THE CRINOID STEREOM

By D. B. Macurda, Jr., D. L. Meyer, and Michel Roux

[Museum of Paleontology, The University of Michigan; University of Cincinnati;
Laboratoire de Paléontologie, Université Paris-Sud]

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INTRODUCTION

The endoskeleton of a crinoid is a porous lattice composed of high-magnesium calcite, an attribute apparently characteristic of all echinoderms. The stereom may be highly differentiated in crinoids, as shown by the study of the skeletal microstructure of modern crinoids (Macurda & Meyer, 1975), and well preserved in fossil crinoids as shown by the study of columnals of Mesozoic-Cenozoic Articulata (Roux, 1970, 1971, 1974, 1975), and of Paleozoic inadunates (Lane & Macurda, 1975; Moore, Jeffords, & Miller, 1968).

Direct observational investigations of modern comatulid and other articulate crinoids (Macurda, 1973; Meyer, 1973a, b; Macurda & Meyer, 1974) have permitted the correlation of life habits with the microstructure of the skeleton, enhancing the paleobiological study of crinoids.

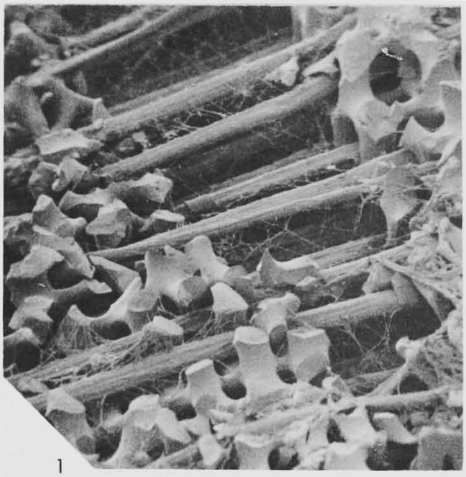
MAIN MICROSTRUCTURAL FEATURES

The crinoid stereom shows two main microstructural features in relation to the organic stroma (Roux, 1970, 1971). The first one is an irregular and labyrinthic lattice of calcite with a thin meshwork of collagen microfibers (Fig. 185,*4;* type β of Roux). The second is a regular galleried stereom with paraxial galleries where collagenous fibers penetrate through the ossicle (Fig. 185,*1;* type α of Roux). The articular ridges of the crenularia have various microstructural features: galleried stereom with short paraxial collagenous fibers or dense labyrinthic stereom without paraxial organic stroma (Fig. 185,*4*). The calcite meshwork of the ligamentary areola is always galleried. Some muscular articulations have a muscle fossa with small needlelike calcite projections to which muscle fibers adhere (Fig. 185,*2; see* 191,*1,2*). The microstructural organization of an articular facet is highly differentiated in stems, cirri, brachials, and pinnules.

STEM

Stem plates of crinoids are ubiquitous in Paleozoic sediments, locally bulking large in volume. They are much less important in the Mesozoic-Cenozoic and are confined to sediments at depths below 100 meters in the recent. The stems of modern crinoids are represented by different types of columnals, which can be compared with fossil specimens.

The heteromorphic column of the isocrinids is composed of stellate, pentagonal, or cylindrical plates, which are divided into five petaloid areolae that are bordered by a symplexial crenularium (Fig. 186,*1*). The stereom of the areola is characteristically galleried (Fig. 186,*3,4*). Each culmen is



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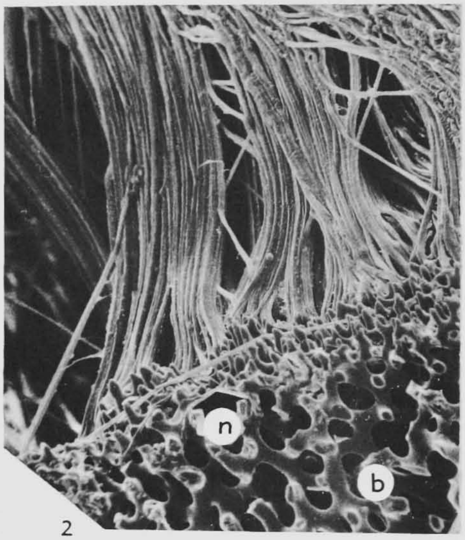

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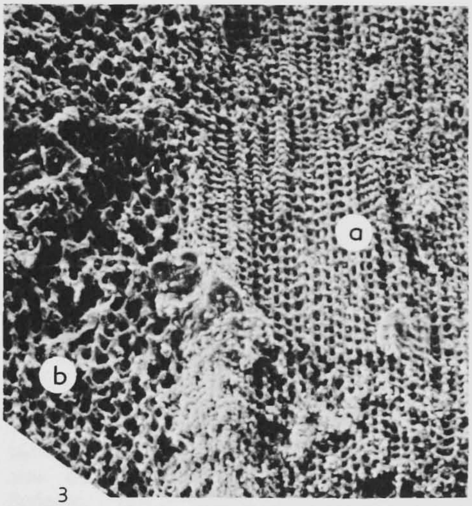

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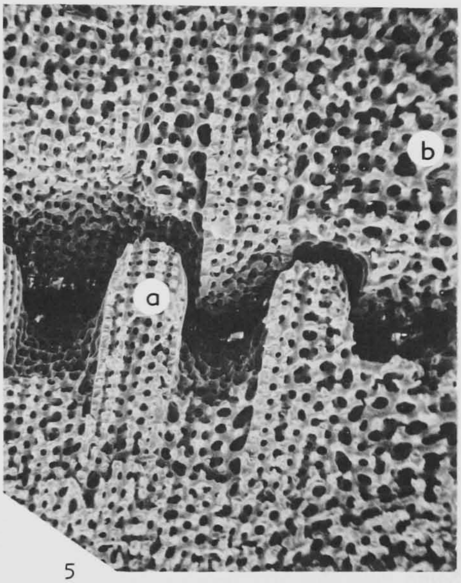

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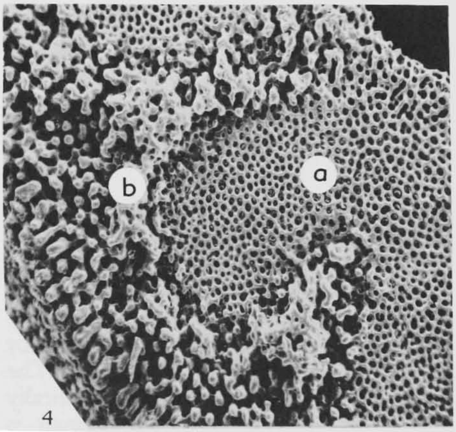

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composed of galleried stereom developed on the labyrinthic stereom of the interpetaloid area. Short and long paraxial collagenous fibers that occupy the galleried pores (Fig. 185,*1*) provide a strong bond between two internodal plates (Fig. 185,*1,5*). The tensile strength of these bonds account for the ability of a recent crinoid such as *Cenocrinus* to elevate the crown almost one meter above the sea floor in currents in excess of 0.5 knots (Macurda & Meyer, 1974).

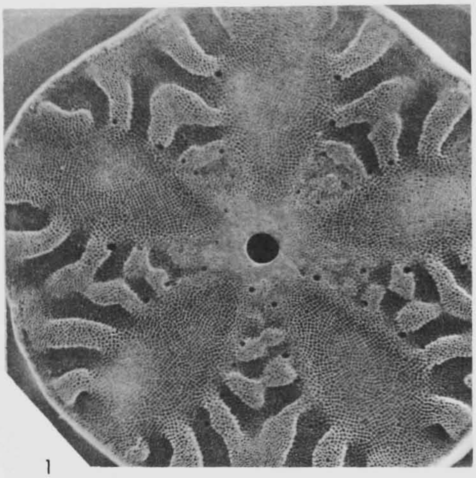
The lower (distal) surface of each nodal is a cryptosymplexy to almost smooth synostosial suture (Fig. 186,*2*), which can result from the secondary development of stereom filling in interarticular space of a symplexy and anchylosing it. The facets appear smooth because of the greatly reduced crenularium and the smaller pores of the synostosial stereom. These may be labyrinthic as in the stem of *Annacrinus,* or galleried as in the stem of *Endoxocrinus.* Proceeding distally on a stem, the synostosial stereom becomes more highly developed and can fill in the lumen. A large mass of labyrinthic stereom may develop below the distal synostosis of an isocrinid stem; with cirri it serves as an anchorage in mud or sand (e.g., *Annacrinus*), or as a terminal attachment disc it may encrust a hard substrate (e.g., *Hypalocrinus*).

The homeomorphic stem of the Hyocrinidae is instructive because this type is very frequently found in fossils. Agassiz's work (1892) on *Calamocrinus* is the most detailed study of such a stem. The proximal part of the stem has very primitive articulations that probably lack galleried stereom and paraxial collagenous fibers. These are present in the middle part of the column where articulations have a symplectic crenularium. Around the lumen, a large annular medulla (like the claustrum of some Paleozoic columnals) is composed of labyrinthic *(β)* stereom characterized by large pores. In the distal part of the stem, the articular facets are plain with a multiradiate crenularium. The main part of the columnal is composed of a labyrinthic stereom, which has circular growth lines.

The recent Bathycrinidae have a xenomorphic column. The proxistele is well developed in *Monachocrinus* and *Bathycrinus;* the first stem plates immediately below the calyx have labyrinthic stereom and synostosial articulations. Quickly, articulations are developed with thick labyrinthic stereom for the crenularium and galleried stereom for the areola (Fig. 185,*4*). A new secondary columnal grows into the interarticular space; it has only galleried stereom. The mesistele of the Bathycrinidae is characterized by elliptical bifascial synarthries (Fig. 186,*5*). Each synarthry is bisected by a large, massive, fulcral ridge (Fig. 186,*6*), which may show abrasive wear. In *Democrinus,* the ridge is bordered on either side by a series of knobs and large pores, which are offset on either side of the ridge. The knobs are the high points of the articulation and apparently fit into corresponding large pores on the opposing plate. This prevents slippage in any direction. This type of fulcral ridge with its bordering knobs and pores also developed in the brachial articulation of some Paleozoic inadunate crinoids. Most of the surface of the synarthrial articulation in the bathycrinids is deeply concave and characterized by a well-developed galleried stereom penetrated by ligament fibers. Since the fulcral ridges are set from 30 to 90 degrees to one another on the opposite ends of each columnal, as seen in a stem of one specimen of *Monachocrinus,* this permits flexure in any direction. The tensile strength of

(See facing page.)

Fig. 185. Ligament fibers and articular surfaces (Roux, n).——*1.* Paraxial collagenous fibers through a symplexy on the stem of *Metacrinus nobilis* Carpenter, recent; with galleried stereom to left and interarticular space to its right, ×900.——*2.* Muscular articulation of brachial ossicle of *Annacrinus wyville-thomsoni* (Jeffreys), recent. Muscular fibers on needlelike projecting surface *(n)* of muscle fossa; labyrinthic stereom of interarticular ligament fossa *(b),* lower right, ×350.——*3.* Paraxial section of a columnal of *Isselicrinus subasaltiformis* (Miller), Eocene, London Clay, showing well-preserved galleried stereom *(a)* on the right and labyrinthic stereom *(b)* on the left, ×60.——*4.* Crenularium of a proximal columnal of *Monachocrinus recuperatus* (Perrier), recent; ×150.——*5.* Symplexial crenularium of a columnal of *Annacrinus wyville-thomsoni* (recent); paraxial section through the articulation with organic stroma removed, ×100. [*a,* galleried stereom (reseau *α*); *b,* labyrinthic stereom (reseau *β*); *n,* needlelike projections.]



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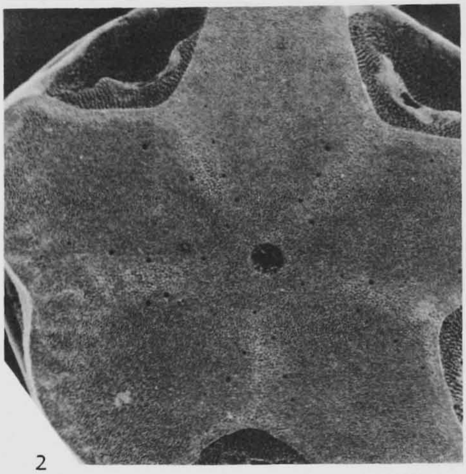

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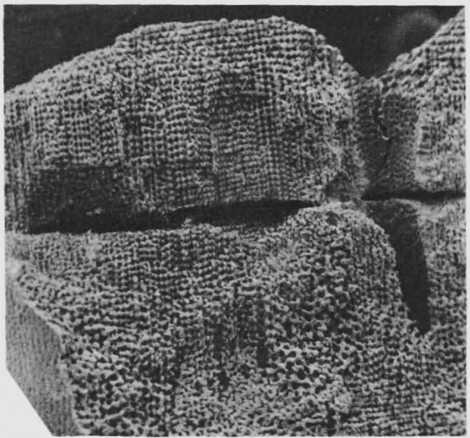

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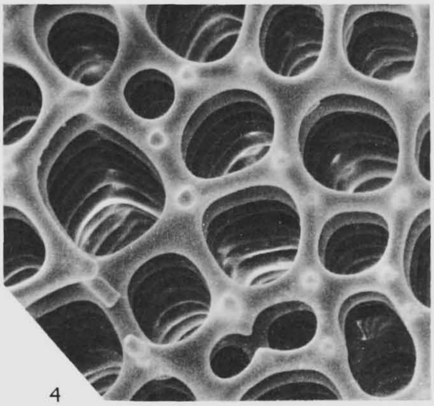

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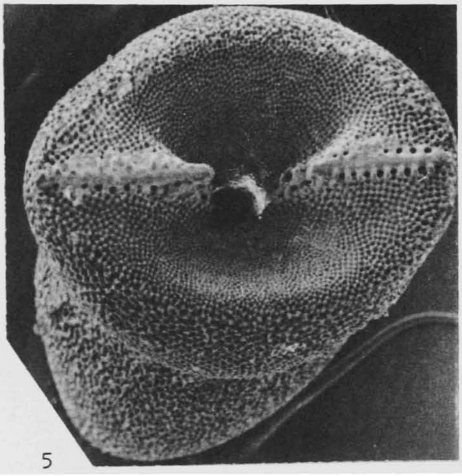

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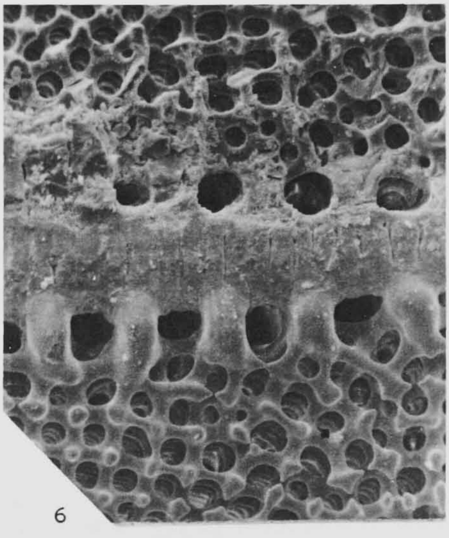

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these articulations is strong enough to hold the calyx upright in moderate currents, only the roots being in contact with the substrate (Macurda & Meyer, 1974).

The most detailed investigation of the stereom of fossil crinoids has involved the stem plates of Mesozoic and Cenozoic articulates (Roux, 1970, 1971, 1974, 1975). During diagenesis, the magnesium that is randomly distributed within the crystal lattice of a crinoid plate is lost. Calcite may secondarily encrust the surface of the plate or penetrate throughout the stereom, being deposited in optical continuity with the original calcite. The original structural detail may be preserved and visible in a thin section, or brought into relief on a surface by natural or artificial etching (Fig. 185,*3*). Further recrystallization may completely destroy the fabric of the stereom. The most fortuitous conditions for stereom preservation appear to be when the plates are preserved in marl or clay. Sometimes pyrite precipitated within the stereom will make an internal cast if the calcite is leached away.

Biometric studies of the stereom of fossil articulate columnals demonstrate that α and β stereom are easily recognizable and that the distributional pattern of these within the stem is of ontogenetic, functional, and taxonomic significance (Roux, 1970, 1971, 1974, 1975). Figure 187,*1* illustrates the growth of the stereom and the gradual increase in pore diameter, the subsequent formation of two smaller pores, and their gradual increase in diameter. The resulting biometrical graph diagrams this process (Fig. 187,*2*). Preparation of a graph for the β stereom of the Jurassic millericrinid *Apiocrinites* (Fig. 187,*4*) shows the ontogenetic development of this plate; the arrows in Figure 187,*4* indicate the directions of growth. The patterns of the stereom may differ between proximal and distal columnals. Thus, in Triassic *Encrinus,* proximal columnals have a highly complex pentalobate crenularium; in median columnals it is radially organized and restricted to near the periphery and in the distal columnals it has become more extensive from the border to near the center (Fig. 188). Thin transverse sections through the columnals show the ontogenetic evolution of the facet morphology during columnal growth and the main stages of microstructural organization. When fossil columnals are dissociated in the sediments, such a study shows that the three types of columnals belong to the stem of one species (Fig. 188,*B,C*). Due to these differences and the pentalobate structure of isocrinid stems, they are best represented by having separate radial biometrical plots of the dimensions of the α stereom of the areola and β stereom of the petalodium in the proximal, median, and distal columnals, as in the Jurassic isocrinid *Balanocrinus subteres* (Fig. 187,*5*). Such graphs are highly distinctive for taxonomic differentiation, summarize the ontogenetic development, reveal functional changes (e.g., Fig. 187,*3a-c*), and can be used for evolutionary comparisons.

CIRRI

The cirri of modern crinoids grow outward from the nodal columnals of the isocrinids or from the centrodorsal of comatulids. In the former, the distal cirri function as anchors or props for the distal part of the stem; in the latter they are used to grasp the substrate (e.g., rocks, sponges, alcyonarians, corals, etc.). They are very tenacious and must be carefully detached. If removed from the substrate they will reattach fairly rapidly if provided an opportunity.

Cirri have basically the same structure in the isocrinids and comatulids. They are cylindrical and pierced by a lumen. The stereom of the isocrinid nodicirral articulation may be organized into two distinct

(*See facing page.*)

Fig. 186. Stem plates (Macurda & Meyer, 1975).——*1.* Plan view of symplexy on internodal stem plate of *Isocrinus blakei* (Carpenter), recent, W.Indies; ×28.——*2.* Plan view of synostosis on nodal stem plate of *Isocrinus blakei,* recent, W.Indies, ×28.——*3.* Lateral view of broken interior of internodal stem plates along axis of areola of *Isocrinus blakei,* recent, W.Indies, lumen at right, ×56.——*4.* Galleried stereom in center of areola on internodal stem plate, *Endoxocrinus parrae* Gervais, recent, W.Indies; ×700.——*5,6.* Synarthrial articulation on stem plate of *Democrinus* sp., and enlargement of fulcral ridge, recent, W.Indies; ×56 and ×350.

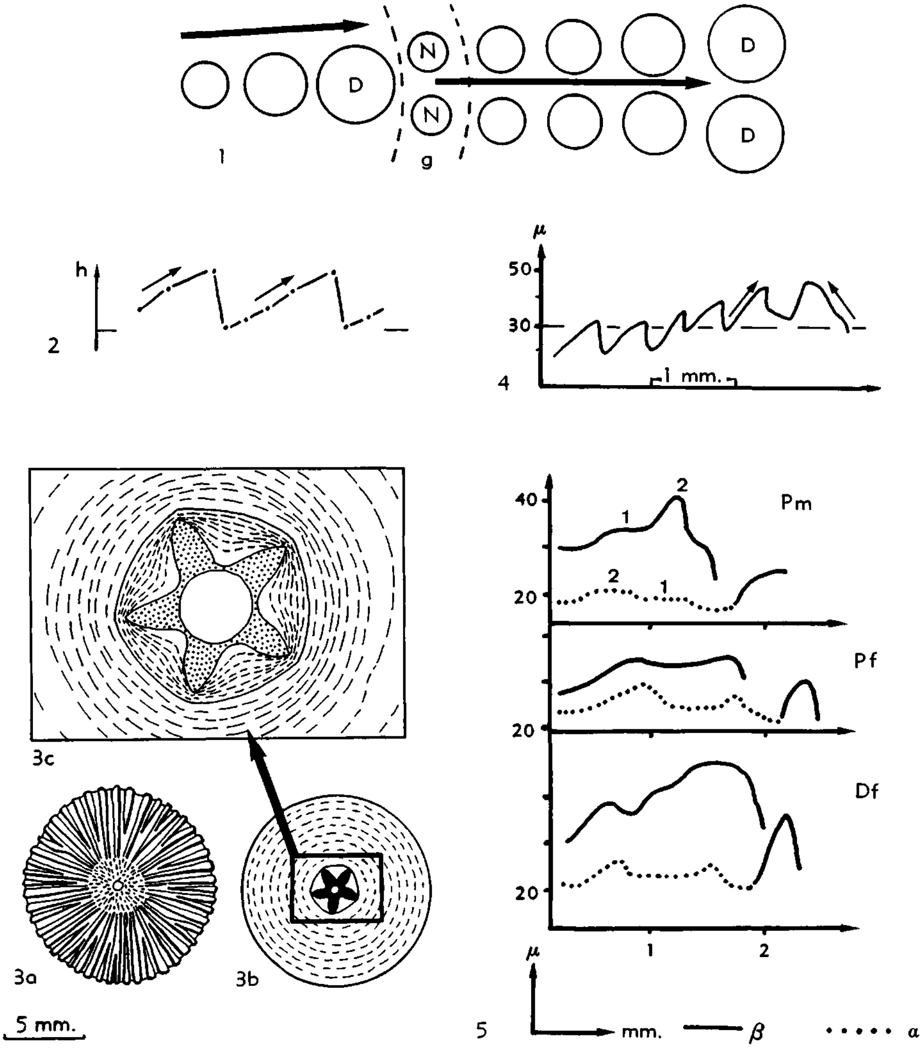


Fig. 187. Biometric graphs of stem growth and ontogenetic modification (Roux, 1975).——*1.* Radial growth of β stereom in stem, subdivision of mesh *(D)*, formation of new mesh *(N)* at growth line *(g)* and continued growth.——*2.* Radial biometric graph of *1* with vertical distance *(h)* equaling dimension of stereom and lateral distance radial growth; arrows indicate directions of growth.——*3a.* Articular facet of a distal columnal of *Millericrinus milleri* (Schlotheim), Jur., France.——*3b.* Transverse section showing the pentalobate organization of the young columnal *(3c)*.——*4.* Radial biometric graph of β stereom of an *Apiocrinites,* Jur., columnal.——*5.* Radial biometric graphs of a and β stereom of proximal *(P)* and distal *(D)* columnals of *Balanocrinus subteres* (Münster), Jur. (*m,* near the median of the thin section; *f,* on the articular facet). Numbers indicate growth stages.

fields, one proximal and one distal as on some centrodorsals; others are undifferentiated. The articulum of a cirral is typically organized into a larger distal field, which has galleried stereom, and a smaller proximal field, also galleried, with some type of articular surface(s) between them (Fig. 189,*1a,b*). The mean pore diameter is smaller in the comatulids than in the isocrinids. The articular faces are of varied structure; they can be two knobs lateral to the lumen with corresponding sockets on the opposing face, a bar or horseshoe-shaped area above the lumen, or flattened elevated surfaces. All have denser stereom; the projecting articular surfaces are on the distal ends of cirrals, the corresponding depressions on proximal surfaces. The greater development of the ligament field in the lower part of the articulum enhances the clasping function of the cirri since the contraction of these pulls the cirrus in toward the stem or centrodorsal, firmly affixing the crinoid. The upper ligament field allows the cirrus to be detached and raised. The most distal cirral is a small, sharp hook; its stereom is usually almost solid, transparent calcite. If short spines are developed along the lower surface of the distal cirrals, these and the hook provide even firmer anchorage for the crinoid.

CALYX PLATES

The calyx plates of the articulates (e.g., basals, radials, centrodorsal) surround and protect the lower part of the crinoid soft body, which includes the chambered organ and main nervous center, located aborally. The nerves, which extend outward from the latter, are richly expressed in the numerous nerve canals (Fig. 189,*2*,*3*) penetrating the plates and extending into the arms, stem, and cirri (MACURDA & MEYER, 1975). In the isocrinids, accessory nerve canals may penetrate the basals to extend well down into the stem (Fig. 186,*1*,*2*). The calyx plates have a porous stereom, except on the exterior, where it is denser as in the arms. The surface of contact between the calyx plates is by definition a synostosis.

BRACHIAL ARTICULATIONS

In crinoids, articulations reach their greatest diversity and complexity in the arms. Four types of articulations are known: a muscular articulation, a syzygy, a symmorphy, and a synarthry. The most common is the muscular articulation that articulates the arm with radials, branching arms with their axillaries, and most brachials with one another. Syzygies are a type of stiffener, particularly just proximal to an axillary. Synarthries are relatively uncommon; the fulcral ridge is vertical and thus accentuates the lateral motions of the arms. Symmorphies are quite rare and their functional significance not fully understood.

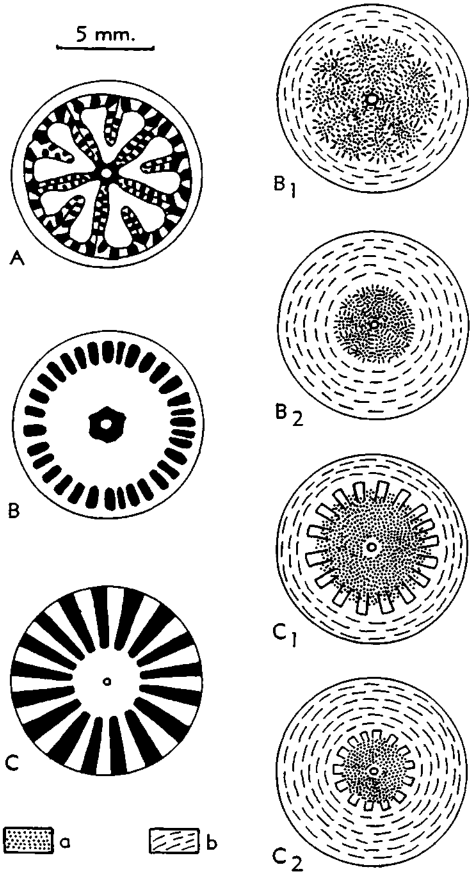
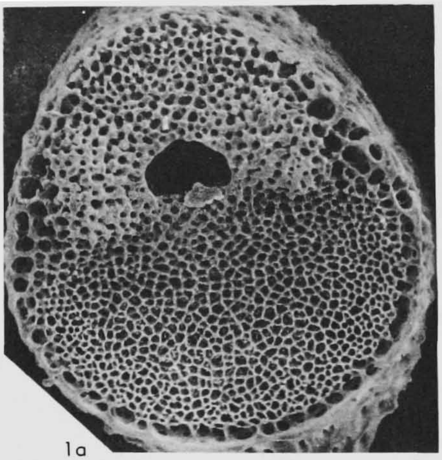


FIG. 188. Microstructural evolution of columnals of *Encrinus liliiformis* LAMBERT, Trias. (Roux, 1975). On the left, the morphology of the facets externally; on the right, microstructural organization as seen within a transverse thin section. [*A*, proximal columnal; *B*, median; *C*, distal; *1*, section near the facet; *2*, section near the median plane, *a*, α stereom; *b*, β stereom.]

The muscular articulation (Fig. 190,*1a*, *b*,*3a*,*b*) has a lower (dorsal) ligament fossa for the extensor ligament, a fulcral ridge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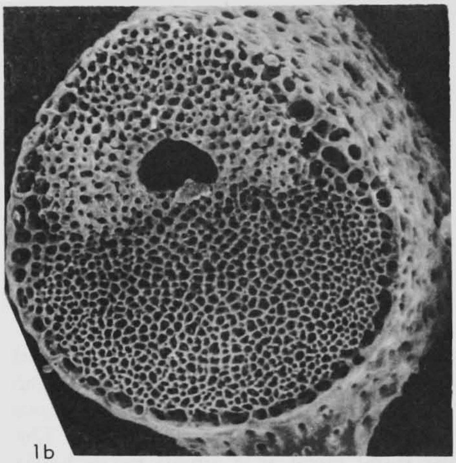
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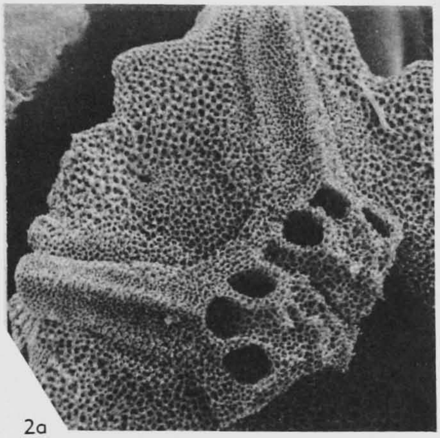
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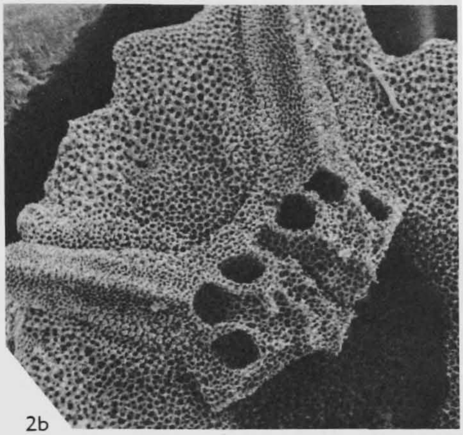
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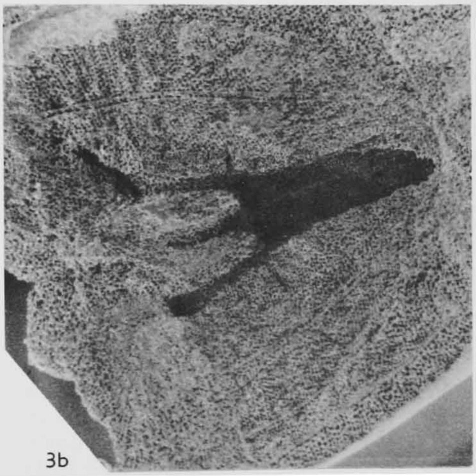
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that may be horizontal or oblique, a subcentral lumen for the brachial nerve above the fulcral ridge, two fossae lateral to the lumen for interarticular ligaments, two fossae above these for flexor muscles, and a gap between the muscle fossae, the intermuscular furrow, which contains an extension of the aboral coelomic canal. Crinoid arms can move rapidly, up to four strokes per five seconds in swimmers as *Analcidometra,* can be used for locomotion by slowly creeping across surfaces by pushing and pulling, or can be held erect in moderate currents to form filtration fans (Magnus, 1967; Meyer, 1973a; Macurda & Meyer, 1974). Arm extension is effected by the dorsal extensor ligament. The stereom of the extensor ligament fossa is porous and galleried (Fig. 190,*3a,b*) and there is commonly a ligament pit in the upper center. The fulcral ridge is composed of rather massive calcite and may show signs of abrasive wear. The stereom of the interarticular ligament fossae is also galleried (Fig. 190,*2a,b*). Long ligament fibers penetrate the stereom in both the extensor and interarticular ligament fossae; these fibers are in part collagenous (Meyer, 1971). The function of the extensor ligaments is presumably to act in conjunction with the muscles to enroll the arm but they might conceivably act in opposition to the interarticular ligaments to stiffen the arm when it is extended for feeding.

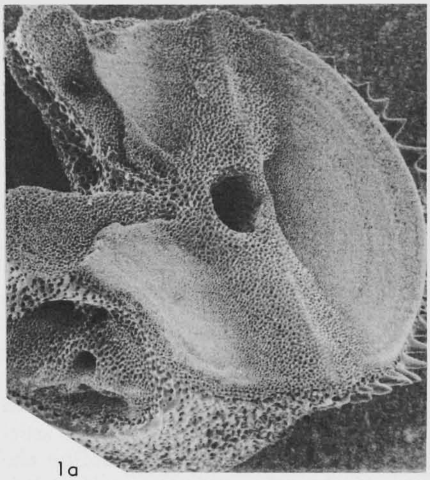
The microstructure of the stereom of the muscle fossae stands in strong contrast to that of the ligament fossae (Figs. 190,*2a,b, 3a,b*; 191,*1a,b, 2a,b*). In the comatulids it usually has a very irregular mesh; the pores are not aligned and this has been called labyrinthic (Macurda & Meyer, 1975). The pore diameters are similar to those of the ligament fossae but are more variable and can be larger or smaller. The surface pore area varies from 15 to 40 percent. In the isocrinids, the surface of the muscle fossae has a clotted appearance produced by many small needlelike projections projecting outward from the fossa (Fig. 191,*2a,b*). Labyrinthic stereom is present just beneath these needles. The labyrinthic stereom of the muscle fossae (and the needles of the isocrinids) is due to the fact that muscles attach to the surface of the stereom and do not penetrate into the skeleton as do ligament fibers. This clear difference in stereomic microstructure has been used by Lane & Macurda (1975) to distinguish muscles and ligaments in brachial and pinnular articulations of the Pennsylvanian inadunate *Aesiocrinus.*

A syzygy is a ligamentary articulation in which the culmina (ridges) of one articulum are opposed to the corresponding elevations of the other articulum (Fig. 191, *3,4*). The culmina radiate from the central lumen and the ligaments are located primarily in the crenellae between them. The syzygy, typically developed only in the comatulids, allows limited mobility in all directions. The tops of the culmina are composed of knobby, massive stereom with small pores; abrasion marks may be visible on the top. The stereom of the crenellae is porous (50 percent pore area) but may or may not be galleried.

A synarthry is a ligamentary articulation in which the opposed articula each bear a medial fulcral ridge all of which are aligned with one another. Each articulum has relatively broad bifascial ligament fields next to the fulcral ridge, which permit mobility in a direction normal to the axis of the fulcral ridge (Fig. 192,*1a,b*). The fulcral ridges may be somewhat porous and show evidence of abrasion. The stereom of the bifascial ligament fields is porous, but may or may not be galleried. In the bathycrinids and some isocrinids, the lower (dorsal) fulcral ridge may be replaced by two divergent ridges radiating dorsally to form a trifascial articulation.

(*See facing page.*)

Fig. 189. Cirral and calyx plates (Macurda & Meyer, 1975).——*1a,b.* Stereo pair of distal cirral articulation of *Analcidometra armata* (Pourtalès), recent, W.Indies; lower edge of plate in lower half of view, ×210.——*2a,b.* Stereo view of oral surface of centrodorsal of *Comactinia echinoptera* var. *meridionalis* (Agassiz & Agassiz), recent, W.Indies, with two basal rays still in position. Latter form cover for concavity of main aboral nerve center in centrodorsal. Outer openings of each basal ray contain nerve canals, which lead to adjacent overlying radials, ×56.——*3a,b.* Stereo view of fractured interior of calyx of *Democrinus* sp. showing internal space for chambered organ and main aboral nerve center and continuation of nerve canals outward (left) toward radial facets, ×35.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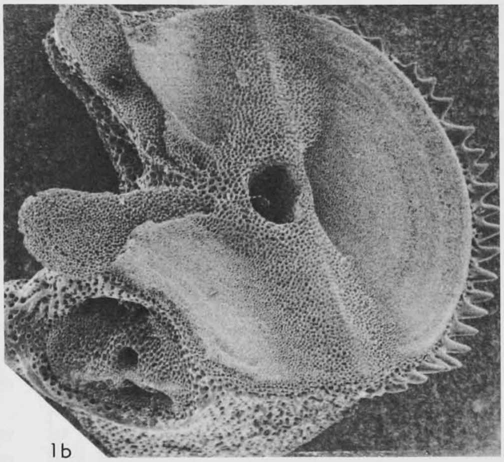
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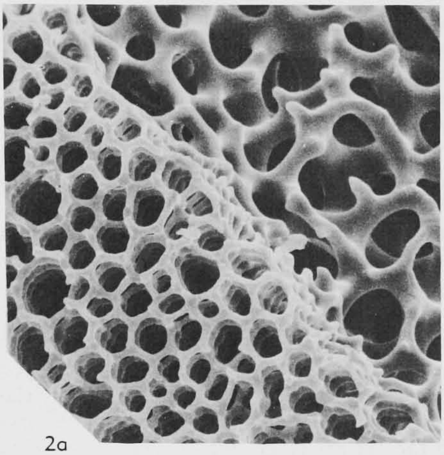
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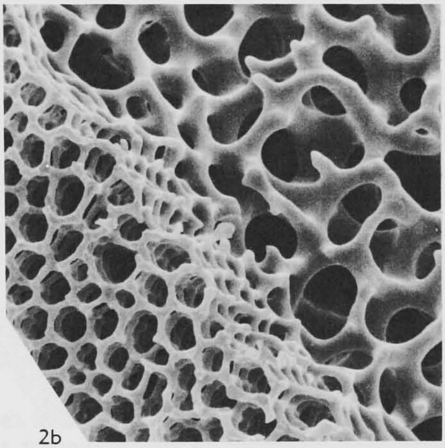
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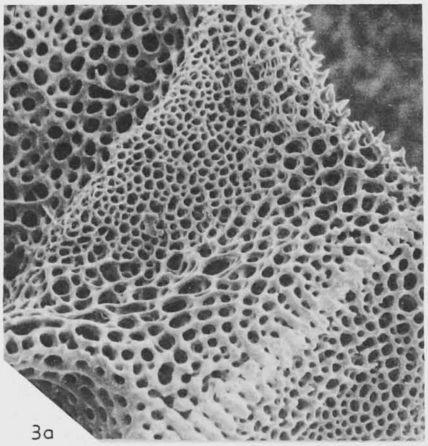
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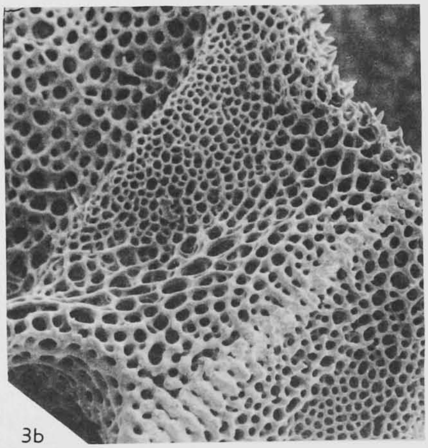
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A symmorphy is a ligamentary articulation in which a prominent transverse culmination of the epizygal brachial fits into a corresponding depression of the hypozygal (Fig. 192,*2a,b*). It is not a common articulation, but is found in the brachials of the isocrinid *Isocrinus,* for example. Sharp, dense culmina border a central flat area of the articulum, which has galleried pores.

PINNULAR ARTICULATIONS

The brachials of the modern articulates bear uniserial pinnules. The pinnules extend outward at a sharp angle from the arm and when the tube feet are extended from the adjacent pinnules to almost touch, a dense filtration fan is formed. Pinnules can stand stiffly in a prevailing current, reverse in a bidirectional wave surge in a few species, extend to increase surface area while swimming as in *Analcidometra,* and then retract to lie parallel to the arm on the upstroke, or twitch and writhe convulsively for unfathomed reasons.

The pinnule articulates with a brachial on its upper lateral surface (Fig. 190,*1a,b;* 191,*1a,b*). The articulation is a muscular articulation similar to that between the brachials except that the muscle fossae have been consolidated in a single, deep muscle concavity (Fig. 192,*3a,b*). This is a result of the rotation of the articulation relevant to the axis of the brachial and the consequent asymmetry and reduction of area available for the inner fossa. The pinnulars themselves have a variety of shapes, from trough-shaped in the isocrinids (Fig. 193,*1*) to rodlike in many comatulids (Fig. 193,*2*). The trough-shaped isocrinid pinnular has cover plates that articulate along the upper edge and the tube feet can thus be protectively retracted within. In many comatulids, the pinnular acts as a stiffening rod for the tissue and the tube feet stand exposed on the surface. Peculiar pores penetrate the upper surface (Fig. 193,*2*).

