentacles digitiform or digitate 8 to 30 in number; body enclosed by a test comprising imbricate plates. *Holo.*

Subclass Aspidochirotacea Brandt, 1835.

Tentacles shield-shaped, 10 to 30 in number; pharyngeal retractor muscles wanting; body with conspicuous bilateral symmetry. *L.Carb.-Holo.*

Order Aspidochirotida Brandt, 1835.

Respiratory trees present. *L.Carb.-Holo.*

Order Elasipodida Theel, 1882.

Respiratory trees lacking. *Dev.-Holo.*

Subclass Apodacea Brandt, 1835.

Tentacles simple, digitate or pinnate; podia reduced, or, more usually, lacking; pharyngeal retractor muscles lacking; sclerites comprising anchor and anchor plates. *Miss.-Holo.*

Order Apodida Brandt, 1835.

Body cylindrical; respiratory trees and anal papillae lacking; deposits commonly including wheels. *Miss.-Holo.*

Order Molpadiida Müller, 1850.

Body fusiform, commonly with tapering caudal portion; respiratory trees present; wheels lacking. *Miss.-Holo.*

Subclass Undeterminate.

Order Arthrochirotida Seilacher, 1961.

Tentacles with articulated axial skeleton; sclerites stout and imperforate. *L.Dev.*

OUTLINE OF CLASSIFICATION OF CRINOIDEA

The following outline of the Crinoidea summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each supra-generic group from class to subfamily. A single number refers to genera; where two numbers are given; the second indicates subgenera additional to nominotypical ones.

Main Divisions of Crinoidea

Crinoidea *(class)* (1009;6). *M.Cam.; L.Ord.-Holo.*
  Echmatocrinea *(subclass)* (1). *M.Cam.*
    Echmatocrinida *(order)* (1). *M.Cam.*
      Echmatocrinidae (1). *M.Cam.*

  Camerata *(subclass)* (209;2). *L.Ord.-U.Perm.*
    Diplobathrida *(order)* (52). *M.Ord.-U.Ord.; M.Sil.-L.Carb.*

      Zygodiplobathrina *(suborder)* (2). *M.Ord.; L.Dev.*

Cleiocrinidae (1). *M.Ord.*
Spyridiocrinidae (1). *L.Dev.*
Eudiplobathrina *(suborder)* (50). *M.Ord.-U.Ord.; M.Sil.-L.Carb.*
Rhodocrinitacea *(superfamily)* (37). *M.Ord.-U.Ord.; M.Sil.-L.Carb.*
Reteocrinidae (3). *M.Ord.-U.Ord.*
Opsiocrinidae (1). *M.Dev.*
Archaeocrinidae (5). *M.Ord.-U.Ord.*
Anthracocrinidae (3). *M.Ord.*
Anthemocrinidae (2). *M.Sil.-U.Sil.*
Rhodocrinitidae (21). *M.Ord.-U.Ord.; M.Sil.; L.Dev.-L.Carb.*
Family Uncertain (2). *M.Sil.*
Dimerocrinitacea *(superfamily)* (12). *U.Ord.; M.Sil.-U.Dev.*
Dimerocrinitidae (8). *U.Ord.; M.Sil.-U.Dev.*
Lampterocrinidae (2). *M.Sil.*
Gazacrinidae (1). *M.Sil.*
Orthocrinidae (1). *L.Dev.-M.Dev.*
Nyctocrinacea *(superfamily)* (1). *M.Sil.*
Nyctocrinidae (1). *M.Sil.*
Monobathrida *(order)* (145;2). *?L.Ord., M.Ord.-U.Perm.*
Compsocrinina *(suborder)* (91). *?L.Ord., U.Ord.-U.Perm.*
Xenocrinacea *(superfamily)* (5). *?L.Ord., U.Ord.; U.Sil.*
Xenocrinidae (1). *U.Ord.*
Tanaocrinidae (3). *?L.Ord., U.Ord.*
Abacocrinidae (1). *U.Sil.*
Periechocrinacea *(superfamily)* (39). *Sil., ?L.Perm.-U.Perm.*
Periechocrinidae (14). *Sil.-Miss.*
Paragaricocrinidae (4). *U.Carb.; U.Perm.*
Amphoracrinidae (3). *L.Carb.(Tournais.)-U.Carb.(Namur.).*
Actinocrinitidae (18). *L.Carb.(L.Miss.)-U.Carb., ?Perm.*
Actinocrinitinae (7). *L.Carb.(L.Miss.)-U.Carb., ?Perm.*
Eumorphocrininae (4). *L.Carb.*
Cactocrininae (5). *L.Carb.*
Physetocrininae (2). *L.Carb.*
Carpocrinacea *(superfamily)* (22). *M.Sil.-U.Sil.; M.Dev.-L.Carb.*
Carpocrinidae (7). *M.Sil.-U.Sil.; M.Dev.*
Batocrinidae (10). *L.Miss.-U.Miss.*
Coelocrinidae (4). *M.Dev.-L.Miss.(Osag.).*
Family Uncertain (1). *L.Miss.*
Hexacrinitacea *(superfamily)* (25). *U.Sil.-U.Perm.*
Hexacrinitidae (5). *U.Sil.-U.Dev., ?Penn.*
Parahexacrinidae (3). *L.Dev.*
Dichocrinidae (7). *L.Miss.-U.Perm.*
Acrocrinidae (10). *L.Miss.-U.Penn., Up.L.Carb.-M.Carb.*
Acrocrininae (3). *U.Miss.(Chester.) or up.L.Carb.(Visean)-L.Penn.(Morrow.).*
Planacrocrininae (1). *L.Penn.(Morrow.).*
Globacrocrininae (6). *L.Miss.-U.Penn.(Missour.).*
Glyptocrinina *(suborder)* (54;2). *M.Ord.-U.Perm.*
Glyptocrinacea *(superfamily)* (3). *M.Ord.-U.Sil.*
Glyptocrinidae (3). *M.Ord.-U.Sil.*
Melocrinitacea *(superfamily)* (10). *U.Ord.-U.Dev.*
Scyphocrinitidae (3). *?L.Sil., U.Sil.-L.Dev.*
Paramelocrinidae (1). *U.Sil.*
Melocrinitidae (5). *U.Ord.-U.Dev.*
Family Uncertain (1). *M.Sil.(Niagaran).*
Eucalyptocrinitacea *(superfamily)* (13). *M.Sil.-M.Dev.*
Clonocrinidae (2). *U.Sil.-L.Dev.*
Eucalyptocrinitidae (2). *M.Sil.-M.Dev.*
Dolatocrinidae (4). *L.Dev.-M.Dev.*
Polypeltidae (4). *U.Sil.-L.Dev.*
Family Uncertain (1). *M.Sil.*
Patelliocrinacea *(superfamily)* (8). *U.Ord.-M.Dev.*
Stelidiocrinidae (1). *U.Sil.*
Patelliocrinidae (7). *U.Ord.-M.Dev.*
Platycrinitacea *(superfamily)* (20;2). *?U.Ord., Sil.-Perm.*
Marsupiocrinidae (1;2). *M.Sil.-L.Dev.*
Hapalocrinidae (12). *?U.Ord., Sil.-M.Dev., ?U.Perm.*
Platycrinitidae (7). *?U.Sil., Dev.-Perm.*
Order, Suborder, Superfamily, and Family Uncertain (12). *M.Ord.-L.Dev.; Miss.; M.Penn.*
Inadunata *(subclass)* (482). *L.Ord.-U.Perm.; M.Trias.*
Disparida *(order)* (93). *L.Ord.-U.Perm.*
Homocrinacea *(superfamily)* (6). *M.Ord.-U.Ord.; M.Sil.*
Homocrinidae (6). *M.Ord.-U.Ord.; M.Sil.*
Calceocrinacea *(superfamily)* (15). *M.Ord.-L.Miss.; L.Perm.*
Calceocrinidae (15). *M.Ord.-L.Miss.; L.Perm.*
Pisocrinacea *(superfamily)* (6). *M.Sil.(Wenlock., Niagaran)-U.Dev.(Chemung.).*
Pisocrinidae (6). *M.Sil.-U.Dev.*
Allagecrinacea *(superfamily)* (23). *Ord.; ?Sil., Dev.-Perm.*
Allagecrinidae (9). *U.Dev.-U.Perm.*
Catillocrinidae (11). *L.Ord.; M.Dev.; L.Miss.-M.Penn.; U.Perm.*
Anamesocrinidae (1). *M.Dev.*
Haplocrinitidae (1). *?Sil., Dev., ?L.Carb.*
Tunguskocrinidae (1). *Ord.*
Heterocrinacea *(superfamily)* (7). *M.Ord.(Mohawk.)-U.Ord.(Cincinnat.).*
Heterocrinidae (7). *M.Ord.(Mohawk.)-U.Ord.(Cincinnat.).*
Myelodactylacea *(superfamily)* (11). *L.Ord.-L.Dev., ?U.Dev.*
Myelodactylidae (5). *L.Sil.-L.Dev.(Helderberg.), ?U.Dev.(Chemung.).*
Iocrinidae (2). *?L.Ord., M.Ord.-U.Ord.*
Eustenocrinidae (4). *L.Ord.-M.Ord.*
Anomalocrinacea *(superfamily)* (3). *M.Ord.-U.Ord.*

Anomalocrinidae (3). *M.Ord.-U.Ord.*
Belemnocrinacea *(superfamily)* (18). *M.Sil.-U.Carb.; U.Perm.*
Belemnocrinidae (2). *L.Miss.(Osag.).*
Holynocrinidae (1). *M.Dev.*
Perissocrinidae (3). *M.Dev.*
Pygmaeocrinidae (2). *U.Sil.-M.Dev.*
Synbathocrinidae (7). *M.Sil.-U.Carb.; U.Perm.*
Zophocrinidae (3). *U.Sil.-M.Dev.*
Perittocrinacea *(superfamily)* (2). *Up.L.Ord. or low.M.Ord.*
Perittocrinidae (2). *Up.L.Ord. or low.M.Ord.*
Superfamily Uncertain (2). *L.Ord., U.Perm.*
Paradoxocrinidae (1). *U.Perm.*
Family Uncertain (1). *L.Ord.*
Hybocrinida *(order)* (7). *L.Ord.-U.Ord.*
Hybocrinidae (3). *M.Ord.*
Baerocrinidae (1). *L.Ord.-M.Ord.*
Hybocystitidae (1). *M.Ord.*
Cornucrinidae (2). *M.Ord.-U.Ord.*
Coronata *(order)* (5). *M.Ord.-U.Ord.; M.Sil.-U.Sil.*
Stephanocrinidae (5). *M.Ord.-U.Ord.; M.Sil.-U.Sil.*
Cladida *(order)* (377). *L.Ord.(Tremadoc.)-U.Perm.; M.Trias.*
Cyathocrinina *(suborder)* (77). *M.Ord.-U.Perm.*
Cyathocrinitacea *(superfamily)* (18). *M.Ord.-U.Miss.; U.Perm.*
Cyathocrinitidae (4). *?M.Ord.; M.Sil.-L.Miss.; U.Perm.*
Barycrinidae (3). *L.Dev.(Ems.); L.Miss.(Osag.)-U.Miss.(Meramec.).*
Euspirocrinidae (7). *M.Ord.(Mohawk.)-L.Carb.(Tournais.).*
Lecythocrinidae (4). *M.Dev.(Givet.)-L.Miss.(Osag.).*
Gasterocomacea *(superfamily)* (21). *M.Ord.(Blackriver.)-U.Ord.; M.Sil.-M.Dev. (Givet.).*
Gasterocomidae (7). *L.Dev.-M.Dev.*
Sphaerocrinidae (3). *M.Ord.; M.Sil.; M.Dev.*
Porocrinidae (2). *M.Ord.(Mohawk.)-U.Ord.(Richmond.).*
Carabocrinidae (1). *M.Ord.-U.Ord.*
Crotalocrinitidae (7). *M.Sil.-M.Dev.(Givet.).*
Petalocrinidae (1). *M.Sil.(Niagaran, Wenlock.).*
Codiacrinacea *(superfamily)* (36). *M.Sil.; L.Dev.-U.Perm.*
Codiacrinidae (18). *M.Sil.; L.Dev.-M.Dev.; L.Miss.-U.Perm.*
Codiacrininae (13). *M.Sil.; L.Dev.-M.Dev.; L.Miss.-U.Perm.*
Bolbocrininae (2). *L.Perm.-U.Perm.*
Thetidicrininae (3). *L.Carb.(Tournais.); U.Perm.*
Sycocrinitidae (5). *L.Carb.(Tournais.); L.Perm.-U.Perm.*
Streblocrinidae (13). *M.Dev.-U.Perm.*
Streblocrininae (7). *M.Dev.-L.Penn.; Perm.*
Pentececrininae (6). *?U.Dev., L.Miss.-L.Penn.; L.Perm.-U.Perm.*
Superfamily and Family Uncertain (2). *M.Sil.; L.Dev.*
Dendrocrinina *(suborder)* (46). *L.Ord.-L.Miss.*
Dendrocrinacea *(superfamily)* (19). *M.Ord.-U.Dev.*
Dendrocrinidae (7). *M.Ord.-U.Dev.*
Botryocrinidae (12). *?M.Ord.; M.Sil.-U.Dev.*
Mastigocrinacea *(superfamily)* (19). *L.Ord.-M.Ord.; M.Sil.-L.Miss.*
Aethocrinidae (1). *L.Ord.(Tremadoc.-Arenig.).*
Thenarocrinidae (1). *M.Sil.*
Mastigocrinidae (17). *M.Ord.; M.Sil.-L.Miss.*
Merocrinacea *(superfamily)* (7). *?L.Ord., M.Ord.-U.Ord.; U.Sil.-L.Dev.*
Merocrinidae (1). *M.Ord.-U.Ord.*
Cupulocrinidae (1). *M.Ord.-U.Ord.*
Ontariocrinidae (1). *M.Ord.*
Ottawacrinidae (1). *?L.Ord., M.Ord., ?U.Ord.*
Metabolocrinidae (3). *M.Ord., U.Sil.-L.Dev.*
Superfamily and Family Uncertain (1). *?M.Dev.*
Poteriocrinina *(suborder)* (251). *L.Dev.-U.Perm.; M.Trias.*
Poteriocrinitacea *(superfamily)* (5). *L.Dev.-L.Penn., ?M.Penn.-?U.Perm.*
Poteriocrinitidae (5). *L.Dev.-L.Penn., ?M.Penn.-?U.Perm.*
Rhenocrinacea *(superfamily)* (10). *L.Dev.-U.Miss.; M.Penn.*
Rhenocrinidae (9). *L.Dev.-U.Miss.; M.Penn.(Atokan).*
Proctothylacocrinidae (1). *M.Dev.*
Scytalocrinacea *(superfamily)* (43). *M.Dev.-U.Perm.*
Scytalocrinidae (22). *M.Dev.-U.Perm.*
Blothrocrinidae (10). *L.Miss.-L.Perm.*
Cercidocrinidae (3). *L.Miss.*
Aphelecrinidae (3). *L.Miss.(Kinderhook.)-U.Miss.(Chester.).*
Corythocrinidae (1). *L.Miss.(Osag.).*
Spaniocrinidae (4). *L.Miss.; L.Penn.-U.Perm.*
Cupressocrinitacea *(superfamily)* (2). *L.Dev.-U.Dev.*
Cupressocrinitidae (2). *L.Dev.-U.Dev.*
Mollocrinacea *(superfamily)* (3). *L.Penn.-U.Perm.*
Mollocrinidae (3). *L.Penn.-U.Perm.*
Lophocrinacea *(superfamily)* (25). *L.Miss.-U.Perm.*
Lophocrinidae (1). *Up.L.Carb.*
Pelecocrinidae (6). *L.Miss.-U.Miss.; M.Penn.-U.Penn.; U.Perm.*
Indocrinidae (3). *L.Perm.-U.Perm.*
Laudonocrinidae (6). *U.Miss.-L.Perm.*
Stellarocrinidae (7). *U.Miss.(Chester.)-L.Perm.*