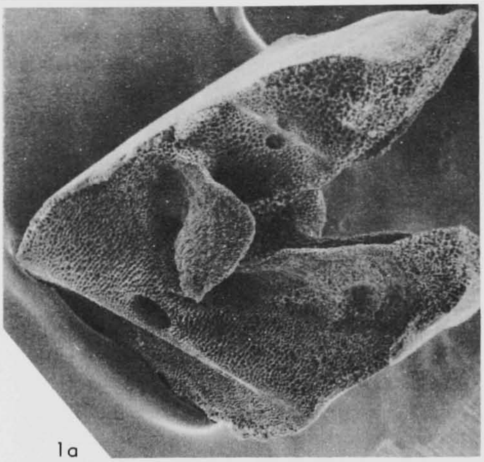
The first two or three pinnulars articulate along a muscular articulation, which has the same transverse ridge, extensor ligament fossa, interarticular ligament fossae, and muscle fossae as the brachials. The transverse ridge between the first and second pinnulars is strongly skewed so that the pinnule extends outward at more of a right angle to the brachial. Most subsequent pinnulars have a modified muscular articulation. The transverse ridge is replaced by two dorsally diverging ridges with thickened stereom (Fig. 193,*3a,b*); a vertical trough with a corresponding ridge on an opposite articulum may be present ventrally (Fig. 193,*4a,b*). Although the form of the articular surface is modified (probably to allow greater flexibility), the stereom is clearly differentiated into galleried pores for ligament fibers and labyrinthic microstructure for muscles.

CONCLUSIONS

The stereom of the crinoid endoskeleton displays a wide variety of structures that reflect the functional morphology and ontogenetic development of the animal. Investigation and interpretation of these by scanning electron microscopy is a recent development (MACURDA & MEYER, 1975; ROUX, 1974), but the study and preservation of similar microstructures in fossil crinoids will enhance the paleobiological interpretation of these animals (ROUX, 1970, 1971, 1975; LANE & MACURDA, 1975).

(See facing page.)

FIG. 190. Muscular articulations (Macurda & Meyer, 1975).——*1a,b.* Inclined oral stereo view of distal muscular articulum of brachial of *Nemaster rubiginosa* (POURTALÈS), recent, W.Indies, with pinnular articulum in lower left, ×28.——*2a,b.* Stereo view of transition from muscle fossa (upper right) to interarticular ligament fossa (lower left) on brachial of *Nemaster rubiginosa,* ×1,050.——*3a,b.* Stereo view of transition from muscle fossa (upper left) to interarticular ligament fossa (upper center); dorsal ligament fossa in lower right, *Analcidometra armata,* recent, W.Indies, ×245.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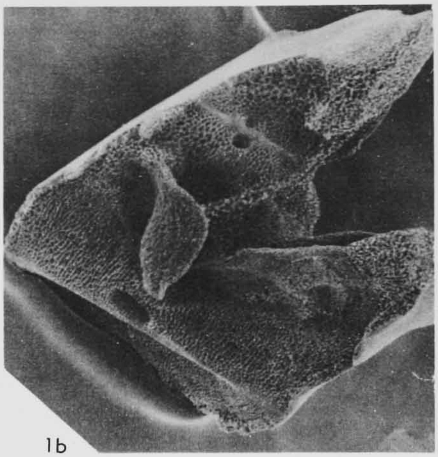
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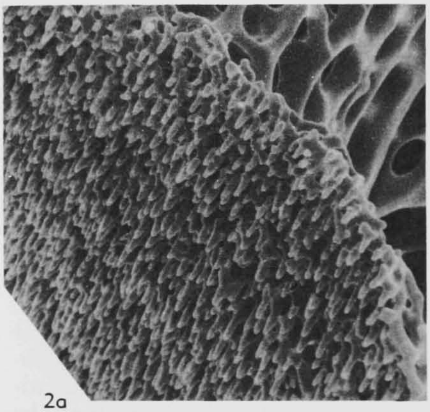
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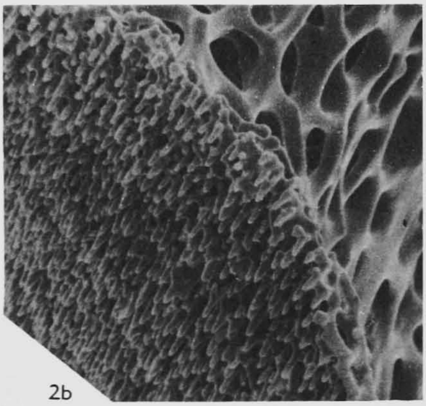
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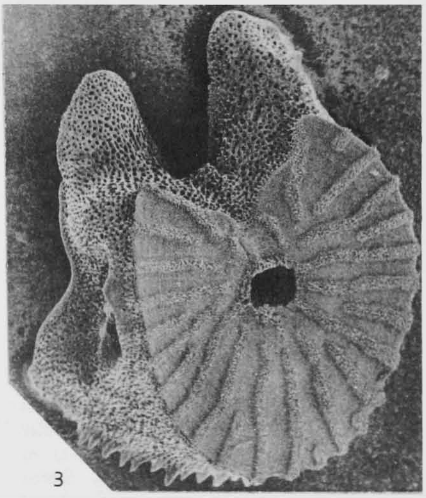
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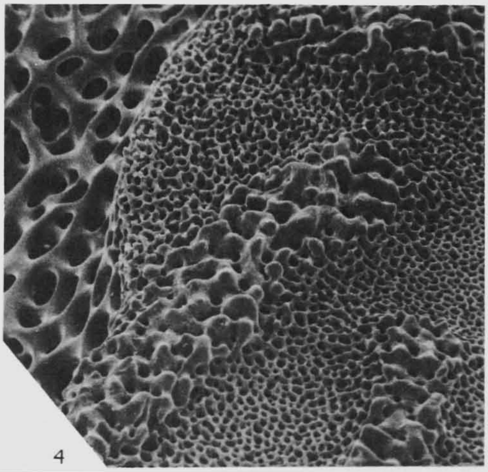
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GLOSSARY OF CRINOID MORPHOLOGICAL TERMS

By RAYMOND C. MOORE, with additions by GEORGES UBAGHS, H. WIENBERG RASMUSSEN, ALBERT BREIMER, and N. GARY LANE

[Obsolete terms are printed in italic type, and if synonyms, also enclosed in brackets]

A ray. Ray (anterior) located opposite interray designated *CD* (posterior), generally wider than others and containing anus or anal plates; includes radial and succeeding brachitaxes with intervening plates as well as pinnules. Other rays are designated *B, C, D,* and *E* in clockwise order from *A,* viewing adoral side of theca.

AB interray. Interray (anterior right) next adjoining *A* ray in clockwise direction when crinoid is viewed from adoral side; between *A* and *B* rays. Other interrays are designated as *BC, CD, DE,* and *EA* in clockwise order from *AB* viewing adoral side of theca.

abactinal. Applied to aboral side of theca or plate (syn., aboral, dorsal); preferred term is aboral.

abmedial. Away from median line of ray (syn., abradial).

aboral. Applied to surface of body opposite adoral surface (syn., abactinal, dorsal); directed away from mouth.

aboral cup. Part of aboral side of body between origins of free arms and column (syn., dorsal cup, calyx).

aboral ligament fossa. Narrowly semicircular depression on aboral side of articular face of any ray ossicle, serving for attachment of ligament fibers that function in opposed pairs of ossicles.

aboral skeleton. Part of calcareous framework located on aboral side of body; includes columnals, holdfast structures, centrodorsal, cirrals, centrale, infrabasals, basals, radials, intercalaries, brachials, and pinnulars.

abradial. Away from median line of ray (syn., abmedial).

abthecal. Applied to side of pinnule or pinnular directed away from theca.

actinal. Side of theca or arm directed toward mouth (syn., adoral, ventral); preferred term is adoral.

adambulacral (*adamb,* pl., *adambb*). Small plate of tegmen or arm between ambulacrals and ventral edges of brachials and pinnulars (syn., side plates).

adapical. See aboral, dorsal (syn., abactinal).

adcentral crenulae (of petalodium). Adradial crenulae of columnar articulum located near lumen; may merge with central area of columnal.

admedial. Toward median line of ray (syn., adradial).

adoral. Applied to surface of body that contains mouth and ambulacra (syn., actinal, ventral); direction toward mouth.

adoral groove. Furrow along adoral surface of free brachials and pinnulars; in life contains food groove and radial extensions from coeloms and water-vascular, hemal, nervous, and reproductive systems (syn., ventral groove).

adoral skeleton. Part of calcareous framework located on adoral side of body; includes orals, ambulacrals, adambulacrals, interambulacrals, interbrachials, and some anals (syn., perisomic skeleton).

adradial. Toward median line of ray (syn., admedial).

adradial crenulae (of petaloid columnal). Crenulae of columnal articulum located along margin of petal adjacent to interpetal radii inside periphery, disposed obliquely or nearly normal to margin of petal.

adthecal. Applied to side of pinnule or pinnular directed toward theca.

alphabrach. Brach of proximal brachitaxis of any axil-arm (typically developed in Calceocrinidae); succeeding brachitaxes not belonging to ramules are designated as betabrachs, gammabrachs, etc.

alpha-ramule. Branchlet borne by axillary alphabrach of calceocrinids, invariably directed abanally; succeeding ramules of a given axil-arm are designated as beta-ramules, gamma-ramules, etc.

ambulacral (*amb,* pl., *ambb*). Small plate of tegmen or arm covering part of food groove; may be separated from brachials or pinnulars by adambulacrals (syn., covering plate).

ambulacral groove. Simple or branched furrow in adoral surface of tegmen, arms, and pinnules, underlain by ambulacral epidermis; serves to convey food to mouth (syn., food groove).

ambulacral lappet. Small epidermal fold bordering ambulacral groove.

ambulacrum. Simple or branched, elongate area on adoral surface of body, extending radially from mouth onto tegmen, arms, and pinnules, formed

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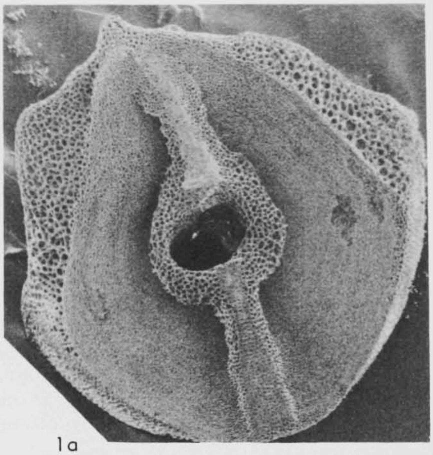
(See facing page.)

FIG. 191. Muscular articulation and syzygy (Macurda & Meyer, 1975).——*1a,b.* Inclined oral stereo view of distal muscular articulum of brachial of *Isocrinus blakei,* recent,. W.Indies, with pinnular articulum in upper center, ×35.——*2a,b.* Inclined view of muscle fossa of brachial *Isocrinus blakei,* recent, W.Indies, such as that of left center of *1a,b,* ×315.——*3,4.* Syzygy on epizygal of *Nemaster rubiginosa,* recent, W.Indies, and enlarged view of culmina at outer edge of syzygy, ×28 and ×280.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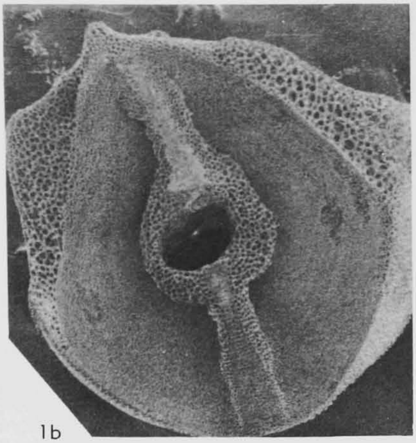
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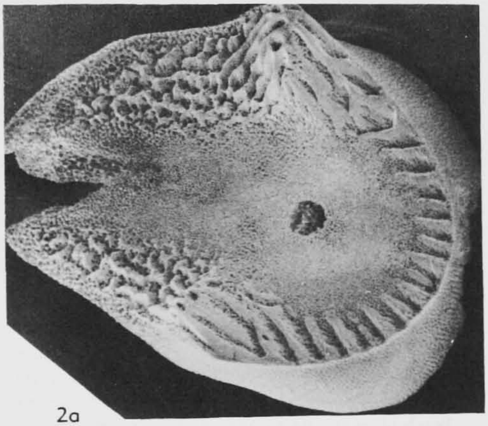
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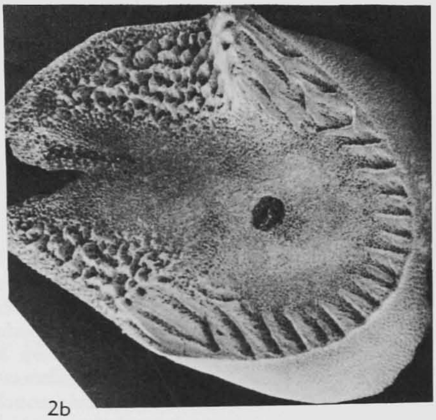
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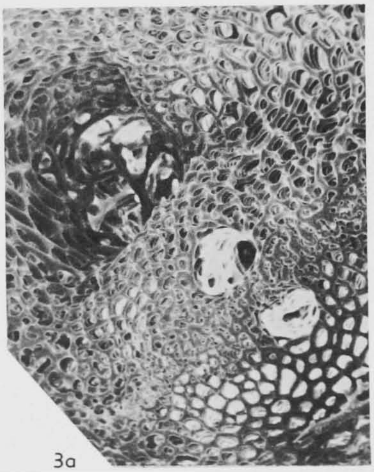
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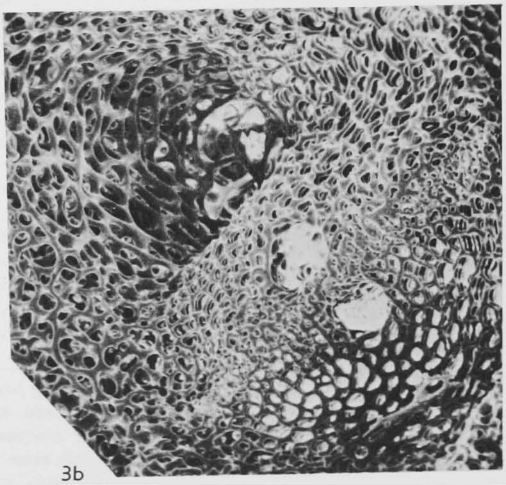
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by ambulacral groove and its associated structures such as ambulacral lappets and tube feet (syn., ambulacral tract).

anal. Any plate of posterior *(CD)* interray, mostly confined to cup but excluding interbrachials and fixed pinnulars and among inadunate and flexible crinoids may include plates of right posterior *(C)* ray other than radial, brachials, and pinnulars.

anal pyramid. Low, generally conical elevation of tegmen around anus.

anal sac. Variously shaped, generally inflated and strongly elevated part of tegmen as developed among inadunate crinoids (syn., ventral sac).

anal tube. Conical to cylindrical structure, usually of considerable height, bearing anal opening at its summit, typically developed in many camerate, flexible, and articulate crinoids (syn., proboscis).

anal *X (X)*. Special anal plate in inadunate and flexible crinoids, typically located between posterior *(CD)* radials, distal to and at left of radianal if present.

angustary. Radial articular facet very much narrower than width of plate, generally horseshoe-shaped.

anibrachial. Axillary brachial plate with left shoulder bearing proximal plate *(X)* of anitaxis and on right shoulder proximal plate of brachitaxis (e.g., *Iocrinus, Merocrinus*). [This plate was undesirably designated as brachianal by MOORE, (1962a, page 28).]

aniradial. Radial (or superradial) plate with left shoulder bearing proximal plate *(X)* of anitaxis or anal sac and on right shoulder proximal plate of brachial series (in some catillocrinine allagecrinids bearing proximal plates of as many as four arms [e.g., *Eucatillocrinus, Isocatillocrinus, Xenocatillocrinus*]). Aniradials are common in monocyclic (disparid) crinoid genera (e.g., *Synbathocrinus, Heterocrinus, Allagecrinus*) and they prevail in most dicyclic (cladid) inadunates.

anisuperradial. *C* superradial supporting proximal anal plate on its left shoulder (e.g., *Ectenocrinus*).

anitaxis. Linear succession of anal plates; commonly raised above laterally adjacent plates of posterior interray (e.g., *Reteocrinus, Xenocrinus*).

ankylosis. Fusion of ossicles effected by calcareous deposits at their interfaces, with or without disappearance of suture lines.

anterior. Referring to direction or ray designated as *A,* located opposite *CD* (posterior) interray, which contains the anus.

anterior left. Equivalent to *EA* interray.

anterior right. Equivalent to *AB* interray.

apical. See aboral, dorsal (syn., abactinal).

areola (pl., **areolae**) *(A)*. Area of columnal articulum between lumen (or perilumen if present) and inner margin of crenularium, generally smooth and featureless but may be granulose or marked by fine vermicular furrows and ridges.

areolar index. Ratio of total width (diameter) of areola to that of columnal articulum multiplied by 100 to avoid fractional numbers (see columnal indices). Areolar index combined with other articular indices has value of 100.

arm. Radial evagination of body above radial, normally extending upward or outward from theca, containing coelomic canals, and composed of pinnulate or nonpinnulate brachitaxes. Restricted by some authors (CLARK) to undivided distal branches.

arm facet. Articulate surface serving for attachment of free arm to theca.

arm trunk. Powerful ramule-bearing arm in some camerates.

armlet. *See* ramule.

articular face (or facet) *(F)*. Smooth or sculptured surface of columnal, cirral, or ray ossicle serving for ligamentary or muscular articulation with contiguous one, also (by some authors) joint face of thecal plate or arm ossicle toward adjacent skeletal element; see articulum.

articular index. Ratio of width (diameter) of columnal articulum to that of entire columnal multiplied by 100, directly measurable in most circular columnals but computed as mean of maximum and minimum values in pentagonal and elliptical columnals.

articular rim. Raised border of articulum.

articulation. Flexible to nearly immovable union of adjoined ossicles effected by ligaments or ligaments and muscles attached to articular faces.

articulum (pl., **articula**). Same as articular face (or facet). All columnal and cirral articula are divisible into lumen and surrounding area designated as zygum.

atomous. Type of ray characterized by lack of branching.

attachment disc. Terminal disc in column of comatulid larva and in some Bourgueticrinida, serving as holdfast.

augmentative regeneration. Replacement of lost part of arm by an axillary (instead of ordinary) arm plate and two branches; common among multibrachiate comatulids.

axial canal. Longitudinal passageway for axial cord penetrating columnals, cirrals, thecal plates, arms,

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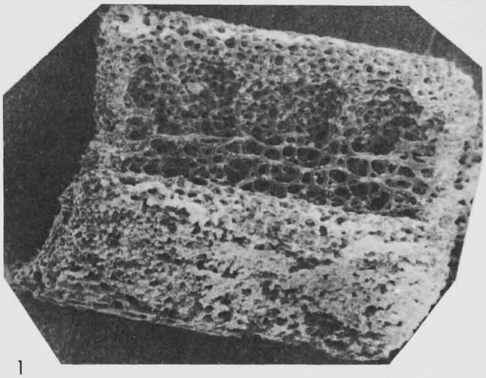
(See facing page.)

FIG. 192. Synarthry, symmorphy, and pinnular articulum (Macurda & Meyer, 1975).——*1a,b.* Stereo view of synarthry on brachial of *Atelecrinus balanoides* CARPENTER, recent, W.Indies, ×42.——*2a,b.* Stereo view of symmorphy on epizygal brachial of *Isocrinus blakei,* recent, W.Indies, ×35.——*3a,b.* Stereo view of pinnular articulum on brachial of *Endoxocrinus parrae* GERVAIS, recent, W.Indies, lower right is adoral direction of brachial, ×112.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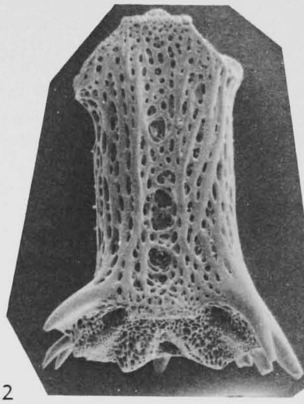
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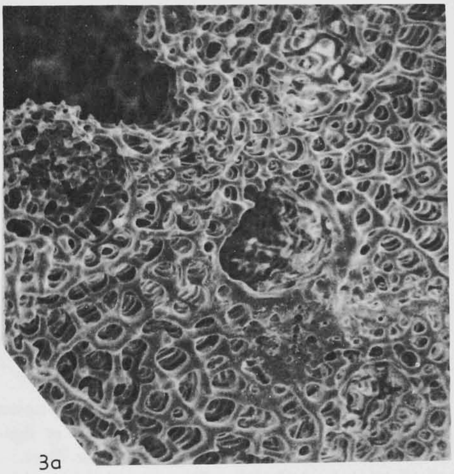
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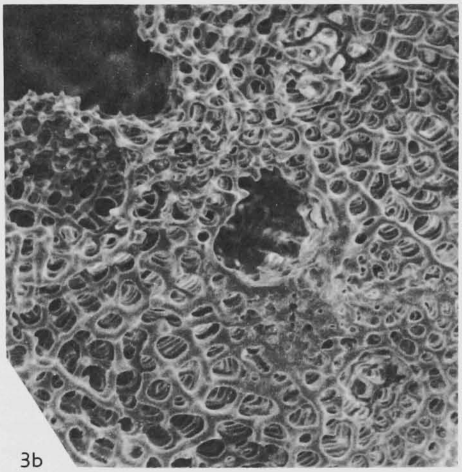
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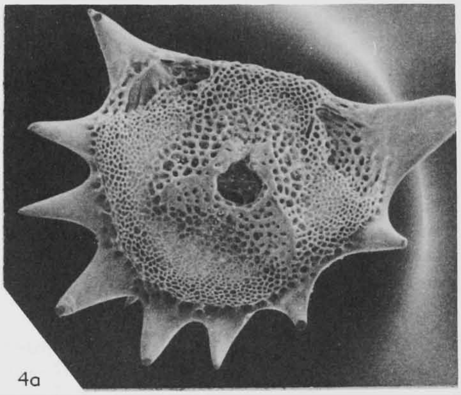
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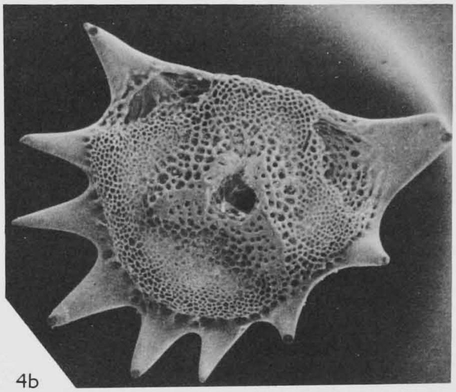
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and pinnules, generally but not invariably located centrally; may be simple or multiple with main canal accompanied by smaller accessory ones.

axial tube. Thin-walled, straight-sided cylindrical passageway within axial canal (found in exceptionally well-preserved pluricolumnals).

axil-arm. Arm including its branches borne by any brach of main-axil as seen in calceocrinids but excluding terminal branchlet termed omega-ramule; may be differentiated as primaxil-arm, secundaxil-arm, etc.

axillary *(AX).* Brachial supporting two arm branches.

axis. Transverse or longitudinal median line defined in theca or longitudinal medial line of ray or stem.

azygous basal. Small plate in 3-basal circlet.

B ray. Right anterior ray (*see A* ray).

BC interray. Lateral interray on right posterior side of cup or calyx (*see AB* interray).

basal (*B,* pl., *BB*). Any plate of circlet next proximal to radials, each basal typically in interradial position.

basal ray. Any of five rodlike structures lying on adoral surface of centrodorsal of some comatulids in interradial position.

base. Part of cup or calyx between radials and stem, normally composed of basals or of basals and infrabasals but in a few articulates and inadunates may include centrale or comprise proximal surface of radial pentagon (Comatulida).

basilarid. One of small number of most proximal columnals which seem to be permanently fixed to base of theca, so that newly added columnals are introduced below them, rather than above most proximal columnal (STRIMPLE, 1963a).

betabrach. *See* alphabrach.

beta-ramule. *See* alpha-ramule.

bifascial articulation. *See* synarthry.

bifascial field. Generally broad smooth area on either side of fulcral ridge of articulum in elliptical columnals, may be bordered on outer side by articular rim, developed also on some cirrals (e.g., *Isocrinus, Austinocrinus, Nielsenicrinus*), may be bordered on outer side by articular rim.

bilateral heterotomy. Type of arm branching characterized by occurrence of ramuli on either side of main arm.

binodal. Paired nodal columnals which share equally in supporting cirri, with distinct apposed articula or with columnals fused together (e.g., *Camptocrinus*); called paired nodals by SPRINGER (1926a).

biradial. Proximal pair of plates in any ray, exclusive of brachials; components of pair designated as inferradial and superradial but in *C* ray may comprise radianal and radial or inferradial and anisuperradial (syn., compound radial).

biserial arm or brachitaxis. Composed of brachs arranged in double row with interlocking sutures along junction of rows (majority of cladid inadunates and camerates, but lacking in disparid inadunates and flexibles).

bivium. Differentiated *C* and *D* (posterior) rays, generally shorter than rays of opposed trivium *(A, B, E)* (e.g., many *Comasterida, Holopodidae*).

bothrospire. Pitlike or slitlike depression on calyx outer surface, presumably serving for respiration (e.g., *Indocrinus*).

brachial (brach) (*Br,* pl., *Brr*). Any ray plate above radial or biradial, exclusive of pinnulars, ambulacrals, and adambulacrals; may be axillary or nonaxillary and incorporated in theca (fixed brachials) or not (free brachials).

brachianal. Fixed brachial of *C* ray supporting proximal and anal plate on its left shoulder (e.g., *Peniculocrinus*).

brachitaxis (pl., **brachitaxes**) *(BrT).* Series of brachials (brachs) extending from radial or biradial to and including primaxil or in arms lacking axillaries to distal extremity of arm; likewise brach series extending from any axillary to and including next one or to distal extremity of arm or branch.

brachium (pl., *brachia*). *See* arm.

C ray. *See A* ray.

calyx. Part of theca excluding tegmen (equivalent to aboral cup) (employed by some authors as equivalent to theca).

canal. *See* axial canal, interarticular radial canal.

canalicula (pl., **canaliculae**). Subhorizontal radially disposed tubular passageway in body of nodal columnal leading from axial canal of stem to axial canal of cirrus, typically grouped in fives with angle of 72 degrees between adjacent canaliculae, but with one or more of these suppressed in many columnals; also, canaliculae may terminate at outer surface of columnal in pimple-like node (aborted cirrus) or small open pore.

cavannulus (pl., **cavannuli**). Low hollow ring in inner medulla of some columnals girdling axial canal and sloping somewhat inward toward mid-plane of columnal, paired with another on opposite side of mid-plane; may contain delicate,

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(See facing page.)

FIG. 193. Pinnulars and pinnular articulations (Macurda & Meyer, 1975).——*1.* Inclined oral view of pinnular of *Endoxocrinus parrae,* recent, W.Indies, ×70.——*2.* Oral view of pinnular of *Nemaster rubiginosa,* recent, W.Indies, ×77.——*3a,b.* Stereo view of muscular articulum on pinnular of *Endoxocrinus parrae,* recent, W.Indies, with upper surface in upper left (compare with *1*), ×210.——*4a,b.* Stereo view of muscular articulum on distal surface of a pinnular of *Nemaster rubiginosa,* recent, W.Indies, upper surface at top, ×140 (compare with *2*).

rather open vesicular tissue (function unknown).

CD interray. *See AB* interray.

[*central area* (BATHER). *See* perilumen, areola.]

central axis. Line connecting aboral and adoral poles or centers (syn., polar axis).

[*central canal. See* axial canal.]

central cavity. Central lumen of cup surrounded by radial and basal circlets.

central nodicirral articulum. Cirrus attachment scar socket located at or very near midheight of latus of nodal, generally facing straight outward (= *central cirrus facet,* BATHER, 1909a).

central plug. Large or small, generally spongy calcareous deposit, on adoral surface of radial pentagon (e.g., some comatulids).

centrale. Noncirriferous thecal plate typically occurring inside infrabasal or basal (if infrabasals are vestigial) circlet of some inadunates and articulates (e.g., *Marsupites, Uintacrinus*).

centrodorsal. Commonly cirriferous columnal or semifused to fused columnals attached to theca of Comatulida (Thiolliericrinidae).

centrodorsal cavity. Depression on adoral surface of centrodorsal containing chambered organ and accessory structures.

centrum (pl., **centra**). Substance of columnal or cirral including luminal septa, if present; may be divisible into parts distinguished by differences in microstructure, such as outer zone (between proximal and distal crenularia), intermediate zone (between proximal and distal areolae), and inner zone (corresponding to perilumina on columnal articular facet).

chiasma. Figure formed by division of aboral nerve trunks within axillary.

cirral. Single cirrus segment.

cirrinodal. Columnal bearing cirrus or cirri; other nodal columnals are termed nudinodals.

cirripore. Small circular opening of canalicula approximately at midheight of columnal latus, commonly accompanied by four others distributed with even spacing around columnal, interpreted as rudimentary type of cirrus structure but of unknown function (e.g., *Mooreanteris*), cirripore-bearing columnal classed as nodal.

cirrus (pl., **cirri**). Unbranched, jointed appendage of crinoid stem of centrodorsal, exclusive of radix.

[*cirrus facet, scar, socket. See* nodicirral articulum.]

cirrus root. *See* radicular cirrus, radix.

cirrus socket. Articular face on nodal or centrodorsal for articulation of cirrus (syn., nodicirral articulum).

claustrum (pl., **claustra**). Thick or thin inward projection of columnal medulla constricting axial canal, inner extremity acuminate to bluntly rounded, truncate with rabbeted edges, or clavate, composed of dense stereom or showing microstructure of fine annular lamellae subparallel to midplane of columnal, with or without intersecting longitudinally disposed lamellae which form microscopic cribwork. Transverse sections of claustra may show pentastellate indentations which are extensions of jugulum and between such indentations inner parts of claustrum may be thickened to form jugular ramparts.

clinate. Distinctly sloping, with inclination gentle, moderate or steep, invariably applied to attitude longitudinally and understood to be essentially straight, unless modified by adjective (e.g., curved, with possible addition of descriptive designation such as gently, strongly, evenly, and the like); refers to attitude of plates in indicated circlet, disposition of mean surface of radial articular facet, or orientation of interbrachial facets and sutures in relation to arm axis.

[*close suture. See* zygosynostosis.]

column. Series of segments composing stem; excludes cirri and anchorage structures (holdfasts).

columnal. Individual ossicle of crinoid stem (exclusive of cirri and holdfast structures).

columnal diameter. Dimension transverse to longitudinal axis, may be uniform in all longitudinal planes or notably dissimilar in different ones.

columnal height. Dimension in longitudinal plane, generally any such plane, but in comparatively rare columnals with opposite articula inclined to one another, plane of measurement needs to be specified for definition of minimum, maximum, and mean height.

columnal indices. See different types: areolar, crenular, epifacetal, facetal, height, jugular, luminal, periluminal, septal, shape, zygal. Variations in outline of facetal elements, as well as facets or columnals in whole introduce difficulties in determining total width factors needed for computation of indices; normally, the sum of measurements along two opposite radii (whether these are identical or different in length) provides the measurement of total width, but in elliptical facets or columnals maximum and minimum radii (disposed at right angles to one another) are chosen.

comb. Peculiar comblike modification of distal part of lower pinnules (in Comasteridae).

commissural canal (ring canal). Passageway within cup plate mainly in transverse direction for entoneural branch (ring-nerve or commissure) connecting neighboring entoneural cords.

complex axial canal. Medial perforation of crinoid column characterized by successive alternating constrictions (jugula) produced by adaxial annular projections (claustra) of columnals and intercolumnal expansions (spatia).

compound basal. Ossicle resulting from union of a basal ray with an interradial process of rosette in some comatulids.

compound nodal. Two or more columnals that share in bearing cirrus or cirri.

[*compound radial. See* biradial.]

concavodeclinate. Downwardly and outwardly sloping circlet of plates or proximal portions of plates located within basal concavity of aboral cup (e.g., *Delocrinus*).

concavoplanate. Horizontal or subhorizontal circlet of plates located within basal concavity of aboral cup.

consolidating apparatus. Peculiarly specialized oral plates (e.g., *Cupressocrinus*).

convoluted organ. Loose calcareous coiled body within theca of many camerates (syn., perigastric coelomic organ).

cortex. Peripheral substance (stereom) of columnal or cirral next to latux, rather clearly distinct from medulla or grading into it; substance of columnals with undifferentiated cortex and medulla referred to simply as stereom.

[*costal. See* primibrach(ial).]

[*covering plate. See* ambulacral.]

craspedospire. Infold at plate margin, presumably serving for respiration.

crenella (pl., **crenellae**). Narrow furrow between culmina of columnal articulum (commonly misapplied to culmina by many authors).

crenula (pl., **crenulae**). Ridge (culmen) combined with adjacent furrow (crenella) of columnal articulum.

crenularial index. Ratio of total width of crenularium to that of columnal articular facet (C/F), multiplied by 100 to avoid fractional numbers.

crenularium. Entire area of columnal articular facet bearing crenulae.

crenulate suture. Externally visible wavy line of contact between symplectically united columnals.

crinoidal plane. Plane of bilateral symmetry passing through *A* ray and *CD* interray.

crown. Whole crinoid exclusive of stem.

cryptodicyclic. Characterized by concealment of infrabasals or by occurrence of these plates only in immature growth stages (syn., pseudomonocyclic).

[*cryptosymplectic articulation. See* cryptosymplexy.]

cryptosymplexy. Weak, ill-defined articulation of symplectial type, as developed between nodals and infranodals of many crinoid columns (e.g., Isocrinidae).

[*cryptosynarthrial articulation. See* cryptosynarthry.]

cryptosynarthry. Weak, ill-defined articulation of synarthrial type, as developed between pairs of brachials of some Articulata.

cryptosyzygy. Weak, ill-defined articulation of syzygial type, as developed between pairs of brachials of Articulata (e.g., some Isocrinidae) in which opposed culmina of articular faces are reduced to discontinuous short ridges or granules, with tendency toward irregular arrangement and disappearance.

culmen (pl., **culmina**). Narrow ridge between adjoining crenellae of columnal articulum (= crenella of many authors).

cup. See aboral cup.

[*cup-brachial. See* fixed brachial.]

[*cup-pinnular. See* fixed pinnular.]

D ray. *See A* ray.

DE interray. Left anterior lateral interray. *See AB* interray.

declivate. Sloping downward and outward (e.g., infrabasal plates of *Delocrinus,* radial articular facets of *Zeacrinites*).

defective pinnulation. Characterized by lack of pinnules in places where they should normally be present.

deltoid. *See* oral.

dichotomous. Characterized by division of arm into two branches (dichotomy), which may be equal (isotomy) or unequal (heterotomy).

dichotomy. Division of arm into two branches.

dicyclic. Having two thecal circlets of plates proximal to radials or (in some inadunates that lack radials) proximal to orals.

disc. Tegminal surface between arm bases or visceral mass resting on aboral cup.

discoid holdfast. Subcircular, depressed, upwardly convex to crateriform plated structure with interior supported by radial walls, base plane or somewhat concave for cementation to foreign object such as shell, central articulum on upper surface for attachment of most distal columnal of crinoid stalk (e.g., *Lichenocrinus, Aspidocrinus*).

distal. Referring to direction or position away from polar or central axis.

distal pinnule. In crinoids provided with oral and genital pinnules, any pinnule beyond the latter.

[*distichal. See* tertibrach.]

dististele. Distal region of crinoid column.

divergence of fulcral ridges. Azimuthal angular difference in orientation of fulcral ridges on opposite articula of synarthrially joined columnals.

[*division series. See* taxis.]

dorsal. Referring to direction or side away from mouth, normally downward and outward; preferred term is aboral.

dorsal cup. Theca exclusive of tegmen; preferred term is aboral cup or cup.

dorsal ligament fossa. See aboral ligament fossa.

dorsal star. Stellate hollow around aboral pole of centrodorsal in some comatulids, often fused with depression.

E ray. Left anterior ray; *see A* ray.

encrinoidal. Characterizing perfect pentamerous cup in which each ray coincides with a plane of bilateral symmetry.

endocyclic. Characterized by central location of mouth with respect to coiled digestive tube, hence at or near center of tegmen.

endospire. Invagination of body wall, serving for respiration.

endotomous. Arm structure characterized by bifurcation in two main arms which give off branches only on their adradial side.

epifacet. Extrafacetal part of crinoid columnal articulum.

epifacetal index. Ratio of total width of epifacet to that of entire columnal multiplied by 100 to avoid fractional numbers (*see* columnal indices). [Combined epifacetal and facetal indices have value of 100.]

epispire. Epithecal structure, open or covered, associated with sutural pore or goniopore, and presumably serving for respiration.

epizygal. Proximal segment of syzygial pair. [Considered by BATHER (1909a) to be equivalent to nodal in crinoid columns, but misnomer, since distal articulum of nodals is not a surface of syzygial articulation.]

eustenocrinoid (eustenocrinoidal) plane. Plane of bilateral symmetry passing through *C* ray and *EA* interray; prominent in some disparid inadunates.

even synarthry. Articulation of synarthrial type characterized by general evenness of opposed faces of two brachials joined by synarthry.

exocyclic. Characterized by location of mouth near or beyond border of coiled digestive tube, hence near margin of tegmen.

exospire. Evagination of body wall, serving for respiration.

exotomous. Arm structure characterized by bifurcation in two main arms which give off branches only on their abradial sides.

facet (articulum). Differentiated part of proximal and distal surfaces of crinoid columnals serving for articulation with contiguous columnals (includes lumen); similarly, in thecal plates and ray ossicles any surface that functions for connection with adjoined skeletal element.

facetal index. In crinoid columnals, ratio of total width of facet to that of entire columnal multiplied by 100 to avoid fractional numbers. [Combined facetal and epifacetal indices have value of 100.]

facetal rim. Raised border of columnal or cirral articular facet.

finial. Ossicle of most distal brachitaxis which does not fork again.

fixed brachial (fixed brach). Ray plate above radial or biradial (exclusive of pinnulars) comprising part of calyx, joined more or less firmly to neighboring plates (e.g., *Ohiocrinus, Dystactocrinus* among inadunates; *Amphicrinus, Artichthyocrinus* among flexibles; *Periechocrinus* and most camerates; *Uintacrinus* among articulates).

fixed pinnular. Plate forming part of pinnule incorporated in calyx (e.g., *Scyphocrinites*).

floor (of columnar articular surface). Generally smooth ligament area in median part of petal, mostly flush with articular surface of columnal but may be depressed or (rarely) slightly elevated, bordered by short crenulae; equivalent to areola.

food groove. Simple or branched furrow running in adoral surface of tegmen, arms, and pinnules; serves to convey food to mouth (syn., ambulacral groove).

fossa (pl., **fossae**). Elongate depression on articular face of ossicle for attachment of muscles or ligaments; less localized than pit.

fossula (pl., **fossulae**). Equivalent of half-canalicula in intercolumnal location, thus traversing articular surfaces of two contiguous columnals and leading peripherally to axial canal of cirrus, distinguished from crenellae in this way (as well as by size, connection with lumen of columnal, and other characters).

free arm. Part of ray exclusive of pinnules not incorporated in crinoid theca, freely mobile.

free brachial (free brach). Ray plate above radial or biradial (exclusive of pinnulars) not incorporated in theca (e.g., nearly all crinoids).

free face. Surface of any ossicle not joined to another.

free pinnular. Plate forming part of aboral skeleton of pinnule not incorporated in theca.

free pinnule. Arm branchlet not incorporated in crinoid theca (essentially synonymous with pinnule).

fulcral ridge. Linear elevation in articular face forming hinge line in synarthrial and muscular articulations of ray plates, synarthry of columnals, and ligamentary articulation of some cirri; facilitates differential movement in directions normal to ridge. Fulcral ridge may be interrupted by lumen or continuous around it and may be simple or variously modified. In cirrus sockets and cirrals, often reduced to pair of lateral tubercles or missing.

gammabrach. *See* alphabrach.

gamma-ramule. *See* alpha-ramule.

genital pinnule. Pinnule used for storage of gametes.

goniopore. Opening at plate corner, presumably serving for respiration.

gonioporoid. Pit or depression generally at plate corner, opening into thecal cavity but not reaching outer surface of skeleton; presumably respiratory.

goniospire. Infold or group of infolds at plate corner, presumably serving for respiration (e.g., *Porocrinus, Triboloporus*).

growth-index line. Graphic plot of selected dimensions of crinoid skeletal elements in graded series of specimens differing in size or number of elements considered.

height. Dimension of columnal, thecal plate, or arm ossicle measured in proximal-distal direction.

height index. For columnals, ratio of height to total width of columnal; for thecal and arm plates, ratio of height to width, multiplied by 100 to avoid fractional numbers (see columnal indices).

heterocrinoid (heterocrinoidal) plane. Plane of bilateral symmetry passing through *D* ray and *AB* interray; prominent in some disparid inadunates.

heteromorphic (column on pluricolumnal). Crinoid column composed of dissimilar columnals, which commonly are classifiable as nodals (with or without cirrus scars) in one group and internodals of first-, second-, or higher-order subgroups in the other.

heterotomous. Arm characterized by division into unequal branches.

heterotomy. Division of arm into unequal branches.

holdfast. Any structure at distal extremity of column serving for fixation.

holotomous. Arm characterized by division on every successive brachial.

homeomorphic (columnal or pluricolumnal). Crinoid column composed of similar columnals throughout observed length but admitting gradual change of characteristics from proximal to distal parts of stem. Pluricolumnals from different parts of xenomorphic stems may be homeomorphic within themselves but dissimilar when compared with one another.

homocrinoid (homocrinoidal) plane. Plane of bilateral symmetry passing through *E* ray and *BC* interray; prominent in some disparid inadunates.

hyperpinnulation. Development of two or more pinnules on a single brachial.

hypozygal (columnal). Distal segment of syzygial pair. [Internodal adjoining distal extremity of nodal (BATHER, 1909); considered inappropriate term because articulation of nodal and this internodal is not syzygial.]

inferradial (*IR*, pl., *IRR*). Proximal plate of biradial; includes radianal.

inferradianal (*IRA*). Plate other than basal on proximal side of radianal, directly in series with it or disposed somewhat obliquely.

infrabasal (*IB*, pl., *IBB*). Any plate of proximal circlet in aboral cup having two circlets of plates (dicyclic) below radials.

infracentral cirrinodal articulum (or facet). Cirrus attachment scar located below midheight of nodal latus, generally directed obliquely downward and outward. In dissociated pluricolumnals (excepting those derived from a few genera of stalked Articulata) infra- and supracentral nodicirral articula are not distinguishable because proximal and distal extremities are indeterminate (= infracentral cirrus-facet, BATHER, 1909a).

infranodal. Internodal adjoining distal face of any nodal (CARPENTER, 1884a).

inner ligament area. Confluent interarticular ligament fossae, located on ventral (inner) side of transverse ridge of articular face.

interambulacral (*iamb*, pl., *iambb*). Any plate of tegmen lying between ambulacrals.

interarticular canal. Simple or branched duct between apposed articular faces of thecal plates (rarely columnals) with outer and inner openings or inner opening only, these openings being invariably located on sutures (sutural pores) or at plate corners (goniopores).

interarticular ligament fossa. Elongate depression on articular face of ray ossicle located on either side of axial canal and on adoral side of transverse ridge.

[*interarticular pore* (CARPENTER). *See* radial pore.]

interarticular radial canal. Small radially directed passageway formed by apposed radial grooves on petaloid articula of some columnals (e.g., *Isocrinus*); not identical to canal produced by apposed fossulae on binodal articula.

interbrach(ial) (*iBr*, pl., *iBrr*). Ossicle of calyx above basals (except anals and fixed pinnulars) between rays and branches of any single ray.

intercalary. One of many calyx plates occurring between radial and basal circlets of some crinoids (e.g., *Acrocrinus*).

[*intercostal. See* interbrachial, interprimibrach.]

[*interdistichal. See* interbrachial, intersecundibrach.]

intermuscular furrow. Linear depression separating muscular fossae of articular face of brachials joined by muscular articulation.

intermuscular ridge. Linear elevation separating muscular fossae of articular face of brachials joined by muscular articulation.

internal suture. Line of contact of apposed columnals or cirrals inside of their latera, as seen in longitudinally cut or in weathered specimens.

internodal (*iN*, pl., *iNN*). Columnal intercalated between pair of neighboring nodals, commonly lacking cirri. Internodals are classifiable according to their different successive generations as first-order, second-order, third-order, etc., each generally distinguished by diagnostic width and height measurements of their own.

internodal index. Ratio of height of internode to height of noditaxis containing it, multiplied by 100 to avoid fractional numbers. [Combined internodal and nodal indices have value of 100.]

internode (*IN*). Section of stem between any two successive nodals.

interpinnular (*iP*, pl., *iPP*). Ossicle between any fixed-pinnulars or fixed-pinnulars and fixed-brachials of same ray.

interprimibrach(ial) (*iIBr*, pl., *iIBrr*). Plate of calyx (except anals and fixed pinnulars) above basals located between rays.

interradial (adj.). Indicative of location between any two adjacent radii.

[*interradial* (noun). Any interray plate above basals (except anals, fixed pinnulars, and tegminal plates). Although used by many authors, this term is rejected here, because the plates referred to are identical in kind and origin to interbrach(ial)s. *See* interbrach(ial), interprimibrach(ial).]

interradial impression. Faint petaloid impression on aboral side of centrodorsal in some comatulids.

interradius. One of five planes, regularly alternating with radii (*see* definition of radius).

interray. Part of calyx between any two adjacent rays.

intersecundibrach(ial) (*iIIBr*, pl., *iIIBrr*). Any ossicle (except pinnulars) between neighboring secundibrach series (brachitaxes) of same ray, including succeeding higher plates.

intertertibrach(ial) (*iIIIBr*, pl., *iIIIBrr*). Any ossicle (except pinnulars) between neighboring tertibrach series (brachitaxes) of same ray, including succeeding higher plates.

isotomous. Characterized by division of arm in equal branches.

isotomy. Division of arm into equal branches.

joint. Connection between any pair of contiguous ossicles.

[*joint face* (BATHER). *See* articulum.]

jugular index. Ratio of total width of jugulum to that of columnal articular facet, multiplied by 100 to avoid fractional numbers (*see* columnal indices).

jugular rampart. Localized thickening of flange in columnal canal at margin of jugulum, typically developed as five petaloid bulges between radiating jugular slits.

jugulum (pl., **jugula**). Localized constriction of axial canal, commonly at midheight of columnals; may be circular transversely or extended by very narrow slits radiating into septa in form of lineate star.

latus (pl., **latera**). Surface of crinoid columnal or cirral exclusive of articular facets, equivalent to epifacet.

left anterior. Ray or radius (designated by letter *"E"*) next to anterior *(A)* ray or radius in counterclockwise direction when crinoid is viewed from adoral side.

left posterior. Ray or radius (designated by letter *"D"*) next to *E* ray or radius in counterclockwise direction when crinoid is viewed from adoral side.

ligament field. Concave or flat part of articular face for attachment of ligaments.

[*ligament fossa. See* ligament field.]

ligament pit. Generally steep-sided small depression in aboral ligament fossa adjoining center of transverse ridge.

ligamentary articulation. Union of ossicles effected solely by ligaments, lacking striated muscle fibers but in some articulations of this type supplemented by more or less calcareous deposition.

longitudinal oblique articulation. Union of ray ossicles characterized by obliquity of articular facet plane in relation to longitudinal axis of ossicles; defined externally by oblique sutures.

loose suture. Externally visible line of contact between movably united ossicles.

lumen (pl., **lumina**). Open space approximately in plane of columnal or cirral articulum comprising intercept of axial canal, generally located centrally, highly variable in size and shape, surrounded on all sides by zygum.

luminal index. Ratio of total width of lumen to that of columnal articular facet, multiplied by 100 to avoid fractional numbers (*see* columnal indices). [Combined luminal and zygal indices have value of 100.]

main axil. Brachial supporting two pinnulate branches on equal or subequal shoulders; in calceocrinids conjoined proximal and following series of contiguous axillary brachials forming a distinctive lowermost part of rays next above lateral radials (e.g., *Synchirocrinus*).

manosynostosis. Ligamentary articulation characterized by relatively large and deep fossae and well-developed peripheral rim that provides contact with adjacent plate; differs from typical synostosis in depth of fossae and presence of rimmed edges; common in flexible crinoids.

medulla. Part of columnal girdled on outward side by cortex, from which it is distinguished by differences in microstructure if discernible at all, may be divided into well-defined or indistinctly bounded inner (proximal) and outer (distal) portions and may consist solely of substance of claustrum, remainder of columnal then being classed as thick cortex.

mesistele. Intermediate part of crinoid column between proxistele and dististele regions, doubtfully distinguishable in pluricolumnals.

monocyclic. Having only single circlet of plates proximal to radials.

multibrachiate. Characterizing comatulids which have more than ten free arms.

muscle field. Concave or flat area on adoral side of articular faces of muscularly articulated ray plates, serving for attachment of muscle fibers.

[*muscle fossa. See* muscle field.]

muscular articulation. Union of ossicles effected by muscle fibers in addition to ligaments, opposed articular faces being characterized typically by presence of aboral ligament fossa, ligament pit, transverse ridge perforated by axial canal, two interarticular ligament fossae, and two muscle fields.

nodal (*N*, pl., *NN*). Columnal generally distinguished by maximum width and height in succession of heteromorphic columnals differentiated as noditaxis. In columns with cirri, these are articulated to cirrus sockets on the nodals (cirrinodals), but in some crinoids apparently lacking canaliculae and cirrus scars entirely. In columns without cirri, nodals are distinguished only by maximum size (nudinodals). Columnals that share in bearing a cirrus, with fossulae on their articular surfaces leading to the intercolumnal cirrus, are defined as compound nodals. In a few crinoids (e.g., *Camptocrinus*) characterized by cirri borne by pairs of fused columnals, having cirrus scars along the line of the vanished intercolumnal suture, cirrus-bearing nodals (separated by internodals) are termed binodals.

nodal index. Ratio of height of nodal to that of noditaxis containing it, multiplied by 100 to avoid fractional numbers. [Combined nodal and internodal indices have value of 100.]

nodicirral articulum (or facet). Scar or socket on latus of nodal for articulated attachment of cirrus.

noditaxis (pl., **noditaxes**). Nodal and contiguous succession of internodals (in most fossil crinoid stems arbitrarily chosen in either direction from nodal, because proximal and distal directions are undeterminable, but in extant stem-bearing crinoids and some fossil forms, such as *Isocrinus,* internodals on proximal side of nodal are joined with it in defining noditaxis, because each nodal precedes in origin next nodal above it and internodal series between pairs of nodals became intercalated after appearance of subjacent nodal).

nonaxil-brach. Plate of any brachitaxis adjoined on its distal side by single brach.

noncrenulate suture. Externally visible straight or curved nonwavy line of articular contact between ossicles.

nudinodal. Nodal lacking nodicirral articula on its latus.

oblique articulation. Union of ray ossicles by ligaments or by muscles and ligaments characterized by obliquity of the articular facet plane of its surface, or both; includes longitudinal oblique articulation and transverse oblique articulation.

oblique ridge. Linear elevation separating interarticular ligament fossa and muscle field on articular face of muscularly articulated ossicles.

oblique suture. Externally visible line of articular contact between contiguous ossicles of brachitaxes and columnals not perpendicular to longitudinal axis of united ossicles (e.g., distal suture of enlarged columnal in abruptly bent stalk of *Nevadacrinus* and *Lampidocrinus*).

omega-ramule. Branchlet borne by terminal axial of main-axil in calceocrinids, invariably directed adanally.

oral (*O,* pl., *OO*). Any of five interradially disposed plates forming circlet on tegmen surrounding or covering mouth.

oral pinnule. Any proximal pinnule differentiated from distal ones in function or structure, or both.

ossicle. Any single calcareous segment of crinoid skeleton (e.g., columnal, cirral, thecal plate, brachial, pinnular).

[*outer ligament area. See* aboral ligament fossa.]

[*palmar. See* tertibrach(ial).]

pararadial. Supplementary arm-bearing plate in radial circlet.

patina. Essential, primitive part of cup or calyx comprising radials, basals, and in some crinoids, infrabasals.

pelma. Stalk and holdfast of crinoid beneath crown.

peneplanate. Almost but not quite same as planate (q.v.), deviating very slightly by upward or downward slope, or with extremely gentle convexity or concavity.

peneplenary. Type of radial articular facet occupying most but not all of distal extremity of plate, leaving nonarticular surfaces (generally narrow) next to sutures at plate margins (e.g., *Zeacrinites, Stellarocrinus*).

pentamere. Fifth part of columnal or column; may be discrete or laterally ankylosed.

[*perigastric coelomic organ. See* convoluted organ.]

perigastric coelomic tube. Contorted conduit above and within convoluted organ in some camerates; possibly part of aboral coelomic system.

perilumen (pl., **perilumina**). Raised inner border of columnal articular zygum, surrounding lumen as rim of tabular field with smooth, granulose, tuberculate, or vermiculate surface. Internally, perilumen of some columnals corresponds to dense inner medulla, which is very distinct from reticulate to spongy outer medulla between areolae and possibly part of crenularia of opposite articula.

periluminal index. Ratio of total width of perilumen to that of columnal articular facet, multiplied by 100 to avoid fractional numbers (*see* columnal indices). [Combined periluminal, areolar, and crenular indices are equal to zygal index.]

peripheral crenulae (of petalodium). Crenulae along abaxial border of petal, generally reaching margin of articulum next to columnal latus.

periproct. Opening in theca for anus, covered in life by membrane or pyramid of small plates.

periproctal. Any plate covering thecal opening for anus, generally part of small pyramid.

perisomic skeleton. Part of skeleton located on adoral side of crown; includes all tegminal plates, interbrachials, and skeletal covering of food grooves in arms and pinnules (syn., adoral skeleton).

peristome. Opening in theca for mouth, may be open or covered by plates.

peristomial. Any plate, probably ambulacral in origin, covering peristome.

perivisceral coelomic organ. Perforate calcareous meshwork separating narrow coelomic compartment adjacent to inner thecal surface from main thecal coelomic cavity of some camerates.

perivisceral coelomic ring. Double-ring commissure connected with perivisceral coelomic organ at summit of thecal cavity in some camerates.

perradial. Precisely in position of some one of crinoid radii.

perradial crenulae (of petalodium). Coalesced or inosculating adradial crenulae near central area of some columnals (e.g., *Balanocrinus*).

petal. One of five main lobate divisions of petaloid columnal articulum (petalodium).

petalodium. Pentalobate, petal-shaped arrangement of short crenulae typically developed on articular faces of some Articulata (e.g., Isocrinidae, Pentacrinidae); equivalent to rosette of BATHER but not of authors referring to Comatulida.

pinnular. Plate forming part of aboral skeleton of pinnule; may be incorporated in theca (fixed pinnular) but almost universally forming part of crown above theca (free pinnular).

pinnular arm unit. Any arm segment giving off one pinnule; may be composed of a single brachial or more.

pinnulation. Arrangement of pinnules.

pinnule. Generally slender, unbifurcated, uniserial branchlet of arm, typically borne on alternate sides of successive brachials except hypozygals and axillaries.

pinnule socket. Articular facet on brachial for attachment of pinnule.

planate. Level or horizontal; refers to shape of aboral-cup base, attitude of basal or infrabasal circlet, or disposition of general plane of radial articular facet.

plate. Tabular ossicle, mostly having articular facets at edges.

plenary. Type of articular facet completely occupying distal extremity of plate and extending laterally to sutures at its margins (e.g., *Delocrinus*).

pluricirral. Two or more cirrals attached to one another.

pluricolumnal. Two or more columnals attached to one another.

posterior. Referring to interray *(CD)* containing anus or anal plates, generally wider than other interrays.

posterior left. Interray or interradius next to left posterior *(D)* ray in clockwise direction when crinoid is viewed with adoral side directed upward.

posterior right. Interray or interradius next to right posterior *(C)* ray in counterclockwise direction when crinoid is viewed with adoral side directed upward.

[*postpalmar.* Any brachial distal from *SBr* series (*see TBrr, QBrr,* etc.).]

primanal. Most proximal anal plate in camerates.

primary skeleton. Part of calcareous framework composed of first ossicles developed in ontogeny; includes columnals, cirrals, infrabasals, basals, radials, brachials, pinnulars, orals, and ambulacrals.

primaxil *(IBrax)*. Axillary primibrach(ial).

primaxillary (primaxil). Axillary plate of proximal brachitaxis.

primibrachial (primibrach) (*IBr,* pl., *IBrr*). Plate of proximal brachitaxis; may be axillary or nonaxillary and fixed or free.

priminternodal. First-order internodal (may be indicated by symbol *iN-1*).

[*proboscis. See* anal tube.]

proximal. Referring to direction or position toward polar or central axis.

proximale. Noncirriferous topmost columnal or fused topmost columnals, distinguished typically by enlargement and permanent attachment to aboral cup.

proxistele. Proximal region of crinoid column near theca, generally not clearly delimited from mesistele. Dissociated columnals and pluricolumnals are rarely identifiable as belonging to proxistele.

pseudocirrus. Unsegmented sideward projection from columnal resembling cirrus in having axial canal but very irregular in form and distribution.

pseudohomeomorphic. Crinoid column with perfect or near-perfect homeomorphic appearance externally possessing internodals which do not reach stem periphery (e.g., *Dianthicoeloma*).

pseudomonocyclic. Characterized by occurrence of infrabasals in immature growth stage only (syn., cryptodicyclic).

[*pseudosyzygy. See* cryptosyzygy.]

quartibrach(ial) (*IVBr,* pl., *IVBrr*). Any ray plate of fourth brachitaxis.

quartinternodal. Fourth-order internodal (may be indicated by symbol *iN-4*).

rabbet. Channel or groove along suture between adjoined skeletal elements formed by beveling of their edges.

radial (noun) (*R,* pl., *RR*). Undivided proximal plate or any ray, may be simple or compound (biradial) and bearing proximal anal plate (aniradial).

radial (adj.). Pertaining to a radius.

radial canal (of petaloid columnal). Radially disposed tubular passageway in apposed articula of contiguous petaloid columnals formed by matched radial grooves between petals, extending to periphery but not reaching lumen (e.g., *Isocrinus*) (syn., interarticular radial canal).

radial cavity. Lumen inside radial circlet.

radial circlet. Same as radial pentagon.

radial dome plate. Prominent ambulacral, especially axillary in nature, on tegmen of some camerate crinoids.

radial facet. Distal face of radial, smooth or sculptured, bearing marks of ligamentary or muscular articulation with first primibrach; facet lacking in radials that bear no arms.

radial groove. Half of radial canal located on either of apposed petaloid articula of adjoining isocrinid or pentacrinitid columnals. Narrow space between adjacent petals of petaloid columnal articulum.

radial pentagon. Subpentagonal ring formed of mutually adherent radials after removal of all other structures.

radial pit. Radially disposed depression in ventral surface of centrodorsal in some comatulids.

radial pore (of petaloid columnals). Small opening in radial position visible at periphery of two attached columnals formed by coincident radial grooves of apposed columnals.

radial ridge groups (of petaloid columnal). Various types of perradial crenulae ranging from alternating, gable-shaped or rectilinear joined crenulae of adjacent petals.

radial space (of petaloid columnals). Area between contiguous petals distinguished by absence of crenulae; may be broadly triangular, with base on rim of columnal and apex at or near central area (e.g., *Pentacrinus*), or very narrow, with apex not reaching central area (e.g., *Isocrinus*), or restricted to narrow radial groove.

radianal *(RA)*. Inferradial of *C* ray adjoining anal *X* or anal opening; may be shifted in position leftward and upward to lie even with *C* radial or rarely somewhat above it.

radicle. Individual rootlike branch of radix.

[*radicular cirrus. See* radicle.]

radius. One of five reference planes passing through polar or central axis and median line of any ray.

radix. Rootlike distal anchorage of column.

ramule. Bifurcating or nonbifurcating minor branch of arms, differing from pinnule in less regular occurrence and in some crinoids by presence of pinnules on it.

ramus. Main arm branch.

ray. Radial plate, together with all structures borne by it.

[*rebate* (BATHER). *See* rabbet.]

regular dichotomy. Bifurcation of arm, constantly repeated in regular manner.

reproductive regeneration. Reproduction of lost part of arm without any increase in number of branches.

right anterior. Ray or radius (designated by letter *"B"*) next to anterior *(A)* ray or radius in clockwise direction when crinoid is viewed from adoral side.

right posterior. Ray or radius (designated by letter *"C"*) next to *B* ray or radius in clockwise direction when crinoid is viewed from adoral side.

right tube plate *(RX)*. A special anal plate in inadunate crinoids commonly located above the radianal and to the right of anal *X*.

rim (of columnal articulum). *See* articular rim.

rosette. Delicate calcareous plate formed of metamorphosed basals, centrally located within radial pentagon in comatulids.

secondary skeleton. Part of calcareous framework composed of ossicles which are intercalated between primary pieces; includes interbrachials, interambulacrals, intercalaries, and some anals.

secundaxil *(IIBrax)*. Axillary secundibrach(ial).

secundibrach(ial) (*IIBr*, pl., *IIBrr*). Any ray plate of second brachitaxis.

secundinternodal. Second-order internodal (may be indicated by symbol *iN-2*).

septal index. Ratio of total width of septum to that of columnal articular facet, multiplied by 100 to avoid fractional numbers (*see* columnal indices).

septum (pl., **septa**). Thick or thin inward projection of columnal centrum which locally constricts lumen, generally comprised of horizontal microlamellae with or without being crossed by vertically disposed annular microlamellae, thus producing a microscopic cribwork. In some crinoids central septa are indented by very narrow radially placed slits extending outward from jugula and opposite septal surfaces may be swollen between neighboring slits in manner that produced petaloid bulges (jugular ramparts).

[*side-plate. See* adambulacral.]

spatium (pl., **spatia**). Localized widening of columnal axial canal opposite interarticular sutures.

stem. Stalklike attachment of many crinoids; column.

straight articulation. Union of ray ossicles by ligaments or by muscles and ligaments characterized by perpendicular orientation of transverse elements of articular surface with respect to longitudinal axis of joined brachials.

straight suture. Externally visible line of articular contact perpendicular to longitudinal axis of adjoined ossicles.

subaxil. Subordinate type of axillary brach bearing pinnule or ramule on one of its distal facets.

subradial cleft. Deep narrow furrow between dorsal surface of radials and opposed surface of centrodorsal in comatulids.

subtegminal. Beneath adoral integument of theca.

superradial (*SR*, pl., *SRR*). Distal plate of biradial; includes *C* radial in crinoids having radianal and anisuperradial.

supracentral nodicirral articulum (or facet). Cirrus attachment scar located above midheight of nodal latus, generally directed obliquely outward and upward.

supranodal (CARPENTER). Columnal adjoining proximal articulum of any nodal.

sursumate. Surface sloping outward-upward, generally refers to radial articular facet.

sursumclinate. Sloping upward and outward (e.g., radial, basal, and distal part of infrabasal plates of *Poteriocrinites,* radial articular facets of *Aesiocrinus* (longitudinal axis of all crinoid facets defined as extending from inner to outer margins at mid-width).

sutural pore. Opening, presumably respiratory, located on line of juncture between ossicles.

suture. Externally visible line of articular contact between adjoined ossicles, employed by many authors as equivalent to joint.

symmorphy. Ligamentary articulation in which one or two prominent ridges or toothlike prominences on one face interlock with corresponding grooves or sockets on opposed face (e.g., *Chladocrinus, Hypalocrinus*); peripheral crenulae may occur on parts of united joint faces; slight differential movement of joined ossicles is possible in two directions.

symplectic articulation. *See* symplexy.

symplexy. Ligamentary articulation in which culmina on one joint face interlock with crenellar grooves on opposite joint face, marked externally by crenulate suture; joined ossicles almost entirely immobile.

synarthrial articulation. *See* synarthry.

synarthry. Ligamentary articulation in which each opposed joint face bears transverse ridge separating two fossae for attachment of ligament bundles; allows moderately flexible differential movement of joined ossicles in two directions. Articular face generally rather flat, but if embayed, articular face is strongly curved, the convexity downward.

synostosial articulation. *See* synostosis.

synostosis. Ligamentary articulation in which opposed joint faces are gently and broadly concave, comprising attachment surfaces for ligament bundles which allow moderately flexible differential movement of joined ossicles in all directions; corresponds to "loose synostosis" of authors.

syzygial articulation. *See* syzygy.

syzygial pair. Two ossicles joined by syzygy, the distal one termed hypozygal, the proximal one epizygal.

syzygy. Ligamentary articulation of brachials and some thecal plates but not observed in columnal or cirrals in which culmina or less well-defined ridges of one articulum are apposed to corresponding elevations of other articulum and crenellae or ill-defined depressions of apposed articula to each other. This term has been misapplied by many previous authors to crinoid columnals, especially articulation of nodals with next-distal internodals; Also used by previous authors for all more or less immovable (close) ligamentary articulations (except symplexy), including cryptosyzygy, cryptosynarthry, symmorphy, synostosis, and even cryptosymplexy (symbol: $+$).

taxis (pl., **taxes**). Definite linear series of plates in any part of crown; superfluous for general application to stem but useful for differentiation of successive nodal-internodal groups of columnals. (*See* brachitaxis, anitaxis, noditaxis.)

tegmen. Adoral part of theca above origin of free arms or occupying space between them; may be calcified or not; may bear anal vent, pyramid, sac, or tube.

[*tergal.* Proximal anal plate in Camerata; *see* primanal.]

[*terminal stem plate.* Most distal columnal in comatulid larva. *See* holdfast.]

tertaxil *(IIIBrax)*. Axillary tertibrach.

tertibrach(ial) (*IIIBr*, pl., *IIIBrr*). Any ray plate of third brachitaxis.

tertinternodal *(iN-3)*. Third-order internodal.

theca. Crinoid skeleton exclusive of pelma and free arms.

transverse oblique articulation. Union of ossicles characterized by oblique position of transverse elements of articular face in relation to longitudinal axis of joined ossicles.

transverse ridge. Generally denticulate fulcral elevation on articular face of ray ossicles, disposed perpendicularly or slightly oblique to greatest width of facet.

trifascial articulation. Union of ray ossicles characterized by presence on articular faces of three gently concave areas for attachment of ligaments; allows distinct mobility in two directions.

trivium. Differentiated *A, B, E* rays, generally longer than rays of opposed bivium (*C, D* rays) in posterior position (e.g., many Comasterida, Holopodidae).

unilateral heterotomy. Type of arm branching characterized by occurrence of ramuli on one side of main arm only; includes endotomous and exotomous arm branching.

uniserial arm or brachitaxis. Composed of brachs arranged in single row, with or without subparallel sutures (e.g., *Barycrinus, Allagecrinus,* inadunates; *Icthyocrinus, Lecanocrinus,* flexibles; *Allocrinus, Lampterocrinus,* camerates; *Saccocoma, Marsupites,* articulates).

united compound basal. Ossicle formed by union of two basal rays with two interradial processes of rosette in some comatulids.

[*vault. See* tegmen.]

ventral. Referring to adoral side of theca and rays, in living crinoids normally directed upward; preferred term is adoral.

ventral groove. Longitudinal trough on adoral side of ray plates (radials, brachials, pinnulars); preferred term is adoral groove.

[*ventral sac. See* anal sac.]

visceral skeleton. Spicules or calcareous network developed within crinoid body, especially in connective tissues surrounding visceral mass and walls of digestive tube.

xenomorphic column. Crinoid stalk containing dissimilar sorts of columnals in proxistele, mesistele, and dististele regions, but dissimilarity excluding contrast between homeomorphic and heteromorphic pluricolumnals, either or both of which may be represented in the xenomorphic differentiates of the stalk.

zygal index. Ratio of total width of zygum to that of columnal articular facet, multiplied by 100 to avoid fractional numbers. *See* columnal indices.

zygocirral. Most proximal segment of cirrus, articulating with cirrus scar on nodal columnal (cirrinodal).

zygosynostosis. Ligamentary articulation in which opposed joint faces are nearly flat areas for attachment of short ligament fibers combined with moderate calcareous deposits; may allow extremely slight differential movement of joined ossicles in all directions but generally forms immovable union; corresponds to "close synostosis" of authors.

zygous basal. One of two large plates in tripartite basal circlet.

zygum *(Z)*. Part of columnal articular facet between borders of lumen and facet; may be divisible into parts (crenularium, areola, perilumen, facetal rim, bifascial fields, fulcral ridge) or contain crenularium alone.

ABBREVIATIONS AND SYMBOLS USED IN CRINOID DESCRIPTIONS

By N. Gary Lane
[University of Indiana]

Beginning with crinoid studies by F. A. Bather (1900), various schemes of abbreviations and symbols have been used to denote certain plates, parts, articulations, or directions of orientation of the crinoid skeleton. There have been considerable revision and changes in usage of this terminology over the years, resulting in a needlessly complex jargon of terms that is surely confusing to the beginning student. Compiled below are selected lists of symbols used in crinoid descriptions. Although not complete, they contain all of the more commonly used abbreviations. The first list contains symbols that begin with a letter and is arranged alphabetically, followed by a list of symbols beginning with a numeral. Miscellaneous symbols that are neither alphabetical nor numerical are listed last. These lists were compiled from the references cited below, and letters in parentheses in the lists indicate the reference from which the symbol or explanation was obtained: Bather, 1900a (B); Clark, 1915a (C); Gislén, 1924 (G); Moore & Laudon, 1943a (ML); Moore, Lalicker, & Fischer, 1952 (MLF); and Moore, Jeffords, & Miller, 1968 (MJM). For a more elaborate list of symbols, see Moore & Laudon, 1941.

ALPHABETICAL SYMBOLS

A	anterior (ML); areola (MJM), anterior ray or radius of authors
A-B	interray between *A* ray and *B* ray (C)
A_1, A_2	left and right brachials, respectively, of *A*-ray arm (C)
Amb	ambulacral (B,ML,MLF); pl., *AmbAmb* (ML), *Ambb* (MLF)
Ant	anterior (MLF)
AntL	antero-left (MLF)
AntR	antero-right (MLF)
ant.R.	anterior radius (B)
AR	anterior radial (ML)
Ax	axillary (ML,MLF); pl., *AxAx* (ML), *Axx* (MLF)
B	basal (B,ML,MLF); pl., *BB* (ML,MLF); *B* ray or radius of authors
B-C	interray between *B* ray and *C* ray (C)
B_1-B_2	left and right brachials, respectively, of *B*-ray arm (C)
Br	brachial (ML,MLF); free brachial (B); pl., *BrBr* (ML), *Brr* (MLF)
Br_1	first brachial (C)
Br_2	second brachial (C)
$\overline{Br}$	fixed brachial (B)
C	columnal (MLF); pl., *CC;* crenularium (MJM); *C* ray or radius of authors
C-D	interray between *C* ray and *D* ray, posterior position (C)
C_1-C_2	left and right brachials, respectively, of *C*-ray arm (C)
CBr	cup brachial (MLF); pl., *CBrr*
CIBr	cup primibrachial (MLF); pl., *CIBrr*
CIIBr	cup secundibrachial (MLF); pl., *CIIBrr*
Cd	centrodorsal plate (G)
Ci	cirral plate (MLF); pl., *Cii*
D	*D* ray or radius of authors
D-E	interray between *D* ray and *E* ray (C)
D_1-D_2	left and right brachials, respectively, of *D*-ray arm (C)
E	*E* ray or radius of authors; epifacet (MJM)
E-A	interray between *E* ray and *A* ray (C)
E_1-E_2	left and right brachials, respectively, of *E*-ray arm (C)
F	finials or brachials of final arm brachs (B)
fBr	fixed brachial (ML); pl., *fBrBr*
IAmb	interambulacral (MLF); pl., *IAmbAmb*
IB	infrabasal (B,C,ML,MLF); pl., *IBB*
IBr	interbrachial (ML); pl., *IBrBr*
IN	internode or internodal (MJM)
IR	interradius (B)
ISBr	intersecundibrachial (ML); pl., *ISBrBr*
ITBr	intertertibrachial (ML); pl., *ITBrBr*
iAmb	interambulacral (B,MLF); pl., *iAmbb*
iIAmb	interprimambulacral (B)
iIIAmb	intersecundambulacral (B)
iBr	interbrachial (B,C,MLF); pl., *iBrr*
iIIBr	intersecundibrachial (B)
iR	inferradial (ML); interradial (MLF); pl., *iRR*
iRA	inferradianal (ML)
L	lumen (MJM)
N	nodal (MJM)
NT	noditaxis (MJM)
P	perilumen (MJM)
P_a	first inner pinnule (C)
P_d	distichal pinnule (C)
P_p	palmar pinnule (C)
P_1	first pinnule (C)
P_2-P_b	second pair of proximal pinnules (C)
P_3-P_c	third pair of proximal pinnules (C)

R	radial (B, ML, MLF)
RA	radianal (B, ML, MLF)
T	taxis (MJM)
Z	zygum (MJM)

NUMERICAL SYMBOLS

IAx	primaxil (B); pl., *IAxx* (MLF)
IAmb	primambulacral (B)
IBr	free primibrach (B); primibrach (C, MLF); costal (C)
IBr_1, IBr_2	free first primibrach, free second primibrach (B); first primibrach, second primibrach (MLF)
$\underline{\text{IBr}_2}$	costal axillary (C)
$\overline{\text{IBr}}$	fixed primibrach (B)
IIAx	secundaxillary (B); pl., *IIAxx* (MLF)
IIBr	free secundibrachial (B); secundibrachial (C,MLF); distichal (C); pl., *IIBrr* (MLF)
$\overline{\text{IIBr}}$	fixed secundibrachial (B)
IIBr_1, IIBr_2	first secundibrachial, second secundibrachial (B,MLF)
IIIBr	tertibrachial (B, C); palmar brachial (C)
IIIBr_{ax}	third postradial axillary (C)
IVBr	first post-palmar brachial (C); tetrabrachials (C)
VBr	second post-palmar brachial (C)
VIBr	third post-palmar brachial (C)

MISCELLANEOUS SYMBOLS

+	syzygy (G)
—	synarthry (G)
□	anchylosis (G)
△	deltoid plate (B)
/	armlet or ramule (G)
$\underline{1},\overline{2}$	bar over or under numeral that stands for brachial indicates position of pinnule (G)

POSTLARVAL ONTOGENY OF FOSSIL CRINOIDS

By J. C. Brower, N. Gary Lane, and H. Wienberg Rasmussen

[Syracuse University; University of Indiana; Geologisk Museum, Universitet København]

CONTENTS

CAMERATES

By J. C. Brower

INTRODUCTION

A recent crinoid crown consists of an internal skeleton composed of a series of adjacent calcite plates. The endoskeleton is mesodermal and occupies the major part of this layer. The outer plate surfaces are covered by a thin epidermal layer, which is not completely developed in some specimens. Plates of the calyx comprise most of the body wall, which encloses the viscera of the crinoid (see Hyman, 1955, p. 47-61, for summary). In simple statement, three processes are seen in recent and fossil crinoid ontogeny: 1) development of new plates; 2) calcite accretion and increase in size of previously formed plates; and 3) complete or partial resorption of plates.

This paper represents a summary of my more detailed discussions of camerate crinoid ontogeny (BROWER, 1973; 1974a; 1974b).

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PLATE GROWTH SEQUENCES

Among recent crinoids complete plate growth sequences can be observed directly. In camerates, this applies only to the later developmental phases, since earliest sequences must be inferred. In general, the plate growth sequences of camerates and comatulids are quite similar, especially with respect to the arms and column (Fig. 194). The basic calyx plate development sequence of all taxa, listed from first to last appearance, comprises: basals, orals, infrabasals (if present), radials, primibrach *1,* primibrach *2* (primaxil), secundibrach *1,* and so forth.

All brachials and pinnulars first appear at the distal tips of the arms or pinnules. In modern crinoids, pinnules do not form until after the arms are well developed. The first pinnule of *Hathrometra sarsii* is seen when about secundibrach *14* is present; in *Antedon bifida,* pinnules occur along with secundibrach *12.* The first pinnules are formed at the arm tips; these are followed by the proximal (oral) pinnules on secundibrach *2.* After these, the intervening ones appear. Pinnules developed earlier in camerates. The smallest known arm-bearing individuals have a calyx height of about 1.0 to 1.3 mm., possess four to nine brachials in an arm, and show a full complement of pinnules.

The development sequence of the stem and arm plates of living species and the camerates follows the same order. Columnals typically are introduced immediately distal to the calyx, below the centrodorsal in pentacrinid growth stages of comatulids and below the infrabasals or basals of camerates. Also, new columnals are generally intercalated between previously formed stem plates. In many living comatulids, the animal discards its column at the end of the pentacrinid growth stage and assumes a more or less free-living existence. This does not occur in camerates and recent isocrinids, in which (barring traumatic accidents) all or part of the column is retained until death.

The main differences between camerate and modern crinoids in sequences of plate development are related to the presence or absence of fixed brachials. During the growth of most camerates, free brachials were incorporated in the calyx, although at variable rates. This does not occur in modern crinoids and inadunates and flexibles, in which the arms remained free above the radials throughout life. Typically, the proximal interprimibrachs of recent crinoids develop late in ontogeny. For example, they are first seen after the primibrach *2* (primaxil) is well defined in *Comactinia meridionalis* (Fig. 194), but the interprimibrachs of *Promachocrinus kerguelensis* do not appear until about five secundibrachs are present. Generally, the living crinoid radianal forms earlier than interprimibrach *1,* ranging from just prior to soon after appearance of the radials. I believe that the radianal and proximal interprimibrachs of living crinoids are homologous with the primanal and proximal interprimibrachs of camerates, as evidenced by similarities of topographic position, ontogeny, and phylogeny (BROWER, 1973, p. 301-304; 1974b). Most likely, the interprimibrach *1* and the primanal of camerates were probably initiated along with or immediately after the radials (BROWER, 1973, p. 301-308; 1974b). Relative to modern crinoids, the camerate interprimibrach *1* is postulated to have appeared earlier, whereas the proximal *CD* interray plates of both camerates and recent forms began at roughly the same time. In turn, this allowed the formation of extensive interbrachials throughout subsequent ontogeny. This plate sequence was probably retained by all camerates including forms both with

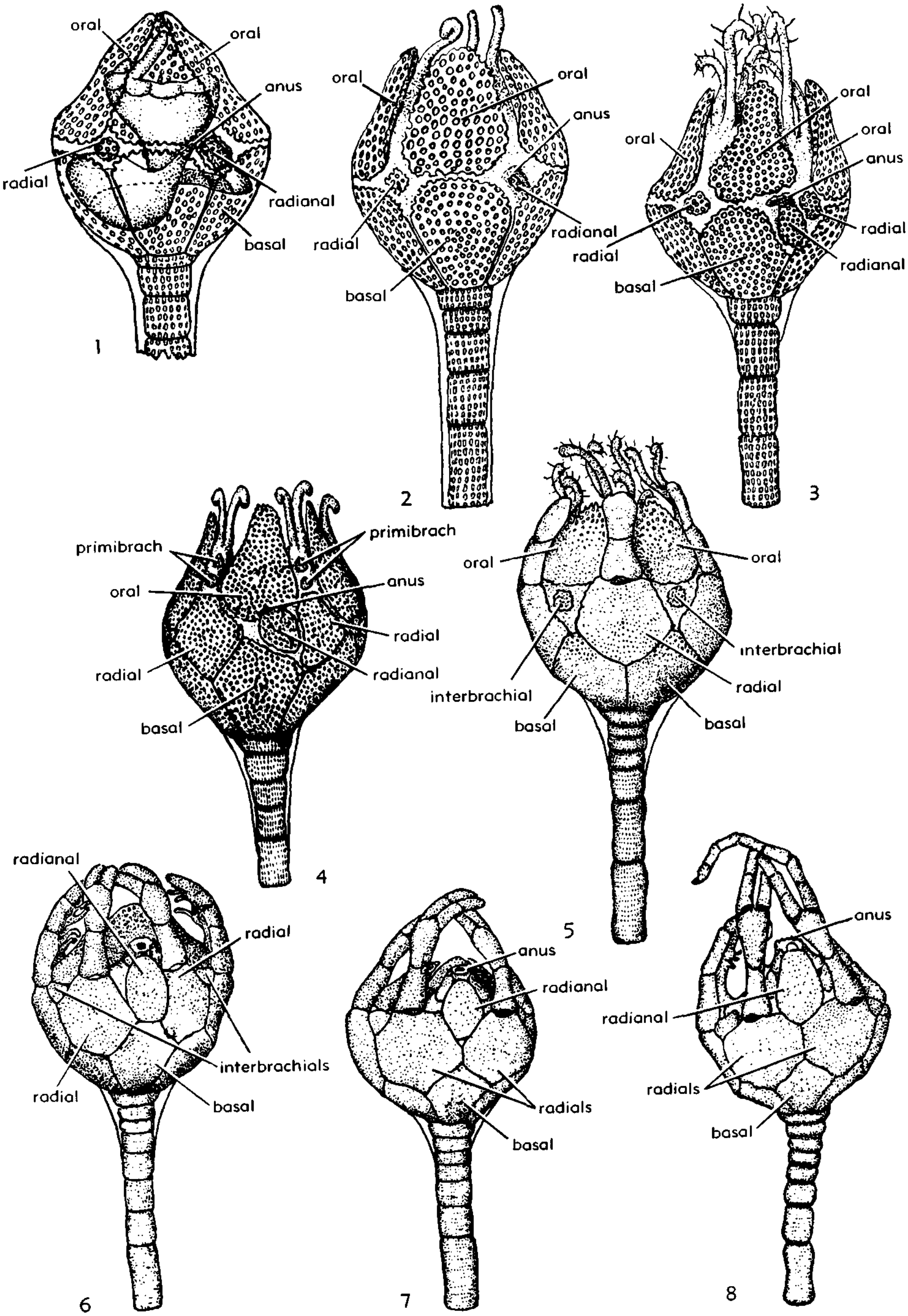

Fig. 194. Growth stages of *Comactinia meridionalis*, recent, from Yucatan, Mexico (Springer, 1920).

numerous and with few fixed brachials.