Pachylocrinidae (2). *L.Miss.-L.Perm.*
Agassizocrinacea *(superfamily)* (28). *L.Miss.-U.Perm.*
Bursacrinidae (3). *L.Miss.*
Ampelocrinidae (9). *L.Miss.-U.Perm.*
Sundacrinidae (6). *L.Perm.-U.Perm.*
Anobasicrinidae (3). *L.Penn.(Morrow.)-U.Perm.*
Agassizocrinidae (5). *U.Miss.-L.Perm.*
Cricocrinidae (1). *M.Penn.(Desmoines.).*
Trimerocrinidae (1). *L.Perm.-U.Perm.*
Decadocrinacea *(superfamily)* (9). *M.Dev.-U.Penn.*
Decadocrinidae (8). *M.Dev.-U.Penn.*
Clathrocrinidae (1). *U.Penn.(Missour.).*
Cromyocrinacea *(superfamily)* (26). *U.Miss.-Perm.*
Eupachycrinidae (2). *U.Miss.(Chester.).*
Phanocrinidae (6). *U.Miss.(Chester.); L.Carb.(Visean)-U.Carb.(Namur.).*
Cromyocrinidae (13). *L.Carb.(U.Miss.)-Perm.*
Ulocrinidae (4). *L.Carb.(Visean); M.Penn.-Perm.*
Cadocrinidae (1). *U.Perm.(Basleo beds).*
Hydreionocrinacea *(superfamily)* (3). *Up.L.Carb., U.Miss.*
Hydreionocrinidae (3). *Up.L.Carb., U.Miss.*
Erisocrinacea *(superfamily)* (29). *L.Carb.(Miss.)-U.Perm.; M.Trias.*
Erisocrinidae (3). *U.Miss.-L.Perm.*
Graphiocrinidae (5). *Low.L.Carb.(Miss.); M.Penn.-U.Penn.; U.Perm.*
Paradelocrinidae (5). *U.Carb.; Penn.(Morrow.); U.Perm.(Basleo beds).*
Arkacrinidae (1). *L.Penn.(Morrow.).*
Diphuicrinidae (2). *L.Penn.(Morrow.)-L.Perm.*
Protencrinidae (2). *U.Carb.(Moscov.); M.Penn.(Atokan)-L.Perm.(Artinsk.).*
Catacrinidae (8). *L.Penn.(Morrow.)-U.Perm.(Basleo beds).*
Stachyocrinidae (2). *U.Perm.(Basleo beds).*
Encrinidae (1). *M.Trias.*
Apographiocrinacea *(superfamily)* (2). *L.Penn.-U.Perm.*
Apographiocrinidae (2). *L.Penn.-(Morrow.)-U.Perm.*
Pirasocrinacea *(superfamily)* (26). *L.Miss.-U.Perm.*
Pirasocrinidae (25). *U.Miss.-U.Perm.*
Adinocrinidae (1). *L.Miss.*
Texacrinacea *(superfamily)* (19). *L.Miss.-U.Perm.*
Texacrinidae (2). *L.Penn.-L.Perm.*
Galateacrinidae (1). *M.Penn.(Desmoines.)-U.Penn.(Virgil.).*
Sellardsicrinidae (1). *M.Penn.(Desmoines.).*
Cymbiocrinidae (8). *U.Miss.-U.Penn.*
Staphylocrinidae (7). *L.Miss.-U.Miss.; M.Penn.-U.Perm.*
Zeacrinitacea *(superfamily)* (17). *L.Miss.-U.Perm.*
Zeacrinitidae (8). *L.Miss.-U.Perm.*
Exocrinidae (3). *L.Penn.(Morrow.)-L.Perm.(Wolfcamp.).*
Timorechinidae (5). *U.Perm.(Basleo beds).*
Scotiacrinidae (1). *Up.L.Carb.*
Calceolispongiacea *(superfamily)* (2). *L.Perm.-U.Perm.*
Calceolispongiidae (2). *L.Perm.(Sakmar.-Artinsk.)-U.Perm.(Word. equiv.).*
Superfamily and Family Uncertain (2). *L.Carb.(Visean).*
Order and Superfamily Uncertain (3). *Ord.; L.Miss.-M.Miss.*
Paractocrinidae (2). *Ord.*
Family Uncertain (1). *L.Miss.-M.Miss.*
Flexibilia *(subclass)* (61). *M.Ord.-U.Perm.*
Taxocrinida *(order)* (10). *M.Ord.-U.Penn.*
Taxocrinacea *(superfamily)* (10). *M.Ord.(Trenton.)-U.Penn.(Missour.).*
Taxocrinidae (6). *M.Ord.(Trenton.)-U.Miss.(Chester.).*
Synerocrinidae (4). *L.Miss.-U.Penn.; L.Carb.-U.Carb.*
Sagenocrinida *(order)* (50). *L.Sil.-U.Perm.(Basleo beds).*
Lecanocrinacea *(superfamily)* (22). *U.Sil.-U.Perm.*
Lecanocrinidae (4). *U.Sil.-M.Dev.*
Nipterocrinidae (4). *U.Sil.-L.Dev.; U.Dev.-L.Miss.*
Mespilocrinidae (5). *L.Miss.(low. L.Carb.)-U.Perm.*
Calycocrinidae (3). *M.Dev.; L.Penn.; U.Perm.*
Gaulocrinidae (1). *L.Miss.*
Prophyllocrinidae (3). *U.Perm.*
Palaeoholopodidae (2). *U.Perm.*
Icthyocrinacea *(superfamily)* (5). *L.Sil.-L.Miss. or low.L.Carb.*
Icthyocrinidae (5). *L.Sil.(Medinan)-L.Miss.(Osag.).*
Sagenocrinitacea *(superfamily)* (23). *U.Sil.-U.Perm.*
Homalocrinidae (3). *U.Sil.*
Sagenocrinitidae (3). *U.Sil.; Miss.; L.Perm.*
Dactylocrinidae (10). *U.Sil.-L.Miss.; L.Penn.-U.Perm.*
Euryocrinidae (7). *M.Dev.-U.Penn.*
Order Uncertain (1). *L.Dev.-M.Dev.*
Edriocrinidae (1). *L.Dev.-M.Dev.*
Articulata *(subclass)* (256;4). *L.Trias.-Holo.*
Millericrinida *(order)* (15). *M.Trias.; L.Jur.-L.Cret.; L.Paleoc.; Holo.*
Millericrinina *(suborder)* (9). *M.Trias.; L.Jur.-L.Cret.*
Dadocrinidae (1). *M.Trias.*
Millericrinidae (5). *L.Jur.-U.Jur.*
Apiocrinitidae (2). *L.Jur.-L.Cret.*
Cyclocrinidae (1). *L.Jur.-L.Cret.*

Hyocrinina *(suborder)* (6). *L.Tert.(Dan.); Holo.*
Hyocrinidae (6). *L.Tert.; Holo.*
Hyocrininae (5). Recent.
Calamocrininae (1). *L.Tert.(Dan.); Holo.*
Cyrtocrinida *(order)* (20;4). *L.Jur.-Mio; Holo.*
Cyrtocrinina *(suborder)* (12;4). *L.Jur.-U.Cret.*
Plicatocrinidae (2). *L.Jur.-U.Jur.*
Sclerocrinidae (2). *U.Jur.(Oxford.)-L.Cret.(Hauteriv.).*
Hemicrinidae (1;2). *U.Jur.(Tithon.)-L.Cret.(Alb.).*
Eugeniacrinitidae (5). *M.Jur.(Bathon.)-U.Cret.(Campan.).*
Phyllocrinidae (2;2). *M.Jur.(Bajoc.)-L.Cret.(Neocom.).*
Holopodina *(suborder)* (7). *L.Jur.; U.Jur.-Mio.; Holo.*
Eudesicrinidae (2). *L.Jur.*
Hemibrachiocrinidae (3). *L.Cret.(Valangin.-Barrem.).*
Holopodidae (2). *U.Jur.(Tithon.)-Mio.; Holo.*
Suborder and Family Uncertain (1). *U.Jur.-L.Cret.(Neocom.).*
Bourgueticrinida *(order)* (11). *U.Cret.(Turon.)-L.Paleoc.(Dan.); ?M.Paleoc.(Heers.); Eoc.-Mio.; Holo.*
Bourgueticrinidae (1). *U.Cret.(Turon.)-L.Paleoc.(Dan.), ?M.Paleoc.(Heers.); Eoc.*
Bathycrinidae (6). *U.Cret.(Maastricht.)-L.Paleoc.(Dan.); Eoc.-Mio.; Holo.*
Phrynocrinidae (2). Recent.
Porphyrocrinidae (2). Recent.
Isocrinida *(order)* (23). *L.Trias.-Mio.; Holo.*
Holocrinidae (2). *M.Trias.*
Isocrinidae (15). *Trias.-Mio.; Holo.*
Genera Dubia (3). *U.Jur., Tert.(Oligo.-Mio.),* recent.
Pentacrinitidae (2). *L.Jur.-U.Jur.*
Proisocrinidae (1). Recent.
Comatulida *(order)* (169). *L.Jur.-L.Paleoc.; Eoc.-Holo.*
Paracomatulacea *(superfamily)* (5). *L.Jur.(Toarc.)-L.Paleoc.; Holo.*
Paracomatulidae (1). *L.Jur.(Toarc.).-L.Cret.(Hauteriv.).*
Atelecrinidae (4). *U.Cret.-L.Paleoc.; Holo.*
Solanocrinitacea *(superfamily)* (11). *L.Jur.(Pliensbach.)-U.Cret.(Coniac.).*
Solanocrinitidae (4). *L.Jur.(Pliensbach.)-U.Cret.(Coniac.).*
Decameridae (3). *L.Cret.*
Thiolliericrinidae (4). *M.Jur.(Bathon.)-L.Cret.(Hauteriv.).*
Comasteracea *(superfamily)* (20). *Tert.(Eoc., Mio.-Plio.); Holo.*
Comasteridae (20). *Tert.(Eoc., Mio.-Plio.); Holo.*
Comasterinae (4). *U.Tert.(Mio.-Plio.),* recent.
Capillasterinae (12). *L.Tert.(Eoc.)*; recent.
Comactiniinae (4). Recent.
Mariametracea *(superfamily)* (34). *Tert.(Eoc.-Mio.);* recent.
Mariametridae (7). Recent.
Zygometridae (2). Recent.
Eudiocrinidae (1). Recent.
Himerometridae (6). *Tert.(Eoc.-Mio.);* recent.
Colobometridae (18). Recent.
Tropiometracea *(superfamily)* (38). *U.Jur.; U.Cret.-L.Paleoc.; Eoc.-Plio.;* recent.
Tropiometridae (1). Recent.
Pterocomidae (2). *U.Jur.; U.Cret.-L.Paleoc.*
Conometridae (5). *U.Cret.(Cenoman.)-L.Paleoc.; Eoc.-Mio.*
Calometridae (5). Recent.
Ptilometridae (1). Recent.
Asterometridae (2). *U.Tert.(Plio.);* recent.
Thalassometridae (14). *U.Tert.(Mio.);* recent.
Charitometridae (8). Recent.
Notocrinacea *(superfamily)* (7). *M.Jur.(Bathon.)-U.Cret.(Maastricht.); ?Eoc.;* recent.
Notocrinidae (6). *M.Jur.(Bathon.)-U.Cret.(Maastricht.), ?Eoc.,* recent.
Aporometridae (1). Recent.
Antedonacea *(superfamily)* (54). *Cret.-L.Paleoc.; Eoc.; Mio.; Pleist.-Holo.*
Antedonidae (52). *Cret.(Alb.-Maastricht.)-L.Paleoc.; Eoc.; Mio.; Pleist.-Holo.*
Antedoninae (11). *Eoc.; Mio.; Pleist.-Holo.*
Perometrinae (4). Recent.
Thysanometrinae (2). Recent.
Zenometrinae (15). *L.Tert.(Eoc.);* recent.
Bathymetrinae (11). Recent.
Heliometrinae (8). *L.Cret.-L.Paleoc.; Mio.;* recent.
Isometrinae (1). Recent.
Pentametrocrinidae (2). Recent.
Uintacrinida *(order)* (2). *U.Cret.(Santon.).*
Uintacrinidae (1). *U.Cret.(Santon.).*
Marsupitidae (1). *U.Cret.(Santon.).*
Roveacrinida *(order)* (14). *M.Trias.-U.Trias.; U.Jur.-U.Cret.*
Roveacrinidae (11). *M.Trias.-U.Trias.; L.Cret.-U.Cret.*
Roveacrininae (7). *L.Cret.-U.Cret.*
Somphocrininae (4). *M.Trias.-U.Trias.*
Saccocomidae (3). *U.Jur.-Cret.*
Saccocominae (2). *U.Jur.-Cret.*
Pseudosaccocominae (1). *U.Jur.-L.Cret.*
Order and Family Uncertain (2). *L.Jur.(Sinemur.)-U.Jur.(Oxford.).*

STRATIGRAPHIC DISTRIBUTION

The stratigraphic distribution of subclasses, orders, suborders, superfamilies, families, and subfamilies of Crinoidea recognized in the *Treatise* is indicated graphically in Table 5 (compiled by JACK D. KEIM).

TABLE 5. *Stratigraphic Distribution of the Crinoidea.*

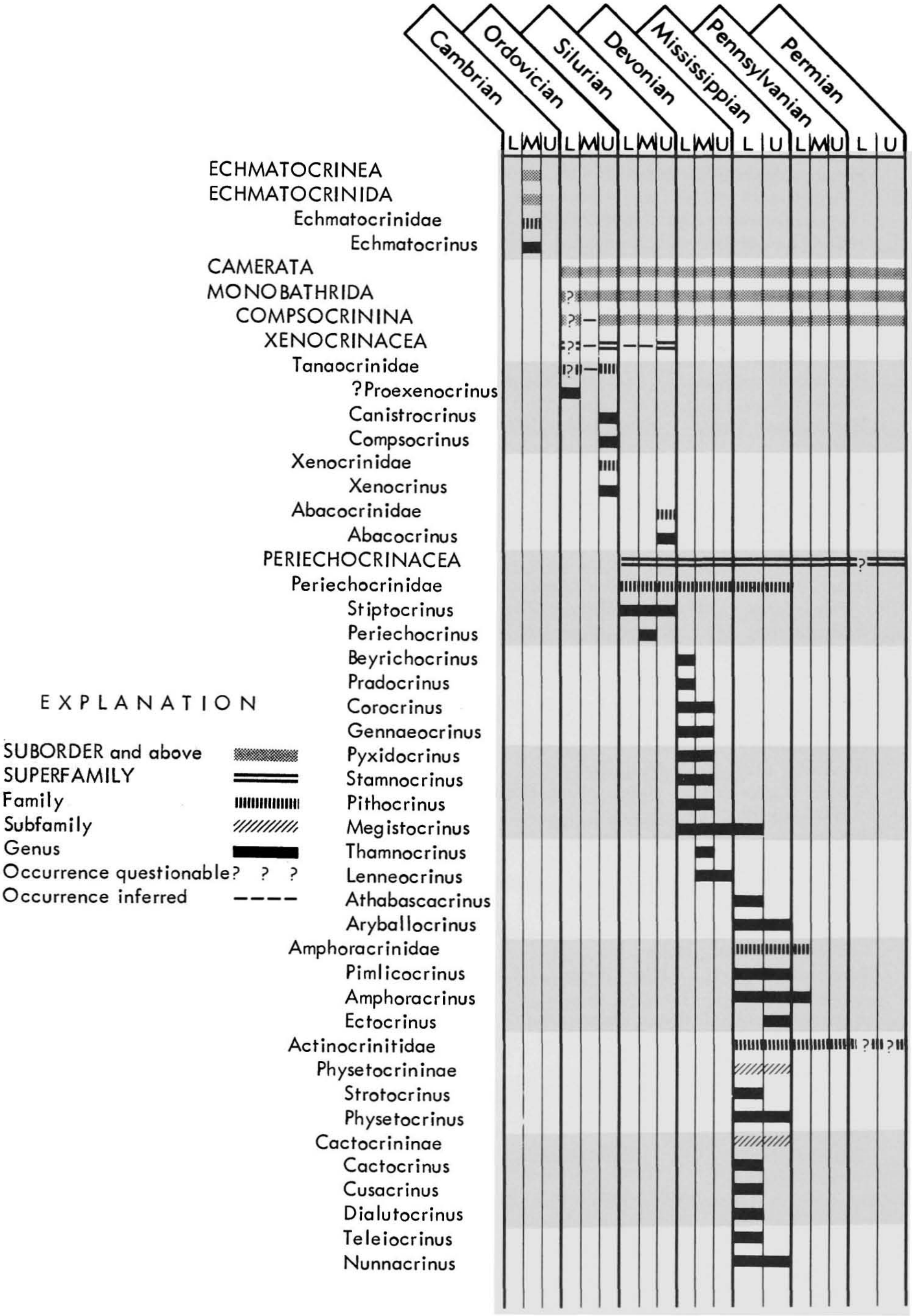


TABLE 5. *(Continued)*

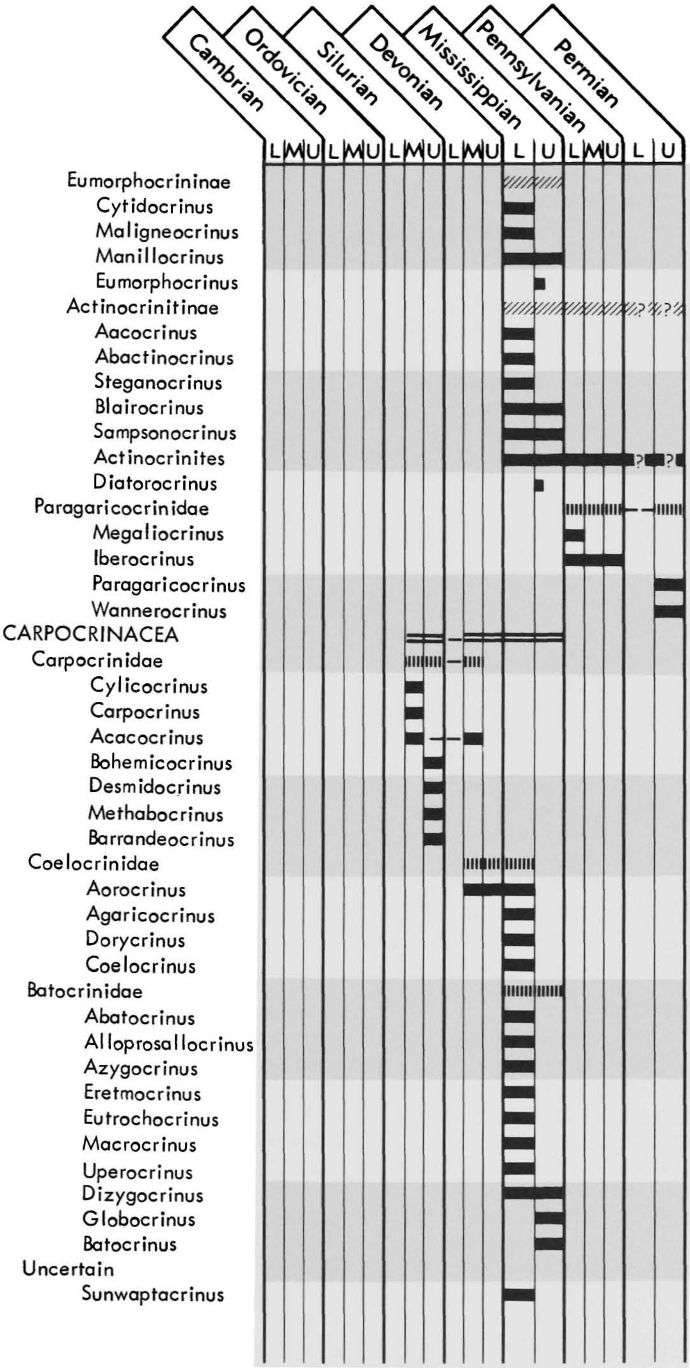


TABLE 5. *(Continued)*

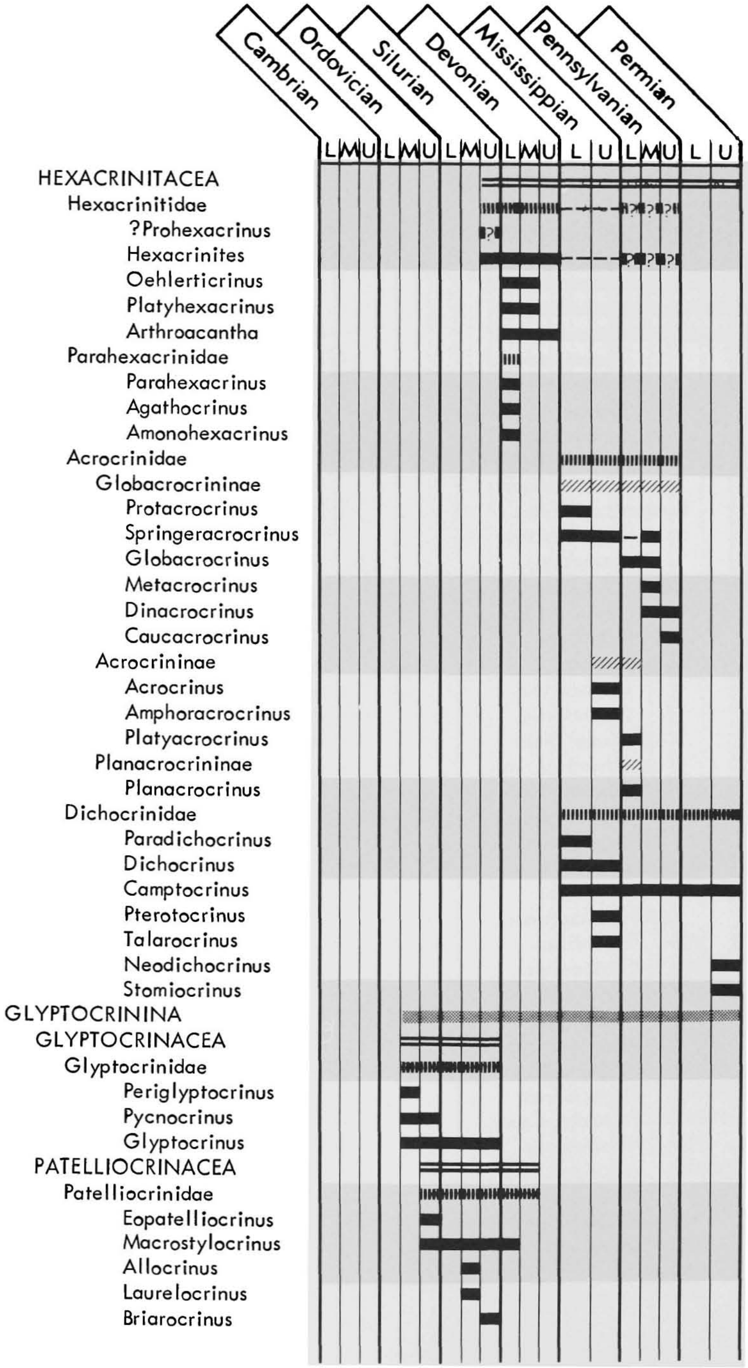


TABLE 5. *(Continued)*

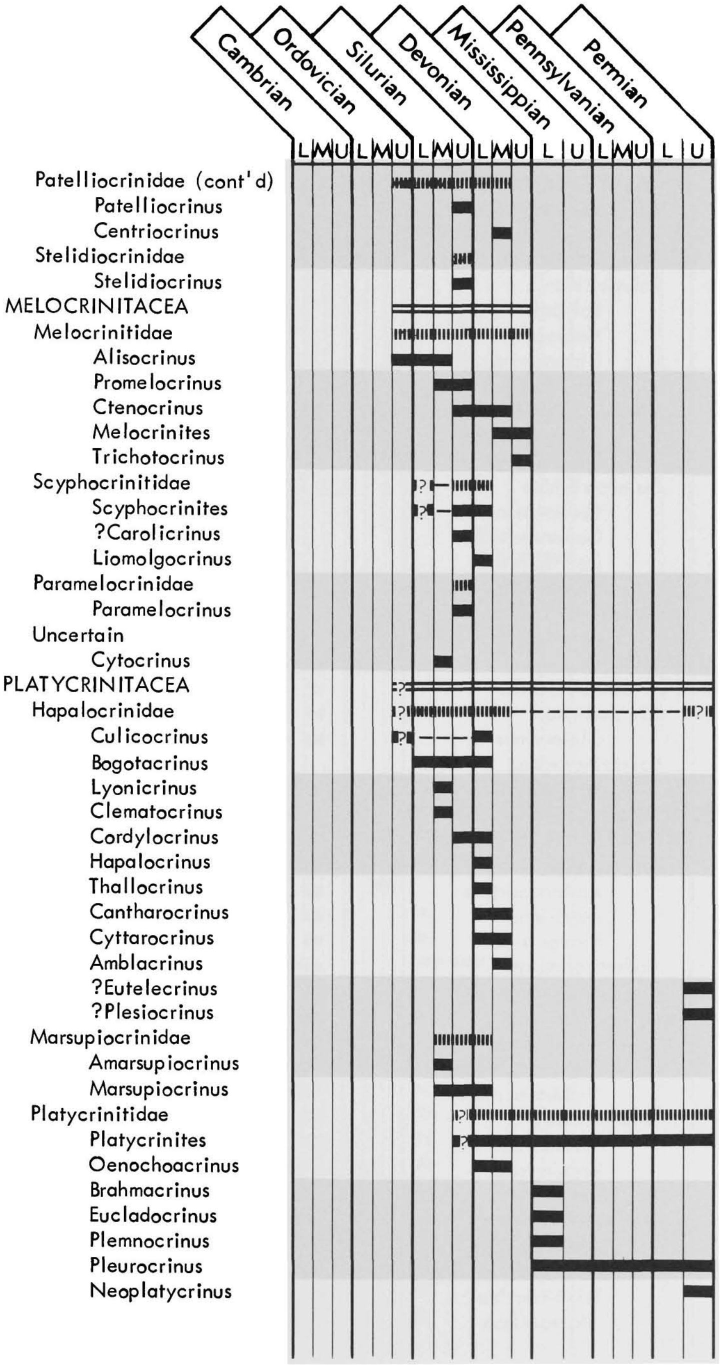


TABLE 5. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U
EUCALYPTOCRINITACEA								═	═	═	═								
Eucalyptocrinitidae								▥	▥	▥	▥								
Eucalyptocrinites								■	■	■	■								
Calliocrinus									■	■									
Polypeltidae									▥	▥									
Polypeltes									■										
Hadrocrinus										■									
Himerocrinus										■									
Trybliocrinus										■									
Clonocrinidae									▥	▥									
Clonocrinus									■	?■									
Technocrinus									■	■									
Dolatocrinidae										▥	▥								
Craterocrinus										■									
Comanthocrinus										■	■								
Dolatocrinus										■	■								
Clarkeocrinus											■								
Uncertain																			
Abathocrinus								■											
DIPLOBATHRIDA					▨	▨	–	▨	▨	▨	▨	▨	▨	▨					
ZYGODIPLOBATHRINA					▨	–	–	–	–	▨									
Cleiocrinidae					▥														
Cleiocrinus					■														
Spyridiocrinidae										▥									
Spyridiocrinus										■									
EUDIPLOBATHRINA					▨	▨	–	▨	▨	▨	▨	▨	▨	▨					
RHODOCRINITACEA					═	═	–	═	═	═	═	═	═	═					
Anthracocrinidae					▥														
Anthracocrinus					■														
Deocrinus					■														
Hercocrinus					■														
Archaeocrinidae					▥	▥													
Archaeocrinus					■														
Balacrinus					■														
Pararchaeocrinus					■														
Neoarchaeocrinus					■	■													
Rhaphanocrinus					■	■													
Reteocrinidae					▥	▥													
Traskocrinus					■														
Reteocrinus					■	■													
Gaurocrinus						■													
Rhodocrinitidae					▥	▥	–	▥	–	▥	▥	▥	▥	▥					
Diabolocrinus					■														
Paradiabolocrinus					■														
Trichinocrinus					■														
Atactocrinus						■													