The few available data suggest that growth rates of size relative to time in modern crinoids fit a "slow-fast-slow" model. "Slow" growth rates seem to occur throughout the microcrinoid growth phase and well into the pentacrinid stage. Apparently, the "fast" growth is initiated just prior to loss of the column. When these growth rates are terminated is uncertain, but probably these end at or immediately prior to maturity. Older crinoids are characterized by "slow" time-size growth rates. These growth rates are evidenced by direct observation on some living crinoids and by the spacing of growth lines in fossil crinoids.

INTEGRATION AND COORDINATION

In the earliest growth stages of extant crinoids, the calyx plates are not fully in lateral contact. They are isolated from one another by the soft tissues (Fig. 194). At this time, the plates commonly are arranged irregularly and vary widely in size and shape. This shows that the growth of a certain plate is poorly coordinated and integrated with other plates during this stage. Due to calcite accretion along the plate sides, the plates eventually join, except for certain "strategic holes," such as the arm openings, anus, and columnal axial canal. This is probably dictated by the functions of the internal plated calcite skeleton. Basically, the plates serve to support and protect the fragile organs housed on the inside of the skeleton. In extremely small and immature individuals of living species, the water-vascular system and other coelomic cavities probably provide the necessary support by hydrostatic means. However, with increasing size, mass, and volume, the (coelomic cavity volume)/(total mass or volume) ratio probably becomes too low to ensure the necessary support, and this function is taken over by the skeleton. Once the plates join, the support problem requires that this configuration be maintained throughout subsequent ontogeny. This probably simplifies growth of the plate mosaic, and it presents an approach to delineation of ontogeny. In general, if one plate increases in size, its neighbors must do the same. Otherwise, gaps would appear between the adjacent plates and the skeleton could not support the animal. In other words, the development of all plates must be integrated and coordinated to prevent the formation of gaps. Matrices of correlation coefficients yield information on this type of integration and coordination. Progressive increase of plate and calyx size is denoted by positive correlation coefficients. Resorption would result in decreased size and would be shown by negative correlations for the plate or plates affected. However, resorption was not common in Paleozoic crinoids except for the stem facet, arm openings, and possibly the anal opening.

Integration and coordination gradients exist, and the dimensions of a given plate correlate best with those of the directly adjoining plates and less well with plates farther away. In general, the ontogeny of calyx plates is slightly better integrated and coordinated than that of free brachials and pinnulars (data are not available for the stem). This is related to basic geometry. In most calyx plates all margins are in contact with adjoining plates and only the inner and outer sides are not opposed by other plates. Conversely, brachials and pinnulars possess one or more free lateral margins not bounded by other plates (Fig. 194). In general, correlations are higher for plates with rapid growth rates than for those with lower developmental vectors.

The mechanism of integration and coor-

(Continued from facing page.)

1. Prebrachiate stage theca consisting only of basals and orals. [Note highly porous plates not fully joined together.]

2. Slightly older specimen with embryonic radials and radianal.

3. Largest prebrachiate stage with radianal and all radials (radianal below and left of *C* radial).

4. Specimen with embryonic primibrachs (proximal plates fully joined but gaps between distal ones).

5. Specimen with well-developed primibrachs and embryonic interbrachials *1*.

6-8. Growth sequence of progressively older individuals. [Note distalward migration of radianal and interbrachials *1*.]

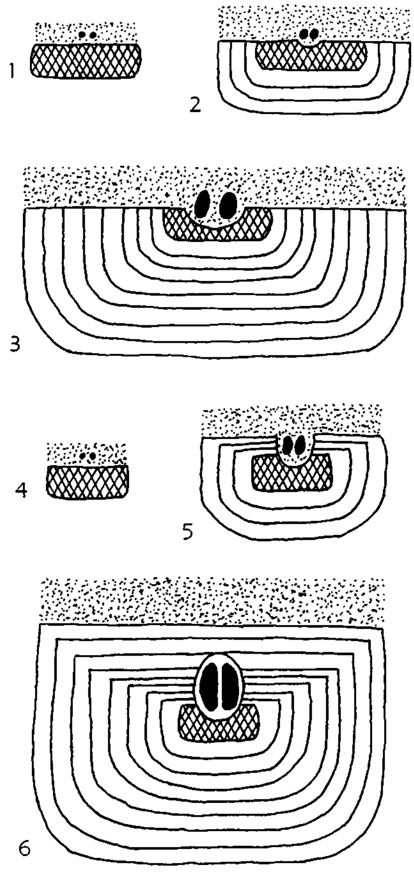

FIG. 195. Schematic cross sections showing growth of crinoid calyx and cup plates by growth lines (Brower, 1974b). [Explanation: soft parts on plate interiors stippled; axial nerve cords black; embryonic plates cross ruled].——*1-3*. Camerate crinoid, plates arranged from youngest to oldest. ——*4-6*. Recent comatulid, plates arranged from youngest to oldest.

dination is conjectural, although a few observations can be presented. Growth of the plate mosaic is adjusted to cause the minimum possible amount of interference with the aboral nervous system. This is the dominant nerve level in crinoids and it controls such basic reactions as flexing the arms, bending the stem, and other movements (A. R. MOORE, 1924). The youngest crinoids lack an aboral nervous system. Consequently, I conclude that the plate geometry and growth of very young crinoids is determined by the physical relationship of the mesenchyme to the ectoderm (RAUP, 1966, p. 393). In older crinoids the aboral nervous system is present and it may integrate indirectly and coordinate growth of the arms and many calyx plates. The control probably operates through the physical relationship of the aboral nervous system and the surrounding mesenchyme. The transition from ectodermal to mesenchyme and aboral nervous system control would be expected prior to the development of secundibrachs.

CALYX PLATES

In Paleozoic crinoids, new calcite was deposited on the margins and exterior surface of calyx plates, but no new calcite was added to the inside of plates (FIG. 195,*1-3*). This is evidenced by the locations of growth lines (BROWER, 1973, p. 293-294; 1974b; MACURDA, 1968; MEYER, 1965b; LANE, 1963b). When present, growth lines are always observed on the interior of calyx plates; this shows that calcite was not deposited on the previously formed plate interior. Growth lines are not seen on the outside of crinoid plates. As noted by LANE (1963b), this is related to placement of the aboral nerve cords. These are located along the plate interior, some simply lying on the flat plate surface, others being housed in grooves on the interior of the plate. Deposition of calcite on the plate interior could have interfered with or disrupted the critical and fragile aboral nerve cords. Growth of Paleozoic crinoid plates simply extended the previously established aboral nervous system. Most tegminal plates seem to have followed the same pattern, although in some cases calcite may have been deposited on the interiors of the plates. All calyx plates are in contact with the aboral nervous system, but this is not true for tegmen plates; however, some tegmen plates were in contact with the hyponeural nervous system (HAUGH, 1973, p. 86).

During the early development of living comatulids such as *Antedon,* the aboral nerve cords lie on the inner sides of the radials (FIG. 195,*4-6*). Subsequent internal calcite deposition on the plates gradually buries the nerve cords within the theca

(W. B. Carpenter, 1866, p. 738, 739; 1876, p. 454). Resorption of calyx plates is more common in recent crinoids than in Paleozoic camerates (A. H. Clark, 1915a, p. 322-340). In general, plate growth of living forms is far more complex than that of most Paleozoic species.

BRACHIAL GROWTH

INTRODUCTION

Development of brachials follows the same pattern seen in the radials of living and fossil crinoids. The radials are the first ray plates formed during ontogeny and they establish the growth pattern of all subsequent ray plates, both fixed and free brachials. The role played by the radials during growth of the rays establishes the paramount importance of these plates in crinoid taxonomy.

Generally, axes of the axial nerve cords constitute constant topographic reference points. Brachial accretion simply extends these throughout ontogeny. Lateral migration of the nerve cords and resorption of the brachials is either absent or minimized as much as possible.

UNISERIAL NONPINNULATE BRACHIALS AND PINNULARS

All flexible and some inadunate crinoids had uniserial nonpinnulate brachials. The axial nerve cord and food-gathering system, and associated organs, were housed in a single V-shaped ventral food groove. By analogy with extant crinoids, the axial nerve cord lay at the base of the ventral groove. The food groove was deepened by calcite deposition along its ventral margins (Fig. 196,*2,* which depicts the ontogeny of a uniserial pinnulate brachial, nonpinnulate brachials developing in the same way). Calcite accretion also extended the other dimensions. In living and, presumably, fossil crinoids, the axial nerve cord diameter increases during ontogeny. This probably causes some resorption along the base and associated sides of the ventral groove.

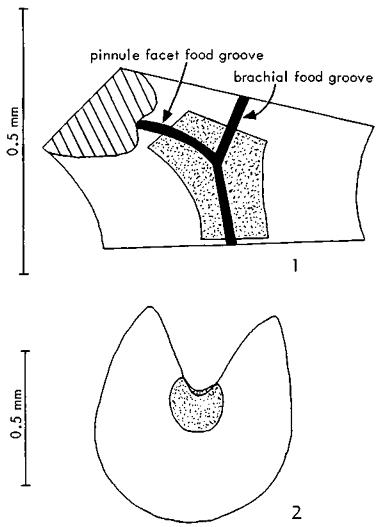

Fig. 196. Growth of uniserial pinnulate brachials in camerates (Brower, 1974b). [Explanation: axial nerve cords cross ruled; food groove axes black; pinnule facet oblique ruled.]——*1.* Ventral views of two superposed brachials of *Eopatelliocrinus latibrachiatus,* Upper Ordovician, Girardeau Limestone, Illinois and Missouri.——*2.* Superposed outlines of two idealized growth stages in articular surface view.

UNISERIAL BRACHIALS OF CAMERATES

All uniserial brachials of camerate crinoids bear pinnules. Throughout development, these plates retained the same basic geometry in which all ontogenetic changes were gradual and incremental (Fig. 196). The brachial ontogeny plan minimized calcite accretion across the articular surfaces as much as possible within basic geometrical limits. Minimizing these growth vectors caused the least possible interference with ligaments and muscles that hinged and flexed the contiguous brachials. Studied relative growth rates toward the articular surfaces, listed from greatest to least, are: pinnule facet, distal brachial, and proximal brachial. The calcite accretion differentials closely correlate with mechanics for support of the developing arms. The rapidly developing vectors of width provided increased supporting area for the growing arms and pinnules. The lowest accretion vector (proximal height) was directed toward the facet which supported the higher brachials. The largest growth rate of an articular surface was toward the pinnule

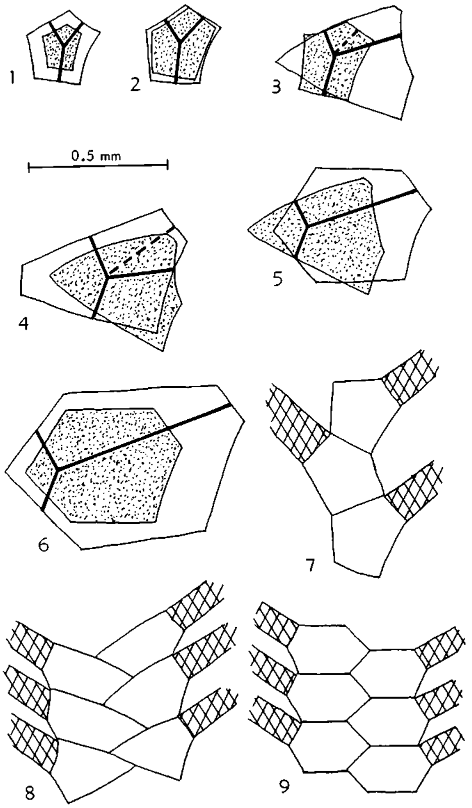

FIG. 197. Ventral view outlines of biserial brachials in free arms of *Macrostylocrinus pristinus,* Upper Ordovician, Girardeau Limestone, Illinois and Missouri (Brower, 1973, 1974b). [Explanation: food-groove axes in heavy black, smaller brachial stippled; if resorption and migration of the pinnule facet food groove was involved, that of the smaller brachial is shown in dashed line.]——*1.* Early uniserial stages.——*2.* Late uniserial stages.——*3,4.* Transitional uniserial to immature biserial stages.——*5.* Immature to mature biserial stages.——*6.* Mature biserial stages.——*7-9.* Schematic sketches of arm segments composed of uniserial, immature biserial, and mature biserial brachials, respectively (pinnules cross ruled; not to any scale).

facet that held only a corresponding pinnule.

The immature brachials present a comparatively high and angular appearance with prominent, roughly horizontal pinnule facets. Mature plates are relatively wider and possess smoother outlines with less prominent and more steeply inclined pinnule facets than juvenile brachials. The convergence angle between proximal and distal faces of brachials decreased throughout ontogeny. In young crinoids and juvenile brachials of adults (near distal arm tips), the height axes of succeeding plates are not parallel, imparting a crooked or bent appearance to the arms. This configuration was produced by unequal angular convergence of the proximal and distal brachial faces. During later growth, the height axes became more or less parallel because equal or nearly equal proximal and distal brachial-face convergence angles were formed by adjustments in the various height growth rates (compare mature and immature brachials in Fig. 196,*1*). This ontogenetic pattern is related to problems of supporting the growing arms (BROWER, 1973, p. 314-315; 1974b).

The ventral calcite accretion rates probably were small or nil at the food groove axes (Fig. 196,*2*). Deepening of the food grooves was produced principally by ventral calcite deposition on the areas flanking the food grooves. Some resorption probably occurred along the base and sides of the food grooves, resulting in increased diameter of the axial nerve cords. The average dorsal developmental vectors probably exceeded the ventral ones.

The most immature brachials, which are located at the distal arms tips, lack pinnules and these closely resemble pinnulars. These terminal brachials exhibit parallel proximal and distal faces. The least mature ones have rounded distal margins, but slightly older terminal plates are characterized by angular distal margins. The highest pinnulate brachials occur immediately below the terminal brachials. Small pinnule facets are present with a short pinnule consisting of one or two pinnulars. The various parts of the brachial did not become differentiated until the pinnule facet and its pinnule appeared.

BRACHIALS OF MODERN CRINOIDS

Except for the aboral nerve cords, the main growth patterns of living crinoids are like those of camerates. Like camerates, in most immature plates, the axial nerve cord and food-gathering apparatus lie in a single ventral groove. During later growth, the food-gathering tissue is displaced ventrally by calcite deposition. Eventually, the axial nerve cords are fully separated from the food-gathering tissue, and the axial nerve cords are housed within the brachial as in cyathocrinids. The most important parts of the axial nerve cords comprise constant topographic reference points throughout ontogeny (Brower, 1973, p. 294-301; 1974b).

BISERIAL BRACHIALS

The food-groove configurations of biserial-armed crinoids resembled those of uniserial forms except that the "pinnule-facet food groove" was straight, rather than curved as in uniserial brachials (Fig. 197). Throughout the early growth stages, the brachials retained a uniserial configuration during which the previously established food groove axes comprised constant topographic reference points (Fig. 197,*1,2,7*). The convergence angle between the proximal and distal faces of the brachials increased, unlike the invariable convergence-angle decrease of uniserial-armed crinoids. This is related to contrasts in the growth rates of brachial height and width of uniserial and biserial-armed crinoids.

As the biserial brachials developed from the uniserial to biserial configuration, major changes took place (Fig. 197,*3-5,8,9*). The convergence angle continued to increase and eventually resorption of the inner sides (opposite the pinnule facet) of the brachials began as the brachials started to interlock on opposite sides of the arm. In some forms, the pinnule-facet food-groove axis underwent resorption and migrated laterally (Fig. 197,*3-5*).

Within the last growth stages, resorption ceased and growth became adjusted so that the brachial faces remained parallel to one another or nearly so (Fig. 197,*6,9*).

COMPARISON OF UNISERIAL AND BISERIAL BRACHIALS

The nonresorption development of uniserial-type brachials is relatively simple and straightforward. Conversely, resorption is a major factor in the development of biserial brachials so that ontogeny is more complex and a higher degree of integration and coordination of the various dimensions is required to prevent gaps from developing between adjacent wedge-shaped brachials. In many crinoids pinnules are more densely packed along biserial arms than uniserial ones, owing to the presence of two rows of pinnulate brachials that alternate from side to side of the arm. The amount of curvature observed in many arm segments indicates that biserial arms are more flexible than uniserial arms, at least in species with ill-developed ligamental articulations between the brachials.

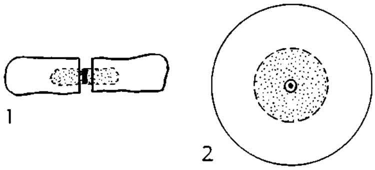

Fig. 198. Diagrams of superposed camerate columnals showing growth stages (Brower, 1973, 1974b). [Explanation: axial canal, black; smaller plate stippled with dashed outline; larger columnal shown by solid line.]——*1.* Side view.——*2.* Axial plane view.

In Paleozoic camerates and pinnulate inadunates, the usual evolutionary sequence was from uniserial to biserial arms, indicating that the advantages of greater food-gathering capacity and more arm flexibility outweighed the disadvantage of ontogenetic complexity. All living crinoids have uniserial arms with well-developed muscular arm articulations, which allow much flexibility. Apparently, muscular arm articulations dictate uniserial arms (Brower, 1973, p. 317, 318; 1974b).

COLUMNALS

The growth of a columnal follows the same pattern in both living and fossil crinoids (Fig. 198). The axial nerve cord penetrates the center of the columnals and passes through the axial canal. As in other plates, the axis of this structure forms a constant point of topographic reference. During ontogeny, the axial canal diameter is augmented by marginal resorption. The principal direction of calcite accretion is outward or peripheral. The much smaller vectors of growth in proximal and distal height are symmetrical for columnals with and without cirri. Typically, the articular

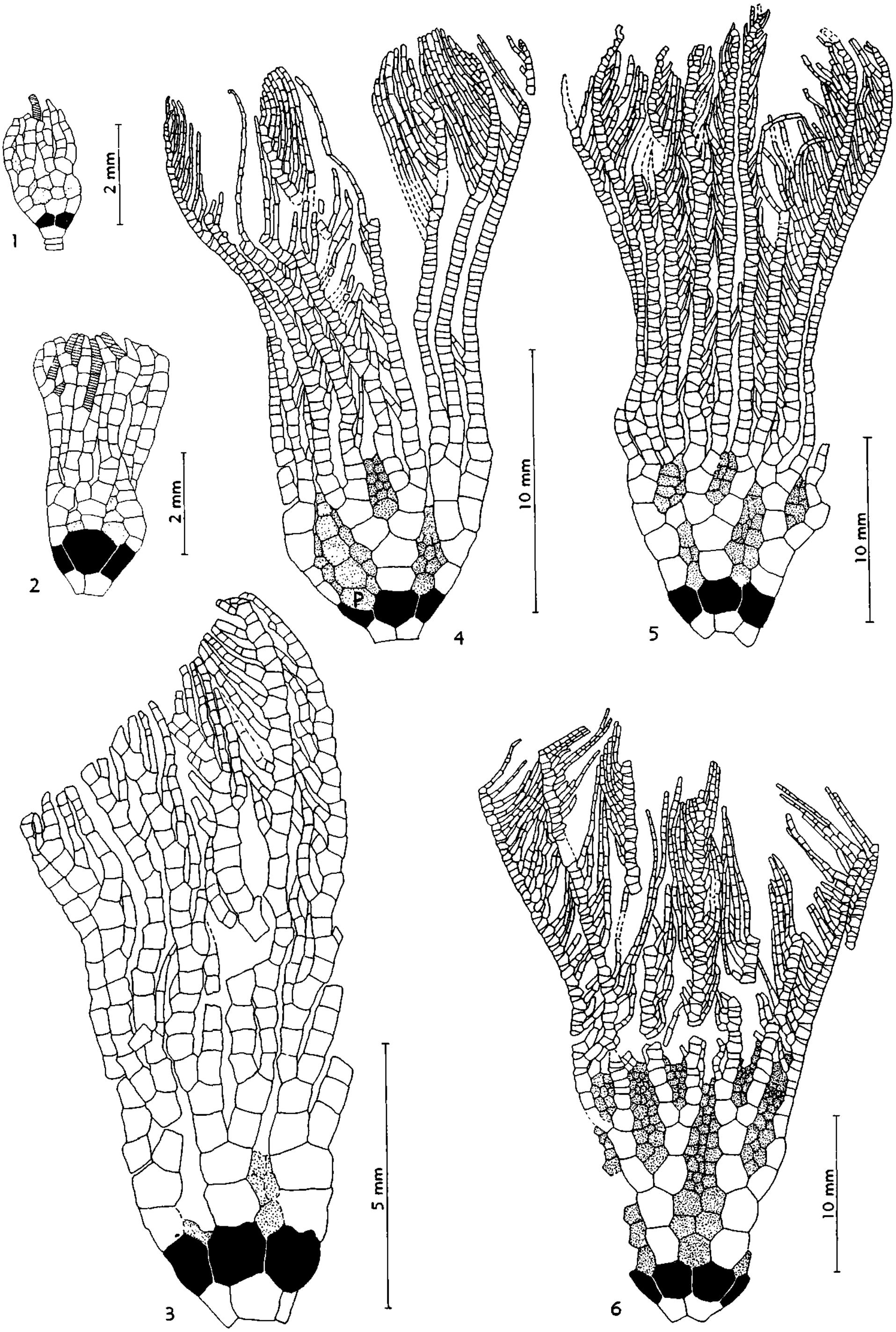

FIG. 199. Growth sequence of *Alisocrinus tetrarmatus* with glyptocrinid-type calyx, Upper Ordovician,

surfaces have culmina or ridges arranged in a radiating pattern (e.g., Jeffords & Miller, 1968, pl. 3). As height and width of the columnals increase, widths of the culmina are augmented and new ones are intercalated between older ones.

ONTOGENY OF THE CALYX

Camerate crinoid calices are divided into five types depending on the extent of fixed brachials, number and nature of interbrachials, and to some degree on number of arms (Brower, 1973, p. 310-313; 1974b). Regardless of calyx type, the youngest camerates are quite similar. For example, crinoids with calyx heights of about 1 mm. typically have primibrach *1* or *2* as the distal fixed brachial, a small number of interbrachials, a calyx which is dominated by the radials, and four to nine free brachials in a single arm (Fig. 199-203). Throughout subsequent ontogeny, the crinoids diverged and adults of the various calyx types are usually easily separated.

GLYPTOCRINID-TYPE CALICES

These crinoids are characterized by many fixed brachials, numerous large and regular interbrachials, and a small number of fixed arms in each ray (Fig. 199). The basic growth pattern of these crinoids was the incorporation of many fixed brachials in the calyx during ontogeny. This caused a series of correlated developmental changes. Young crinoids which lack intersecundibrachs have closely spaced arms within a single ray and the different rays are separated by wide interray areas. Older crinoids formed intersecundibrachs and, in some cases, intertertibrachs. Consequently, the adjacent arms within a single ray were spread apart so that the arms became spaced evenly around the calyx. High rates of fixed-brachial incorporation resulted in rapid distal extension of the calyx and viscera. A lobate tegmen was formed because the intersecundibrachs and intertertibrachs generally reached higher than the lateral and *CD* interray interprimibrachs. Young crowns have calices in which radials are the dominant ray plates. The subsequent growth rates of the radials and primibrachs relative to calyx height were roughly equal. This resulted in an adult calyx with primibrachs and radials roughly equal in height.

XENOCRINID-TYPE CALICES

The morphology and development of an xenocrinid calyx is similar to the glyptocrinid type except for the interbrachials (Fig. 200). The interbrachials of all camerates probably comprise tegmen interambulacrals, which shifted downward to become fixed in the calyx. In glyptocrinids, the number of interbrachials at any one level is small and was stabilized after the fixed brachials were incorporated in the calyx. The interbrachials show large height and width growth rates relative to calyx height and the interbrachial areas were probably rigid during life of the animal. Conversely, xenocrinid interbrachials remained small throughout ontogeny and the interbrachial areas became wider in larger individuals mainly owing to the intercalation of new interbrachials between older plates. Xenocrinid-type calyces were derived from ancestors with large and regular interbrachials (Brower, 1974a). The growth pattern of the xenocrinid interbrachials is unique among camerates and probably represents a specialized adaptation, perhaps in response to respiration.

ACTINOCRINITID-TYPE CALICES

The basic morphological and developmental features of crinoids having actinocrinitid-type calices parallel the more primitive glyptocrinid group with one exception.

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Girardeau Limestone, Illinois and Missouri (Brower, 1973, 1974b). [Explanation: radials black; interbrachials stippled; pinnules oblique ruled in fig. *1* and *2;* specimens arranged in order of increasing calyx height.]

1. Side or *CD*-interray view of smallest crinoid showing few fixed brachials and short arms composed of few brachials.

2. D-ray view of slightly larger young specimen with better developed arms.

3. Side view of juvenile crinoid.

4. C-ray view of young adult showing development of proximal intersecundibrachs.

5. Side view of submature adult.

6. Side view of largest crinoid with numerous interprimibrachs, intersecundibrachs, intertertibrachs, and fixed brachials.

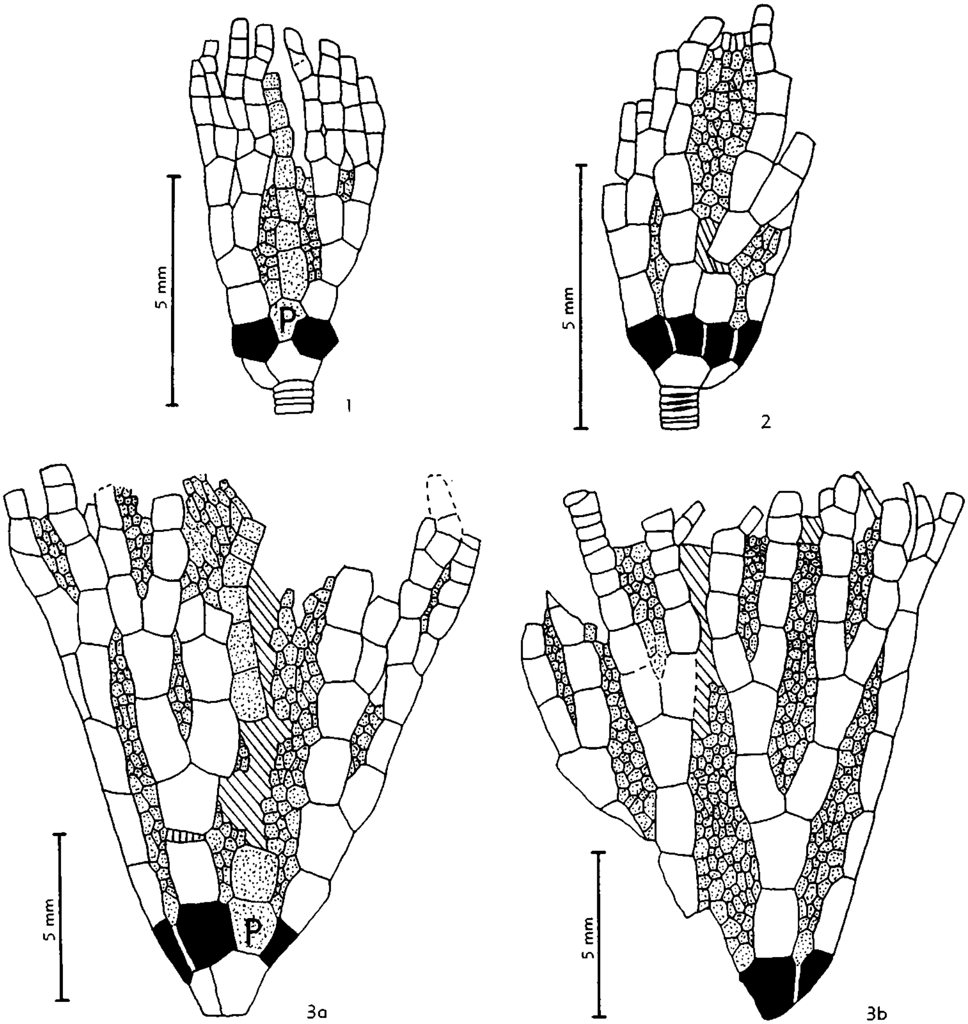

FIG. 200. Growth sequence of *Xenocrinus multiramus,* Upper Ordovician, Scotland, with xenocrinid-type calyx (Brower, 1974a, b). [Explanation: *P,* primanal; radials black; interbrachials stippled; damaged parts of specimens oblique ruled; specimens arranged in order of increasing calyx height.]

1. *CD*-interray view of young specimen with relatively few interbrachials.

2. *A*-ray view of another young specimen with more interbrachials; the *A* ray is abnormal and fails to branch.

3a,b. *CD*-interray and *A*-ray view of adult individual with numerous small and irregular interbrachials.

The glyptocrinids have few fixed arms in a single ray (usually two or four), whereas six or more fixed arms generally occur in rays of actinocrinitid calices. The development of numerous arms and associated axillaries fixed in the calyx tended to spread the arms apart, because the axillaries are roughly pentagonal and expanded distally (Fig. 201). The large number of axillary fixed brachials appears to be correlated with fewness of intersecundibrachs, intertertibrachs, and higher interbrachs, which are decidedly less well developed than in the more primitive glyptocrinid camerates (compare Fig. 199, 201).

PATELLIOCRINID-TYPE CALICES

These crinoids show a small number of fixed brachials which are joined into the calyx by large and regular interbrachials. Each ray bears a small number of arms, usually two or four (Fig. 202). Adults of all species examined have the proximal secundibrachs as the distal fixed brachials. The youngest crinoids lack intersecundibrachs and have closely spaced arms within a single ray that are separated by wide interray areas. Adults retained the juvenile condition because of the low rates of fixed brachial fixation in the intersecundibrach and intertertibrach areas. The lower rate of development of fixed brachials dictated slower distal extension of the calyx compared to glyptocrinid-type calices with the same shape. The radials are the largest ray plates in the youngest crinoids. The subsequent growth rates of the ray plates are adjusted so that mature patelliocrinids either retained or accentuated this juvenile radial and primibrachial arrangement.

PLATYCRINITID-TYPE CALICES

These crinoids are most similar to and doubtless were derived from patelliocrinid-type calices from which they diverged in two respects. The arms remained free above the fixed primaxil throughout platycrinitid ontogeny (Fig. 203). The patelliocrinids joined fixed brachials (both primibrachs and secundibrachs) in the calyx throughout development and proximal secundibrachs usually comprise the most distal fixed brachials in mature individuals. Primitive platycrinitid-type calices exhibit two primibrachs, but more advanced types tended to lose the primibrach *1,* and primibrach *2* (primaxil) rests on the radial. The primibrach width and height growth rates are much smaller in platycrinitids than in patelliocrinids. Thus, the platycrinitid primibrachs become progressively smaller in relation to size of the calyx throughout growth. For example, in young *Platycrinites bozemanensis* (Fig. 203), a pentagonal primaxil completely supports the secundibrachs *1.* Mature individuals have a triangular primaxil, which only partially serves this function; the outer secundibrach *1* margins rest on the radials.

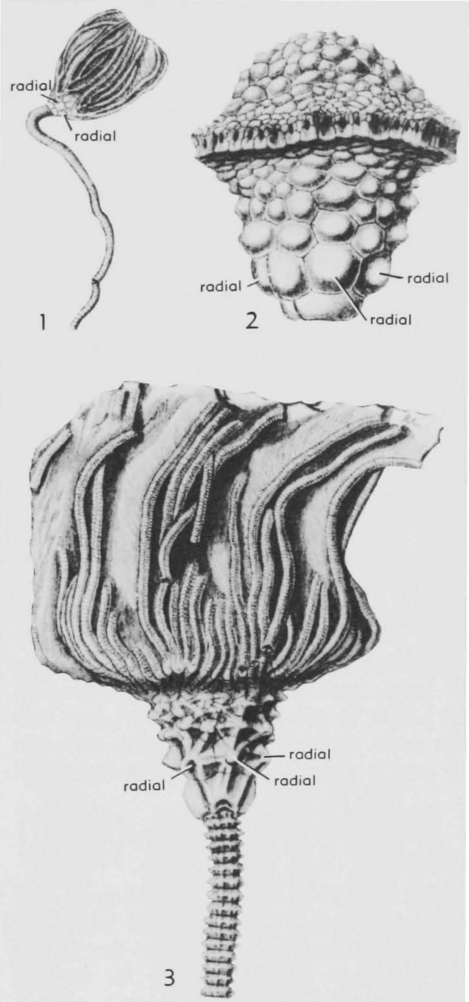

FIG. 201. Growth sequence of *Teleiocrinus umbrosus,* Lower Mississippian, Midcontinent, with actinocrinitid-type calyx (Wachsmuth & Springer, 1897). ——*1.* Side view of a young crinoid with arms free above the secundibrachs, ×1.——*2. A*-ray view of adult with many fixed brachials and fully developed wheel-like rim of free-arm bases, ×1. ——*3.* Side view of submature adult with moderately numerous fixed brachials and incipient wheel-like rim at free-arm bases, ×1.

GEOLOGICAL HISTORY OF CAMERATE CALYX TYPES

Consideration of lineages and the overall distribution of calyx types suggests a se-

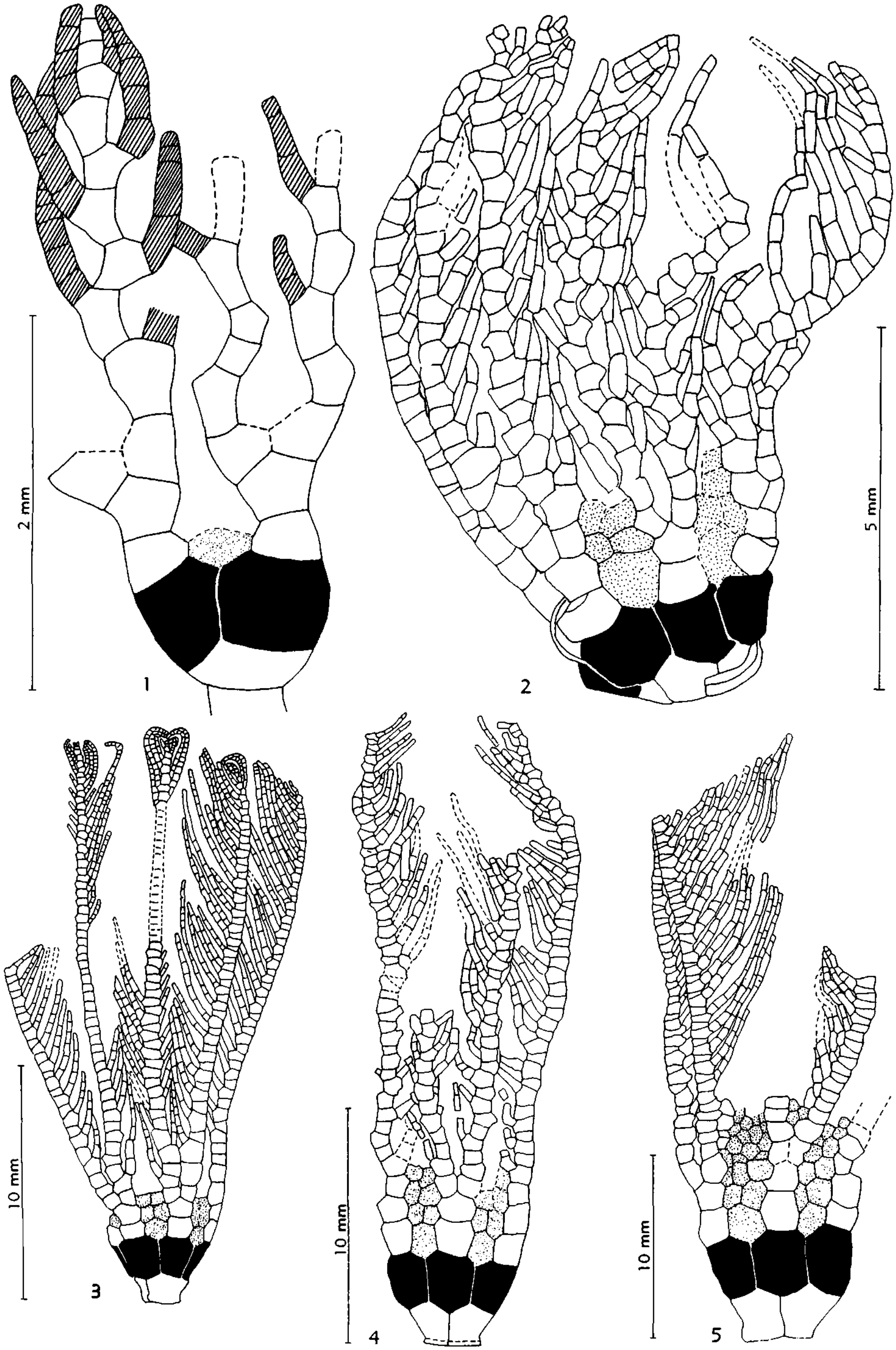

FIG. 202. Growth sequence of *Eopatelliocrinus scyphogracilis,* a patelliocrinid-type calyx, Upper Ordo-

ries of successions and replacements (see Brower, 1973, p. 401-407; 1974b). During the early and middle Paleozoic, xenocrinid-type calices evolved from glyptocrinid types but because these were not successful, they were replaced probably by glyptocrinid types (Brower, 1974a); extinct glyptocrinid groups were succeeded by actinocrinitid and patelliocrinid types; and platycrinitids supplanted patelliocrinids and perhaps some others. Camerates became extinct in the Permian. During the late Paleozoic, camerates probably were replaced by inadunates and flexibles (Lane, 1972) that almost exclusively had arms free above the radials. This indicates that crinoids lacking fixed brachials were most successful in the long run.

ONTOGENY OF THE FOOD-GATHERING SYSTEM

Crinoids face the same problems of growth as most filter-feeding marine invertebrates. The food-gathering capacity is, at best, an area or (linear dimension)^2 function, but the tissue to be supplied with food is a volume or (linear dimension)^3 function. Throughout ontogeny, the length of the food-gathering system is augmented by formation of new plates and increase in height of older ones. Addition of new plates, both in the arms and pinnules, results in the development of more food-catching tube feet. All new plates are initiated at the distal tips of the arms and pinnules. The following variables are the most critical (see Brower, 1974b, for more details): 1) the total volume of tissue is approximated by external volume of the calyx since total amount of tissue cannot be determined because of complex geometry of the crown and unknown complete stems. Both the entire tissue volume and calyx volume are (linear dimension)^3 functions and should scale similarly during ontogeny; 2) length of the entire food-gathering system including the arms and pinnules is substituted for the area of water covered by the food-gathering system because it is impractical to measure the area due to its geometrical complexity; 3) number of food-catching tube feet. The latter two variables are highly correlated and both scale the same way during ontogeny. Later discussion will emphasize the length of the food-gathering system which is easier to measure.