TABLE 5. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U
Rhodocrinitidae (cont'd)					┅	┅	–	┅	–	┅	┅	┅	┅	┅					
Maquoketocrinus						━													
Elpidocrinus								━											
Emperocrinus								━											
Lyriocrinus								━											
Paragazácrinus								━											
Condylocrinus										━									
Diamenocrinus										━									
Sphaerotocrinus										━									
Ophiocrinus										━									
Monstrocrinus										━	━								
Thylacocrinus										━	━								
Acanthocrinus										━	━								
Cadiscocrinus											━								
Rhipidocrinus											━								
Gilbertsocrinus											━	━	━	━					
Cribanocrinus													━	━					
Rhodocrinites													━	━					
Anthemocrinidae								┅	┅										
Wilsonicrinus								━											
Anthemocrinus									━										
Opsiocrinidae											┅								
Opsiocrinus											━								
Uncertain																			
Paulocrinus								━											
Siderocrinus								━											
DIMEROCRINITACEA						═	–	═	═	═	═	═							
Dimerocrinitidae						┅	–	┅	┅	┅	┅	┅							
Ptychocrinus						━													
Cyphocrinus								━											
Eudimerocrinus								━											
Dimerocrinites								━	━	━	━								
Ambicocrinus										━									
Griphocrinus										━	━	━							
Macarocrinus										━	━	━							
Pterinocrinus										━	━	━							
Gazacrinidae								┅											
Gazacrinus								━											
Lampterocrinidae								┅											
Lampterocrinus								━											
Siphonocrinus								━											
Orthocrinidae										┅	┅								
Orthocrinus										━	━								
NYCTOCRINACEA								═											
Nyctocrinidae								┅											
Nyctocrinus								━											

TABLE 5. *(Continued)*

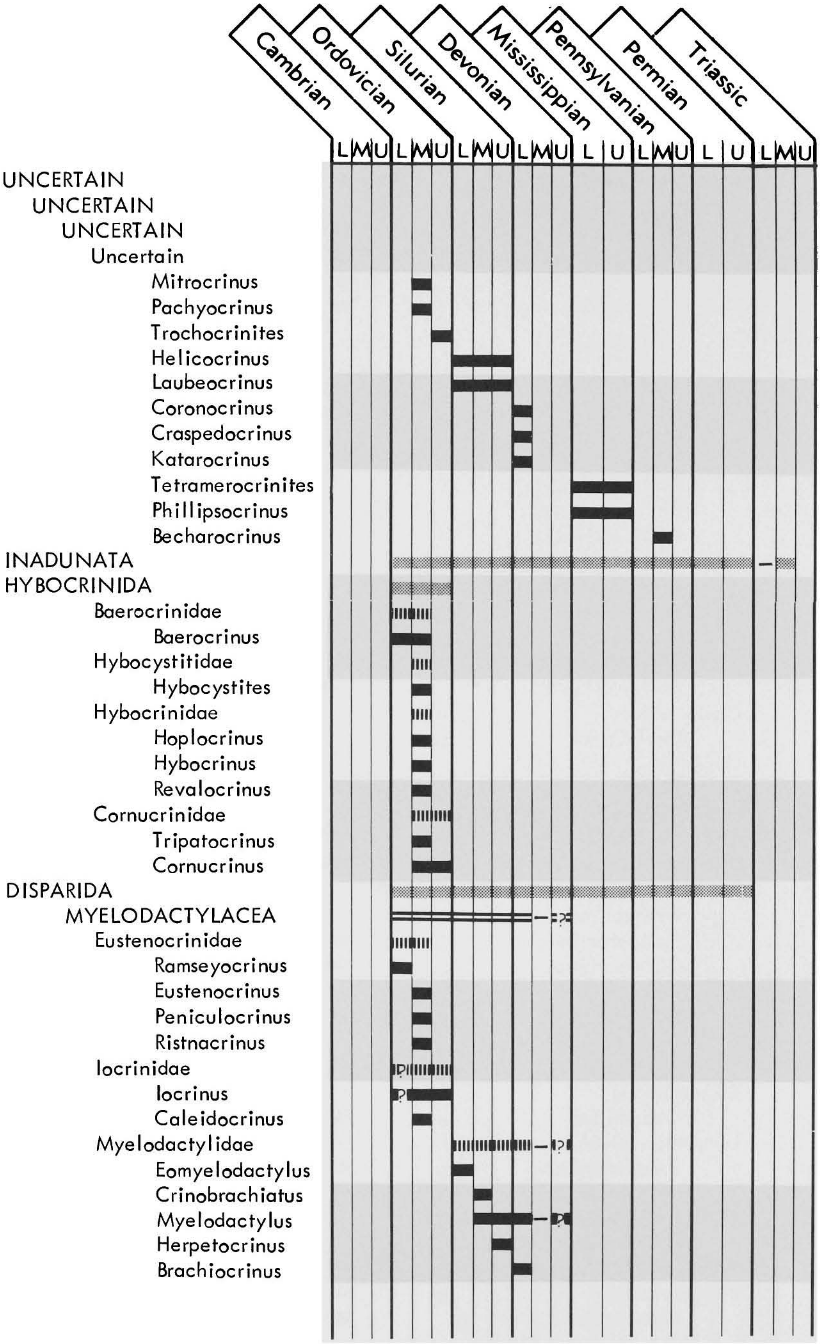
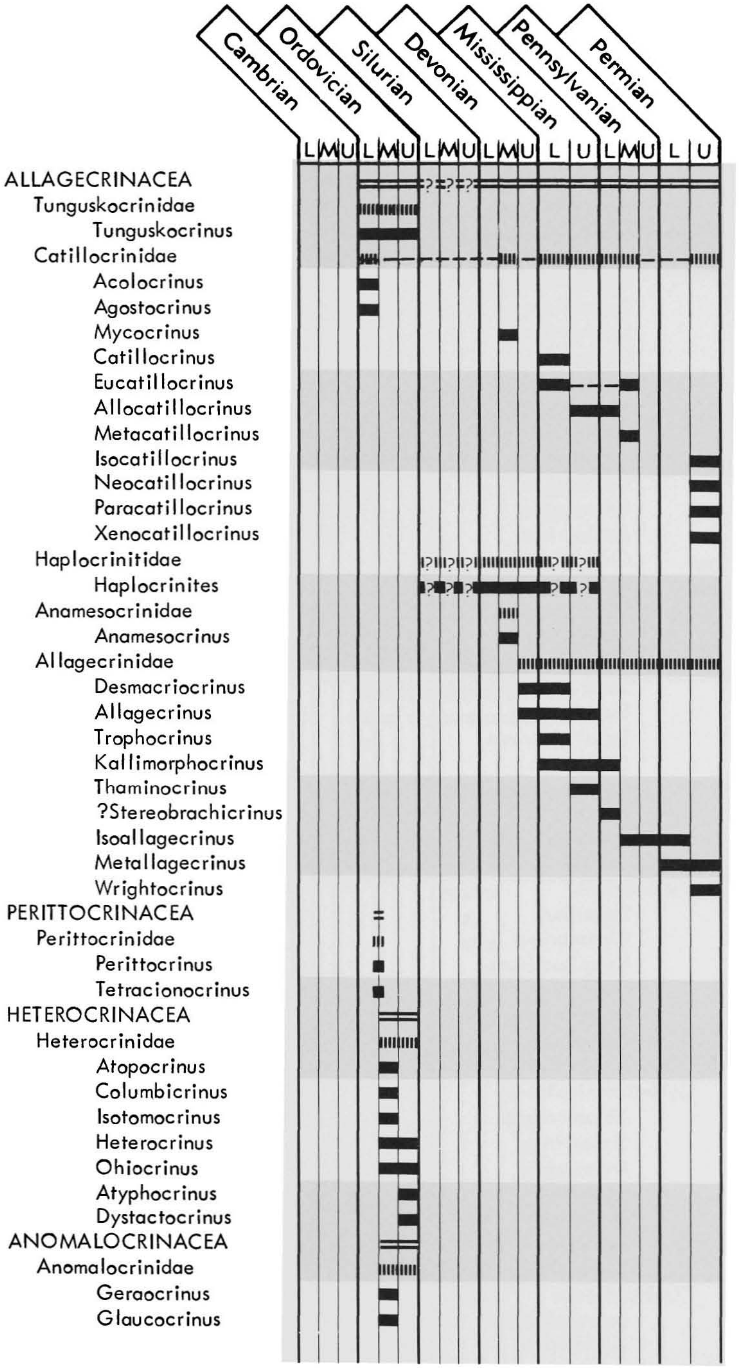


TABLE 5. *(Continued)*



For *Atopocrinus* (Heterocrinidae), read *Othneiocrinus.*

TABLE 5. *(Continued)*

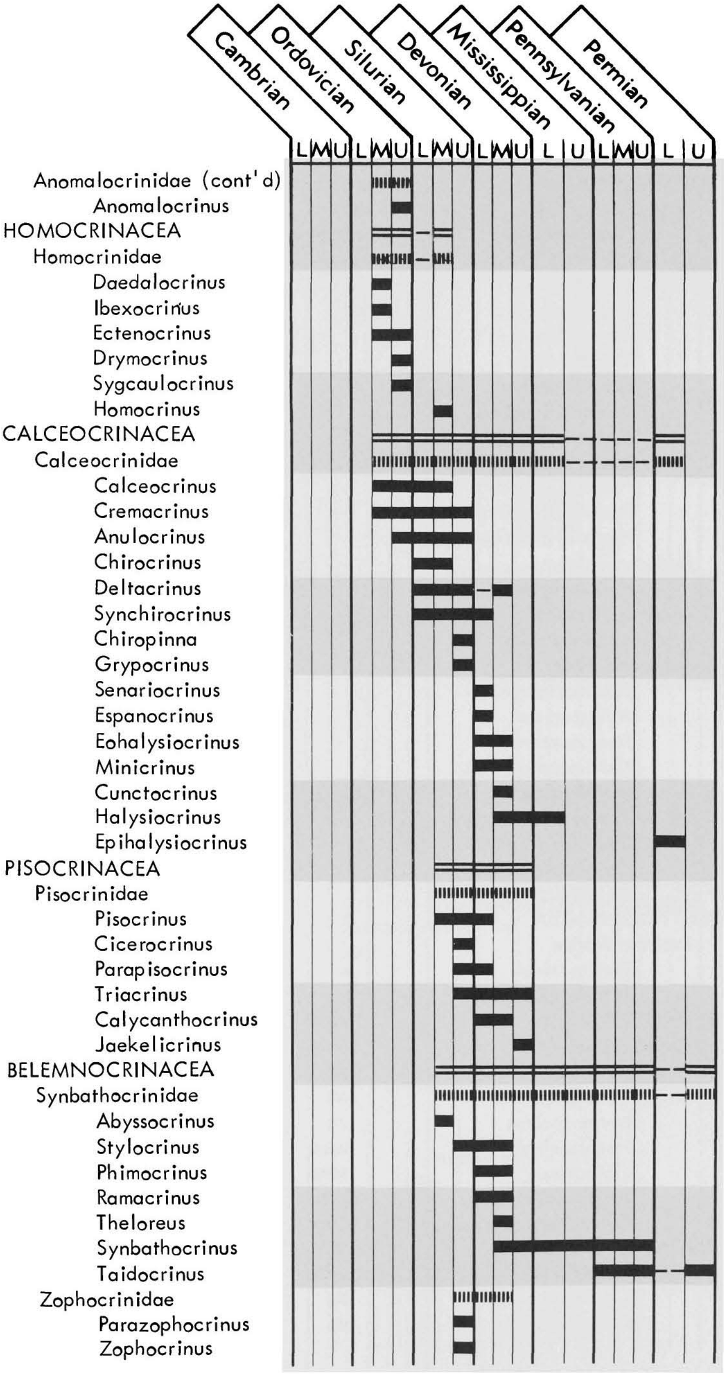


TABLE 5. (Continued)

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian		Triassic		
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U	L	M	U
Zophocrinidae (cont'd)									┅	┅	┅											
Tiaracrinus										■	■											
Pygmaeocrinidae									┅	┅	┅											
Pygmaeocrinus									■	■	■											
Storthingocrinus										■	■											
Holynocrinidae											┅											
Holynocrinus											■											
Perissocrinidae											┅											
Hypsocrinus											■											
Perissocrinus											■											
Quiniocrinus											■											
Belemnocrinidae													┅									
Belemnocrinus													■									
Whiteocrinus													■									
UNCERTAIN																						
Paradoxocrinidae																			┅			
Paradoxocrinus																			■			
Uncertain																						
Vosekocrinus				■																		
CLADIDA				▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	—	▒	
DENDROCRININA				▒	▒	▒	▒	▒	▒	▒	▒	▒	▒									
MASTIGOCRINACEA				═	═	– –	– –	═	═	═	═	═	═									
Aethocrinidae				┅																		
Aethocrinus				■																		
Mastigocrinidae					┅	– –	– –	┅	┅	┅	┅	┅	┅									
Polycrinus					■																	
Mastigocrinus								■														
Bathericrinus								■	■	■												
Antihomocrinus								■	■	■												
Streptocrinus									■													
Dictenocrinus									■	■												
Eifelocrinus										■												
Follicrinus										■												
Nassoviocrinus										■	■	■										
Lasiocrinus										■	■	■	■									
Belanskicrinus											■											
Kalpidocrinus											■											
Quantoxocrinus											■	■										
Iteacrinus												■										
Cradeocrinus												■	■									
Atelestocrinus													■									
Goniocrinus													■									
Thenarocrinidae								┅														
Thenarocrinus								■														
MEROCRINACEA				?═	═	═	– –	– –	═	═												
Ottawacrinidae				┅?	┅	?┅																
Ottawacrinus				■?	■	?■																