The basic statistics derive from the simple power function or allometric equation $Y = b \cdot X^k$ (see Huxley, 1932, and Gould, 1966, for discussion of the equation) in which X and Y are the independent and dependent variables, respectively. The intercept b gives the value of Y when X equals unity. The exponent k is the ratio of the specific growth rates of Y and X. "Ideal cases" may be defined for the development of food-gathering system length *(Y)* relative to calyx volume *(X)*. For a crinoid without pinnules, the length of the food-gathering system is a simple linear dimension, i.e., the length of all free arms. In this case, the ideal exponent is 0.33. All camerate crinoids bear pinnulate arms and the length of the food-gathering system is:

$$\left[\begin{pmatrix}\text{average}\\ \text{pinnule}\\ \text{length}\end{pmatrix} \times \begin{pmatrix}\text{number of}\\ \text{pinnule-bearing}\\ \text{brachials}\end{pmatrix}\right] + \begin{pmatrix}\text{length}\\ \text{of all}\\ \text{free arms}\end{pmatrix}$$

The length of the food-gathering system is a linear dimension that is mainly a product of two other linear dimensions, namely, number of pinnule-bearing brachials and average pinnule length. The length of the arms is negligible relative to the food-gathering system length represented in the pinnules. For a crinoid with pinnulate arms, the approximate ideal exponent comprises 0.67.

Table 1 presents the statistical data for several Ordovician camerates from the

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vician, Girardeau Limestone, Illinois and Missouri (Brower, 1973, 1974b). [Explanation: radials black; interbrachials stippled; pinnules oblique ruled in smallest specimens; crinoids arranged in order of increasing calyx height.]

1. Side view of young specimen with few fixed brachials and one interbrachial in each interray.

2. *E*-ray view of juvenile with more numerous fixed brachials and interbrachials.

3. Side view of small adult.

4. Side view of mature crinoid.

5. Side view of largest crown, showing moderately numerous interbrachials and fixed secundibrachs.

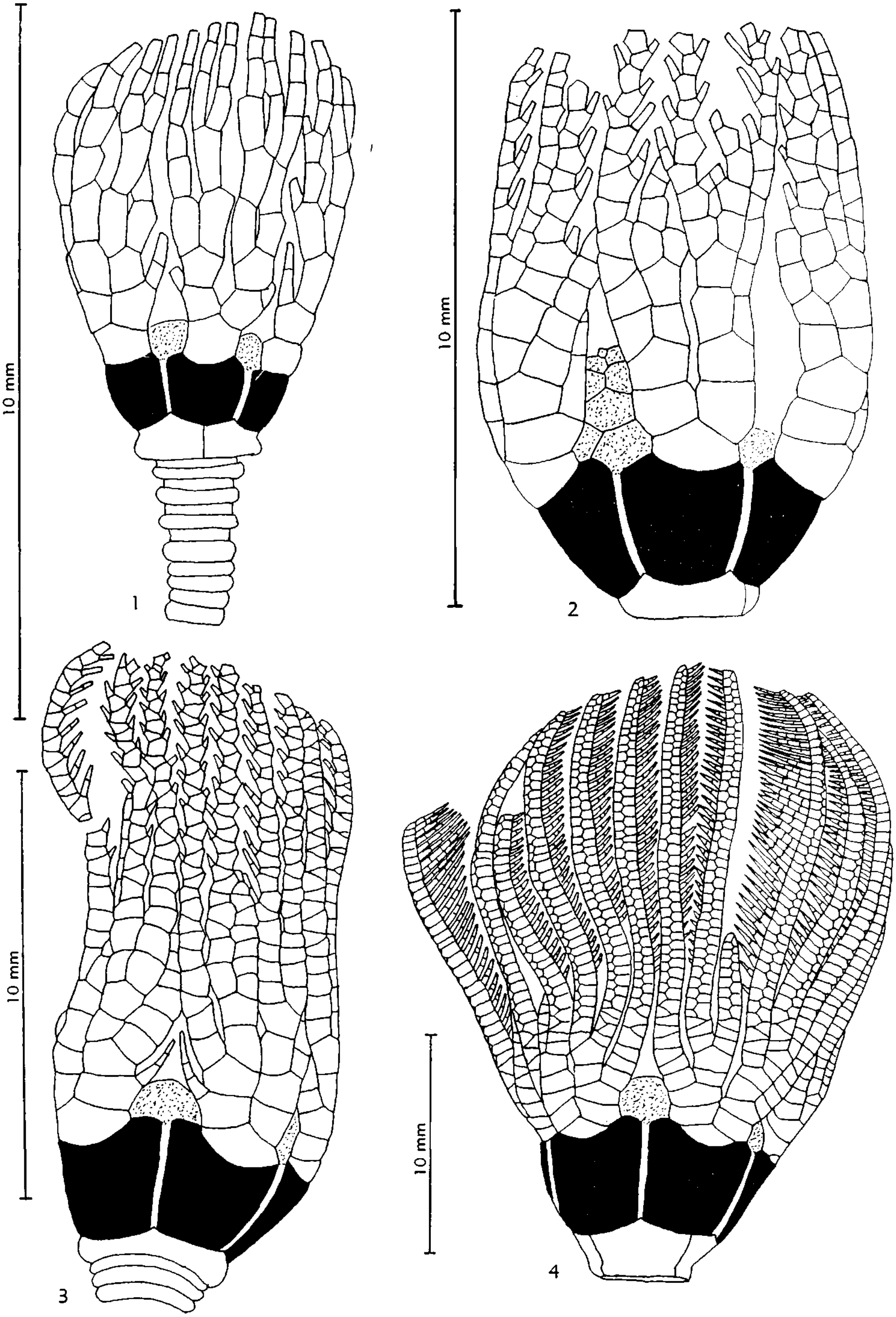

FIG. 203. Growth sequence of *Platycrinites bozemansis,* Lower Mississippian, Montana, wth platycrinitid-

TABLE 1. *Growth of Calyx Volume and Length of Food-gathering System in Some Girardeau Limestone Camerates (Ordovician).*

[X = calyx volume in cc.; Y = length of food-gathering system in cm.]

Species	Initial Intercept	Exponent	Minimum X	Predicted Minimum Y	Maximum X	Predicted Maximum Y	(Minimum Predicted Y)/(Minimum Observed X)	(Maximum Predicted Y)/(Maximum Observed X)	Correlation Coefficient	Number of Specimens
Eopatelliocrinus scyphogracilis	2,134	0.807	0.0007	6.07	0.220	629	8,670	2,860	0.976	16
E. latibrachiatus	1,337	0.717	0.0006	6.56	0.132	313	10,900	2,370	0.937	10
Macrostylocrinus pristinus	2,900	0.872	0.0003	2.46	0.237	826	8,200	3,480	0.988	10
Alisocrinus tetrarmatus	4,360	0.920	0.001	7.57	0.216	1,060	7,570	4,910	0.996	12
Ptychocrinus splendens	1,390	0.729	0.012	55.4	0.865	1,250	4,620	1,370	0.912	16
P. fimbriatus	482	0.452	0.006	47.8	0.184	224	7,970	1,220	0.885	6

Girardeau Limestone (BROWER, 1974b). The youngest crinoids all have similar food-gathering systems (Fig. 199, 202), but divergence occurred throughout subsequent development. Ontogeny of length of food-gathering system relative to calyx volume was curvilinear in all Girardeau camerates in which the growth rates of length of food-gathering system per 0.01 cc. of calyx volume increment dropped with increasing volume and age, i.e., negative allometry (Table 1). Except for *Ptychocrinus fimbriatus,* the food-gathering system grew more rapidly than one would predict based on the ideal case. In *P. fimbriatus,* the food-gathering system developed more slowly than in the ideal case. In general, crinoids with pinnulate arms seem to have maximized the growth rates of length of the food-gathering system with respect to calyx volume as much as possible within the inherent geometrical limits of the food-gathering system. This was accomplished by several basic mechanisms:

1) Development of pinnules must greatly accelerate the rate of development of the food-gathering system. Once pinnules are present, further increases in the rate of growth are achieved through augmenting the number and length of pinnulars in each pinnule.

2) Crinoids have several ways of accelerating the rate of formation of new brachials in a ray. This increases the number of pinnules because usually all plates within a free arm bear pinnules except for one or two distal free brachials, free axillaries, and free brachials located immediately above the free axillaries. Development of biserial brachials augments the number of brachials per unit free arm length compared to crinoids with uniserial brachials of roughly

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type calyx (mod. from Laudon, 1967). [Explanation: radials black; interbrachials stippled; crinoids arranged in order of increasing calyx height.]

1. Anterior view of young specimen with relatively large axillary primibrach *1* and uniserial free arms consisting of relatively high brachials.

2. Side view of older crown with relatively wider and shorter uniserial brachials.

3. Juvenile crown with strongly cuneiform brachials in upper arms.

4. Mature specimen with biserial arms, small primaxil and outer edges of secundibrachs *1* resting on radials, proximal part of free arms above axillary secundibrach *2* uniserial but regularly biserial higher.

TABLE 2. *Ontogeny of Feeding Tube Feet in* Alisocrinus tetrarmatus, *Ordovician, Girardeau Limestone.*

"Size" (mm.)	Calyx volume (cc.)	Feeding tube feet per arm	Feeding tube feet in pinnules of single arm	Total number of feeding tube feet	Total number of feeding tube feet/ calyx volume
1.1	0.001	150	60	4,200	4,200,000
1.4	0.002	180	150	6,600	3,300,000
4.2	0.20	1,710	5,700	148,000	740,000
5.5	0.20	1,950	4,550	130,000	650,000

the same height (compare Fig. 202, 203). The number of fixed or free arms can be increased. For example, *Alisocrinus tetrarmatus* has four unbranched uniserial free arms per ray, whereas eopatelliocrinids have only two free arms in a single ray (Table 1, compare Fig. 199, 202). *Ptychocrinus splendens* has about eight uniserial free arms in each ray, which results in very rapid formation of new brachials as the arms are extended distally. Development of hypertrophied arms, such as in melocrinitids, probably also accelerates the rate of formation of new brachials.

3) Length of the arms can also be increased through the growth of higher brachials, although this does not affect the number of food-gathering tube feet.

4) Many crinoids combine two or more of the above mechanisms. For example some actinocrinitids have numerous branched free arms composed of biserial brachials that bear long pinnules with many pinnulars.

The "food-gathering ratio" equals (food-gathering-system length)/(calyx volume). Despite the fact that camerate crinoids seem to have maximized the rate of growth of the food-gathering system as much as possible, the food-gathering ratio invariably declined during progressive development of a single species (Table 1).

In an attempt to evaluate ontogeny of the food-gathering system further, the approximate number of food-catching tube feet was computed for several individuals of *Alisocrinus tetrarmatus* (Table 2; see BROWER, 1973, p. 323; 1974b, for details). The capacity of the food-gathering system, as measured by the number of feeding tube feet in relation to calyx volume, decreased throughout ontogeny (Table 2). The initial downtrend of the ratio was most rapid, for more than half of the total decline occurred over roughly five to 10 percent of the calyx volume interval. It is notable that (food-gathering-system length)/(calyx volume) and (number of food-catching tube feet)/(calyx volume) behaved similarly during development. Both ratios declined as the crinoids became larger, indicating that the food-gathering capacity relative to volume dropped throughout growth. Continuation of this ontogenetic pattern could produce a "hypothetical crinoid" in which the number of food-catching tube-feet is too low and the food-gathering system too short to provide the volume of soft tissues with food. Obviously no crinoid reached this critical limit, although some forms may have approached it. Perhaps some ratio of (food-gathering-system length)/(tissue volume) or (number of food-catching tube feet)/(tissue volume) serves as a limit beyond which further increase of tissue cannot take place.

GROWTH OF SUPPORTING STRUCTURES

A crinoid endoskeleton is a complex of supporting relationships. Essentially, each plate bears all higher ones. For example, the proximal columnal supports the crown, basals underlie the radials and all higher plates, distal fixed brachials elevate the arms, and pinnule facets hold the pinnules. Not all supporting relationships have been evaluated and attention is focused on the proximal columnal area and the area of the distal fixed brachial (see data on Girardeau camerates in BROWER, 1973; 1974b). In both cases, the supporting ratio (area of supporting plate)/(weight of structure supported) declines throughout ontogeny and mature crinoids are "less well supported" than youngsters. Seemingly, continuation of this decrease eventually could have produced a stem too small to have elevated and supported the crown or arms which were too long and heavy for the crinoid to support, or both. Perhaps critical ratios provide limits, beyond which further size growth cannot proceed. Whether or not any camerate crinoid approached or reached this limit is not known.

GROWTH OF THE STEM

During development of most living and fossil crinoids, new plates form in the stem. Typically some of these are initiated immediately below the calyx (nodals), whereas others grow between previously formed columnals (intercalation of internodals). In most camerate crinoids which I have examined, more than half of the columnals formed by intercalation. In a few crinoids (e.g., some *Pisocrinus*) all new columnals are developed just below the calyx.

The function of a crinoid stem is to elevate the crown above the substrate. Elevation is progressive and continues throughout life of a stalked crinoid. The rate of elevation is dictated by two growth vectors —the rate of initiation of new columnals and the height growth rates of old ones. During growth, crinoid stems must achieve a balance between two factors—suitable rate of lengthening and maintenance of an appropriate amount of flexibility in the column. Flexibility allows the crinoid to bend the stem so as to attain advantageous feeding orientation and to avoid undue stress on the column that might break the stem (BROWER, 1973, p. 283-290, 298-299; 1974b). Most camerates show the usual flexibility gradient of stalked crinoids in which maximum flexibility generally occurs in the middle 67 to 75 percent of the column (SEILACHER, *et al.*, 1968). Relatively rigid stem segments are associated with the rooting device and immediately below the calyx. This allows the crinoid to flex the stem against a rigid holdfast, thus achieving maximum mechanical leverage. With a certain articular type, column flexibility is directly proportional to the ligament volume/external columnal volume ratio.

In most crinoids, growth of width in the columnals tends to decrease stem flexibility because the ligament volume/external columnal volume ratio of mature plates is lower than that of young columnals. Consequently, a continuous supply of intercalated plates is required to maintain a flexible stem. Some crinoids develop more strongly depressed articular surfaces in larger columnals and in such crinoids the ligament volume/external columnal volume ratio increases throughout ontogeny. Such forms need not depend on intercalation to maintain a flexible stem.

COMPARATIVE ONTOGENY OF CAMERATES AND LIVING CRINOIDS

Camerates and recent crinoids show the same plate-growth sequence with respect to the arms, column, and most calyx plates. In many living crinoids (comatulids), the animal discards the column at the end of the pentacrinid growth stage and assumes a more or less free-living existence. This does not occur in camerates and recent isocrinids, where, barring traumatic accidents, all or part of the stem is retained until death. Nevertheless, growth of the comatulid larval column and the camerate and isocrinid stem follows the same pattern. The sequences of calyx-plate development of camerates and comatulids are the same except for proximal interbrachials. During the ontogeny of most camerates, free brachials became incorporated in the calyx, although at rates varying with calyx type. This does not occur in modern crinoids, among which the arms remain free above the radials throughout life. Typically the interprimibrachs *1* of recent crinoids develop late in ontogeny, usually after primibrach *2* is present or still later. In camerates, these proximal interbrachials probably were initiated along with or soon after the radials. Camerate crinoids were probably also characterized by early interprimibrach

1 development. It is notable that the contrasts between the plate-growth sequences of living crinoids and camerates can be correlated with the presence or absence of fixed brachials.

Growth of the camerate and modern crinoid calyx plates follows different paths. Most camerate crinoids probably had a calcitic convoluted organ located inside the calyx. I believe that this structure both supported the gut and separated it from the chambered organ and aboral nerve cords. If so, the camerate convoluted organ served roughly the same purpose as the basal rosette in comatulids. The basic camerate calyx functions were to enclose, protect, and support the viscera, and to bear the free arms. These free arms were supported by distal fixed brachials, which in turn rested on more proximal plates. All camerate calyx plates performed more or less the same functions. Consequent on this functional morphology, major resorption was rare in calyx plates of camerates. I believe that resorption in camerate calyx plates was largely confined to plates located near the openings for free arms, anus, and axial canal of the column.

As noted by A. H. Clark (1915a, p. 344-348), comatulids depart greatly from the camerate plan (see Brower, 1974b, fig. 4). The principal specializations of comatulids are related to reduction of the cup plates and increase in cup strength. Different parts of the comatulid cup served different functions. The comatulid infrabasals, if present, are reduced. Early in ontogeny these fuse with the distal columnal to form the centrodorsal with cirri which the crinoid uses to grasp the substrate or foreign objects after the column is discarded. The comatulid basals are also insignificant cup elements that are metamorphosed and shifted upward to form the basal rosette during growth. The mature chambered organ is almost completely enclosed within the centrodorsal on its base and sides, by radials on its sides, and the basal rosette at its top. The viscera proper (i.e., inner and outer coelom, gut, etc.) rests on the distal margin of the basal rosette and radials. Thus, the basal rosette serves as a platform that largely separates the chambered organ from the viscera proper. The principal function of the comatulid radials is probably to support the arms, which are free above the radials. Lateral protection and support for the viscera proper are provided by the primibrachs. Thus, in comatulids and to a lesser extent in isocrinids, the infrabasals, basals, and radials do not serve to support and protect the sides of the viscera as in camerates. Consequently, the cup-plate growth patterns of modern crinoids and less complex camerates diverge. As mentioned above, resorption was rare in camerate calyx plates. Conversely, in comatulids (isocrinid ontogeny is not well known), resorption during cup-plate growth is common and can be documented for basals, centrodorsals, radianal, orals, and other tegminal plates (A. H. Clark, 1915a, p. 322-340).

The initially formed comatulid radials have flat inner and outer surfaces with axial nerve cords located inside of the plates (Fig. 195,*4-6*). Throughout ontogeny, calcite is deposited on the inside of the comatulid radials, and the axial nerve cords are completely buried within the radials during the last development stage (W. B. Carpenter, 1866, p. 738-741). Growth of comatulid brachials follows the pattern established for radials. In camerates, calcite was not deposited on the interior of the calyx plates and the axial nerve cords were housed on the plate interiors throughout life (Fig. 195,*1-3*). Growth of the brachials produced a distal extension of the calyx plate type (Fig. 196) and the axial nerve cord lay at the base of the brachial food grooves regardless of age.

The camerate type of uniserial brachial growth predominated in the Paleozoic, whereas living forms are characterized by the comatulid type. This suggests progressive evolution and adaptation. Obviously, the recent crinoid-axial nerve cords are better protected. Damage to the food-groove tissue need not harm the axial nerves. This is important because the aboral nervous system, including axial nerve cords of the arms, is the major level that controls posture and other basic reactions. Conversely among camerates, many injuries to the food-gathering structures probably also damaged the axial nerve cords. Geometrically, the comatulid growth pattern is far more complex than the camerate one. This implies that comatulid brachials require a higher degree of developmental integration and coordination than camerate plates. Perhaps this partially explains why camerates retained their type of growth, despite vulnerability of their axial nerve cords.

Compared to cup or calyx plates and brachials, the main growth patterns of columnals are highly conservative. As far as can be determined, these are uniform in living crinoids and all fossil forms.

INADUNATES

By N. GARY LANE

Ontogenetic studies of inadunate crinoids have been confined to two groups of these fossils, each of which is classified informally as microcrinoids. These small crinoids are included in the monocyclic, disparid superfamily Allagecrinacea, and the dicyclic suborder Cyathocrinina, superfamily Codiacrinacea. The ontogeny of larger, and more diverse, macroscopic inadunates is as yet unstudied, although immature or very small specimens of some species are known.

The three dicyclic inadunates for which ontogenetic development is best known are three species from the Artinskian of the U.S.S.R., described by ARENDT (1970a): *Monobrachiocrinus oviformis* YAKOVLEV, *Cranocrinus praestans* ARENDT, and *Hemistreptacron abrachiatum* YAKOVLEV (Fig. 204).

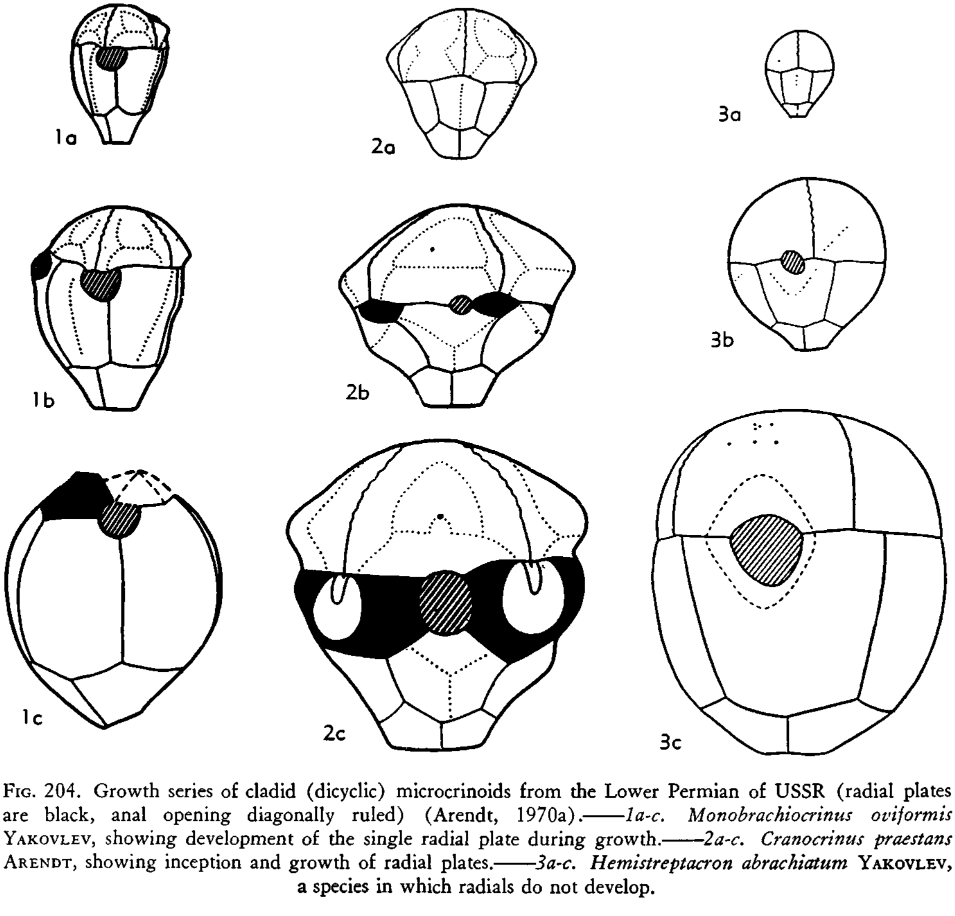

FIG. 204. Growth series of cladid (dicyclic) microcrinoids from the Lower Permian of USSR (radial plates are black, anal opening diagonally ruled) (Arendt, 1970a).——*1a-c. Monobrachiocrinus oviformis* YAKOVLEV, showing development of the single radial plate during growth.——*2a-c. Cranocrinus praestans* ARENDT, showing inception and growth of radial plates.——*3a-c. Hemistreptacron abrachiatum* YAKOVLEV, a species in which radials do not develop.

The growth series for *Monobrachiocrinus oviformis* begins with a high, pyriform theca about 4.5 mm. high, consisting of three infrabasals, five basals, and five oral plates. Radials are completely absent and a large opening, presumably an anal opening, exists between the upper lateral edges of two of the basals. In the next stage, a single radial plate appears as a small, transversely lens-shaped element, directly atop one of the basals, bounded above by two oral plates. This radial plate, the only one that develops in this crinoid, increases abruptly in size, and a radial facet for the single arm appears on thecae that are about 6.9 mm. high. Subsequent changes during growth include change in thecal shape from high and pyriform to a globular shape, occasioned by enlargement and bulging out of the basal plates. The oral plates seemingly cease growth at an early stage and form a small cap-shaped pyramid perched on top of the theca in mature stages, maintaining their same relative position to the single radial and basals.

The earliest known growth stage in *Cranocrinus praestans* consists of a small theca composed of five large orals, five basals, and an uncertain number of infrabasals. In the next, slightly larger, stage, an anal opening appears above one of the basals, followed shortly by appearance of a small, diamond-shaped radial adjacent to and just to the right of the anal opening. This radial is judged to be the *C* radial. Next, three additional radials appear virtually simultaneously, those of the *B, D,* and *E* rays. The *A* radial is the last to appear. All radials develop at the top of interbasal sutures; they are small, diamond or lens-shaped, where they first appear, and none of them bears an arm facet until they have become conspicuously larger. An arm facet appears first on the *C* radial, followed by a facet on the *D* radial and very small facets on the *B* and *E* radials. The arm facet of the *A* radial is the last to appear. The facets of the *C* and *D* rays gradually enlarge until they are conspicuously larger than the facets of the other three rays.

Differential growth of the lateral edges of the oral plates results in gradual shift in orientation of these plates relative to the basals during growth. In smallest known specimens interoral sutures are directly above the midlines of the basals. As growth continues the interoral sutures are gradually displaced to the left, until in largest known specimens the orals are directly in line with the basals, and are, therefore, in normal interradial position.

In *Hemistreptacron abrachiatum* radial plates are lacking and the principal changes during growth include the appearance of an anal opening after smallest known stages, and rotation of the oral plates relative to the basals. Where the anal opening first appears, it is directly above the midline of a basal, and one of the interoral sutures is directly above the anal opening. During growth the basal plate that bounds the anal opening exhibits slightly greater growth along its right lateral edge than along the left side, so that in large specimens the anal opening is shifted slightly to the left of center of the basal. The oral plates alternate with the basals in early stages, so that interoral sutures are in line with the midlines of basals, as in *Cranocrinus.* The interoral sutures become progressively shifted to the right during growth, indicated especially by rightward shift of the interoral suture that was directly above the anal opening in early stages. The orals stop short of being aligned directly above the basals, however, their sutures being slightly offset to the left of interbasal sutures in largest specimens.

The growth series of these three species indicate that the anal opening appears after basal and oral plates are well formed and in close contact with each other. The radial plates appear quite late in ontogeny, and arm facets are relatively slow to develop on these plates. The oral plates undergo rotation during growth, perhaps in response to internal shifts in the main visceral components.

Reasonably complete growth series are known for several disparid crinoids, one of the most complete and most interesting being that of *Allocatillocrinus rotundus* Moore, described by Moore (1940) (Fig. 205). The smallest specimens of this species have a single arm facet on each of three radials, the other two radials lacking facets. These first three facets are on the *B, C,* and *E* rays. In the next stage there

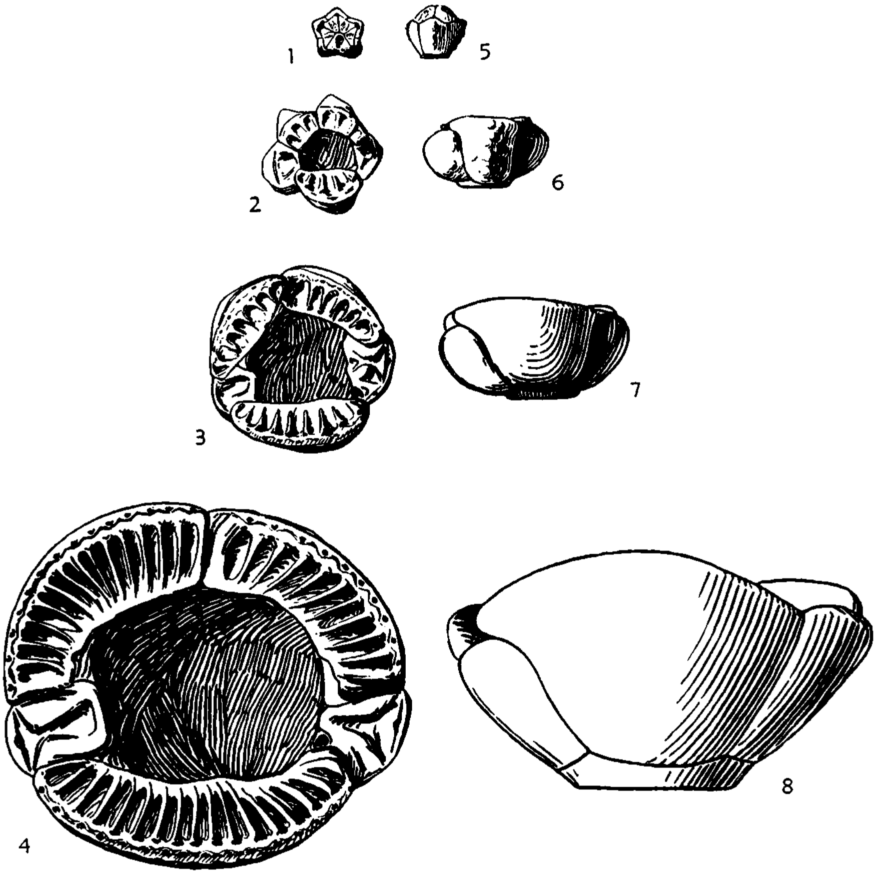

Fig. 205. Growth series of a monocyclic, disparid crinoid, *Allocatillocrinus rotundus* Moore, all ×5 (Moore, 1940a).——*1-4.* Oral views of cup showing increase in number of arm facets on the *A, B,* and *D* radials, *D* radial at the bottom, and retention of a single facet on the *E* and *C* radials.——*5-8.* Lateral views of same specimens showing allometric lateral growth of *D* radial.

is a single facet on the *A, E,* and *C* radials, and two facets, side by side, on each of the other two radials. As growth continues, additional facets continue to be added to the *A, B,* and *D* radials; the *C* and *E* radials continue to have a single radial facet. Each radial facet supports a single, uniserial, unbranched arm. As the number of arm facets increases, there is a corresponding increase in width of the three multifaceted radials, so that they become conspicuously larger than the two small single-facet-bearing radials. Largest individuals with greatest number of facets have 10 facets on the *B* radial, 14 on the *A* radial, and 16 on the *D* radial. During growth, new arms and arm facets appear either at one end of a radial plate, so that the oldest facet is at one end and the most newly formed facet at the other, or the oldest facet is in the center of the radial, with new facets, and arms, added at both extremities of the plate. In *Allocatillocrinus,* the oldest facet is at the anterior edge of the *B* radial, and the newest facet at the posterior end. On the *A* radial, new facets are added at each end.

Specimens of *Allagecrinus* show a reasonably complete growth series that resembles the early growth stages in *Allocatillocrinus.* In *Allagecrinus pecki* Moore (1940), small specimens, about 1 mm.

wide, have a cap of five conspicuous oral plates and one arm facet on the *C* radial only. A facet develops next on the *E* radial, then on the *B* and *D* radials almost simultaneously. The facet for an arm on the *A* ray develops last, in specimens that are about 2 mm. wide. In fully mature individuals, the oral cap of plates is typically lost, and two facets are developed on the *A, B,* and *D* radials, with single facets on the other two radials. Other species of *Allagecrinus* may have three or more facets on the three multifaceted radials. Presumably the oral plates are firmly fixed to the radials in early growth stages, but become progressively more loosely bound to the radials as growth continues, so that they are rarely preserved in larger specimens.

A growth series for *Synbathocrinus texanus* has been described by Moore & Ewers (1942). Smallest specimens of this species have a very low basal circlet, five conspicuous radials and five orals; the radials completely lack arm facets. The first arm facet appears on the *C* radial, closely followed by facets on first the *E* and then either the *D* or *B* radials. The facet on the *A* radial is the last to be developed. The arm facets are initially small, rounded, and smooth. With continued growth the facets become progressively wider until they occupy the entire distal faces of the radials. The facets also become progressively more prominently sculptured, with a strong transverse ridge, outer ligament pit, and other features typical of advanced arm facets in inadunate crinoids. The basal circlet grows in height, becoming a more conspicuous part of the lateral wall of the cup. The five oral plates are found in position in all of the small specimens, but mature specimens invariably have the oral plates missing, perhaps indicating a change in the strength of oral-radial articulations with growth.

FLEXIBLES

By N. Gary Lane

Knowledge of morphological change consequent upon individual growth in flexible crinoids is scanty, and has been little studied since Springer's (1920) monograph on these crinoids. The smallest known specimens of flexible crinoids, less than one centimeter in crown height, are probably best judged to be young adult, rather than immature, individuals. The plates of the cup—infrabasals, basals, radials, and plates of the posterior interray—undergo little change in number or relative proportion of plates from smallest to largest individuals. These plates increase in size with growth, but maintain constant relations to each other and to the arms and stem, resulting in a cup that maintains the same outline and shape during growth. The only observed change in these plates was reported by Springer (1920) in *Homalocrinus parabasalis* Angelin, in which the infrabasal plates expanded differentially during growth so that in large individuals the infrabasals cover most of the proximal parts of the basals and the radianal, plates that are mostly exposed in small specimens.

Two growth features that affect the stem have been reported in flexible crinoids. The proximal part of the stem, the proxistele of Moore and Jeffords (1968), is sharply differentiated from more distal stem parts in many flexible crinoids. The proxistele is composed of wide, very thin columnals that are firmly united and commonly preserved attached to the cup. In at least one flexible, *Eutaxocrinus curtus* (Williams), discussed by Goldring (1923), small individuals have very few columnals distinguishable as a proxistele, whereas large specimens of this species have many columnals in the proxistele, indicating a progressive increase in number of plates in the proxistele during growth. In other flexible crinoids the number of plates in the proxistele changes very little, if at all, from quite small to large individuals. A growth series of specimens of *Taxocrinus colletti* White, illustrated by Springer (1920), indicates that the number of plates in the proxistele in this species remains relatively constant from small to large individuals. Increase in height of the proxistele with growth is accomplished by slight increase in thickness of individual columnals, four per mm. in small specimens

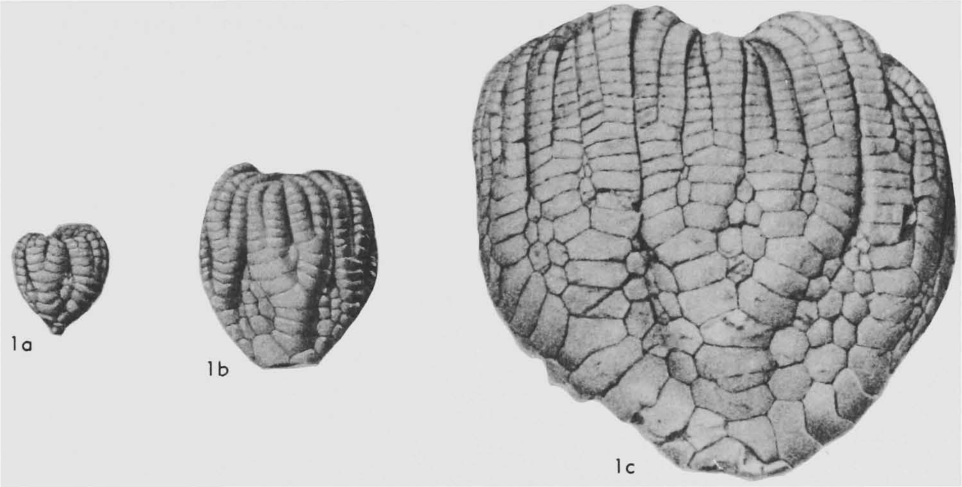

FIG. 206. Growth series of *Forbesiocrinus multibrachiatus* LYON & CASSEDAY, Miss.; *1a-c*, ×1 (Springer, 1920).

and 2.5 to three columnals per mm. in large specimens, according to SPRINGER. Consequently, the slight evidence that is presently available concerning growth of the proxistele is equivocal and deserves further study.

The more distal parts of the stem, the mesistele andististele, also have been observed to undergo conspicuous changes during growth in a number of flexible crinoid species. In young, or small, individuals this part of the stem consists of highly elongate, barrel-shaped columnals, the degree of elongation increasing distally. Large specimens of species that show this character have relatively short, wide columnals with lateral faces evenly rounded. Presumably, these columnals attain their full height quite early in growth, with subsequent additions of stereom serving to increase the width of the column. This mode of growth, with emphasis first on increasing the overall length of the stem, and then on making the stem wider and sturdier, may be related to an adaptive strategy on the part of the crinoid to first raise itself up off the sea floor a given distance as rapidly as possible, and once this minimum height is attained, to concentrate on providing as firm and strong a support as possible for the increasingly bulky crown. SPRINGER illustrated small specimens with highly elongate distal columnals for *Taxocrinus colletti* WHITE, *Eutaxocrinus alpha* (WILLIAMS), *Icthyocrinus laevus* CONRAD, and *Asaphocrinus ornatus* (HALL). Specimens of *Mespilocrinus* retain these stem characteristics, typical of small specimens in other flexibles, in fully adult specimens.

One of the most conspicuous changes in the crown of flexible crinoids during growth is the increase in number of interradial plates in the four interrays other than the posterior interradius. This growth trend is best seen in specimens of *Forbesiocrinus multibrachiatus* LYON and CASSEDAY, in which small specimens have one, two, or three interray plates per interray, whereas large specimens have 19 or 20 such plates (Fig. 206). SPRINGER (1920) observed this increase in number of interradial plates in virtually every flexible crinoid for which he had both small and large specimens available. The interray plates served to bind flexibly together the proximal parts of the arms, thus as the interray plates increased in number with growth, an increasingly higher part of the arm was laterally bounded by such plates. This increasing support of proximal arms may have added needed strength and support for the presumably highly flexible arms during arm movement.

An increased height of interradial plates also resulted in a proportionately greater volume to the visceral cavity of the crinoid. In small individuals with only one or two interradial plates per interray the tegmen was situated very little above the bases of the arms, and the main visceral organs were confined mostly to the cup. With increase in number of interradial plates the tegmen was situated progressively higher on the crown and space internal to the arm bases would have been a significant part of the visceral cavity. Presumably the internal organs grew sufficiently large that they could not be accommodated within the cup in large individuals, at least partly because cup plates did not increase in size proportionate to the increase in volume of vital organs. This adult configuration would have provided an additional reason for restricting movement of proximal parts of the arms by laterally bounding interray plates—excessive movement of the proximal parts of the arms could conceivably have jostled adjacent internal organs sufficiently to be disadvantageous to the crinoid.

With increase in size, most flexible crinoids also exhibit an increase in the number of arm branches per ray. Small specimens, on the order of 1 cm. or less in crown height, typically have either secundibrachs or tertibrachs as the highest arm plates in the crown. Large specimens of the same species, as for instance *Taxocrinus ungula* Miller and Gurley as illustrated by Springer (1920), have quartibrachs and additional higher arm divisions preserved. As new series of brachials are added to the tips of the arms during growth, proximal brachials constitute a progressively smaller portion of the total crown height. The mechanism by which additional arm branches are added at the ends of the arms is not known. Living multibrachiate comatulids add new divisions to the arms by autotomically casting off a series of distal arm plates and regenerating a new axillary plate and higher brachials on the brachial above which the rupture took place. Whether flexible crinoids utilized the same, or a similar, mode of increasing the number of arm divisions per ray is not known.

ARTICULATES

By H. Wienberg Rasmussen

INTRODUCTION

Larval ontogeny and early development have been studied in a few recent crinoids, mainly comatulids, and are described in the *Treatise* section on recent crinoids. No such information on fossil crinoids exists, but the influence of larval ontogeny in recent comatulids on phylogenetic interpretation of some Articulata is mentioned in the section on evolution of Articulata, especially in connection with Comatulida and Bourgueticrinida.

Postlarval growth and change of skeletal form is very important in the determination of fossil and recent Articulata. Several morphological features undergo considerable change during growth of the crinoid skeleton and single skeletal elements. Nominal species based on specimens differing only in age and growth stages has resulted in a large number of synonyms. Thus, 17 species have been based on growth stages of the Cretaceous *Glenotremites paradoxus,* according to Rasmussen (1961, p. 284). Growth series of fossil Articulata have been described by Springer (1901) and Rasmussen (1961). Moore (1967), Rasmussen (1972), and Peck & Watkins (1972) have given information on growth in fossil Articulata. Studies on growth have been based on correlation of size with change of form, and must be closely connected with the species concept, but also direct evidence of growth seen as growth rings in sections of skeletal elements has been mentioned by Gislén (1927) for recent *Democrinus,* by Rasmussen (1961) for *Phyllocrinus,* and by Moore (1967) for *Dunnicrinus.*

In different parts of the crinoid skeleton the form changes during growth according to a few general patterns common to all Articulata or to large groups of the subclass. Identification of fossil Articulata is not possible without familiarity with these general patterns of postlarval ontogeny, which are therefore also to some extent included in the systematic description of Articulata in the *Treatise*.