TABLE 5. *(Continued)*

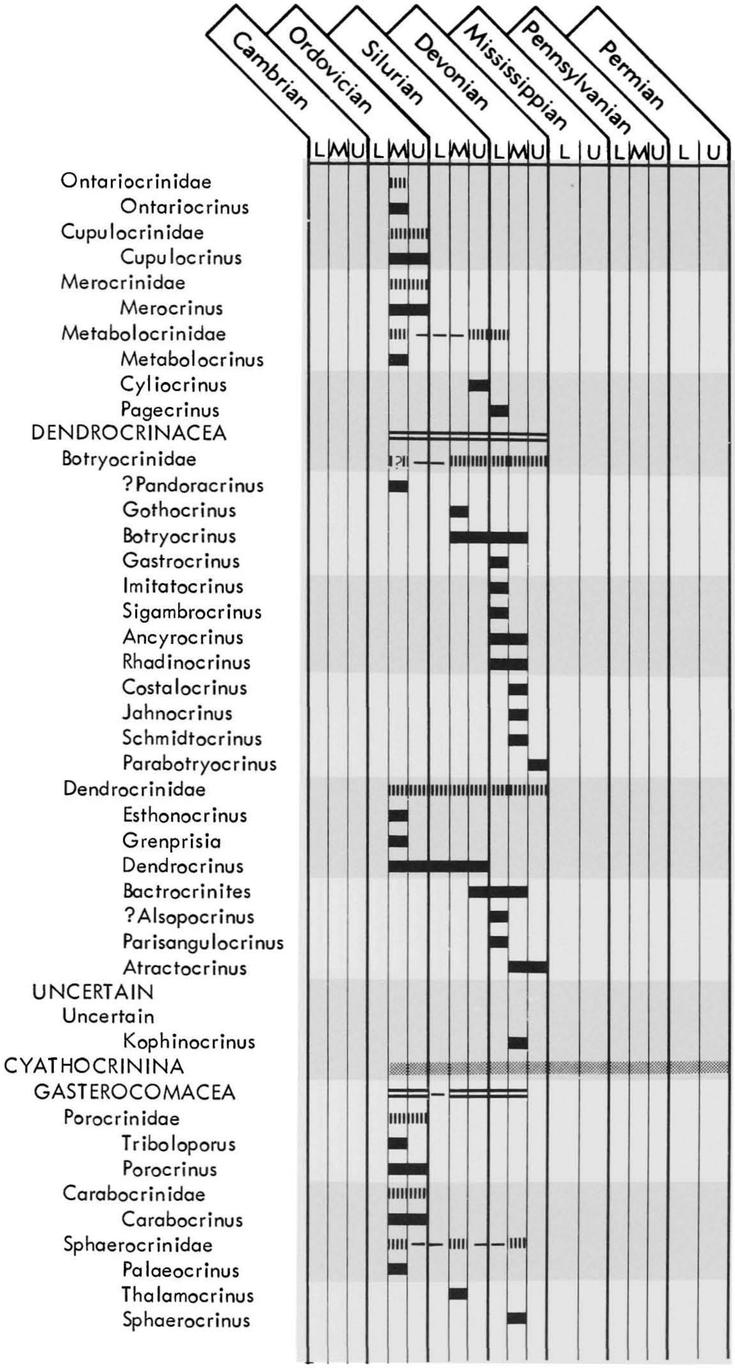


TABLE 5. *(Continued)*

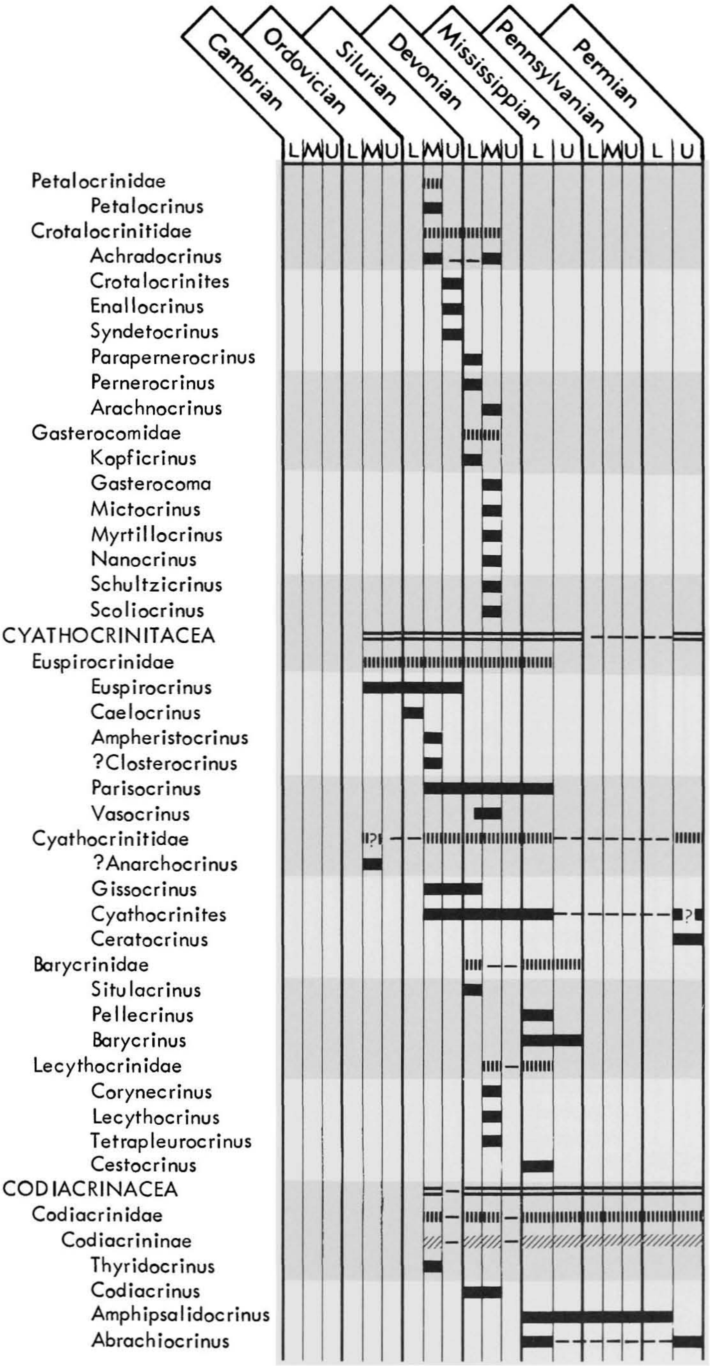


TABLE 5. *(Continued)*

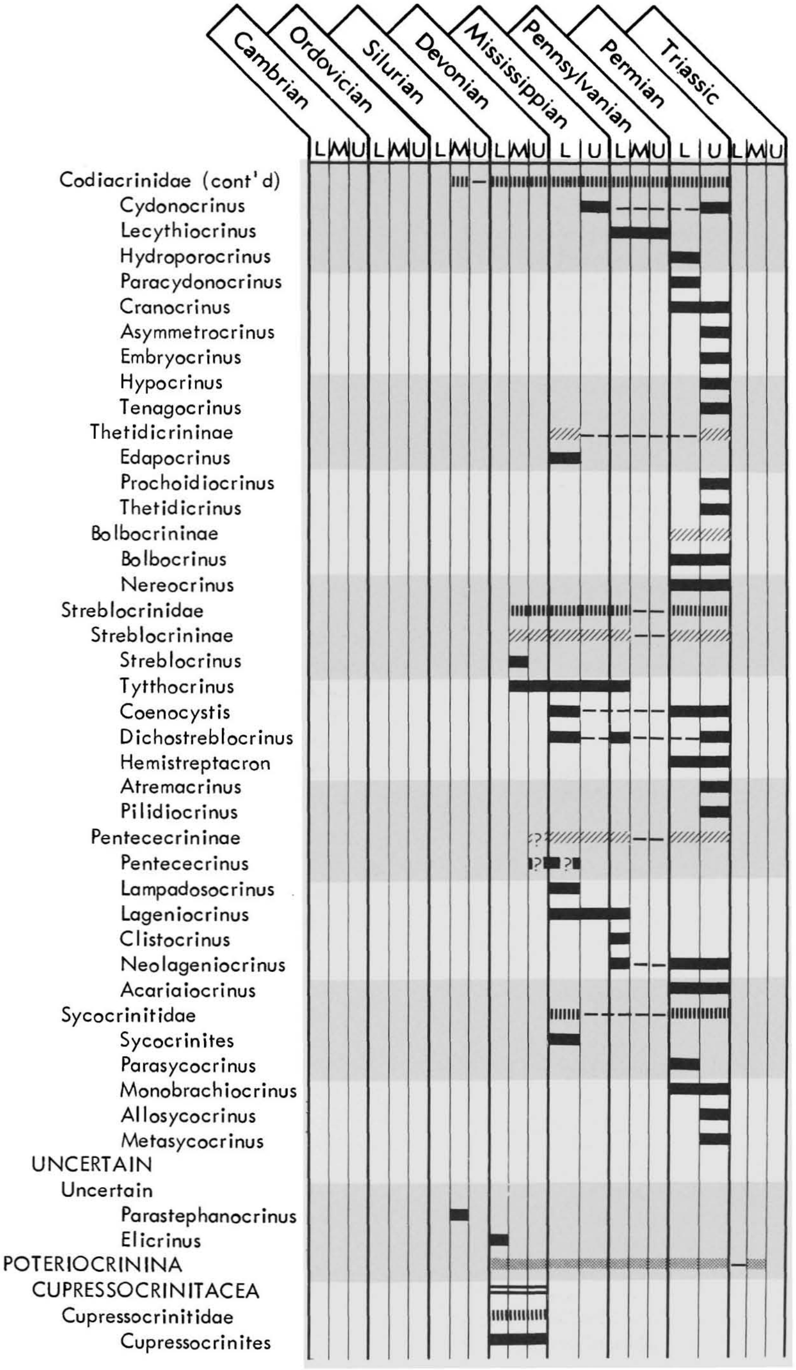


Table 5. *(Continued)*

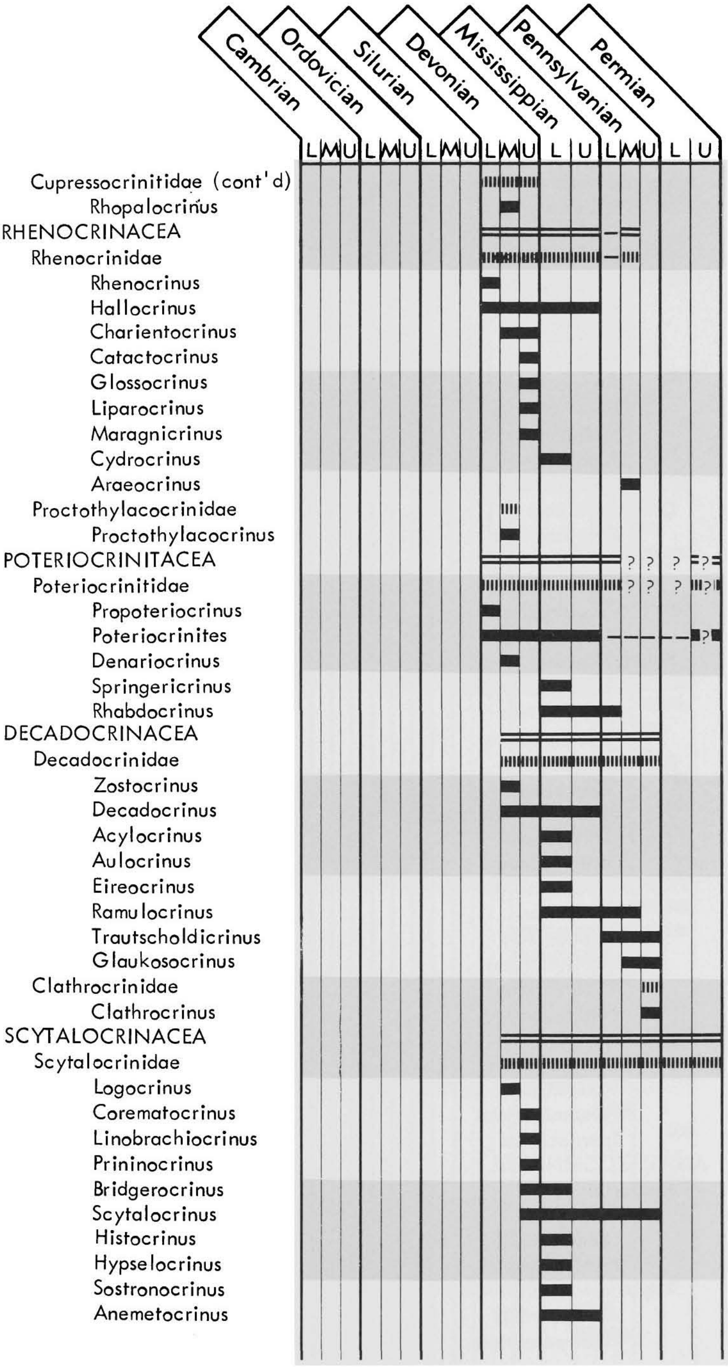


Table 5. *(Continued)*

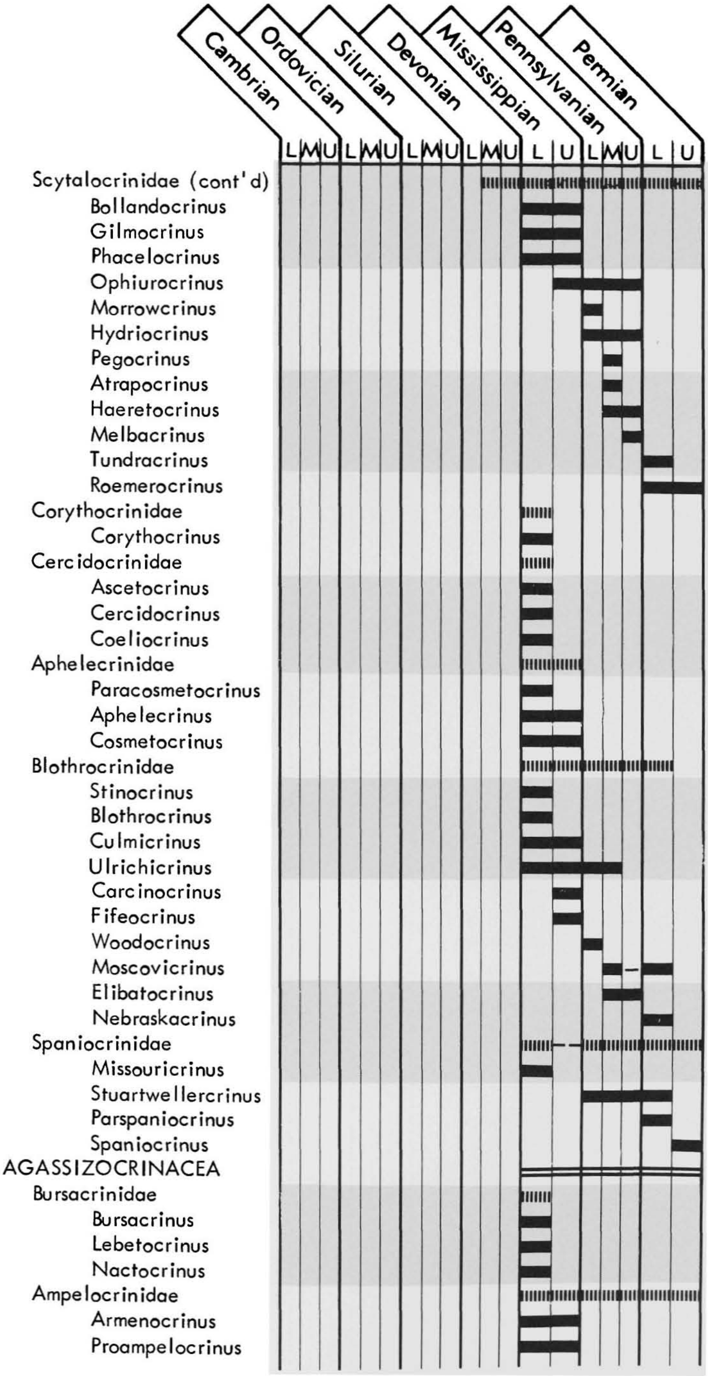


TABLE 5. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U
Ampelocrinidae (cont'd)													┇	┇	┇	┇	┇	┇	┇
Ampelocrinus														▬	▬				
Chlidonocrinus														▬	▬	▬	▬		
Halogetocrinus																	▬		
Moundocrinus																	▬		
Polusocrinus																	▬		
Arroyocrinus																		▬	
Spheniscocrinus																			▬
Agassizocrinidae														┇	┇	┇	┇	┇	
Agassizocrinus														▬					
Anartiocrinus														▬					
Paragassizocrinus															▬	▬	▬		
Epipetschoracrinus																		▬	
Petschoracrinus																		▬	
Anobasicrinidae															┇	┇	┇	┇	┇
Anobasicrinus															▬	▬	▬		
Synyphocrinus																▬	▬	▬	▬
Terpnocrinus																	▬		
Cricocrinidae																┇			
Cricocrinus																▬			
Sundacrinidae																		┇	┇
Hemiindocrinus																		▬	
Tribrachyocrinus																		▬	
Basleocrinus																			▬
Laccocrinus																			▬
Parindocrinus																			▬
Sundacrinus																			▬
Trimerocrinidae																		┇	┇
Trimerocrinus																		▬	▬
LOPHOCRINACEA													═	═	═	═	═	═	═
Pachylocrinidae													┇	┇	┇	┇	┇	┇	
Pachylocrinus													▬	▬	▬	▬	▬		
Plummericrinus															▬	▬	▬	▬	
Pelecocrinidae													┇	┇	–	┇	┇	– –	┇
Pelecocrinus													▬						
Forthocrinus													▬	▬					
Exoriocrinus																▬	▬		
Tetrabrachiocrinus																			▬
Depaocrinus																			▬
Malaiocrinus																			▬
Lophocrinidae														┇					
Lophocrinus														▬					
Laudonocrinidae														┇	┇	┇	┇	┇	
Paianocrinus														▬					
Anchicrinus															▬	▬			
Laudonocrinus															▬	▬	▬		

TABLE 5. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U
Laudonocrinidae (cont'd)														┅	┅	┅	┅	┅	
Bathronocrinus																■	–	■	
Athlocrinus																■	■		
Schistocrinus																■	■		
Stellarocrinidae														┅	┅	┅	┅	┅	
Pedinocrinus														■					
Rhopocrinus														■					
Heliosocrinus														■	■				
Brychiocrinus																■			
Brabeocrinus																■	■	■	
Stellarocrinus																■	■	■	
Celonocrinus																	■	■	
Indocrinidae																		┅	┅
Proindocrinus																		■	
Indocrinus																			■
Metaindocrinus																			■
PIRASOCRINACEA													═	═	═	═	═	═	═
Adinocrinidae													┅						
Adinocrinus													■						