During growth of a crinoid, the single skeletal elements increase in size and new columnals are added at the top of the stalk, and new brachials in the tip of the arms. Therefore, distal columnals and proximal brachials are older than proximal columnals and distal brachials of the same specimen. However, the new skeletal elements, especially columnals, introduced in an old individual are different from those introduced in a young specimen. This complicates the growth pattern and makes a concise terminology necessary in the description of ontogenetic features, so as not to confuse age of specimen with age of skeletal element.

A general rule for all Articulata is that during growth of a brachial its width increases more than its height. Young brachials are high and slender, but during growth they become wider and more robust. This change is found from juvenile to adult specimen as well as from the distal to the proximal part of an arm. Division of arms may take place either by two branches growing out from an axillary in the tip of the arm, or as augmentative regeneration, the distal part of an arm being shed from a nonmuscular articulation and replaced by an axillary with two branches. Except in damaged specimens, augmentative regeneration is found only from an axillary following a nonmuscular articulation. It has been observed in recent *Endoxocrinus, Teliocrinus,* and after the first division in most or all multibrachiate comatulids. Also, modification of pinnules may lead to a multibrachiate structure in some Isocrinida. Crinoids with arms divided at primibrachs *1* are extremely few, but have been observed among Cyrtocrinida and a few Comatulida. They have often been explained away by suggesting fusion of two primibrachials, but there has been no observation supporting the premise that brachials may fuse during growth.

The radials follow the same pattern of growth as the brachials, increasing in width, and in many groups also leaning progressively outward. The growth of basals is more variable. In Millericrinida the growth of basals and radials is almost equal, the cup becoming wider, but not changing much in form during growth. In most Isocrinida and Comatulida the basals increase less in size than the radials, or they may be reduced in size during growth. In some Bathycrinidae, especially *Democrinus,* the height of basals is very greatly increased.

Growth of the column and columnals is more complicated. An articulated column is developed together with other skeletal elements early in the larval embryology of recent comatulids, and the crinoid attaches itself by a terminal disc of the column. The juvenile column of stalked crinoids is small and slender, and consists of single columnals, which are small in diameter, but may well be rather high. During growth the columnals increase in size, and new columnals are added in the proximal end of the column. These new proximal columnals are concealed between adjacent proximal columnals or between the uppermost columnal and the cup until they have reached the columnal diameter and show up as extremely low ("thin") discs. By continued introduction of new proximal columnals, the previously formed columnals gradually move to a more and more distal position in the column, and at the same time they rapidly increase to their final height, and may also change in outline and ornament. It follows from this that diameter of the column and of single columnals is a function of the size and age of the individual, but height of the columnals is mainly correlated with its proximal or more distal position within the column. Very slender columnals, whether low or high, are found only in juvenile specimens, but low columnals are formed proximally throughout the lifetime of the specimen or, rather, its growing period. Some recent and fossil crinoids have very few or no low (new) proximal columnals in large specimens, and this indicates a final decrease or cessation of columnal formation (RASMUSSEN, 1961, pl. 24, fig. 16; pl. 27, fig. 14; pl. 30, fig. 1; pl. 32, fig. 3; A. M. CLARK, 1973b, fig. 5).

The diameter of the column, although increasing during growth of the individual, is often the same or almost the same throughout its entire length, but a slight increase toward the distal end is not unusual, and a slight decrease distally is found in some Isocrinida. Also, proximal columnals may be enlarged and modified, especially in Apiocrinitidae, some Millericrinidae, and in *Bourgueticrinus*.

New columnals in the proximal end of the column may be identified by their very low height. They may all be introduced at the boundary between cup and the preceding uppermost columnal, which is generally considered the most common pattern of growth in crinoid columns, such as in Bathycrinidae, but it is uncertain how common it is among other Articulata. Differences in height of proximal columnals indicate other patterns in the succession of new columnals in several groups of Articulata.

ISOCRINIDA

In Isocrinida, the proximal part of the column with low columnals shows strong variation in height and generally in diameter as well. In this zone the new columnals are introduced. The largest columnals, provided with cirri, are called nodals or cirrinodals. Immediately below the cup only cirrinodals occur, generally, and then nodals separated by a single internodal succeeded by parts with an increasing number of internodals regularly alternating in size. This arrangement leads to the conclusion that all nodals are introduced at the boundary between cup and column, and the first and largest internodals introduced between two nodals are succeeded by several generations of internodals intercalated in alternation with previous columnals in the proximal zone until the full number of internodals is reached. This number may vary even within the single column, but variation within a species is often rather small. These proximal columnals display a considerable difference in height and commonly some variation in diameter according to succession of generations, but during further growth they gradually reach the same diameter and almost the same height except for the larger cirrinodals.

New proximal columnals are always strongly stellate or deeply pentalobate, with radial canals (radial pores) between. During growth, stellate columnals become pentagonal and pentalobate columnals become more rounded subpentalobate, in some specimens even circular. Also, different kinds of ornamentation such as ridges, tubercles, or spines are gradually formed during growth. The symplectial articular face of columnals in Isocrinida is characterized by five interradial petals (areolae) surrounded by crenulae. The number of crenulae increases during growth by the addition of new culminae in the interradial points. The change in outline of columnals from pentalobate to subcircular may influence the pattern of petals and crenulae so that petals grow wider and crenulae may be more or less restricted to the marginal zone. This is most distinct in *Isselicrinus,* where the pattern of small or proximal columnals is similar to *Isocrinus,* but during growth these are transformed to large and circular columnals similar to those of *Balanocrinus.* Many species of fossil Isocrinida are characterized by size, form, and ornamentation of the columnals, but the affinities of proximal columnals where these features are not yet developed are in most cases indeterminable.

The column of Isocrinida generally has almost the same diameter in its entire length, but a few species show a slightly increasing diameter toward the distal end. This is most distinct in *Proisocrinus,* but the same is presumably the case in the column of *Austinocrinus.* The articular face of columnals in *Austinocrinus* shows a petaloid central pattern of crenulae, which cover the entire articular face of proximal columnals, but apparently never increases in size. In the distal part of the column, formed when the crinoid was young, this petaloid pattern covers only a narrow central area of the articular face, but during growth, a marginal zone with radiating crenellae is formed outside the petaloid area, and this marginal zone increases in width toward the distal end.

In the very short stem of recent *Endoxocrinus maclearanus* the diameter does not change, and the entire column maintains its juvenile features with low, pentalobate, strongly alternating columnals and very short internodes.

In a few species early columnals do not keep up with diameter of later columnals during growth, so that diameter of the column decreases toward the distal end, and also other juvenile features may be maintained in the distal part of the column, such as alternating size, pentalobate outline, and rather short internodes. This is most evident in the very long stem or Jurassic *Seirocrinus,* but to some degree similar features or at least a distal decrease of diameter and of internodal length may occur in *Pentacrinites* and in young specimens of some recent *Annacrinus, Chladocrinus, Metacrinus,* and *Teliocrinus.* The reason this is not seen in most old specimens may well be that all Isocrinida from time to time break off distal parts of the column.

The cup and brachials of Isocrinida increase in diameter more than in height, and the radials constitute an increasing part of the cup and become more outwardly directed. The basals are rather variable in size, quite often meeting as a contiguous circlet on the surface of small specimens, but in larger specimens separated by the lower point of the radials.

MILLERICRINIDA

In Millericrinida the column is generally very long and columnals rather uniform. The diameter of the column may remain almost the same in its entire length or may increase a little toward the distal end. In all or most species a permanently uppermost columnal, the proximale, different in form and often rather large, is included as a five-sided plate in the dorsal side of the thecal structure inside the basal circlet. Introduction of new columnals during growth must either be restricted to juvenile specimens or take place in the upper part of the column below the proximale. These new, low columnals occurring in the proximal zone may be rather uniform or, in several species, distinctly alternating. So it seems that at least in some species small, new columnals are introduced in succeeding generations between previous columnals in a zone below the proximale. In other specimens no small, new columnals are seen, so it is quite possible that introduction of new columnals ceases early in the adult. In some species there are a few enlarged, proximal columnals below the cup and a zone with smaller columnals below this proximal cone. It is uncertain whether new columnals are introduced within the conical part or only below it, or possibly the conical part is not formed until formation of new columnals has ceased. Some variation in height of columnals, less frequent in diameter, may be maintained in more distal parts of the column but is generally inconspicuous. Form of columnals generally does not change much during growth, although in some species a nearly five-sided section may occur in the proximal part of the column.

The articular face of columnals in Millericrinida is more or less completely covered by radiating crenulae, the number of which increases during growth by division or by insertion of new culminae.

Some species generally referred to Apiocrinitidae are very similar to Millericrinidae and show similar indications of columnal growth with a zone of low columnals below a proximale.

In typical *Apiocrinites,* a conical, enlarged, uppermost part of the column forms a gradual transition to the large, wide cup, and the columnals within this cone are generally higher and more uniform than in the zone below, thus indicating that new columnals are probably not formed within the conical part.

Growth and development of cup and arms in Millericrinida have never been studied. In Apiocrinitidae the cup and conical uppermost part of the column seem to increase in width during growth. The relative size of basals to radials is rather variable, but no distinct change in this relation during growth has been observed.

The radial and proximal brachial articulations of Apiocrinitidae are more or less modified by reduction of the fulcral ridge and of ventral and interarticular fossae and by the greatly enlarged and modified dorsal ligament fossae, which may have a feeble ornament of radiating crenellae or irregular rugosity. These modifications, which may also be indicated in some Millericrinidae, are no doubt introduced or increased during growth, although this has not been studied in detail.

BOURGUETICRINIDA

Columnals of small Bourgueticrinida, including juvenile *Bourgueticrinus* and most species of Bathycrinidae, are very slender, rather high, reel shaped or hourglass shaped, and twisted with elliptical, synarthrial articulations and with a funnel-shaped axial canal enlarged toward the articular face. They may be similar in size or slowly increasing toward the distal end.

During growth the columnals increase in diameter more than in height, as shown in recent *Rhizocrinus,* and in large specimens (e.g., *Bourgueticrinus*), may become very stout, cylindrical to barrel shaped and with a narrow axial canal not widening toward the articular face.

New columnals are introduced at the proximal end of the column, presumably immediately below the cup, since height of proximal columnals gradually decreases toward the cup without alternation. These proximal columnals are low discs with smooth articular faces, but gradually change to the size, form and synarthrial articulation found in more distal columnals. The number of low disc-shaped proximal columnals has been used by GISLÉN (1938a) for discrimination between recent genera and species, but this must be taken with some reservation since the number decreases in adult specimens and large specimens devoid of any low disc-shaped proximal columnals may be found. This has been demonstrated by A. M. CLARK (1973b) for recent Phrynocrinidae. It is obvious that introduction of new columnals decreases and may stop in adult specimens.

Bourgueticrinus has a large, cylindrical, conical or pyriform proximale composed of a few fused columnals, generally without trace of sutures. The articular face of the proximale toward the free columnals may vary within a species, either smooth and flat synostosial with circular outline or synarthrial and with elliptical outline. It is presumed, therefore, that if new columnals are introduced in *Bourgueticrinus,* it must be below a proximale with smooth, circular articular face, and when introduction of new columnals has ceased, the articulation between proximale and column may become synarthrial as in more distal parts of the column. This interpretation is supported by the proximal decrease of columnal height in some specimens and not in others (RASMUSSEN, 1961, pl. 27, fig. 12 and 14; compare with pl. 24, fig. 16 and pl. 30, fig. 1).

A considerable variation is seen in the cup of *Bourgueticrinus,* but no ontogenetical change or correlation between size and form of cup has been observed except that the proximale, at least in some species, increases in size more than the radials and basals during growth.

A juvenile specimen of *Dunnicrinus* shows radials and first brachial to be as high as wide, while in larger specimens width is greater than height.

In *Democrinus* growth of the cup mainly affects the basal circlet, height increasing much more than width. Adult specimens thus attain a very high, slender, more cylindrical form. GISLÉN (1927) demonstrated change in growth lines in a recent *Democrinus* from a low, conical to a high, slender, almost cylindrical cup. Juvenile *Conocrinus* is very similar to *Democrinus,* but during growth the basals and radials fuse, and there is an excessive growth of basals and maybe radials, so that in large specimens no suture is seen, and the arms are separated by ventral projections from the cup. Also, the uppermost columnals may be overgrown by the basals.

Studies of recent *Rhizocrinus* show that height of cup increases during growth more than diameter, but in *Zeuctocrinus* it seems that diameter of cup and brachials increase more than height. Considering the few specimens of *Zeuctocrinus* known, and the large individual variation, this must be taken with some reservation, however.

Development of cup and arms in *Bathycrinus* has not been studied, but GISLÉN (1938a) suggested that the small species *B. gracilis* with its keeled arms may well be a juvenile specimen. Figures by CARPENTER (1888) of *B. aldrichianus* and its synonyms indicate almost no change of form during growth.

CYRTOCRINIDA

Cyrtocrinida live attached to a hard substrate by a short column or directly by the cup, including a nonarticulated dorsal element. Growth and change of the column are unknown.

Irregular or excessive growth, increasing compactness, and fusion of skeletal elements are found during growth of most Cyrtocrinida. In Sclerocrinidae, width and stoutness of the cup increase. In *Phyllocrinus,* and presumably in *Eugeniacrinites,* the ventral projections of the cup separating the arms increase in size during growth, and a study of growth lines in *Phyllocrinus* shows the cup changes from stellate to a more rounded outline. In *Hemicrinus* fusion of cup and proximal columnals take place, and compactness, irregularity, and possibly angular growth increase. Cups and dorsal elements generally fuse in the adults of Hemibrachiocrinidae. In *Cyathidium* small juvenile specimens are very low and shield shaped, but during growth the height is greatly increased and the form is variable, dependent on the space available. Thus, specimens from the Danian coral limestone at Fakse in Denmark may occur in narrow pipes from dissolved coral branches and are extremely slender, following the form of the pipe until they reach the surface of the limestone, where they expand as a cone, but other specimens found on the ceiling of larger crustacean burrows or on the underside of overhanging walls are wide, conical or columnar, and rather low. A juvenile specimen of recent *Holopus* is low and shield shaped, and similar juvenile specimens of recent *Cyathidium* have been recorded from the mid-Atlantic. More detailed studies of brachial growth and apparent change in arm division or fusion of primibrachials of recent *Holopus* and *Cyathidium* are needed.

COMATULIDA

Larval Comatulida are the only Articulata known to agree with Bourgueticrinida in having a column with synarthrial articulations, a radix, and no true cirri until late in the pentacrinid stage. The possibility that Bourgueticrinida may be derived in the early Cretaceous by proterogenesis from the Comatulida seems not to have been previously considered.

The juvenile centrodorsal of most comatulids is conical to hemispherical, and this form is maintained in many genera. In most comatulids, however, the diameter increases during growth more than the height, and the form develops from conical through hemispherical to truncated or discoidal, and by obliteration of apical cirri, and presumably resorption in the apical area, they may obtain a large, flat or concave, cirrus-free dorsal area. Further reduction of the centrodorsal to a low disc or plate with few or no cirri is found in some Comasteracea.

The centrodorsal cavity, lodging the chambered organ and its surrounding nerve capsule, is large in small and juvenile specimens, often more than half of centrodorsal diameter, but is reduced in relative size during growth, generally to about a third or a quarter of the centrodorsal diameter. Exceptions are found in the Atelecrinidae and some Antedonacea, especially Zenometrinae and Pentametrocrinidae.

The first five cirri of the larval centrodorsal are radially placed. New sockets grow out at the ventral edge of the centrodorsal and are commonly seen as a ridge on the ventral face. The sockets at the edge of the centrodorsal are at first very small, but rapidly increase to the same size as preceding sockets or larger, so that only one or two small, juvenile sockets may be seen in each radial side. Generally the first sockets are placed alternately right and left of the midradial line, thus forming ten vertical columns on the centrodorsal, two in each radial side. This form is maintained in the adult stage of many conical centrodorsals. In other species new sockets are intercalated during further growth also in the radial areas between the first ten columns, the number of columns in each radial side thus increasing to three or four, and the arrangement may become irregular. The first sockets near the dorsal pole are often obliterated during growth, so that in low, disc-shaped centrodorsals the sockets remaining form a single or a few irregular, marginal circles surrounding a large, cirrus-free dorsal area. Further reduction of sockets is found in some Comasteracea and Thiolliericrinidae.

The most enlightening studies of growth series of fossil comatulids have been described by Rasmussen (1961) for *Glenotremites,* and by Peck & Watkins (1972) for *Decameros.*

The cup and arms of comatulids follow a pattern of growth similar to that of the Isocrinida. Basals are well developed in the larval comatulids, but during growth radials increase in size and basals are rapidly reduced. Generally, the basals of adult comatulids are reduced to narrow rods exposed only in the interradial point, or in many groups are further reduced to a tiny, perforate, central plate, the rosette. Even in Atelecrinidae, where basals are large plates exposed on the surface, a reduction takes place during growth.

Radials and brachials increase in width more than in height, and many comatulids have a radial circlet that is exposed and contiguous on the surface of juvenile specimens, but with a very low, free surface in larger specimens, and often exposed only near the interradial edge.

UINTACRINIDA

In small specimens of *Marsupites,* the basals are the largest plates of the cup, but during growth the centrale and infrabasals increase to the same size as basals and radials or slightly larger, and the greatest diameter of the cup moves from the upper end of the basal circlet in small specimens to the lower part of basals or upper part of infrabasals in large specimens. In the basal plates the upper and lower angle and the height of the lateral edges decrease during growth. The surface ornament of ridges and granules on thecal plates, although extremely variable, seems to weaken during growth. It thus seems that both change in relative size of the plates and in ornament of these planktonic crinoids is opposite to that of most other crinoids.

In *Uintacrinus* thecal size cannot be determined exactly, the specimens generally being flattened by fossilization and the boundary between thecal structure and free arms being more or less indistinct. Still, it appears that width of theca increases more than height during growth. The number of interbrachial plates, although quite variable, increases during growth by intercalation of small, new plates at arbitrary points of the interbrachial areas. The presence or absence of infrabasals are not correlated with growth and size of the specimens. Growth of brachials follows the usual pattern, increasing in width more than in height, and the same change is found from distal to proximal part of an arm.

ROVEACRINIDA

Growth in Roveacrinida has not been studied, but it was demonstrated by RASMUSSEN (1961, 1971) that basals are overgrown by downward prolongations of the radials, and this undoubtedly took place during early growth. Also, spines, ridges, and flanges serving as floats in Roveacrinida increase during growth; thus, several species and subspecies of *Plotocrinus* and *Poecilocrinus* are interpreted by RASMUSSEN (1961) as probable synonyms based on different ontogenetical stages.

EVOLUTION

By GEORGES UBAGHS, N. GARY LANE, H. WIENBERG RASMUSSEN, and H. L. STRIMPLE

[Université de Liège; University of Indiana; Geologisk Museum, Universitet København; The University of Iowa]

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ORIGIN OF CRINOIDS

By GEORGES UBAGHS

INTRODUCTION

The earliest known undisputed crinoids are Early Ordovician in age. They are *Ramseyocrinus cambriensis* (HICKS) from the Lower Arenigian of Wales (BATES, 1968), *Aethocrinus moorei* UBAGHS from the Lower Arenigian or possibly the Upper Tremadocian of France (UBAGHS, 1969), *Hybocrinus* sp. and two undetermined inadunate species from near the Tremadoc-Arenig boundary of Utah (LANE, 1970), and *Proexenocrinus inyoensis* STRIMPLE & MCGINNIS, from the Al Rose Formation (upper Arenigian) of California (STRIMPLE & MCGINNIS, 1972). To these perhaps may be added *Perittocrinus radiatus* (BEYRICH) and *Tetracionocrinus transitor* (JAEKEL) of uncertain provenience but reputed to be from the Kunda Formation (Arenig-Llanvirn) of the Baltic regions (UBAGHS, 1971a). Among these identified Lower Ordovician species, one *(Aethocrinus moorei)* is a dicyclic inadunate, one *(Proexenocrinus inyoensis)* is a monocyclic camerate, and all the others are monocyclic inadunates belonging to two or possibly three different orders. Such considerable taxonomic diversity indicates that crinoid ancestry must extend far back in pre-Ordovician time—a conclusion fully supported by the fact that the just-mentioned forms already have all the distinguishing features of normal crinoids.

The brachiole-bearing echinoderms—particularly the Cambrian eocrinoids—often have been suggested as being the ancestral stock of the crinoids. This seems quite improbable, considering the differences that exist between a brachiole and a crinoid arm. A brachiole is a purely exothecal appendage that has no direct connection with the interior of the theca and, consequently, could not have carried extensions from the main coelomic cavity, the hemal, genital, and entoneural systems. An arm or brachium of a crinoid is an evagination of the central body mass, carrying extensions from the various coeloms, as well as from the hemal, genital and entoneural systems. Arms and brachioles, therefore, are structures of a different nature and are not homologous.

Unlike crinoids, intimate correlation between brachia and theca does not exist in the Paracrinoidea, which have asymmetrical food-gathering appendages, provided with an ambulacral tract on one side and a row of uniserial side branches along the other side. A canal, connecting with the thecal cavity at its proximal end, runs internally through the main appendages, but does not penetrate into the branches (Parsley & Mintz, 1975); it is unlikely that such a canal could have contained the same extensions (certainly lacking in the side branches) as those present in the arms of crinoids. Here again fundamental differences appear to exist between crinoid arms and paracrinoid armlike processes.

If the presence of true brachia seems to be very distinctive of the crinoids, other features serve also to distinguish them from the brachiole-bearing and paracrinoid classes. Examples of these are: 1) the clear division of the theca into an aboral cup and an adoral tegmen; 2) the invariable presence of a radial plate at the origin of each ray; 3) the mainly radial growth pattern, which finds its expression in the powerful development of the arms, directed away from the theca; 4) the fact that the aboral nervous system is the main motor system; 5) the occurrence of the gonads outside the theca, in the arms or pinnules (at least in recent members). Because of these many and considerable differences, derivation of the crinoids from the brachiole-bearing and paracrinoid echinoderms may be regarded as very unlikely.

However, certain similarities in the arrangement of thecal plates in some Eocrinoidea and Rhombifera, the presence of respiratory structures comparable to epispires or pectinirhombs in some early crinoids, and continuation of the ambulacral tracts over the thecal plates in the hybocrinid inadunate *Hybocystites* have led some authors to look for the origin of crinoids among Rhombifera (Yakovlev, 1918, 1927; Moore, 1954), hypothetical minute Cystoidea (Kirk, 1911), Eocrinoidea (Fell, 1962, 1963b; Jaekel, 1918; Moore, 1954; Nichols, 1969), or proto-blastoids (Bather, 1900a). But such analogies are no proof of close affinities. They may merely reflect the fundamental unity of the stem-bearing echinoderms, and they may have arisen independently in each class. After all, the crinoids and the brachiole-bearing echinoderms must have met the same sort of problems, having the same attached mode of life and probably highly similar food-catching methods.

Some earliest known crinoids have features judged to be very primitive, and thence possibly significant for the problem of the origin of the class. These features are: 1) the merging of the calyx into the column and of the thecal cavity into the wide lumen of the stem (e.g., *Aethocrinus, Ramseyocrinus*); 2) the partition of the column into pentameres, accompanied by irregular interlocking of the columnal plates and passage to a distal mass of tiny skeletal elements (e.g., *Aethocrinus*); 3) the extension of this columnal interlocking into the theca, the proximal circlets of which are not arranged in quite regular circlets (e.g., *Aethocrinus*); and 4) the occurrence of supplementary plates (anals, interbrachials, accessory plates) in the cup (e.g., *Aethocrinus, Perittocrinus, Tetracionocrinus*). These characters suggest derivation of the crinoids from an elongate ancestor, provided with an irregular many-plated calyx that graded downward into an irregularly plated hollow holdfast and extended upward into radial outgrowths of the central body mass.

Similar views were first advocated by Jaekel (1918), who stated that in the beginning there was no simplicity, but lack of regularity. He thought that originally the stem and root were the rear extension of the body, and that some forms like the Middle Cambrian eocrinoid *Acanthocystites* with its many and irregularly arranged plates might well represent the ancestral type of the crinoids. Consequently he strongly opposed the opinion, generally accepted in his time, that the crinoids originated from small and simple forms, the Inadunata Larviformia of Wachsmuth &

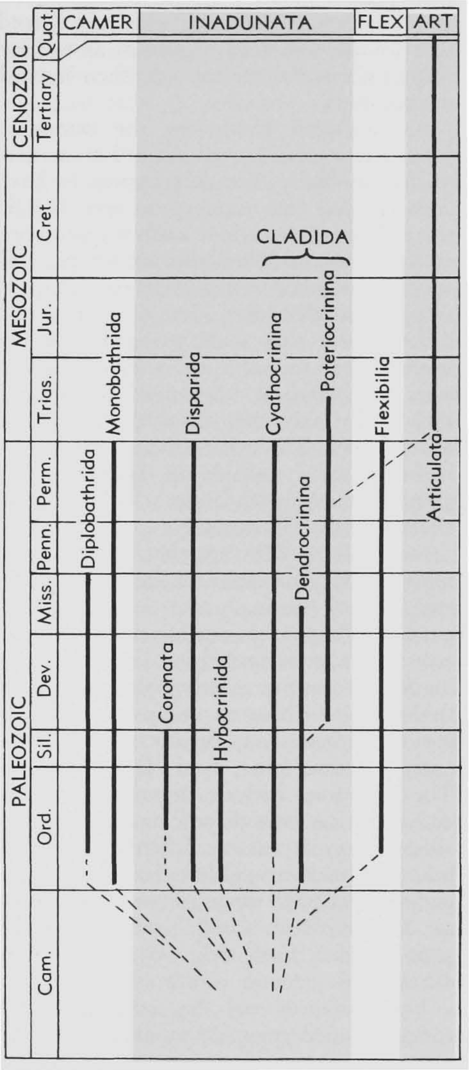

FIG. 207. Stratigraphical distribution and presumed phylogenetic relationships of major groups of crinoids (Ubaghs, n).

SPRINGER (1885), or passed through a larviform stage, as imagined by BATHER (1900a). The discovery of new Lower Ordovician crinoids and revision of those already known have brought partial support to JAEKEL's judgment, except that the eocrinoids or other brachiole-bearing pelmatozoans are probably not the forerunners of the crinoids.

As yet no Cambrian echinoderm has been recorded that could be accepted with certainty as the ancestor of the crinoids. However, in this connection one form deserves much attention. It is *Echmatocrinus brachiatus* SPRINKLE, a very primitive attached echinoderm from the Middle Cambrian (Burgess Shale) of western Canada (SPRINKLE, 1973a). With its stalk barely differentiated from the theca, and its many irregularly arranged plates, it does recall some very archaic eocrinoids. It has armlike uniserial processes with apparently soft appendages (? tube feet, ? uncalcified armlets) given off alternately (?) left and right. Because of these processes, it was placed by SPRINKLE in an indeterminate crinoid subclass and order, though in most other respects it does not fit the definition of a crinoid. Besides, it is not certain that its armlike processes are really homologous with the crinoid brachia, that is to say, that they are outgrowths from the central body mass. At any rate, the regular arrangement of the plates of these processes contrasts with the poorly organized plating of the theca. Even if *Echmatocrinus* seems to be separated from any unquestioned crinoid by a wide gap, at least it furnishes evidence that pelmatozoan echinoderms provided with arms similar in outer appearance to those of crinoids were living in the Cambrian seas. From such forms the crinoids could have arisen.[1]

ORIGIN OF MAJOR GROUPS

From the outset of their known geological record the Camerata and the Inadunata, which seemingly represent the two main branches of the Crinoidea, were already clearly differentiated (Fig. 207). In many respects, the Camerata stand apart from the other crinoids. They are morphologically fairly distinct, and never gave rise to any other subclass. The Inadunata, on the other hand, are the basic stock from which both the Flexibilia and the Articulata proceeded. There seems, therefore, to be some justification in the classification advocated by JAEKEL (1894, 1901, 1918), accord-

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[1] In the systematic part of this *Treatise*, *Echmatocrinus* is considered by SPRINKLE and MOORE to represent a new order Echmatocrinida and new subclass Echmatocrinea, both by SPRINKLE and MOORE (see p. *T*405).—CURT TEICHERT.

ing to whom the Camerata, which he named Cladocrinoidea, should be separated from the rest, named Pentacrinoidea.

It has sometimes been suggested that the Camerata and the Inadunata could have originated separately, and also that each of them was polyphyletic (Brower, 1969). Jaekel (1894, 1902, 1918) went even so far as to suppose that the arms, pinnules, and most thecal plates of the Camerata were different in origin and morphological significance from the corresponding plates and structures of the other crinoids. Such views do not appear consistent with the fact that all crinoids share the same basic organization and are composed of highly similar elements, which are arranged in the same manner and obviously had the same functions. So many and far-reaching resemblances can hardly be explained as the result of convergent evolution. Besides, some early inadunates (e.g., *Aethocrinus, Cupulocrinus, Ottawacrinus*) have fixed brachials and interbrachials like camerates, a condition that rather favors judgment that both Inadunata and Camerata are derived from a common source.

The division of the Crinoidea into two subclasses, the Monocyclica and the Dicyclica, as proposed by Bather (1899b, 1900a), would signify at least an early dichotomous branching of the class and a large number of parallel modifications, since each main branch would have produced a camerate and an inadunate type of theca and arms. It is true that the structure of the base has been a fundamental, highly distinctive and generally constant feature of the major groups of crinoids throughout their history. Nevertheless, the monocyclic camerates have more characters in common with the dicyclic camerates than with the monocyclic inadunates, and the same is true for the monocyclic and dicyclic inadunates. Among early camerates, *Reteocrinus,* which is dicyclic, and *Xenocrinus,* which is monocyclic, are so essentially alike, except for characters of the base, that it is improbable that they could have been derived from widely separated ancestors. Similarly among inadunates, the dicyclic *Merocrinus* is practically like the monocyclic *Iocrinus* but for the presence of infrabasals. Such examples tend to indicate that the differentiation of the monocyclic and dicyclic types of base took place separately within the camerates and the inadunates though it must be agreed that we are completely ignorant as to how they originated and what were their mutual relationships.

As described previously, the camerates form a group fairly well defined on a morphological basis. Yet they appear to have been divided into monocyclic and dicyclic stocks from their earliest known appearance in Lower or Middle Ordovician time, and we do not know which of these stocks is ancestral to the other. But once they had differentiated they seem to have kept the fundamental monocyclic or dicyclic character of their base unchanged throughout their entire existence, allowing recognition of two orders within the subclass; the Diplobathrida, which include all dicyclic camerates, and the Monobathrida, which comprise all monocyclic camerates.

Such sharp cleavage into two main branches does not seem to characterize the evolution of the inadunate crinoids. Comparison of their representatives rather indicates either an early division into six clearly marked groups, or a polyphyletic origin of the subclass. These six groups are the Disparida, Hybocrinida, Perittocrinacea, Coronata, Cyathocrinina, and Dendrocrinina. The first four include monocyclic inadunates, the last two, dicyclic inadunates. Inasmuch as important differences existed between them throughout their whole geological record and as no intermediate forms are known which could have reduced the gaps between them, their origin and interrelationships remain problematical.

The Disparida are the most important and diversified group of monocyclic inadunates. They largely correspond to the Inadunata Larviformia of Wachsmuth & Springer (1885)—a term referring to their generally small size and simple structure, and to the belief formerly held that they were the most primitive crinoids and that they represented the ancestral type of the class. In fact, they disclose evolutionary trends very different from those shown by the other crinoids. Thus they show a common tendency to develop bilateral symmetries in planes different from the so-called crinoidal plane *(A-CD)* prevalent in most other crinoids; they commonly have compound radial plates in rays other than the *C* ray; their proximal *C*-ray plate never takes the appearance or function of a radianal; the median line of ossicles supporting the anal tube is ordinarily so intimately related to the adjacent *C* ray that it may replace it or its proximal left ramus. Such highly distinctive features probably evolved within the stock and were not inherited from an ancestor common to all crinoids. Apparently the disparid inadunates form a separate group, which became extinct in Upper Permian time, and did not give rise to any other group.

Hybocystites and other genera now included in the order Hybocrinida were thought by Bather (1900a) as possibly derived from early forms of Protoblastoidea. Consequently, and because of their simple structure, they were placed at the starting point of his classification. As clearly shown, however, by Jaekel (1902, 1918), and largely confirmed by Regnéll (1948a), the peculiarities of these genera and similarities with blastoids are purely secondary. They resulted from the progressive (or degenerative) evolution from an ordinary five-rayed crinoid, and were largely brought about through the progressive reduction, and eventually the loss, of the arms and replacement of these processes by recumbent ambulacral tracts. The hybocrinid inadunates differ markedly from the disparid inadunates by lack of compound radials, and presence of a radianal situated obliquely below the *C* radial and that supports the anal *X*. On the other hand, in such other features as the shape of the cup, the narrowness of the arm facets, and absence of an anal tube, they resemble primitive Cyathocrinina (e.g., Palaeocrinidae), except that they are monocyclic instead of being dicyclic. These similarities are not sufficient, however, to indicate any close relationships between these crinoids. The hybocrinids are among the earliest recorded crinoids. So far as we know, they disappeared in Late Ordovician time, without giving rise to any other group.

The Perittocrinacea are represented by two monotypic genera of probably Early Ordovician age. Like the Disparida and Hybocrinida, they are monocyclic inadunates. They differ from both in having numerous triangular accessory plates and only four basals. Also, they are clearly separated from the Disparida by the presence of a radianal and lack of compound radials. They are less distinct from the Hybocrinida, for, like them, they have simple radials, a typical radianal and anal *X,* a *C* radial smaller than the other four and located above their level, and relatively narrow and rounded arm facets. In other words, the pattern of the main cup plates in Perittocrinacea is similar to that in Hybocrinida and in primitive Cyathocrinina. Of course, such resemblances may result from an evolutionary convergence, but they may also indicate inheritance from a common ancestry (Ubaghs, 1971a). On the whole, however, their peculiarities suggest tendencies of their own, so that they appear to form a rather aberrant offshoot of the inadunate stock, which apparently left no descendants. They certainly are not transitional between the camerates and the other crinoids, as supposed by Jaekel (1902, 1918).

Perhaps still more puzzling are the few Ordovician and Silurian genera known as the Coronata. Because they look very much like blastoids in general appearance and arrangement of thecal plates, they have been considered as such by some workers, including Jaekel (1918, 1927), Wanner (1924), and Regnéll (1945). However, they lack lancet plates, hydrospires, gonopore and brachioles—all features typical for blastoids. On the other hand, they have biserial arms and armlets comparable to those of crinoids (Springer, 1926a; Bather, 1900a; Fay, 1961). For that reason they were accepted as crinoids first by Wachsmuth & Springer (1885), and then by Bather (1900a), Springer (1926a), Fay (1961), and others. They certainly are quite different from any typical crinoid. They may be considered, at least for the time being, as representing a particular evolutionary development from an inadunate stock, though their origin and relationships remain equally enigmatical.

The Cyathocrinina and the Dendrocrinina comprise the earliest known cladid, or dicyclic, inadunates. The former first appear in the Middle Ordovician, the latter in the Lower Ordovician. Both were clearly differentiated from the outset and were subject to an early diversification—two conditions that point to a long previous history. There is no evidence at present for a common origin or derivation of one group from the other. Relationship with monocyclic inadunates is also obscure. As stated above, the thecal pattern of some Ordovician Cyathocrinina resembles that of the Hybocrinida, except for characters of the base. But such similarities are no proof of phylogenetic relationships. As to the Dendrocrinina, they display a number of features and evolutionary tendencies quite different from those exhibited by the monocyclic inadunates. If one compares, for instance, their earliest known representatives, the Lower Ordovician *Aethocrinus moorei,* with the disparid *Ramseyocrinus cambriensis* of about the same age, one is struck by the many differences which exist between them. Most of their characters are contrasting and certainly none indicates unquestionable origination from a common source.

Although the Cyathocrinina appear not to have given rise to any other group, the Dendrocrinina are reputed to include the direct ancestors of the Poteriocrinina and the Flexibilia. The former are the most advanced dicyclic inadunates. They probably arose during Devonian time from such dendrocrinine families as the Botryocrinidae or the Mastigocrinidae, which, in several respects, approximate primitive Poteriocrinina very closely. The passage from one type to the other assuredly was quite progressive and possibly repeated several times. It was especially characterized by the development of the pinnulate condition from a strongly heterotomous condition, the appearance of muscular articulation between the radial and first primibrach, and the more and more prevailing occurrence of three (or more) anal plates in the cup.

The earliest known representatives of the Flexibilia are two species of the genus *Protaxocrinus* from the lower Trenton rocks (Middle Ordovician) of Canada. They closely resemble species of the dendrocrinine genus *Cupulocrinus,* which occur in the same beds, in that they have erect infrabasals, a radianal in primitive position, a series of anal plates bordered by finely plated integument, interbrachial areas largely occupied by numerous small and irregular plates, arcuate brachial sutures, and a pliant tegmen. The main differences lie in number of infrabasals, number and distribution of primibrachs, and presence of an anal sac. *Protaxocrinus* has three unequal infrabasals, two primibrachs per ray, and no distinct anal sac. *Cupulocrinus* possesses five equal infrabasals, three or more primibrachs, which are unequally distributed among the rays, and a prominent anal sac. These divergences are not so important as to prevent accepted judgment that both genera derive from a common Ordovician or slightly pre-Ordovician ancestor.

The exact origin of the Articulata is still obscure. Their earliest known representatives are Middle Triassic in age. They belong to three distinct families (Dadocrinidae, Holocrinidae, and Roveacrinidae) that cannot be derived with certainty from any known Paleozoic genera. Yet the poteriocrinine inadunates may display features or evolutionary tendencies which approach and in some cases reach the articulate condition. Thus, all poteriocrinid inadunates are dicyclic (all articulates are dicyclic or cryptodicyclic), and several have the infrabasals reduced in number and size. Some may have all anal plates eliminated from the cup, as is invariably the case in articulates. Their arms are pinnulate like those of articulates, and free above the radials, as in most articulates. Many of them have uniserial arms, as do all articulates. Typically, their radial facets and proximal arm plates bear marks of well-developed muscular articulations similar to those of articulates. These articulations may be oblique and perforate, and distributed in exactly the same manner as those of the living comatulids (LANE & MACURDA, 1975). Finally, the mouth and the ambulacral furrows were probably exposed in some advanced poteriocrinine members such as the Encrinidae, which have lost the large anal sac so typical of most poteriocrinine inadunates and acquired a flattened tegmen quite similar to the disc of articulates. For these reasons it is generally agreed that the Poteriocrinina comprise the stock from which the Articulata originated.

There is no evidence that the Articulata or even some of the members of the subclass descended from the Flexibilia. It is true that the Flexibilia also had a pliant tegmen, with exposed mouth and food grooves, and that certain Permian forms, such as *Palaeoholopus* and *Permobrachypus,* were outwardly remarkably like the articulate Holopodidae. But the Flexibilia as a whole are characterized by a combination of structural peculiarities very different from those of the Articulata. They never have pinnulate arms, and their arm-branching never really tended toward the pinnulate condition. Their radial facets and brachial articulations do not resemble the muscular articulations of the recent crinoids, but are of a rather special type of movable ligamentary juncture. Peculiar also are the articulations between the calyx plates. The brachials usually have undulate sutures, resulting from the fact that the lower edge of each has a projection that fits into a depression of the plate below. Almost invariably there are three infrabasals, two large plates and a small one, which always occur in the *C* radius, whereas in articulates the infrabasals generally number five. In short, the Flexibilia practically do not show any feature that could suggest an articulate descent. They rather appear as a specialized group that became extinct in Permian time.

Even if all the Articulata were derived from the Poteriocrinina, as indicated by their essential unity of structure, they did not necessarily originate from the same poteriocrinine ancestor. Their early diversification and large diversity speak rather in favor of a moderate polyphyletism. In any case, the origin and affinity of their various orders remain largely conjectural, if not entirely unknown. This problem will be discussed in the chapter devoted to the phylogeny of these crinoids.

EVOLUTION OF CAMERATE CRINOIDS

By Georges Ubaghs

As for the other crinoid subclasses, the phylogeny of the Camerata is essentially based on comparative morphology of genera. Practically no lines of ancestry and descent are known at the species level. The most comprehensive treatments of the evolutionary development of these crinoids are purely qualitative (Wachsmuth & Springer, 1897; Bather, 1900a; Jaekel, 1918; Moore & Laudon, 1943a; Ubaghs, 1953). Few quantitative phyletic studies have been undertaken, and they all concern restricted groups (Brower, 1973, 1974a; Lane, 1963b; Macurda, 1974). For the present, the study of the phylogeny of Camerata appears very subjective and still in its infancy.