Pirasocrinidae														┅	┅	┅	┅	┅	┅
Dasciocrinus														■					
Zeusocrinus														■					
Exterocrinus															■				
Lasanocrinus															■				
Metutharocrinus															■				
Affinocrinus															■	■			
Utharocrinus															■	■	■		
Sciadiocrinus															■	■	■		
Stenopecrinus															■	■	■		
Metaperimestocrinus																■			
Pirasocrinus																■			
Platyfundocrinus																■			
Polygonocrinus																■			
Psilocrinus																■			
Retusocrinus																■			
Schedexocrinus																■			
Eirmocrinus																■			
Metaffinocrinus																■			
Aatocrinus																■	■		
Plaxocrinus																■	■		
Perimestocrinus																■	■	■	
Simocrinus																	■		
Separocrinus																	■		
Vertigocrinus																	■		
Triceracrinus																		■	■

Table 5. *(Continued)*

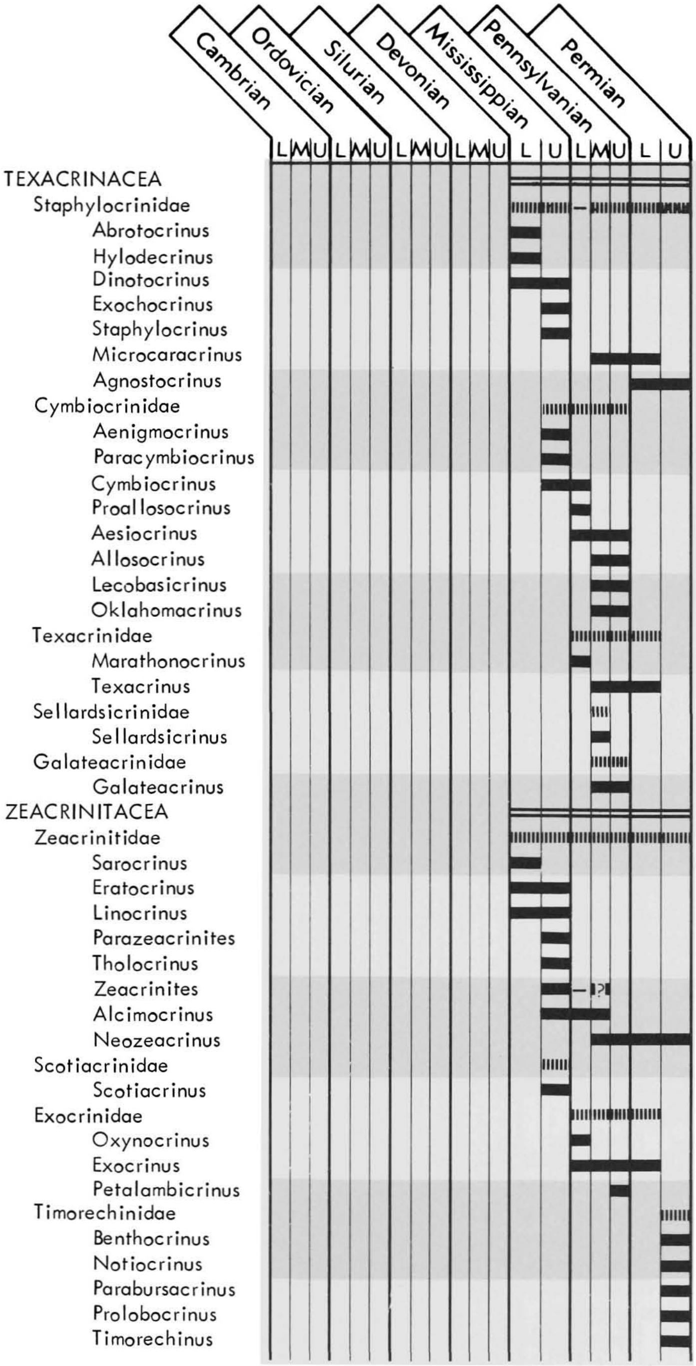


TABLE 5. *(Continued)*

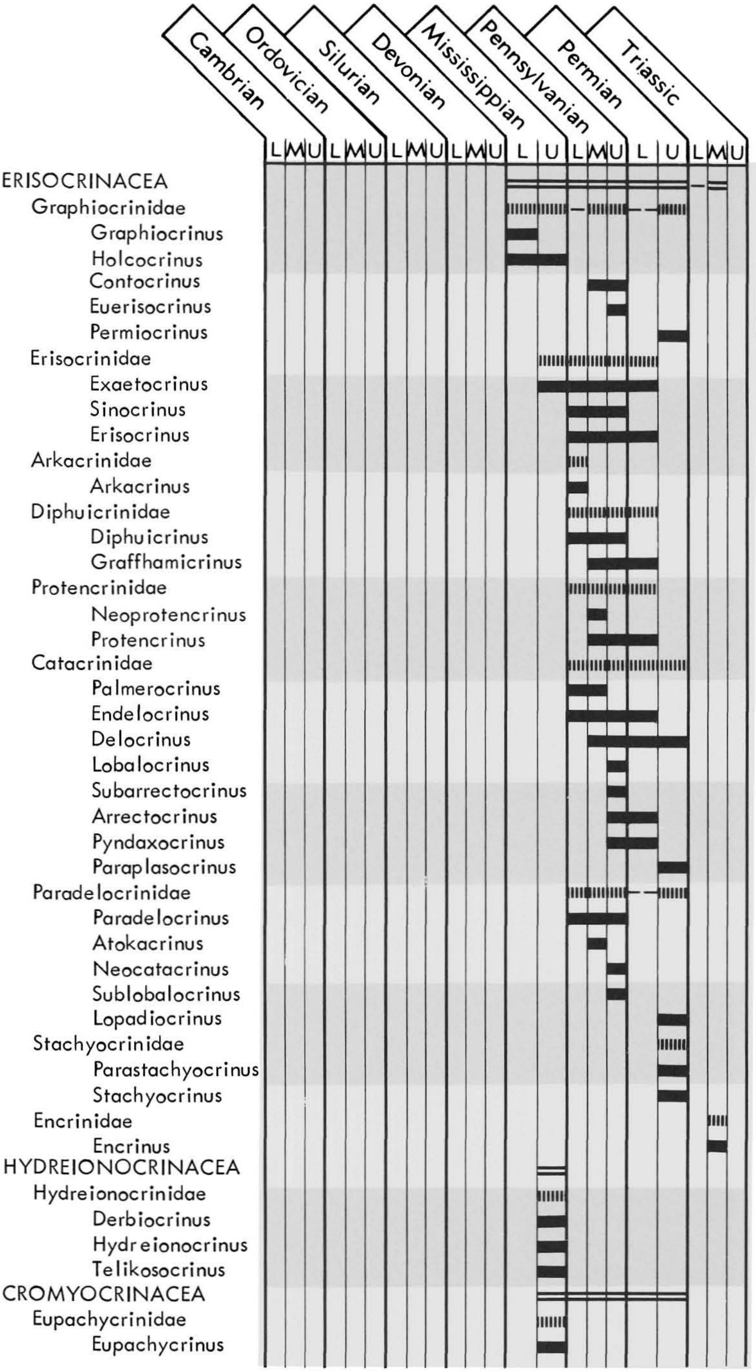


TABLE 5. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U
Eupachycrinidae (cont'd)														┅					
Intermediacrinus														▬					
Phanocrinidae														┅	┅				
Bronaughocrinus														▬					
Cryphiocrinus														▬					
Hosieocrinus														▬					
Idosocrinus														▬					
Phanocrinus														▬					
Pentaramicrinus														▬	▬				
Cromyocrinidae														┅	┅	┅	┅	┅	┅
Mantikosocrinus														▬					
?Goleocrinus														▬	▬	▬			
Metacromyocrinus															▬	▬			
Dicromyocrinus															▬	▬	▬		
Synarmocrinus															▬	▬	▬	▬	
Paracromyocrinus															▬	▬	▬	▬	
Cromyocrinus															▬	▬	▬	▬	▬
Mooreocrinus																▬			
Parethelocrinus																▬			
Aglaocrinus																▬	▬	▬	
Ethelocrinus																	▬		
Parulocrinus																	▬	▬	
Moapocrinus																		▬	
Ulocrinidae														┅	—	┅	┅	┅	┅
?Tyrieocrinus														▬					
Ureocrinus														▬					
Ulocrinus																▬	▬	▬	▬
Probletocrinus																	▬		
Cadocrinidae																			┅
Cadocrinus																			▬
APOGRAPHIOCRINACEA															═	═	═	═	═
Apographiocrinidae															┅	┅	┅	┅	┅
Apographiocrinus															▬	▬	▬	▬	▬
Paragraphiocrinus																			▬
MOLLOCRINACEA															═	═	═	═	═
Mollocrinidae															┅	┅	┅	┅	┅
Strongylocrinus															▬	▬	▬	▬	▬
Hemimollocrinus																		▬	
Mollocrinus																			▬
CALCEOLISPONGIACEA																		═	═
Calceolispongiidae																		┅	┅
Jimbacrinus																		▬	
Calceolispongia																		▬	▬
UNCERTAIN																			
Uncertain																			
Aulodesocrinus														▬					
Carlopsocrinus														▬					

TABLE 5. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian	
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U
CORONATA					░	░	—	░	░										
Stephanocrinidae					▥	▥	—	▥	▥										
Mespilocystites					■														
Paracystis					■														
Tormoblastus						■													
Stephanocrinus								■											
Stephanoblastus									■										
UNCERTAIN																			
UNCERTAIN																			
Paractocrinidae				▥	▥	▥													
Paractocrinus				■	■	■													
Parorthocrinus				■	■	■													
Uncertain																			
Passalocrinus													■						
FLEXIBILIA					░	░	░	░	░	░	░	░	░	░	░	░	░	░	░
TAXOCRINIDA					░	░	░	░	░	░	░	░	░	░	░	░	░		
TAXOCRINACEA					═	═	═	═	═	═	═	═	═	═	═	═	═		
Taxocrinidae					▥	▥	▥	▥	▥	▥	▥	▥	▥	▥					
Protaxocrinus					■	■	■	■	■	■									
Gnorimocrinus									■										
Meristocrinus									■										
Eutaxocrinus									■	■	■	■	■						
Taxocrinus											■	■	■	■					
Parichthyocrinus													■						
Synerocrinidae													▥	▥	▥	▥	▥		
Onychocrinus													■	■					
Enascocrinus														■	■				
Synerocrinus															■	■	■		
Euonychocrinus																	■		
SAGENOCRINIDA							░	░	░	░	░	░	░	░	░	░	░	░	░
ICTHYOCRINACEA							═	═	═	═	═	═	═						
Icthyocrinidae							▥	▥	▥	▥	▥	▥	▥						
Clidochirus							■	—	■	■	—	■	■						
Icthyocrinus								■	—	■									
Cleistocrinus									■										
Synaptocrinus											■	■							
Metichthyocrinus													■						
LECANOCRINACEA									═	═	═	═	═	═	═	═	═	═	═
Lecanocrinidae									▥	▥	▥								
Mysticocrinus									■										
Lecanocrinus									■	■									
Miracrinus										■									
Geroldicrinus											■								
Nipterocrinidae									▥	▥	—	▥	▥						
Cholocrinus									■										
Hormocrinus									■										

TABLE 5. *(Continued)*

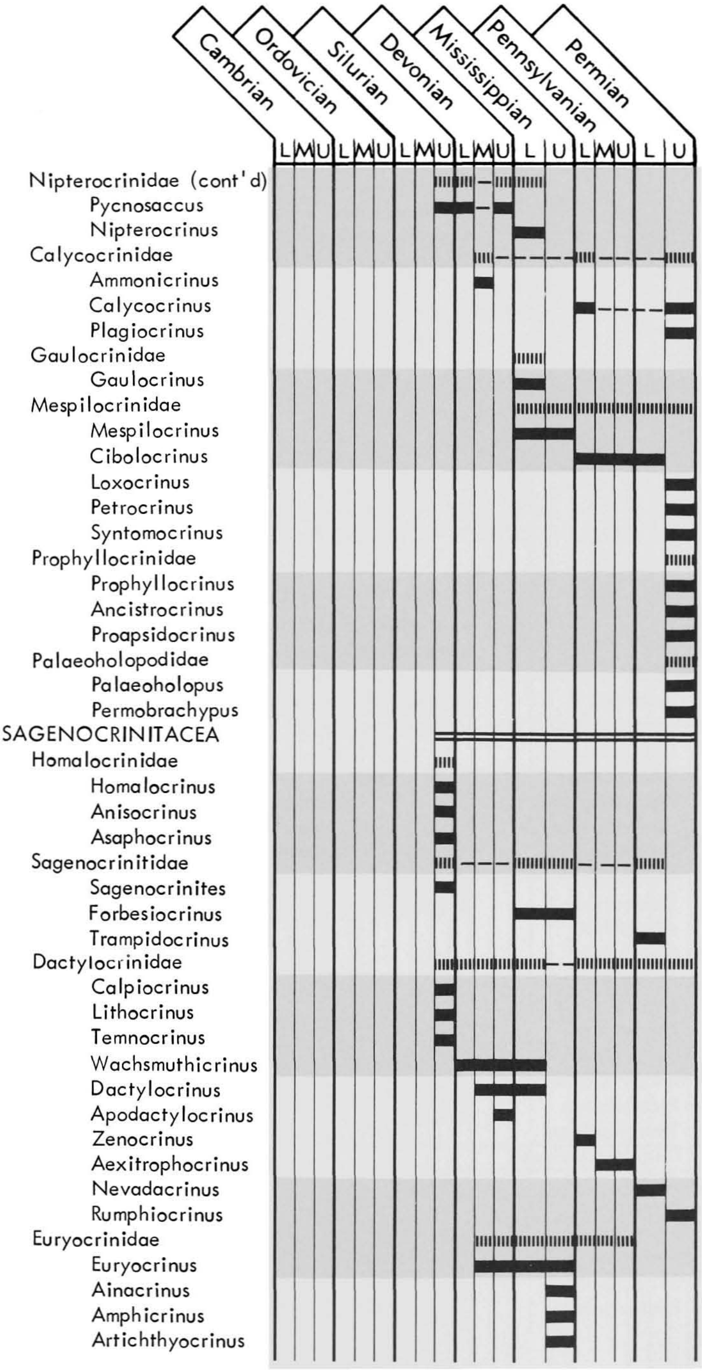


Table 5. *(Continued)*

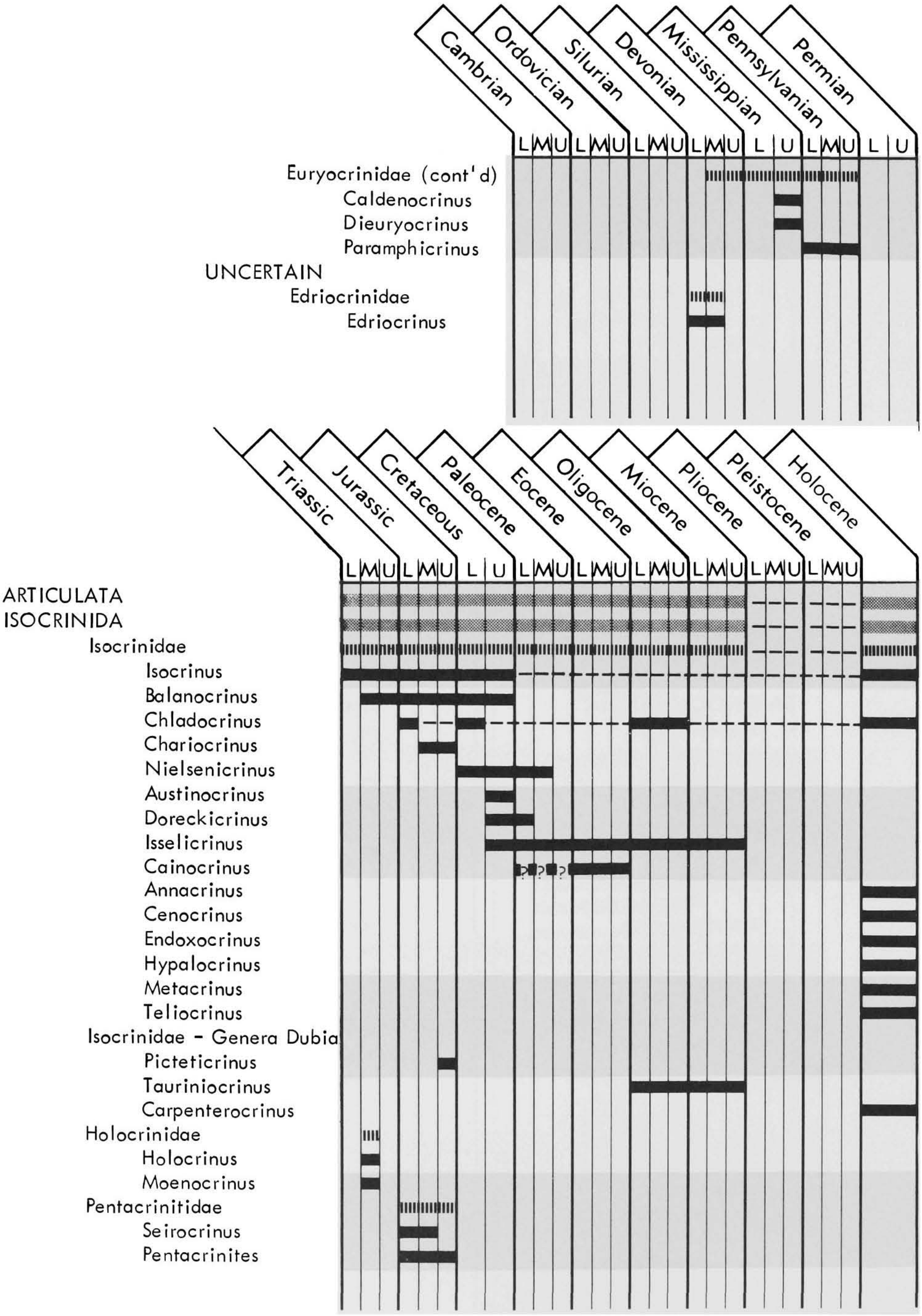


TABLE 5. *(Continued)*

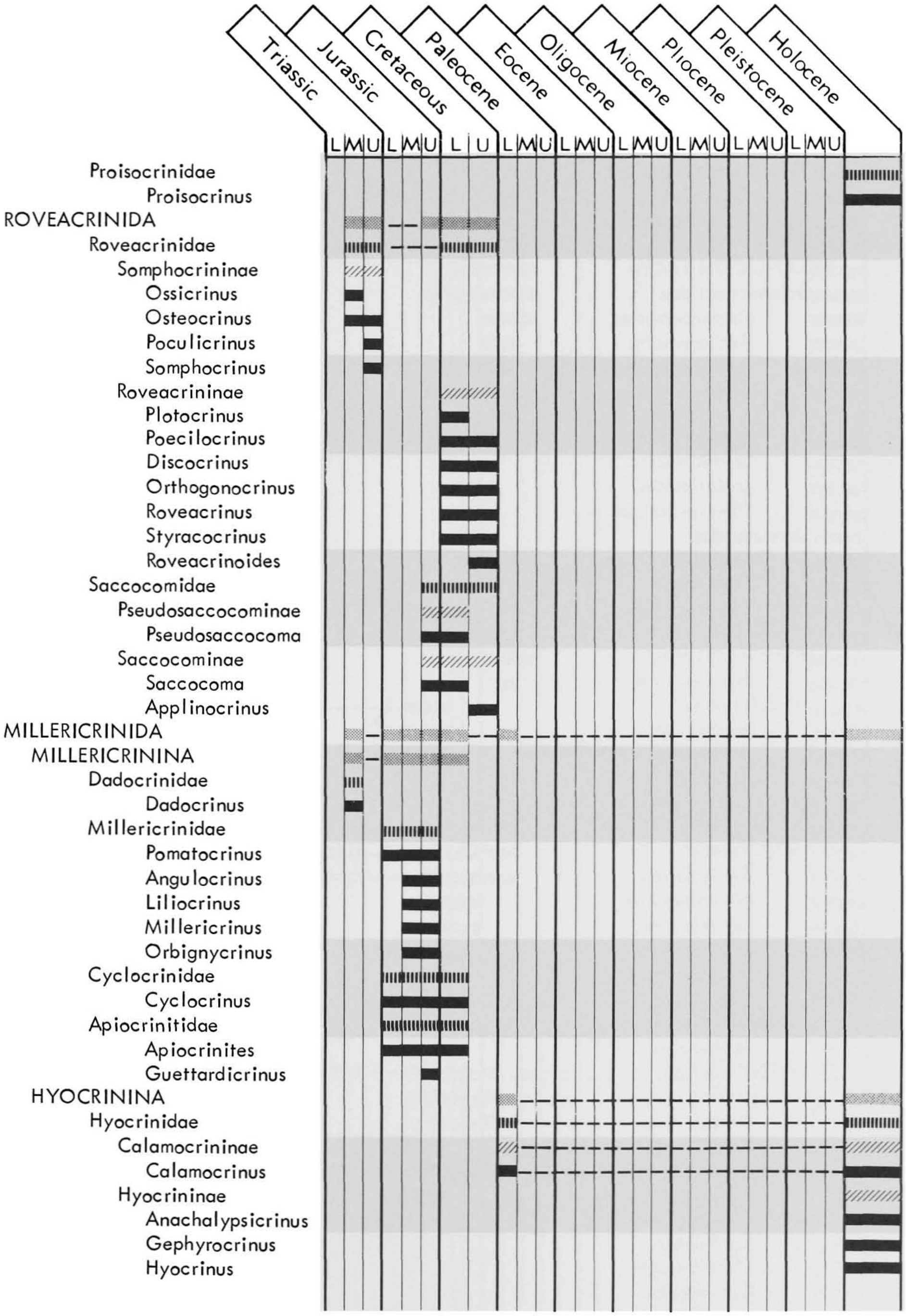
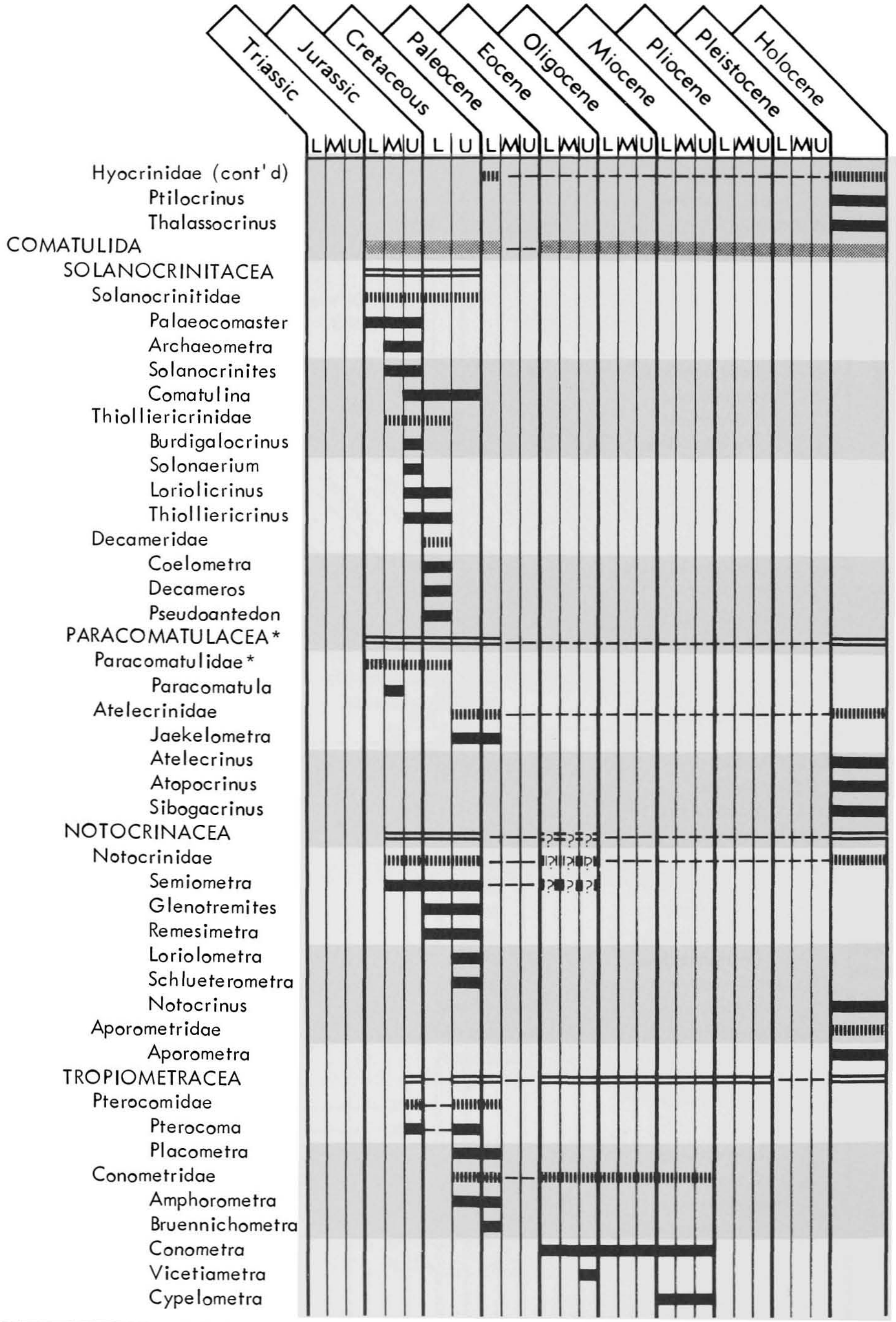


TABLE 5. *(Continued)*



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* Range extended, based upon two new unpublished genera (see p. T870).