The earliest known camerate is *Proexenocrinus inyoensis* Strimple & McGinnis from the Lower Ordovician Al Rose Formation of California. It was classified as belonging to the family Xenocrinidae by Strimple and McGinnis (1972). Uncertainty concerning the structure of the proximal part of its calyx up to the radial circlet makes its systematic position somewhat uncertain, however. Nevertheless, it demonstrates that the Camerata had already acquired all their distinguishing features by Early Ordovician time, suggesting a more remote, probably Cambrian, origin for these crinoids.

This premise is strongly supported by the early diversification of the subclass. At least six distinct camerate families occurred in the Middle Ordovician, to which four or possibly five more were added in the Late Ordovician. At the end of this period, all orders and suborders, and no less than six superfamilies of the twelve recognized in this *Treatise* were differentiated.

Which of the camerate orders and suborders are the most primitive is unknown, for all of them were clearly separated since their first appearance in the geological record. In particular there is no convincing evidence suggesting derivation of the monocyclic camerates from dicyclic camerates, or descent of the Glyptocrinina from the Compsocrinina. Since all these major groups are distinguished throughout their history by the structure of the proximal part of the theca, it appears that when once evolved this structure stabilized (except for minor changes), so that the modifications occurring afterwards mainly affected the distal part of the theca and (or) the free arms, more rarely the column.

EVOLUTIONARY TRENDS IN CAMERATES

The geological succession of the main calyx types (as recognized by Brower, 1973) and the comparison of the earliest known stages with more advanced members in some lineages allow recognition of some definite trends in the evolutionary development of the camerates. Some of these trends were restricted to a few genera, others were widespread, but none seem to have involved the whole subclass. They probably affected the young crinoids at various growth stages and caused divergences during the later ontogeny (Brower, 1973).

EVOLUTION OF THE CALYX

One of the most remarkable trends was the elimination of fixed brachials, interbrachials, and anal plates from the calyx, so that eventually the arms became entirely free. This condition is partly filled by the Gazacrinidae, Carpocrinidae, Coelocrinidae, Eucalyptocrinitidae, Stelidiocrinidae, Patelliocrinidae, some Dimerocrinitidae, and a few Hapalocrinidae; members of these families have few fixed brachials and few but large interbrachials. The trend is still more advanced in the Nyctocrinidae, Hexacrinitacea, and Platycrinitacea, which generally have no brachials and no interbrachials incorporated in the calyx. The genera included in the two last superfamilies were referred by Bather (1899b, 1900a) to a monocyclic order, the Adunata, which he considered to have been derived from the Inadunata and modified after the fashion of the Camerata. This view is not accepted in the present *Treatise*. The earliest known representatives of these so-called Adunata already had the arms fully pinnulated, that is to say, long before Inadunata acquired pinnules. Their many-plated tegmen generally was of a camerate type. The Silurian Marsupiocrinidae and some Hexacrinitidae and Hapalocrinidae had fixed brachials and large interbrachials. These crinoids, therefore, are not morphologically distinct from typical Camerata. They are regarded here as highly specialized members of this subclass, which became superficially similar to some Inadunata.

In camerate crinoids, as in other animal groups, the different parts of the body evolved more or less independently and at various rates, so that many genera share primitive and advanced features. For instance, *Melocrinites* combines an archaic type of calyx with a most specialized kind of arms, as do also *Thamnocrinus, Manillocrinus,* and several other genera.

The main changes observed in the base of the calyx are related to size, shape, and number of component elements, and already have been discussed in the chapter devoted to the skeletal morphology of the crinoids (p. *T*107). Here it will be merely noted that primitively the base was probably erect and composed of one or two circlets of five elements each. Bases flattened or concave, or with proximal circlet reduced and concealed by stem, or having less than five infrabasals or five basals are judged to be specialized. All or at least some of these modifications may have benefited the crinoid. Thus the reduction of the number of plates in the proximal circlet probably increased the mechanical strength of the calyx, better protected the chambered organ, and simplified the problem of integration and coordination of calyx growth (Brower, 1973). The number of basals—the number of infrabasals less so—is an important diagnostic feature on the family or even the suprafamilial level. It was generally established very early and commonly persisted throughout the history of the families. For instance, the Periechocrinacea and the Carpocrinacea, which flourished abundantly from the Late Silurian to the Early Carboniferous, invariably have three basals, which most generally are equal. All the Melocrinitacea have four basals. Two is the characteristic number of these plates for the Dichocrinidae and Acrocrinidae, and other similar examples could be given.

The fixed ray plates are usually more numerous in Ordovician and Early Silurian genera than in later forms. This suggests, as seen above, a rather general tendency toward reduction of the number of these plates up to their complete elimination (except radials) from the calyx—a stage represented by the dicyclic Nyctocrinidae and the most advanced representatives of the monocyclic Hexacrinitacea and Platycrinitacea. In some lineages, however, an opposite trend seems to be recognizable. The Polypeltidae and some genera like *Scyphocrinites, Strotocrinus,* and *Teleiocrinus* have, for example, such a high number of fixed ray plates there is little doubt that in these crinoids a progressive incorporation of the arms into the calyx took place.

Another feature of the fixed part of the ray which tends to disappear with time is the presence of a median ridge on each ray of the calyx. These ridges, strongly marked in various Ordovician genera, were ordinarily replaced by faint ridges in later forms, and ultimately vanished completely.

Accompanying these changes, modifications in number, size, and arrangement of interbrachials occurred in many lineages. Generally, in the Ordovician genera, they were numerous, small or moderately large, and more or less irregular. Also, they were continuous with the interambulacrals. The Reteocrinidae, Archaeocrinidae, Xenocrinidae, and Glyptocrinidae are good examples of this condition, which is regarded as primitive. In most later camerates, the interbrachials tended to diminish in number, to increase in size, to become more definitely arranged, and, in some lineages, to be separated from the tegminal plates by fixed brachials and pinnulars in lateral contact. It must be noted, however, that by the Middle Ordovician the interbrachials were lacking in the Cleiocrinidae and separated from the interambulacrals by fixed ray plates in the Anthracocrinidae. On the other hand, the extremely numerous, small and irregular interbrachials of the Ordovician genera *Reteocrinus* and *Xenocrinus* probably represent an advanced rather than a primitive evolutionary character. Indeed, while the rays and interrays of *Xenocrinus* (and doubtless of *Reteocrinus*) expanded continuously during ontogeny, the interbrachials showed small growth rates and a complex intercalatory type of development. This mode of growth contrasted with that observed in other camerates, such as the Glyptocrinidae. In those, the growth rates for dimensions of the interbrachials were large relative to size, and all new interbrachials developed at distal borders of the interbrachial areas. Multivariate, statistical information about phylogeny suggest this condition to be more primitive than that shown by *Xenocrinus* and *Reteocrinus* (Brower, 1974a).

A consequence of the progressive enlargement of the interprimibrach in several lineages consists of a change in the shape of the adjacent primibrachs. In primitive genera or in lineages which retain a primitive type of calyx, as in the Melocrinitidae or the Periechocrinidae, the interprimibrachs are ordinarily small or of moderate size, and the first and second primibrach are, respectively, hexagonal and heptagonal in outline. But in more advanced or specialized forms (e.g., the Paragaricocrinidae, Batocrinidae or Eucalyptocrinitidae, which have well-developed interprimibrachs), the first primibrach becomes quadrangular and the primaxil usually pentagonal in outer appearance. This apparently unimportant difference serves as a significant diagnostic feature for separating most Periechocrinacea from the Carpocrinacea.

In dicyclic Rhodocrinitacea, the proximal interprimibrachs lie between adjacent radials and rest on basals. The basic change to the organization seen in the Dimerocrinitacea seems to be the displacement of these first interprimibrachs to a position above the radial circlet. Whether such displacement really took place in evolution remains conjectural. It must be noted, however, that both types of structures occur in some specimens of *Dimerocrinites icosidactylus, Lyriocrinus melissa, L. dactylus,* and *Griphocrinus nodulosus.* Also, in the ontogeny of some recent comatulids, interradial plates having the same location as the proximal interray plates of camerates develop between adjacent radials and then migrate to above the radial circlet. Possibly a similar process occurred in the evolution of the dimerocrinitid from the rhodocrinitid camerates. Such elimination of plates from the radial circlet was perhaps advantageous, for it must have increased the strength of the proximal part of the radial circlet (Brower, 1973).

The structure of the posterior *(CD)* interray of the calyx seems to have evolved in many lineages. Primitively this interray was wider than others, contained more plates, and was commonly marked by a prominent sagittal and generally ridged series of extra plates. Subsequently, this ridge disappeared, the plates were reduced in number, and the posterior interray became similar to the other interrays. As a consequence, an almost perfect pentamerous symmetry was acquired by the calyx, contrasting with the strongly marked bilateral symmetry of many early forms. The similarity of the median anal series of plates in some archaic camerates with a series of fixed brachials has led some authors (Moore & Laudon, 1943a; Spreng & Parks, 1953) to assume that the anal series might have had its origin in a sixth ray. Until now no fossil has been recorded to support this hypothesis. Neither do we have proof that the primanal migrated effectively from a primitive position between *C* and *D* radials to a more advanced position above these plates, or, on the contrary, was secondarily interpolated into the radial circlet. Both explanations have been advocated, but no definitive solution to this problem has ever been found.

EVOLUTION OF THE TEGMEN

The phylogeny of the tegmen of camerate crinoids has not been studied in detail. It appears that in many Ordovician genera judged to be primitive in many respects the tegmen consists of an incompetent and many-plated structure, in which the orals, ambulacrals, and interambulacrals are not clearly differentiated. Rather surprisingly, in many lineages, it is in advanced members that these plates become really distinct. But an opposite tendency may also occur. For instance, in the Platycrinitidae, there seems to have been a definite trend toward loss of differentiation of orals and ambulacrals through incorporation of a large number of interambulacrals. On the whole, the tegmen of camerates has been modified in various ways, forming, for instance, protective devices for the free arms, such as grooves, niches, bladelike processes, wing plates, and gigantic spines, or being provided with an anal tube that in some species was elevated well above the summit of the arms. Most of these changes developed at the generic level, probably as a response to some particular need.

EVOLUTION OF THE FREE ARMS

During and after evolution of the main calyx structures, the arms generally evolved toward greater complexity and efficiency. Several trends may be recognized in their evolution. One of them consists of the change from a uniserial to a biserial arrangement of the arm plates. Species with uniserial free arms were prevalent in the Ordovician, progressively less frequent in the Silurian, and rare after the Early Devonian. Members of some lineages went a step further toward the biserial condition; they acquired compound brachials that carried one or more pinnules on each side of every brachial. These changes are interpreted as adaptative, for they allowed a considerable increase in the number of pinnules and thence in the food-gathering capacity of the brachial system.

Increase in the number of free arms is another dominant trend in many camerate lineages. All camerates, including the earliest known, had two arms per ray at least. It is true that a few camerate genera have only one arm per ray, but this is because the two arms of each ray fused together (as in *Melocrinites*) or developed so unequally that one of them took the appearance of a mere armlet (as in *Cytidocrinus*). Two arms per ray is certainly a primitive stage in camerates, which persisted in some lineages (e.g., *Scyphocrinites, Stelidiocrinus, Patelliocrinus*) but generally was replaced by a more advanced one characterized by four or six arms per ray, more rarely three, five, seven or even more (large specimens of *Strotocrinus* may have up to 30 arms per ray). This increase in number of free arms resulted from either the transformation of a proximal pinnule into a pinnulate arm or the incorporation of one or several bifurcations of arms into the calyx. An example of the first case seems to be furnished by the transition from the Middle Ordovician *Pycnocrinus ornatus,* with two arms per ray, to the Late Ordovician

Glyptocrinus decadactylus, with four arms per ray (Brower, 1973). The second case may be illustrated by batocrinid and actinocrinitid genera which have many brachitaxes incorporated in the calyx and consequently many free arms given off by the theca.

Primitively the free arms were probably undivided. At least they are so in several archaic genera, such as *Cleiocrinus, Rhaphanocrinus, Proexenocrinus, Xenocrinus,* and *Compsocrinus.* The next step was marked by isotomous bifurcations repeated at long intervals. Examples of this stage include Ordovician genera like *Archaeocrinus* or *Canistrocrinus.* Subsequently other types of arm branching (heterotomy, endotomy, exotomy) evolved in various lineages, forming diagnostic features for many genera and sometimes species. At the same time there was a widespread tendency to concentrate ray division within the calyx or immediately above it—a probably advantageous modification, for any accidental loss of an arm involved only a small part of the whole system. This tendency was frequently accompanied by the grouping of the arms, thus producing lobation of the calyx at arm regions (as in Actinocrinitidae or Platycrinitidae), or was manifested by their arrangement in a continuous belt around the calyx (as in many Batocrinidae).

A special type of arm structure peculiar to camerate crinoids resulted from the hypertrophy and very unequal, heterotomous branching of arms. It arose independently in various families (i.e., Rhodocrinitidae, Lampterocrinidae, Actinocrinitidae, Melocrinitidae, Polypeltidae, and Platycrinitidae), and consisted of the formation of one or two powerful arm trunks in each ray. These trunks carried relatively slender ramuli that were pinnulate, whereas the trunks themselves usually (if not invariably) lacked pinnules. In advanced melocrinitids, the two adradial arms of each ray coalesced and produced a compound ramule-bearing trunk. These structures probably originated in response to a need for enlargement and strengthening of the food-gathering apparatus.

Another specialization which appeared independently in several camerate families (i.e., Rhodocrinitidae, Carpocrinidae, Dichocrinidae, Aorocrinidae, Patelliocrinidae, and Platycrinitidae), but very rarely in Inadunata (and never in Flexibilia and Articulata), lies in the downward growth of the arms. That in such cases the pendent or recumbent attitude was permanent and not accidental is shown by its association with various structural devices which prohibited, or at least hindered, any motion in upward direction. This curious peculiarity developed at the specific level, except in the desmidocrinid genus *Barrandeocrinus,* the whole crown of which is transformed in connection with a fixed recumbent position of the arms.

These were the dominant trends that affected the evolutionary development of the camerate crinoids. Now, guided by this knowledge, we may endeavor to trace the phylogeny of this subclass, taking the Diplobathrida first and then the Monobathrida (Fig. 208).

PHYLOGENY OF CAMERATES

DIPLOBATHRIDA

Reteocrinus has been commonly accepted as the most primitive known camerate crinoid (Moore & Laudon, 1943), and certainly it has many archaic features. However, as explained above (p. *T*283), its pliant interbrachial areas studded with numerous small and irregular plates seem to represent a specialized and advanced feature, suggesting that this genus derived from a form with larger and more regular interbrachials. Such an ancestor may perhaps be visualized as an archaeocrinid which, like *Rhaphanocrinus,* would have an erect calyx, prominent ray-ridges, moderately large and regular interbrachials, a primanal supporting an anal median series of plates, and uniserial unbranched free arms, but, in contrast to *Rhaphanocrinus,* should be provided with infrabasals visible from the side. These characters are widespread among Ordovician genera belonging to various lineages, and consequently can be considered as primitive.

Rhaphanocrinus is a member of a widely diversified assemblage of dicyclic camerates, all of which have the radials separated by interbrachials in contact with basals, and are conveniently grouped in the superfamily

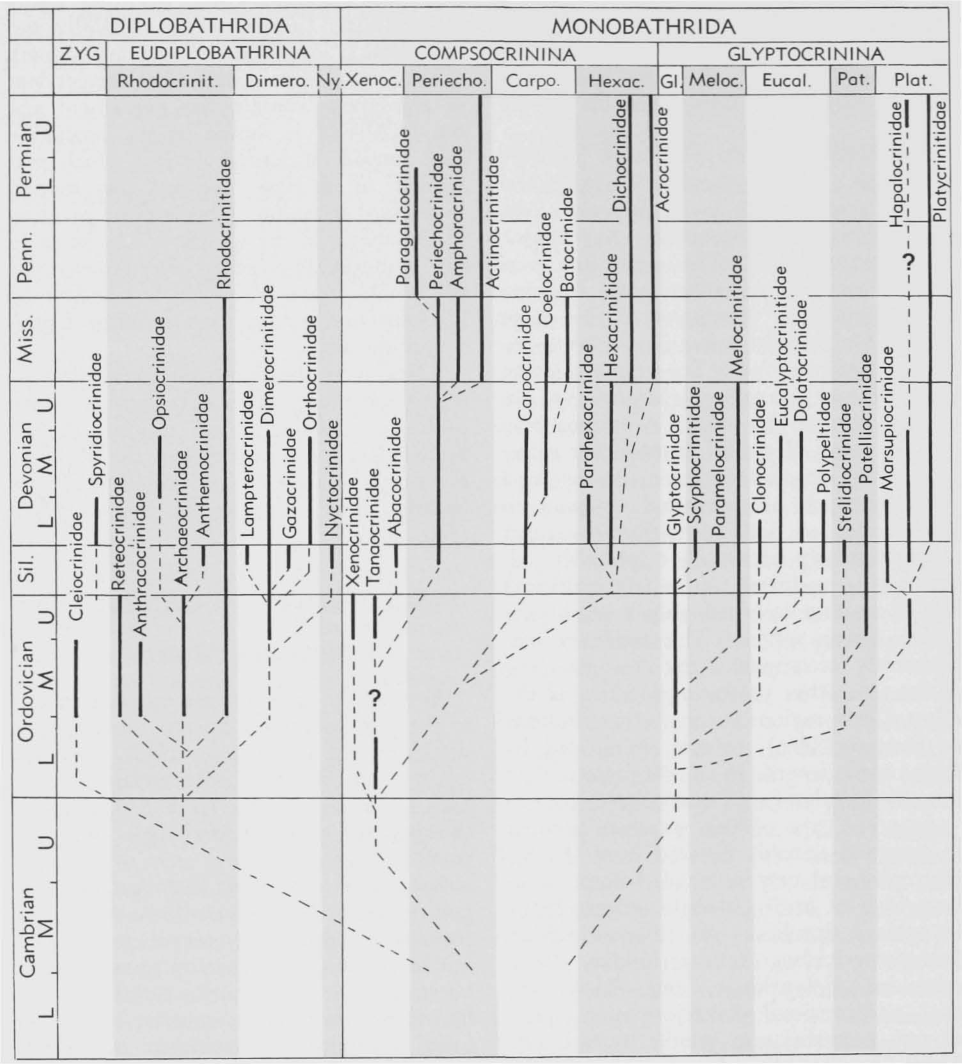

FIG. 208. Diagram showing evolutionary trends of the Camerata (Ubaghs, n).

Rhodocrinitacea. This classification is admittedly artificial, for the phyletic relations of these forms are practically unknown. By middle Ordovician time they already had reached a high degree of diversification and, in some cases (e.g., Anthracocrinidae), of specialization, which suggests a long previous history and possibly a polyphyletic origin.

The relations of the Rhodocrinitacea with the Cleiocrinidae and Spyridiocrinidae (here placed in the suborder Zygodiplobathrina) are obscure. *Cleiocrinus* is one of the most puzzling crinoids. It was referred successively, and generally with doubt, to the Crotalocrinidae (ZITTEL, 1879), Ichthyocrinidae (WACHSMUTH & SPRINGER, 1885), and the Flexibilia Impinnata (BATHER, 1900a); it was also regarded as an intermediate form between the Camerata and the Flexibilia (SPRINGER, 1905), an *incertae sedis* echinoderm (SPRINGER, 1911b, 1920), and an aberrant crinoid-like offshoot from the cystoids (Moore & Laudon, 1943a). Because of its pinnulate arms and subtegminal mouth, it was classified as a camerate closely related to *Reteocrinus* by Springer (1913), as a camerate by Bassler (1938) and Bassler & Moodey (1943), a monocyclic camerate by Jaekel (1918), and a dicyclic camerate by Ubaghs (1950, 1953). It differs, however, from all other dicyclic camerates in having the infrabasals overlapped by the basals and radials, which form a circlet of ten plates that project downward over the column like a collar. Furthermore, in contrast to all other camerates provided with many fixed brachials, it lacks interbrachials completely. However, the location of the basals between the radials (zygodiplobathrid type of base) does not seem to be fundamentally distinct from the eudiplobathrid type in which the basals and radials are arranged in two different circlets, for in some species (e.g., *Dimerocrinites pentlandicus, Paulocrinus biturbinatus, Rhipidocrinus crenatus*) some or even all radials may be inserted between the basals and thus be in contact with infrabasals. According to Brower (1975) the zygodiplobathrid base can be derived from the eudiplobathrid type by reducing the growth rates of the basals. *Cleiocrinus,* however, appears in many respects as an aberrant camerate, which presumably separated early from the ancestral diplobathrid stock. As to *Spyridiocrinus,* whether it is related to *Cleiocrinus* or not remains conjectural. If its basals, like those of *Cleiocrinus,* alternate with the radials in a circlet of ten plates, they rest on the distal edge of the infrabasals but do not overlap them, and with them and other calycal plates participate in the formation of a deep basal concavity which, as generally in crinoids, results from an invagination of the thecal wall. Moreover, contrary to the preceding genus, *Spyridiocrinus* has well-developed interbrachials and no anal plates. These and other differences, as well as the chronological gap (Middle Ordovician-Lower Devonian) that separates these two forms make a direct phylogenetic connection between them very doubtful. A rhodocrinitid ancestry is postulated for *Spyridiocrinus* by Brower (1975), who considers the zygodiplobathrids to be probably polyphyletic, and proposes to drop the suborder Zygodiplobathrina and to group the two genera *Cleiocrinus* and *Spyridiocrinus* within the Eudiplobathrina along with the most closely related families.

The Dimerocrinitacea originated probably from one or several archaeocrinid ancestors through upward displacement of the first interprimibrachs, so that the radials were brought into lateral contact except at the posterior side, where a single anal plate (primanal) remained. This line of ancestry is strongly suggested by: a) specimens of several species (e.g., *Atactocrinus wilmingtonensis, Dimerocrinites icosidactylus, Griphocrinus nodulosus, Lyriocrinus melissa, L. dactylus*) in which the proximal interprimibrachs separate the radials and rest on basals as in archaeocrinids, or occur above the radials in lateral contact as in dimerocrinitids; b) the similarities that exist between an archaeocrinid such as *Rhaphanocrinus* and the dimerocrinitid *Ptychocrinus.* Both genera have the same type of theca, except for the presence or absence of interbrachials between the radials, and very similar arms. The primitive dimerocrinitids had two or four unbranched uniserial arms per ray, as does *Rhaphanocrinus.* They were followed by forms provided with more or less numerous arm branches and biserial arms, although the uniserial arrangement of brachials persisted in at least one genus *(Macarocrinus)* until Devonian time. Other evolutionary trends in dimerocrinitids include formation of arm trunks in *Lampterocrinus,* development of tegminal ridges forming grooves for protection of arms in *Gazacrinus,* and allometric growth of base relative to height of calyx in *Orthocrinus*—three genera widely divergent from most other dimerocrinitids.

The Silurian genus *Nyctocrinus* was interpreted, probably correctly, by Moore & Laudon (1943a), as representing the most advanced evolutionary stage of the dicyclic camerate crinoids, inasmuch as the fixed brachials, interbrachials, and anals have been eliminated from the cup, thus establishing perfect pentamerous symmetry in this part of the theca. Unfortunately, the ancestors of *Nyctocrinus,* which may be regarded as a dicyclic homeomorph of *Platycrinites,* are unknown.

MONOBATHRIDA

Whether the monobathrid camerates derived from the diplobathrid camerates is uncertain. Both groups coexisted in the Ordovician, and no intermediate forms between them have ever been recorded. The earliest known (presumably) monobathrid species is *Proexenocrinus inyoensis* from the Lower Ordovician of California. It is a small crinoid with ten uniserial, unbranched free arms, few relatively large and regular interbrachials, and a well-defined median series of anal plates. Its systematic position remains somewhat obscure, because the structure of its depressed base has not been elucidated. Nevertheless, comparison of this species with later monobathrid camerates points to the probable line of development of these crinoids.

The monobathrid camerates comprise a large and diversified group which, in this *Treatise,* is divided into 28 families (against 13 for the diplobathrid camerates). They include two main stocks characterized by persistent structures of the calyx, namely, the occurrence of the primanal in the radial circlet in the Compsocrinina and its absence from the radial circlet in the Glyptocrinina.

COMPSOCRININA

So far as we know, all Ordovician, and probably primitive, members of the compsocrinine stock had a quadripartite base of hexagonal outline. [*Tanaocrinus,* erroneously reported as having five basals, has only four such plates; it is here considered to be a subjective synonym of *Canistrocrinus.*] This type of base was maintained in the Upper Silurian *Abacocrinus,* but in most other compsocrinine camerates it was replaced by an equally or subequally tripartite type that persisted throughout the history of the group, except in some terminal members, which evolved an equally bipartite type of base.

The Upper Ordovician genera *Canistrocrinus* and *Compsocrinus* stand closest to *Proexenocrinus,* inasmuch as they have retained its (probably primitive) kind of interbrachial structure. At the same time, *Xenocrinus* developed very small and irregular interbrachials and a complex mode of ontogeny of these plates. Like its homeomorph dicyclic *Reteocrinus,* this genus is therefore considered as representing a specialized offshoot, which apparently died out at the end of the Ordovician period.

Proexenocrinus had only two arms in each ray. This arm number was maintained in some species of *Xenocrinus,* but other xenocrinid species and most tanaocrinids acquired three or, more commonly, four arms per ray, presumably through conversion of the first pinnule (prominent in *Proexenocrinus*) of each arm into a pinnulate arm (Brower, 1974a). The free arms of *Proexenocrinus* were unbranched, as were also those of *Xenocrinus* and *Compsocrinus.* Those of *Canistrocrinus* became isotomously forking, but only once or twice, and at long intervals. The same type of arm branching occurs in the Upper Silurian *Abacocrinus*—possibly a descendant of *Canistrocrinus.*

During the Silurian period, three large branches of compsocrinine camerates appeared, namely the Periechocrinacea, Carpocrinacea, and Hexacrinitacea. Their precise origin and interrelations are not known, but they are supposed to be derived from tanaocrinid ancestors.

The Periechocrinacea contain the families Periechocrinidae, Paragaricocrinidae, Amphoracrinidae, and Actinocrinitidae. All these crinoids are characterized by having an equally tripartite base, a generally large number of fixed brachials, large and regular interbrachials, a first primibrach with hexagonal outline becoming quadrangular only in advanced members, and branching free arms, commonly. The Upper Silurian *Periechocrinus* is the earliest known representative of this group. Its primitiveness is indicated by its high conical calyx, its upflaring basal plates, its numerous fixed brachials, interbrachials and anal plates, its interbrachials connected with interambulacrals, its median ray and anal ridges, its many-plated tegmen, and its relatively small number of free arms per ray. From this or a similar form, various genera, some of them highly specialized (e.g., *Gennaeocrinus, Megistocrinus, Thamnocrinus*), evolved within the Periechocrinidae during the Devonian.

In Early Carboniferous time, or probably somewhat earlier, the Periechocrinidae gave rise to the Actinocrinitidae and to the closely related Amphoracrinidae, which both (mainly the former) flourished abundantly in the Mississippian. The less advanced actinocrinitids (e.g., *Maligneocrinus*) closely resemble periechocrinids. The principal difference between them lies in the number of plates in the second range of the *CD* interray: three in the periechocrinids, two in the actinocrinitids and amphoracrinids. However, many actinocrinitid specimens still have the primanal followed directly by three plates. Another difference appears in the number of free arms. The periechocrinids usually have two to four free arms per ray (exceptionally, as in *Gennaeocrinus,* six or eight), whereas six or more free arms in the ray are common among actinocrinitids, reaching a maximum of approximately 16 per ray in *Teleiocrinus* and 30 per ray in *Strotocrinus.* In the two latter genera, incorporation of many brachitaxes (up to the twelfth order in *Strotocrinus*) resulted in the formation of a prominent calycal flange from the edge of which the unbranched free arms arose in a belt around the theca. Such genera are among the most specialized camerate crinoids.

Another, rather late, offshoot probably derived from the periechocrinids is the Paragaricocrinidae, a small group restricted to Pennsylvanian and Lower Permian deposits. These crinoids are very advanced camerates, as indicated by the low, rounded shape of their theca, the occurrence of a basal concavity commonly including the radials, the quadrangular outline of their first primibrachs, and the large size and small number of their interray plates, which are separated from the tegmen by the arm bases except generally on the posterior side.

The second branch that possibly originated from tanaocrinid ancestors comprises the superfamily Carpocrinacea, which includes the Carpocrinidae, Batocrinidae, and Coelocrinidae. Like the Periechocrinacea they have three, generally equal, basals, but their first primibrach is typically quadrangular instead of hexagonal in outline, their interbrachials are generally fewer, larger and more regular, and they have a lesser number of fixed brachials, and ordinarily fewer free arms, and those mostly unbranched. These features and their early appearance in the Silurian indicate that the Carpocrinacea are more progressive than the Periechocrinacea. They coexisted with the latter, but disappeared earlier, at the end of the Mississippian period, during which they showed an extraordinary development followed by a rapid decline.

Among the Carpocrinacea, the Carpocrinidae are believed to be the ancestral family. They are practically restricted to rocks of Silurian age, while the Coelocrinidae, which are not known before Middle Devonian time, are found mainly, and the Batocrinidae exclusively, in Mississippian deposits. On the other hand, the Carpocrinidae contain genera which seem well fitted to represent the source from which the Coelocrinidae could be derived. *Desmidocrinus,* for instance, combines primitive features, such as uniserial free arms, interbrachials connected with interambulacrals, a median series of extra plates in the *CD* interray, and a variable number of free arms, with typical carpocrinacean characters. Between *Desmidocrinus* and the oldest known coelocrinid *Aorocrinus* there is not a wide morphological gap. In its turn, *Aorocrinus* does not seem to be very far from the less advanced batocrinids. Those differ essentially from the coelocrinids in having an anal tube, the interrays commonly separated from the tegmen by fixed brachials, and no median series of anal plates; in addition, they are generally provided with cup-pinnule openings, which are lacking in coelocrinid genera. But all batocrinids do not have all these distinguishing features. For instance, in *Uperocrinus,* which is classified among the Batocrinidae because it has an anal tube, the interbrachials are connected with the interambulacrals and there are no cup-pinnule openings. Such a form constitutes a morphological transition between the two families and suggests that the Batocrinidae originated from the Coelocrinidae.

The third branch with a possible tanaocrinid ancestry is composed of the Hexacrinitidae, Parahexacrinidae, Dichocrinidae, and Acrocrinidae, which together form the superfamily Hexacrinitacea. As here interpreted, these crinoids are the most advanced and specialized compsocrinine camerates. Known from Upper Silurian to Upper Permian, they are characterized by a cup that typically comprises only two circlets of plates: a basal circlet and a radial circlet, the latter including a primanal in line with the radials. This simple structure may not be considered primitive, but probably results from elimination from the cup of all plates above the radial circlet and derives from a more complex stage. Like the Periechocrinacea and Carpocrinacea, the Hexacrinitidae have an equally tripartite hexagonal base, and the primanal located between the *C* and *D* radials. They seem to be nearer the Carpocrinacea than to the Periechocrinacea, for the former have fewer fixed brachials and interbrachials, and generally larger radials than the latter. A form like *Prohexacrinus,* considered by YAKOVLEV (1946) as a primitive hexacrinitid, might well be regarded as a carpocrinid insofar as concerns its cup (the only part of this crinoid known). This concept of a carpocrinid origin of the Hexacrinitidae is opposed by those who think that these crinoids are closely related to the Platycrinitidae or their hypothetical ancestors (BATHER, 1900a; WILSON, 1916; STRIMPLE, 1969; STRIMPLE & WATKINS, 1969).

Several hexacrinitacean camerates (e.g., some *Hexacrinites, Talarocrinus, Pterotocrinus*) show a marked tendency toward reduction of the primibrachs: they have only one such plate left in each ray, and this plate, which is axillary, is commonly not visible and may even be lacking, so that the secundibrachs become supported partly or completely by the radials. One would expect a similar origin for the multiple-arm bearing radials of Parahexacrinidae. However, the known stratigraphic succession of the three genera now included in this family is not consistent with this theory. According to SHEVCHENKO (1967), it is in the oldest genus that the free arms are directly borne by the radials, whereas they are carried by short, cuneate, irregular proximal brachials in the youngest.

The Dichocrinidae are commonly regarded as directly related to the Hexacrinitidae, from which they differ mainly in the structure of their tegmen and in having two, instead of three, equal basals, but in fact their origin is unknown. This prolific family, restricted to Upper Paleozoic deposits (Lower Mississippian-Upper Permian), contains genera which, like *Camptocrinus* or *Pterotocrinus,* are among the most unusual camerates. In these, as well as in other members, of this lineage, the tegmen, arms, or column were modified, in some cases very markedly, but the cup showed no significant change. The Acrocrinidae, which are distinguished from all other crinoids by the presence of supplemental calyx plates (intercalaries) between the basal and radial circlets, exhibited an explosive evolution in Late Mississippian, followed by a decline in the Pennsylvanian. Although they share possession of an equally bipartite base with the Dichocrinidae and are generally regarded as a specialized offshoot from *Dichocrinus,* their precise origin remains obscure (MOORE & STRIMPLE, 1969).

GLYPTOCRININA

The Glyptocrinina are the other main stock of monobathrid camerates. Their earliest known representatives, the Glyptocrinidae, occur in Middle Ordovician deposits. Their great antiquity combined with primitiveness of features designates them as the main source of the monocyclic camerates which, like them, have no anal plate in the radial circlet and, consequently, have a pentagonal base. Whether this type of base is primitive or not is a much debated but still unsolved problem (see discussion in section on skeletal morphology of crinoids, p. *T*102). In fact, no transition form between compsocrinine and glyptocrinine camerates has ever been recorded. The origin of both groups is unknown.

The Glyptocrinidae are regarded as primitive Glyptocrinina because they have a conical calyx with five upflaring basals, prominent ray and anal ridges, numerous fixed brachials, medium-sized and regular interbrachials connected with interambulacrals, a many-plated tegmen, and few arms (2 to 4 per ray), which are unbranched or fork only once or twice, and are ordinarily uniserial.

A first branch probably given off from the Glyptocrinidae is represented by the superfamily Melocrinitacea, which includes the Scyphocrinitidae, Paramelocrinidae, and

Melocrinitidae. Those camerates have retained the primitive glyptocrinid type of calyx, except that the number of basals was reduced from five to four. Also, in the Scyphocrinitidae, loose articulations evolved between cup plates, and very many brachials and pinnulars were incorporated in the calyx, separating the interbrachial areas from the tegmen. But the major evolution concentrated on the free arms, increasing the food gathering system considerably. This was accomplished by a) transition from the uniserial to biserial arrangement of brachials, b) by branching of the arms: those of the Scyphocrinitidae and Paramelocrinidae divided isotomously several times, whereas those of the Melocrinitidae were transformed into powerful arm trunks bearing a large number of pinnulate ramuli.

The principal steps in the evolution of these arm trunks, as elucidated by JAEKEL (1895, 1902, 1918), OLSSON (1912), KIRK (1929c), UBAGHS (1958b), and BROWER (1973), include: 1) development of four arms per ray from two arms per ray in the Upper Ordovician—a change already accomplished at the glyptocrinid level, probably by converting the first pinnule of each arm into a pinnulate arm; 2) exotomous branching of the inner arms of each ray, followed or accompanied by loss of the pinnules proximal to the arm branches, in the Silurian; 3) fusion together of the inner arms, starting proximally and extending progressively distalward, thus forming arm trunks, in the Upper Silurian and Lower Devonian; 4) disappearance of the unbranched outer arms, in the Middle Devonian; 5) division of the arm trunks themselves into ramule-bearing branches, in the Upper Devonian. Worth mentioning also about the Melocrinitacea is the unique type of root that evolved in the genus *Scyphocrinites:* a large, hollow, spheroid body that probably served as a float.

A second main section presumed to be derived from glyptocrinid ancestors consists of the families Clonocrinidae, Eucalyptocrinitidae, Dolatocrinidae, and Polypeltidae. For convenience they are placed in the superfamily Eucalyptocrinitacea, although their origin and interrelations are admittedly obscure. They have few distinctive features in common. In most of them, the calyx is low and wide, and the tegmen is stoutly plated. The base comprises four (or three) unequal basals, which may be fused together. The posterior side of the cup is barely, if at all, differentiated from the other interrays. The free arms are typically biserial. But all these characters could have evolved independently, and they do not serve to designate any precise forerunner. The Eucalyptocrinitidae and Clonocrinidae are probably related, for they have four basals, a relatively small number of fixed brachials and interbrachials, and ordinarily few free arms per ray. Different in appearance are the Dolatocrinidae, which have three, commonly fused, basals and comprise a well-diversified, mainly North American, group of Lower and Middle Devonian species. Still more distinct are the Polypeltidae, with their huge theca generally deeply modified proximally and including an extremely large number (up to about 700 in *Himerocrinus*) of fixed brachials. Their relatively short free arms may be as few as two per ray *(Hadrocrinus)* but as many as 16 or 17 per ray *(Himerocrinus).* This type of theca is certainly not primitive, but rather suggests the existence of a peculiar tendency to incorporate a very large number of ray plates into the calyx.

The superfamily Patelliocrinacea, which includes the Stelidiocrinidae and Patelliocrinidae, constitutes a third main branch from the glyptocrinid stock. Compared to their presumed Middle Ordovician ancestors, they appear to be very progressive, and, with their few fixed brachials and interbrachials, morphologically intermediate between the Glyptocrinidae and Platycrinitidae. Although the Stelidiocrinidae retained the primitive number of five basals, in most other respects (particularly in the stoutly plated structure of their tegmen) they are highly specialized, and probably represent an isolated offshoot of unknown origin and descent.

The ancestry and evolution of the Patelliocrinidae is better documented, thanks to the discovery of an early representative of this family in Upper Ordovician rocks, *Eopatelliocrinus,* which differs only from Middle Ordovician glyptocrinids in having three, instead of five, basals, a lesser number of fixed brachials, interbrachials and anal plates, and larger radials but relatively smaller primibrachs; in addition, its first primibrach is commonly quadrate instead of being hexagonal. On the other hand, *Eopatelliocrinus* resembles the Glyptocrinidae in its general habitus, in showing traces of median ray and anal ridges, in the structure of its many-plated tegmen, and in having few unbranched and uniserial free arms. In the evolution of the family, which became extinct in the Lower Devonian, the following trends are recognizable: 1) reduction of the number of fixed brachials and interbrachials; 2) change in shape of the first primibrach and primaxil, which by Late Silurian time became generally quadrangular and pentagonal, respectively; 3) gradual reduction of the heights of these two plates relative to calyx size; 4) progressive disparition of the median ridge and extra plates in *CD* interray; 5) formation of biserial arms (Brower, 1973).

The fourth and last branch from the glyptocrinid stock comprises the Marsupiocrinidae, Hapalocrinidae, and Platycrinitidae, which together form the superfamily Platycrinitacea. As interpreted here, they represent the end products of one of the most dominant evolutionary trends of camerates, namely the elimination of the fixed brachials, interbrachials and anal plates from the calyx, which thus tends, and eventually is, confined to the sole basal and radial circlets. They are presumed to have a common ancestor with the Patelliocrinidae or to be descended from them, and to represent a more advanced stage along a similar line of evolution. Their precise origin is unknown, and their occurrence in rocks older than Upper Silurian doubtful. The Hapalocrinidae are antecedents to the Platycrinitidae, and in some respects they seem to be more primitive. As in these two families the main characters of the cup were stabilized very early, it is in the structure of the tegmen, the arms and the column that the principal changes occurred. Whereas the hapalocrinid stem remained cylindrical, the platycrinitid column became elliptical in cross section, twisted, and provided with synarthrial articulations, except proximally. The Hapalocrinidae had two primibrachs in each ray, generally more than two secundibrachs in each half ray, and, the arm bases not being in close contact with the calyx, the arms never formed proximal trunks; on the contrary, the arms of the Platycrinitidae ordinarily comprised only one, commonly very small, primibrach followed in each half ray by two secundibrachs; those arm plates therefore tended to be in close contact with interambulacrals and commonly were covered by tegminal ambulacrals, so that the arm bases became connected. The hapalocrinid tegmen, mainly composed of five orals, did not incorporate a large number of ambulacral and interambulacral plates, nor show a loss of differentiation of its component elements. Very different was the platycrinitid tegmen, which primitively had ambulacra protected by alternating orals, with axillar ambulacrals, but exhibited a strong tendency toward incorporation of many interambulacrals, sinking of ambulacra under those plates, and loss of differentiation of its plates. As to the Marsupiocrinidae, they do not seem to have shared the same tendencies, and probably were distantly related to the hapalocrinid-platycrinitid line of evolution.