Table 5. *(Continued)*

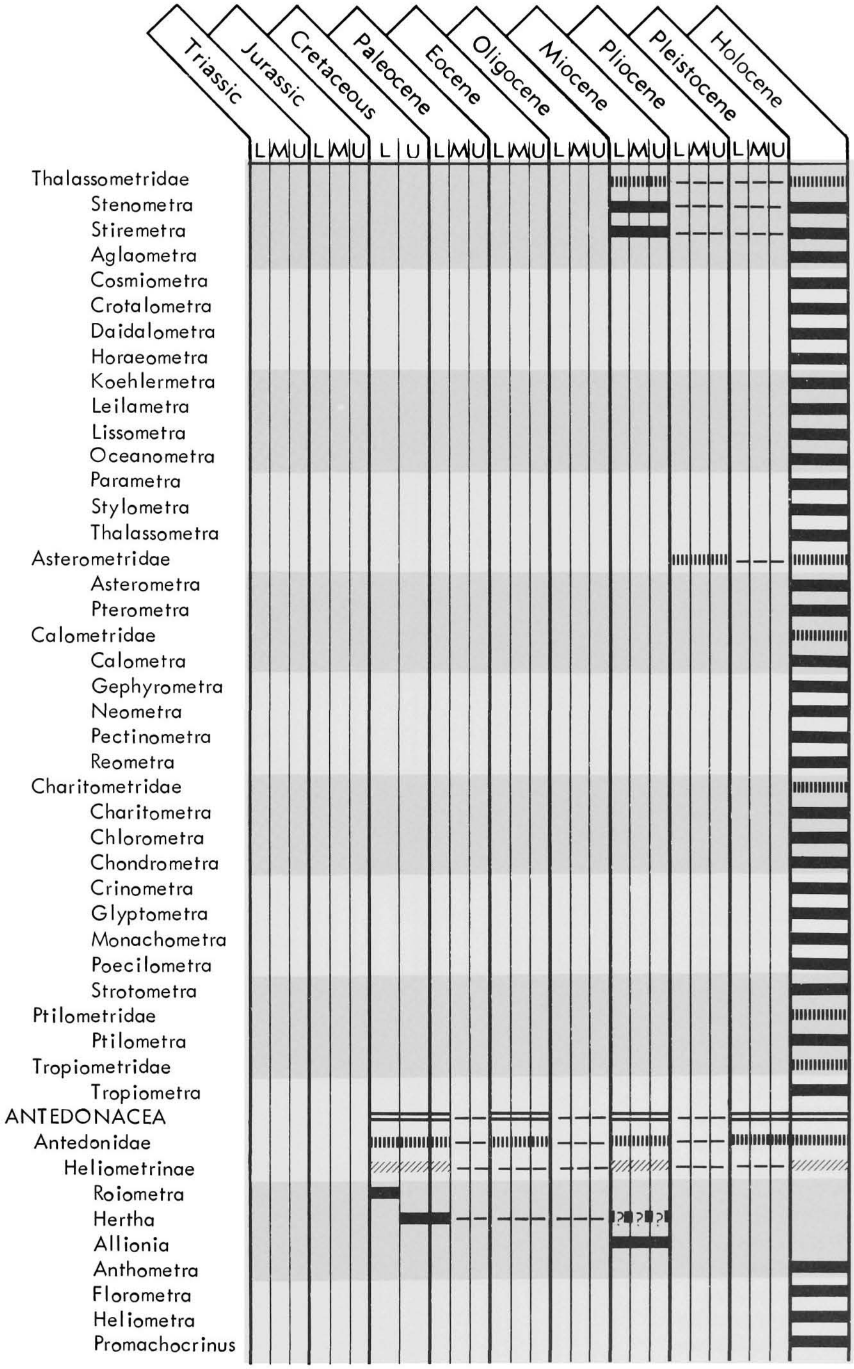
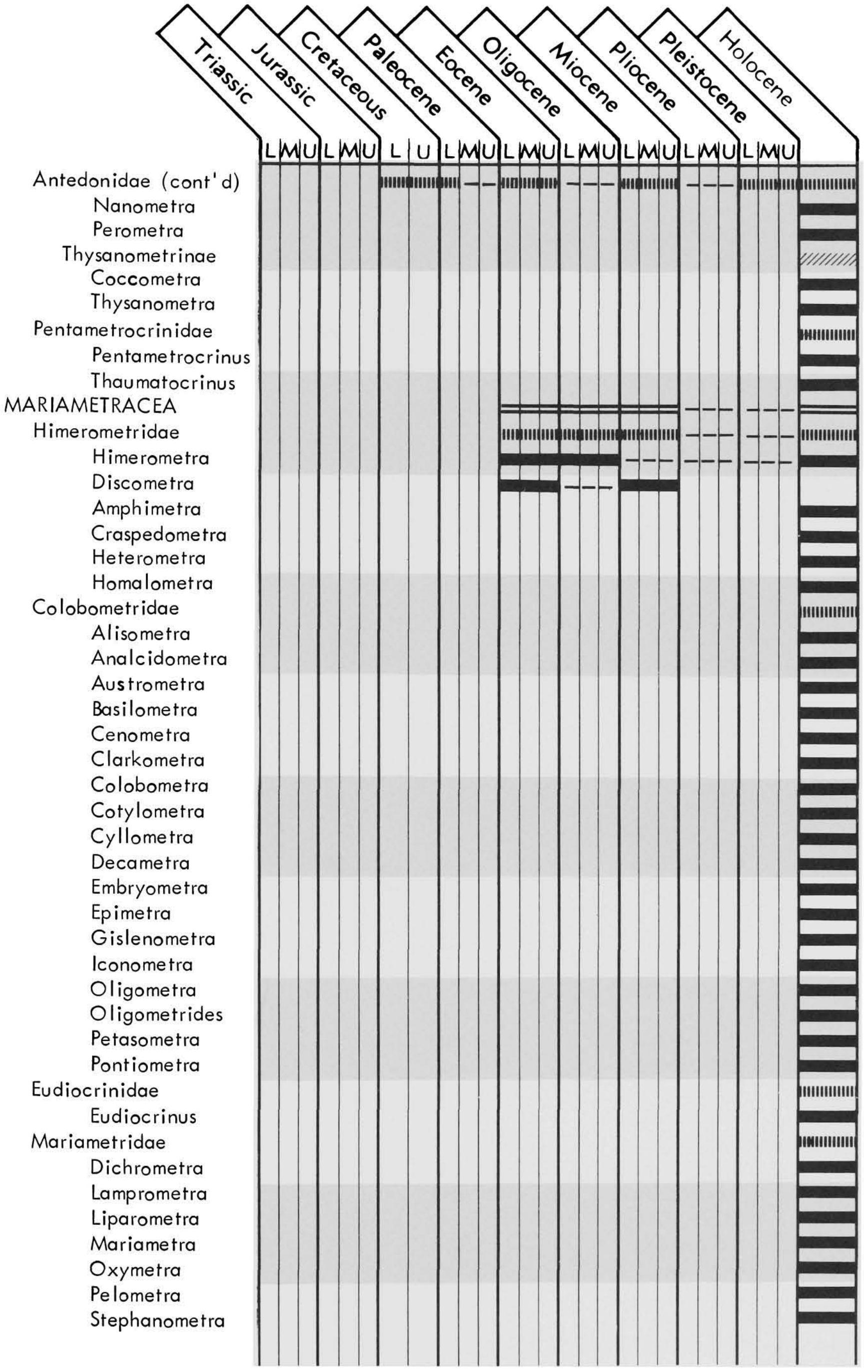


TABLE 5. *(Continued)*

	Triassic			Jurassic			Cretaceous		Paleocene			Eocene			Oligocene			Miocene			Pliocene			Pleistocene			Holocene
	L	M	U	L	M	U	L	U	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U	
Antedonidae (cont'd)							▥	▥	▥	—	—	▥	▥	▥	—	—	—	▥	▥	▥	—	—	—	▥	▥	▥	▥
Solanometra																											▮
Antedoninae												▨	▨	▨	—	—	—	▨	▨	▨	—	—	—	▨	▨	▨	▨
Palaeantedon												▮	▮	▮	—	—	—	▮	▮	▮	—	—	—	▮	▮	▮	▮
Andrometra																											▮
Annametra																											▮
Antedon																											▮
Argyrometra																											▮
Dorometra																											▮
Euantedon																											▮
Eumetra																											▮
Iridometra																											▮
Mastigometra																											▮
Toxometra																											▮
Zenometrinae												▨	▨	▨	—	—	—	—	—	—	—	—	—	—	—	—	▨
Microcrinus												▮	▮	▮													
Adelometra																											▮
Anisometra																											▮
Balanometra																											▮
Caryometra																											▮
Cyclometra																											▮
Eometra																											▮
Eumorphometra																											▮
Hybometra																											▮
Kempometra																											▮
Leptometra																											▮
Poliometra																											▮
Psathyrometra																											▮
Sarametra																											▮
Zenometra																											▮
Bathymetrinae																											▨
Bathymetra																											▮
Boleometra																											▮
Fariometra																											▮
Hathrometra																											▮
Nepiometra																											▮
Orthometra																											▮
Phrixometra																											▮
Retiometra																											▮
Thaumatometra																											▮
Tonrometra																											▮
Trichometra																											▮
Isometrinae																											▨
Isometra																											▮
Perometrinae																											▨
Erythrometra																											▮
Hypalometra																											▮

TABLE 5. *(Continued)*



For *Discometra* (Himerometridae), read Tert.(Mio.).

TABLE 5. *(Continued)*

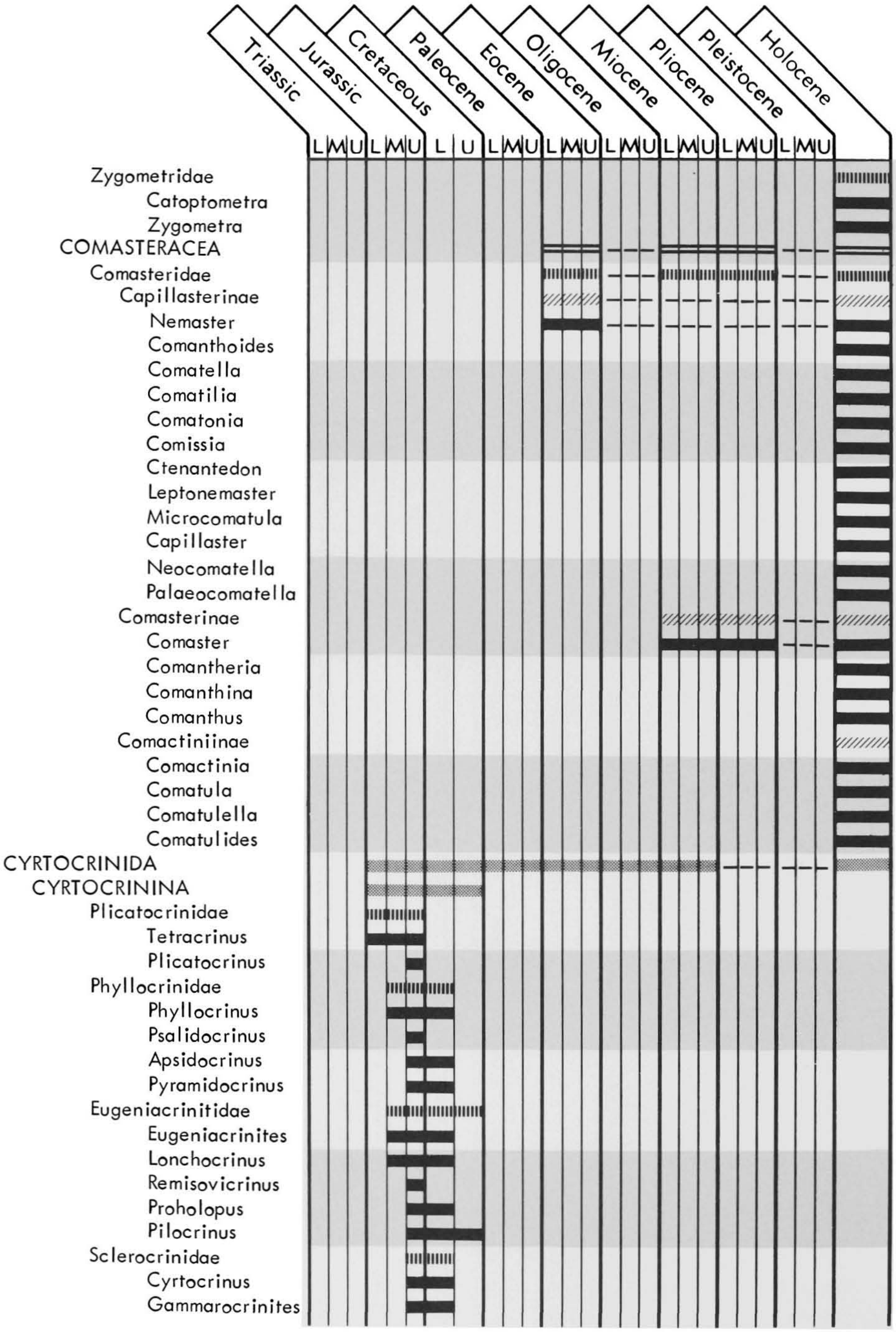


TABLE 5. *(Concluded)*