EVOLUTION OF INADUNATE CRINOIDS

By N. Gary Lane and H. L. Strimple

DISPARIDA AND HYBOCRINIDA

By N. Gary Lane

Disparid and hybocrinid monocyclic inadunates are highly diverse and common Ordovician crinoids. Of the nine superfamilies of disparids and hybocrinids recognized in this *Treatise,* six are first represented in the Ordovician. They appeared very early in the Ordovician and had undergone an extensive adaptive radiation before Silurian time. Most of these inadunates are characterized especially by having a plane of bilateral symmetry through the crown situated other than through the anterior ray and posterior interray, the bilateral plane typical of most crinoids. In Ordovician disparids these other symmetry planes are expressed especially by presence of compound radial plates in certain rays and undivided ones in other rays.

Seemingly, the most primitive and archaic disparid crinoids belong to the Eustenocrinidae of the superfamily Myelodactylacea. *Ramseyocrinus* is one of the oldest known crinoids and possesses features such as infer- and superradials in all rays and *C*-ray supporting an anal sac, but not an arm, which are judged to be very primitive. *Peniculocrinus* is only slightly advanced beyond and younger than *Ramseyocrinus.* These crinoids, which have a *C-EA* symmetry plane, provide evidence that the distinctive homocrinoidal and heterocrinoidal symmetry planes of other Ordovician disparids evolved within this stock and were not inherited from a pre-disparid ancestor. The Eustenocrinidae are thought to have evolved directly into Ordovician *Iocrinus,* which lacks compound radials in all rays, but is distinguished by the presence above the cup rim of an anibrachial in the *C*-ray. *Iocrinus,* in turn, evolved in the Silurian into the Myelodactylidae, characterized by an *Iocrinus*-like crown enclosed within a coiled bilateral stem.

The Eustenocrinidae also gave rise, by Middle Ordovician time, to two stocks of crinoids that are characterized by retention of a high, narrow primitive cup and advanced, complexly heterotomous arms. The Heterocrinacea, exclusively Ordovician, with two compound radials, and the Homocrinacea, dominantly Ordovician, with three, record experimentation with various patterns of arm-branching, differing from each other mainly in presence or absence of compound radials in the *B*-ray. The heterocrinoids died out by the end of Ordovician time without known descendants in the Silurian, but, before they became extinct, they may have given rise to one small superfamily of Ordovician disparids, the Anomalocrinacea. These crinoids display a heterocrinoid symmetry plane and heterotomous arms, but have a globose cup and other features that may point to an origin independent of the Heterocrinacea.

The Homocrinacea surely were the ancestral source for the unique Calceocrinacea, the "bent-crown" crinoids which appear to have lived with the stem prostrate and the crown bent upward just above the bottom. These disparids first appeared in the Middle Ordovician and were reasonably successful Paleozoic crinoids, achieving maximum generic diversity in the Silurian and persisting into the Early Permian. The calceocrinids have a homocrinoidal symmetry plane *(E-BC)* and heterotomous arms that point clearly to an origin within the Homocrinacea.

The superfamilies discussed above constitute the bulk of known Ordovician disparids and groups remaining to be treated below, including the majority of post-Ordovician disparids. Three distinct, and presumably separate, evolutionary trends are evident among these younger disparids. One trend was toward fusion of all infer- and superradial plates to produce a cup with five equal, large radials. This was accompanied, in some, by evolution of five simple atomous arms, one to a ray. This trend is seen especially well-developed in the Belemnocrinacea with a crinoidal *(A-CD)* symmetry plane, which had achieved this much simplified crown by Silurian time with appearance of the Pygmaeocrinidae, Zophocrinidae and oldest representatives of the Synbathocrinidae.

A second trend was development of a small bowl-shaped cup in which compound radials were retained in one or more rays. Conspicuous differences in size of radials became evident, especially by hypertrophy of the *A* and *D* radials. The arms tended to be simple and atomous. This trend is present in the Pisocrinacea, Allagecrinacea, and the Perissocrinidae and Holynocrinidae of the Belemnocrinacea, and is especially well-represented among Silurian and Devonian disparids.

The third trend was for multiple simple atomous arms to be developed on broad radial facets, an adaptive alternative to branched arms in effecting an increased ambulacral surface. This innovation appeared first in the Middle Devonian Anamesocrinidae and is extensively developed in the dominantly late Paleozoic Catillocrinidae, and Allagecrinidae, all families of the Allagecrinacea.

These three trends point up one of the most conspicuous differences between Ordovician and post-Ordovician disparids in that the great majority of the former have heterotomous arms and most of the latter have simple atomous arms. Although evolutionary simplification of the arms may have occurred once, or several times, it seems unlikely that any of the Ordovician disparids with elaborate arm-branching led directly to younger disparids with atomous arms. All post-Ordovician disparids have either the homocrinoidal *(E-BC),* eustenocrinoidal *(C-EA),* or crinoidal *(A-CD)* symmetry plane. Therefore, a likely ancestor for at least some of these younger crinoids is an Ordovician form that had a rather generalized cup exhibiting homocrinoidal symmetry and simple isotomous arms that might have evolved directly into atomous arms. Based on these qualifications, the most likely ancestor for many of the post-Ordovician disparids is *Tunguskocrinus,* known from the Ordovician of Russia. Specimens of *Tunguskocrinus* have homocrinoidal bilateral symmetry, and simple isotomous arms that could readily have evolved into the atomous arms typical of so many younger disparids. The steeply conical cup of this genus is closely similar in construction to that of the oldest known synbathocrinid, *Abyssocrinus,* which has a crinoidal *(A-CD)* bilateral symmetry. It seems likely that *Tunguskocrinus* stands closest morphologically to the ancestral type for many of the Belemnocrinacea.

The Pisocrinacea, which display a homocrinoidal *(E-BC)* type of symmetry, appeared abruptly in Upper Silurian rocks and their origin is obscure. The only Ordovician disparids with a bowl-shaped cup are the Anomalocrinacea, which can be ruled out as precursors of the pisocrinoids because they possess the wrong kind *(D-AB)* of bilateral symmetry, have specialized heterotomous arms and other features which indicate that they are a specialized sterile offshoot of the Heterocrinidae.

The origin of the multi-armed radial plates of the Allagecrinacea is also unknown. The Anamesocrinidae are known only from the Middle Devonian and are contemporaneous with oldest known Catillocrinidae. The development of multiple atomous arms was not confined to this superfamily, but also occurred in very different fashion, and clearly polphyletically, in some genera of the Pisocrinacea.

The prevailingly globose form of the theca observed in the Hybocrinida differs from that of disparid superfamilies, as does the tendency toward suppression of arms accompanied by placement of ambulacra on the surface of cup plates. Also, the Hybocrinida are unlike Disparida in having a radianal plate directly or obliquely beneath the *C* radial. The hybocrinid *Baerocrinus* and disparid *Ramseyocrinus* are the only monocyclic inadunate genera recorded from lower Ordovician rocks. Beyond doubt, one type was not derived from the other; rather both descended from unknown pre-Ordovician ancestors.

CLADIDA

CYATHOCRININA AND DENDROCRININA

By N. Gary Lane
[University of Indiana]

The two most primitive groups of cladid, or dicyclic, inadunates are the suborders Cyathocrinina and Dendrocrinina. The latter is first represented by specimens in the Lower, the former in the Middle Ordovician. The Cyathocrinina are dominantly a lower and middle Paleozoic group of crinoids, being represented in the late Paleozoic mainly by a group of microcrinoids. The Dendrocrinina, on the other hand, gave rise in the Middle Ordovician to the subclass Flexibilia, and in the Devonian, evolved into the suborder Poteriocrinina, the most successful and diverse group of late Paleozoic crinoids. The nature of Ordovician genera of the cyathocrinids and dendrocrinids is so disparate, that it is virtually impossible to postulate a common ancestor for these two early groups of dicyclic inadunates, and it seems quite likely, therefore, that the Cladida arose polyphyletically from two or more pre-Ordovician crinoids or other pelmatozoans.

TABLE 3. *Comparison of Morphological Features of Ordovician Genera of Cyathocrinina and Dendrocrinina.*

CYATHOCRININA	DENDROCRININA
Cup large, bowl- or egg-shaped	Cup small, low, or conical
Infrabasals large, conspicuous	Infrabasals generally small and low
Tegmen low or with a small, short sac	Tegmen produced into a conspicuous anal sac
Goniospires or trace of them present	Goniospires absent
Posterior oral a madreporite	Posterior oral not known
Arms narrow, rounded, less than one-half width of radials	Arms mostly wide, one-half to two-thirds width of radials
Arms branch isotomously once or a few times	Arms richly branching, isotomous or heterotomous

In the Ordovician, the cyathocrinids are represented by six genera, which are placed in five families assigned to two superfamilies in the *Treatise* classification. The contemporaneous dendrocrinids include 11 genera assigned to ten families in three superfamilies. Consequently, even though the number of genera and specimens known is small, these crinoids do show a wide range of morphological features which point to an extensive evolutionary history that is as yet unknown.

A summary of conspicuous differences between Ordovician cyathocrinids and dendrocrinids is provided in Table 3. Comparison of the lists points up the difficulty of postulating a common origin for the two suborders. The presence of goniospire slits or traces of these structures in several cyathocrinid genera may well represent a hold-over from some kind of slit-bearing noncrinoid pelmatozoan such as the cystoids. If this should prove to be true, then the major adaptive innovation of the cyathocrinids was the evolution of true crinoid arms from brachioles. The inflated egg-shaped theca of several Ordovician cyathocrinids superficially resembles the theca of the monocyclic Hybocrinida inadunates, but this similarity is judged here to be convergent and not indicative of phyletic relationship. The quite large, prominent infrabasals of early cyathocrinids seemingly precludes any close relationship with monocyclic inadunates, the disparids or hybocrinids.

The Dendrocrinina, on the other hand, exhibit several features that point toward a much closer relationship between these dicyclic crinoids and monocyclic disparids. Early dendrocrinids tend to have quite small, low infrabasals that could have disappeared in pre-Middle Ordovician time, resulting in monocyclic inadunates, or conversely, the small infrabasals could have been a new feature, evolved in dendrocrinids from a disparid ancestor. Both the dendrocrinids and disparids have infer- and superradial plates in most primitive, and oldest, representatives. Both groups include types with a small, high, conical cup, have arms that are densely branched, and a conspicuous anal sac. It seems likely, therefore, that disparids and dendrocrinids may have had a common ancestor, or one group may have evolved from the other. Only discovery of new Early Ordovician, or better, Cambrian, crinoids will resolve these phyletic problems.

Ordovician genera of the Dendrocrinina can be arranged into four morphological grades that may approximate the principal early evolutionary pathways within this group. At the base of the series stands *Aethocrinus,* the oldest dicyclic inadunate known, which possesses several very primitive features, especially the arrangement of cup or calyx plates. The next grade contains *Ottawacrinus,* which has five compound radials in the cup, that of the *C*-ray consisting of a superradial classed as a radial and an inferradial identified as the radianal plate. The third stage, as represented by *Cupulocrinus* and *Dendrocrinus,* consists of crinoids that retain an inferradial, identified as a radianal, in the *C* ray only. A fourth grade is defined by *Merocrinus* in which the *C* radial is an undivided plate, exactly like the four other radials, but unlike them is followed above the cup rim by an axillary anibrachial, which on its left articular facet supports an anal *X* plate followed by other plates of the anal sac and on its right facet a series of normal primibrachs.

Four nominal Ordovician genera assigned to the Dendrocrinina are omitted from this ranking because they are poorly known. All were described by JAEKEL (1918) and may be very important crinoids for understanding the early history of this group of crinoids. JAEKEL's descriptions are so incomplete and his illustrations so unreliable, as recently demonstrated by UBAGHS in redescription of JAEKEL's 1918 genus *Perittocrinus,* that it would be foolhardy to discuss these four genera *(Esthonocrinus, Pandoracrinus, Polycrinus, Metabolocrinus)* as if we really understood their significance.

The Dendrocrinina constitute a reasonably homogeneous group of crinoids displaying few striking modifications of the basic morphological types established in the Ordovician. The main interest in post-Ordovician dendrocrinoids concerns their phylogenetic relationship to the advanced dicyclic cladids assigned to the Poteriocrinina. The two advanced groups of dendrocrinids are the Botryocrinidae, a family of the Dendrocrinacea, and the Mastigocrinidae of the Mastigocrinacea. Either, or both, of these families may have served as the phyletic source of the Poteriocrinina, which assuredly evolved from the Dendrocrinina during Devonian time. The two key characters used for judging phyletic derivation of the poteriocrinids are the appearance of muscular articulation between radials and first primibrachs, and the development of pinnules from nonpinnulate heterotomous arms with closely spaced ramules. Two other features of secondary value are relative width of the radial articular facets, generally narrow in more primitive, and wide in advanced forms, and the number of anal plates in the cup. Width of radial facets as a criterion for discriminating early Poteriocrinina is a feature of dubious value. Many earliest known pinnulate cladids have relatively narrower radial facets than even very generalized Ordovician dendrocrinids, like *Cupulocrinus,* for instance. Advanced genera of the Mastigocrinidae have wider radial facets than do many primitive poteriocrinids.

The evolution of pinnules during the transition from dendrocrinids to poteriocrinids was taking place on a broad front within more than one lineage, resulting in a mosaic of crinoids that independently achieved or closely approximated a pinnulate condition. Advanced genera of both the Botryocrinidae and Mastigocrinidae exhibit a sequence of arm types in which two main isotomous branches occur above the primaxils. In less advanced genera, ramules are developed at irregular intervals on alternate sides of brachials, spaced from four to nine brachials apart, as in *Lasiocrinus* and *Cradeocrinus.* In more advanced genera, the ramules are attached to alternate sides of every second brachial, as in Devonian *Pagecrinus* and *Iteacrinus.* Only one further step is necessary, having alternate ramules on alternate sides of each successive brachial in a series, to achieve a truly pinnulate condition. It is quite clear that true pinnules did evolve within crinoids classed as members of the Dendrocrinina. Both *Imitatocrinus* and *Dictenocrinus,* of Devonian age, have pinnulate arms, each brachial having a side branch. These two genera are placed within the Mastigocrinidae and neither could have been the direct ancestor of the Poteriocrinina, because they possess only two anal plates in the cup, like most other genera of this family with less advanced arm structure. One Silurian dendrocrinid, *Cyliocrinus,* records a precocious, independent origin of pinnules in which proximal brachials have pinnules on alternate sides of each brachial, and distal brachs each bear a pinnule on both sides of each plate, a hyperpinnulate condition that did not evolve in the Poteriocrinina until Mississippian time.

The pinnulate dendrocrinids discussed above cannot reasonably be accorded importance as potential ancestors of the Poteriocrinina, but one genus, *Quantoxocrinus,* stands as close to such an ancestral type as is now known. This crinoid has well-developed pinnules, and three anal plates in the cup, but is placed in the Dendrocrinina because its anal sac is closely comparable to that of other genera grouped in the Mastigocrinidae.

The relationship between these two suborders is still more complicated by the fact that two genera of Devonian poteriocrinids, *Rhenocrinus* and *Charientocrinus* of the Rhenocrinidae, are not pinnulate but have ramules on every second brach above the primaxils. Consequently, the arms of these genera are less advanced than those of some dendrocrinids. They are placed in the Poteriocrinina because three anal plates occur in the cup and because features of the sac and configuration of the cup ally them with several other Devonian genera, all of which have pinnules and otherwise qualify as belonging in the Poteriocrinina.

The pinnulate condition in dicyclic inadunates clearly evolved gradually and separately in more than one distinctive stock of advanced dendrocrinids and primitive poteriocrinids and cannot be utilized as an all-or-nothing "key" character to differentiate the two suborders.

A second feature used to distinguish dendrocrinids from poteriocrinids is the presence or absence of muscular articulation in the arms, especially at the base of the arm between the radials and first primibrachs. The condition of muscular articulation is recognized traditionally in fossil skeletal morphology of crinoids by presence of a transverse articular ridge on the facet. Adjacent to the ridge externally is a pit that housed ligaments and two or more internal fossae that contained ligaments and muscles. Strictly ligamentary articulation is judged to have been present on radial and other facets that lack a prominent ridge and associated fossae, although other less conspicuous structures may be present (VAN SANT, 1964). The radial articular facets of most primitive poteriocrinids and advanced dendrocrinids are not known in sufficient detail to allow direct observations concerning morphological steps leading to this important advance. Not all of the crinoids now placed in the Poteriocrinina had muscular articulations, for genera such as *Poteriocrinites* and *Springericrinus* lack necessary fossae, and none of the Dendrocrinina attain this condition. Consequently, muscular arm articulations evolved within the Poteriocrinina and appeared somewhat later in the phyletic history of inadunate crinoids than did the pinnulate condition, which is present in both suborders. The time-sequential relationship between these adaptations may provide a clue to the evolutionary pathway by which muscular articulations evolved in the Poteriocrinina.

If one examines the articular facets between brachials and first pinnular plates in many crinoids that possess pinnules, whether camerate, inadunate, or articulate, these facets have a closely similar construction. There is a distinct, short transverse ridge with rather large fossae on either side. In living crinoids the external fossa houses ligaments and the internal one muscle fibers, acting in opposition to each other. Contraction of the muscle pulls the pinnule up over the arm into a closed position, and relaxation of the muscle allows the ligament to contract, extending the pinnule into a feeding posture. Because of the close skeletal similarity of these facets in living crinoids and fossils it seems reasonable to postulate that many camerates and advanced inadunates, all of which have pinnules, possessed muscle fibers that helped to move the pinnules. With very rare exceptions *(Planacrocrinus)*, camerates never evolved beyond this stage to one wherein muscles developed between brachials or between radials and arms.

Ramules of dendrocrinids generally have smooth or only faintly sculptured articular surfaces between plates and presumably were united to brachials by ligaments. Pinnular facets of advanced poteriocrinids clearly had both muscles and ligaments. The evolution of ligament-muscle from strictly ligamentary articulations is therefore thought to have occurred in cladid inadunates contemporaneously with or shortly after attainment of the pinnulate condition. The presence of muscle-activated pinnules was a necessary pre-condition for the evolution of muscular articulations in the main part of the arms. Instead of stopping at the point reached by camerates early in their development, with muscles confined to helping move pinnules, the cladids went a step further and sites of muscle insertion spread from pinnular facets to the main part of arms, first between radials and arms, then on either side of axillary plates, and later, in articulates, between most of the brachials. If this interpretation of evolution is correct, the development of pinnules or "near-pinnules" was a necessary first step toward incorporation of muscle fibers into the main part of the arms. The sequential appearance of, first, pinnules, and then muscular articulation on the radial facets, in the phyletic transition from dendrocrinids to poteriocrinids is thus explained.

EVOLUTIONARY TRENDS AMONG POTERIOCRININA

By H. L. Strimple

The general trend in evolution of the Poteriocrinina is toward increase in overall size and moderate thickening of cup plates. As an example, the cup of *Ulocrinus elongatus* Strimple (1961d), Middle Pennsylvanian, is known to have attained a height of 39.5 mm. and width of 44.7 mm., as compared to the similarly shaped *Glossocrinus naplesensis* Goldring (1923), Late Devonian, with a height of 3.5 mm. and width of 6.0 mm., an increase in size of about 85 percent.

Evolution of the primitive cup outline (high conical) may have proceeded along different paths such as 1) retention of primitive straight-sided form modified by reduction in height, 2) longitudinal curvature of sides with constriction of the summit producing globose shapes, and 3) broadening of the cup base accompanied by development of a shallow to deep basal concavity.

The mechanics for changing cup shape appear to be fairly simple: 1) infrabasals developed a flattened surface about the stem attachment with only their distal tips flexed upward, producing narrow, flat-based cups as in *Decadocrinus* Wachsmuth & Springer (1880), Middle Devonian-Lower Mississippian; 2) subhorizontal distal tips of infrabasals joined upwardly curved proximal ends of basals providing a broad flat base as in *Laudonocrinus* Moore & Plummer (1940), Middle Pennsylvanian-Upper Pennsylvanian, 3) horizontal or downflared infrabasals were surrounded by downflared proximal parts of basals or entire basals, which was characteristic in many genera of Mississippian to Permian age.

Although most Poteriocrinina became stabilized with a moderately deep, broad, bowl-shaped cup by Chesterian or Pennsylvanian time, some continued to lower cup height by extending proximal ends of the radials into the basal plane and eventually most of these plates became horizontal so that the cup became little more than a platform beneath the visceral mass. Examples of the latter condition are *Galateacrinus* Moore (1940a), *Oklahomacrinus* Moore (1939), and *Sciadiocrinus* Moore & Plummer (1938), all Lower or Middle Pennsylvanian to Upper Pennsylvanian. Among the Pirasocrinacea (Lower Mississippian to Lower Permian), loss of body space in the cup was partially compensated by extension of the steep, outward-downward, radial articular facets; however, contributing factors were probably the prominent musculature of the arm facets and large number of arms found in these genera. A similar condition is found in Chesterian species of *Zeacrinites* Troost in Hall (1858) in which the arms are numerous, the cup is very shallow, and large, outward-downward sloping, radial articular facets appear. Reduction in capacity of the cup may be compensated also by enlargement of the anal sac.

Primitive Poteriocrinina had ridges extending across sutures from plate to plate in the cup, strengthening the thin plates. Evolution normally trended toward thicker plates with reduction or disappearance of the ridges as in *Exoriocrinus* Strimple & Moore (1971a), Upper Pennsylvanian; *Elibatocrinus* Moore (1940a), Middle to Upper Pennsylvanian; and *Indocrinidae* Strimple (1961d), Lower to Upper Permian. Thin plates and surficial ridges persisted in various post-Devonian Poteriocrinina (e.g., the Stellarocrinidae Strimple, 1961, Upper Mississippian-Lower Permian), which retained the ridges or remnants of them even though plates of the cup were considerably thickened.

Primitive (normal) anal plates in the cup of Poteriocrinina numbered three, consisting of radianal placed obliquely left below the *C* radial and above the *BC* basal, followed obliquely left by anal *X* resting on the truncate distal edge of the posterior *(CD)* basal, and directly or obliquely above by a right tube plate (= *RX,* of older usage). No representative of the Poteriocrinina possessed a radianal in its most primitive position, directly beneath the *C* radial, as found in some Dendrocrinina (e.g., *Dendrocrinus* HALL, 1852, Middle Ordovician-Upper Silurian, and *Ottawacrinus* BILLINGS, 1887, Middle Ordovician).

Evolution of anal plates in cups of crinoids belonging to this suborder is readily demonstrable to have produced a step-by-step reduction in size and number until they became eliminated completely. First, the right tube plate was squeezed upward out of the cup, leaving the first two anals in their normal positions. Then the anal *X* was expelled and the radianal shifted leftward and upward so as to replace the anal *X*. Very exceptionally the radianal was resorbed (e.g., *Zeacrinites*[1] MOORE & PLUMMER, 1940, text-fig. 43a,c), leaving the anal *X* next above the posterior basal to take over as radianal. Many Pennsylvanian and Permian genera of the Poteriocrinina had only one anal plate (radianal) in their cup. In such crinoids as *Erisocrinus* MEEK & WORTHEN (1865b), Lower Pennsylvanian-Lower Permian, *Arkacrinus* KNAPP (1969), Lower Pennsylvanian, and *Paradelocrinus* MOORE & PLUMMER (1940), Lower to Upper Pennsylvanian, this anal plate generally was not visible externally, for it was reduced in size and confined to a notch on the inner edges of the posterior radial articular facets. Bilateral symmetry had nearly vanished. Finally, perfect pentameral symmetry was attained in *Encrinus,* Middle Triassic, which genus is usually considered to belong to the Articulata. Normally the arms were pinnulate and in later genera with uniserial arms the arms tended to become hyperpinnulate (more than one pinnule to each brachial). Uncommonly, syzgial pairs of brachials developed for increased flexibility of the arms, although with loss of pinnules borne by infrazygals. The latter structure is known only in the families Ampelocrinidae and Cymbiocrinidae and the genus *Araeocrinus* (Rhenocrinidae).

In some lineages the number of arms was reduced to five, which generally but not invariably became very long.

The delicate arms of primitive forms diverged upward with no apparent tendency ever to be closed. Addition of arms led to crowding so that they abutted one another when closed. Most Middle Mississippian and later genera, even those with relatively few arms, tended to close them in a compact manner and if their structure did not allow them to abut (e.g., Stellarocrinidae) spaces between proximal parts of the arms might be occupied by interlocked pinnules. Most pre-Pennsylvanian Ampelocrinidae and Cymbiocrinidae did not attain the ability to close their arms and some genera, never.

A tendency for brachials of adjacent arms to interlock when closed, particularly in proximal sections, is found in the Pirasocrinacea, many genera of the Erisocrinacea, in the Laudonocrinidae of the Lophocrinacea, and Ampelocrinidae of the Agassizocrinacea (e.g., *Arroyocrinus*).

The arms of oldest Poteriocrinina are mostly very numerous as result of isotomous branching in the middle and upper parts of the crown (e.g., Poteriocrinitidae BASSLER, 1938, L.Dev.-U.Perm.; Proctothylacocrinidae KIER, 1952, M.Dev.; Blothrocrinidae MOORE & LAUDON, 1943a, L.Miss.-L.Perm.; Bursacrinidae KIRK, 1947, L.Miss.), or endotomous heterotomous branching (e.g., Zeacrinitidae BASSLER, 1938, L.Miss.-U. Perm.). Generally, the course of evolution led to crinoids having only ten arms, as seen in the host of genera grouped in the families Scytalocrinidae MOORE & LAUDON, 1943a (M.Dev.-U.Perm.); Apographiocrinidae MOORE & LAUDON, 1943 (L.Penn.-U. Perm.); Erisocrinidae S. A. MILLER, 1890 (L.Penn.-L.Perm.); Decadocrinidae BATHER, 1890 (M.Dev.-U.Penn.); Graphiocrinidae WACHSMUTH & SPRINGER, 1886 (L.Carb.-U. Perm.); Diphuicrinidae STRIMPLE & KNAPP, 1966 (L.Penn.-M.Penn.); Paradelocrinidae KNAPP, 1969 (L.Penn.-U.Perm.); Protencrinidae KNAPP, 1969 (M.Penn.-L.Perm.); Catacrinidae KNAPP, 1969 (M.Penn.-U. Perm.); Stachyocrinidae MOORE & STRIMPLE, 1973 (U.Perm.); and others.

Some small crinoids belonging to the Poteriocrinina appear to have been very successful and thus survived through considerable lengths of time. For example, the Ampelocrinidae and Cymbiocrinidae, with long slender arms, were common throughout the Chesterian and by Pennsylvanian

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[1] Misidentification by MOORE & PLUMMER.

time increased in size and general resemblance to associated forms of other families. The ampelocrinids and cymbiocrinids retained many of their unique characters, however, and some genera *(Allosocrinus, Halogetocrinus)* reduced the number of their arms to five. The Decadocrinidae remained small throughout their history but were never very abundant, the last survivors *(Ramulocrinus, Glaukosocrinus)* apparently dying out in the Middle or Late Pennsylvanian.

Most of the Phanocrinidae are small but dominant crinoids in Chesterian deposits. Their affinities with Pennsylvanian derivatives have not been determined, although nearly identical cup shape and small, tubelike anal sac of *Delocrinus* (Catacrinidae) suggest that this widely distributed, very common genus may be one of them. The ten arms of *Delocrinus* are biserial, whereas the arms of *Phanocrinus* are typically uniserial. One large species (*P. imoensis* BURDICK & STRIMPLE, 1973) from the uppermost Chesterian of northern Arkansas has distinctly biserial arms, however.

Crinoids with ten arms, of small or moderate size and with relatively small anal sacs, were very successful in Pennsylvanian time, as indicated by their abundance and variety. The most common genera are *Delocrinus* and *Erisocrinus* with biserial arms and *Apographiocrinus* with uniserial arms. *Apographiocrinus* reached its peak in the Upper Pennsylvanian (Missourian). All ranged into the Permian.

At least moderate mobility on or slightly above shallow sea floors is judged to characterize such late Paleozoic stemless genera as *Agassizocrinus, Paragassizocrinus, Cryphiocrinus, Staphylocrinus,* and *Exochocrinus.* The same habitat is thought to have characterized some stalked crinoids also (e.g., *Calceolispongia, Jimbacrinus, Utharocrinus, Metutharocrinus, Lasanocrinus*), as indicated by pronounced downward projections of their basal or radial plates or both, which served to lift the crinoids slightly above bottom sediment. The stems of these crinoids were relatively slender and probably acted as tethers or sea anchors rather than as upright stalks.

Some lineages display a tendency toward reduction in width of the *B* and *E* radials and ultimately disappearance of arms in these rays. Also, like *B* and *E,* the *C* and *D* rays are mirror-image pairs; changes in the *B* ray simultaneously or eventually appear also in the *E* ray and those in the *C* ray are duplicated in the *D* ray or vice versa. In one of the few available studies of crinoid ontogeny, STRIMPLE (1938, p. 5, 7) observed that primibrachs *1* in the *B* and *E* rays of *Graphiocrinus carbonarius (= Apographiocrinus typicalis)* and *Erisocrinus typus* are shorter (weaker) than in the other three rays. It thus follows that any tendency toward suppression of arms should appear first in the *B* and *E* rays, enhancing bilateral symmetry of the cup oriented in the crinoidal *(A-BC)* plane. Among Permian-age Indocrinidae suppression of one arm took place in the *B* ray of *Metaindocrinus* and in both *B* and *E* rays in *Indocrinus* and *Proindocrinus. Sundacrinus* WANNER (1916a) and *Tribrachyocrinus* M'COY (1847), of Permian age, have two armless radials located in the *B* and *E* rays. STRIMPLE (1951b, p. 200) reported a specimen of *Delocrinus* sp. of Pennsylvanian age in which the *B* radial lacks an arm. *Hosieocrinus* WRIGHT (1952, p. 137) from the Visean of Scotland is reported to have *B* and *E* radials "on which is fused a small triangular *PBr* [primibrach *1*] curved over the top of the cup," or these radials bear no arms. Thus, the evolutionary tendency discussed is recognized in widely different crinoid stocks of Poteriocrinina.

Primitive columns were quinquelobate or quinquestellate and moderately large. Evolution of them was toward pentagonal and then subpentagonal outlines, ultimately to transversely circular, accompanied by reduction in diameter to the point of complete atrophy in some genera. Large quinquestellate columnals are known as late as Morrowan (Early Pennsylvanian) in species of *Heliosocrinus* and quinquelobate stems of *Chlidonocrinus* in Missourian (Upper Pennsylvanian) rocks. Pentagonal or subpentagonal columnals are known in at least proximal portions of the stems of several genera of the Ampelocrinidae and Cymbiocrinidae as late as Virgilian (Late Pennsylvanian) and in *Hydriocrinus* from Missourian (Upper Pennsylvanian) formations. The vast majority of stems belonging to

Mississippian, Pennsylvanian, and Permian Poteriocrinina are circular in cross section.

Search for a possible Paleozoic ancestor of the Jurassic *Pentacrinites* and *Isocrinus* points to Pennsylvanian Ampelocrinidae because several of its genera possess axillary primibrachs 2, syzygial pairs of brachials, and have highly cirriferous pentagonal or quinquelobate stems. *Chlidonocrinus* from the Upper Pennsylvanian has such a stem and therefore may belong to the lineage containing the Mesozoic crinoids mentioned.

EVOLUTION OF FLEXIBLE CRINOIDS

By N. Gary Lane

The origin of flexible crinoids is known much more precisely than for any of the other three subclasses of crinoids. The only and earliest known flexible crinoid from Ordovician rocks is *Protaxocrinus,* which closely resembles associated *Cupulocrinus,* classed as a dicyclic inadunate. The principal differences between these two genera are that *Protaxocrinus* has three unequal infrabasals, rather than the five of *Cupulocrinus,* possesses a distinctive series of anal plates in the posterior interray, and displays a different number and arrangement of primibrachial plates. *Cupulocrinus* has arcuate sutures between brachials which somewhat resemble those associated with the patelloid processes of brachials in many flexible crinoids. This close relationship between flexibles and dicyclic inadunates has been accepted by crinoid workers since first pointed out by Bather in 1900. The probable evolution of *Protaxocrinus* from *Cupulocrinus* provides one of the closest evolutionary links known between major groups of crinoids.

After the Ordovician appearance of *Protaxocrinus,* a great gap exists in our knowledge of flexible crinoids until Late Silurian time. No crinoids of this type are known from Upper Ordovician rocks which yield a variety of camerate and inadunate crinoids, and information is lacking concerning this interval of geologic time when flexible crinoids must have undergone relatively rapid diversification. A single genus of flexibles *(Clidochirus)* is known from the Early Silurian and when next younger Late Silurian flexibles appeared, five families are represented. The order Sagenocrinida is dominant, represented by 46 genera, and the family Homalocrinidae is especially characteristic. Silurian representatives of the Taxocrinida, presumably derived directly from *Protaxocrinus,* include only three genera, in addition to *Protaxocrinus.* It is assumed that the Sagenocrinida evolved from the Taxocrinida, but there is little or no direct fossil evidence for this evolutionary step, which mainly involved changes in the posterior interray.

Phylogenetic relationships among the families of the Sagenocrinida are poorly known. The Icthyocrinidae are recorded in Early Silurian deposits. Five of the 12 families in this order appeared more or less simultaneously in the Late Silurian. Whether the pre-Devonian families each evolved independently from the Taxocrinida, or whether post-Silurian families radiated after the Sagenocrinida had become established, is not known.

Several broad evolutionary trends are evident within the flexible crinoids. The superfamily Lecanocrinacea and the Homalocrinidae among Sagenocrinitacea developed an arrangement of cup and lower arms that is closely similar to and essentially homeomorphic with the cup and arms of inadunate crinoids. Careful study of articular facets and individual brachials has been necessary in order to distinguish some of these flexibles from advanced poteriocrinitid inadunates. The Pennsylvanian and Permian flexible *Cibolocrinus* is a case in point as this genus was classified as an inadunate crinoid for many years before its affinity with other Flexibilia was documented. Specialized end products of flexible evolution, shortly before they became extinct near or at the end of the Permian Period, have been described from the Upper Permian of Timor. These include inadunate-like genera of the Lecanocrinacea, as well as small compact sessile forms adapted for rough-water reef habitats which resemble superficially the modern articulate *Holopus.* Several of these last-surviving flexibles have very short, unbranched arms, that are tightly folded over the top of the theca. Two unusual Permian genera have been reported that have a "bent-stem," analogous with, but not related to, the "bent-crown" of the disparid inadunate family Calceocrinidae. This adaptation permitted lowering of the crown to a position just above the sea floor and may have been an adaptation for rough-water environments. Early flexibles have simple, isotomous arms, but in various groups in both orders of flexibles, heterotomous arm branching developed at various times during the Paleozoic. This trend reached a peak with the late Paleozoic taxocrinoid *Onychocrinus,* which has closely spaced much-branched heterotomous ramules.

Other evolutionary trends include the following: 1) Change in lateral outline of the cup or calyx from steeply conical to a low bowl shape and, in some genera, development of a basal concavity. 2) Infrabasals evolved from high plates that form a conspicuous part of the lateral wall of the cup or calyx to low plates that are completely hidden beneath the proximal stem columnal. In some late Paleozoic flexibles the infrabasals may become fused into a single plate. 3) The primanal shifted from directly below the *C* radial in *Protaxocrinus* to an oblique position. The radianal, or the anal *X* plate, or both, may be eliminated from the cup. 4) Evolutionary trends affecting the development of interbrachial plates between rays are not clearly understood. Many early flexible crinoids have small areas of interbrachial plates, and SPRINGER (1920) believed that the general trend was toward increase in size and number of plates in the interbrachial areas. However, the Sagenocrinitidae have many interbrachials between the rays when they first appear in the Late Silurian. Presumably there were trends both to increase and decrease the importance of these plates in the crown, because some late Paleozoic lecanocrinacean genera lack interbrachials altogether. These plates served to bind together in a flexible way the lower parts of the arms. Perhaps the development of interbrachials was related to the relative strength of the arms and to the strength of waves or currents in various habitats.

EVOLUTION OF ARTICULATE CRINOIDS

By H. WIENBERG RASMUSSEN

The subclass Articulata includes all Mesozoic to Holocene crinoids except Encrinidae, which are now generally referred to Inadunata. No Paleozoic member has been recorded.

Since the time of JAEKEL (1892), it has been generally thought that the Articulata evolved from the dicyclic Inadunata, and more specifically from the Poteriocrinina, by complete elimination of all anal plates from the cup, reduction in size of the five infrabasals as well as the height of tegmen, exposure of mouth and ambulacral groove on the surface of tegmen, enclosure of the axial nerves in canals penetrating basals, radials, and brachials, by formation of well-developed muscular articulations in radials and arms, and by the arms being invariably uniserial and pinnulate.

In the Poteriocrinina the infrabasals are commonly reduced in number to three, or are fused. The radial articular face has a fulcral ridge and ligament fossae, and may have muscular fossae. Anal plates are generally present in the cup, but may disappear. The tegmen generally forms a large ventral sac, but may be flattened in Triassic members. The arms are pinnulate, generally branched, and uniserial or biserial; the column may or may not bear cirri on the nodals. Several of these characters show a trend toward the Articulata.

The Encrinidae, often referred to Articulata, have five small infrabasals, a low tegmen similar to that of the Articulata with exposed mouth and ambulacral groove, and there is no anal plate in the cup. They were considered by BATHER (1896b, 1897a) to be the ancestors of the Isocrinida and the Millericrinida, but the arms are biserial and brachial articulations less advanced. According to JAEKEL (1892) and HILDEBRAND (1926), the Encrinidae are closely related to *Erisocrinus* [= *Stemmatocrinus*] (Erisocrinidae), now referred to the Poteriocrinina. The Triassic Articulata, the Dadocrinidae and Holocrinidae, according to HILDEBRAND, are more similar to *Poteriocrinites* in structure of the cup than to the Encrinidae.

It has not yet been demonstrated whether the Articulata had a monophyletic or polyphyletic origin, nor which of the many families of the Poteriocrinina may have been ancestral.

The Triassic fauna of the Articulata is poor, yet it contains the first representatives of three orders important in the Mesozoic fauna (Fig. 209).

1) The Millericrinida, represented in the Triassic by the Dadocrinidae and perhaps by incompletely known specimens of the Millericrinidae, include the Articulata in which the column has simple symplectial articulations with radiating crenulae and no cirri. Nonmuscular articulations are synarthrial in Millericrinina and synostosial in the Hyocrinina. This order may be ancestral to the Cyrtocrinida with their more or less reduced column and basal circlet and generally without nonmuscular articulations in the arms, and maybe to the Bourgueticrinida, which have synarthrial articulations in the column and synostosial or synarthrial articulations in the arms.

2) The Isocrinida, represented in the Triassic by the Holocrinidae and by various incompletely known Isocrinidae, includes Articulata with a generally five-sided column with symplectial articulations, the crenellae forming a petaloid pattern, and with nodals with a verticil of five radially directed cirri. Nonmuscular brachial articulations include synarthry as well as cryptosyzgy. This order is ancestral to the large order of Comatulida, in which the larval column is discarded and proximal nodals are fused to a centrodorsal with cirri. Nonmuscular articulations include synarthry as well as typical syzygy.

It is possible that the Bourgueticrinida may have been derived by proterogenetic evolution from the Comatulida.

3) The Roveacrinida, represented in the Triassic by the subfamily Somphocrininae, include planktonic microcrinoids with a small cup of radials, more or less reduced basals, and with or without a dorsal plate or rod-shaped element, but no true column. The nonmuscular articulations are synarthrial.

The order Uintacrinida, including only the two Upper Cretaceous genera *Uintacrinus* and *Marsupites,* are large planktonic species with a cup formed by infrabasals, basals, radials and a centrale, but no trace of a column. The arms are connected by a variable number of interbrachial plates. The nonmuscular brachial articulations are syzygial. The affinity of the Uintacrinida with other orders of Articulata is unknown.

It is remarkable that, with very few exceptions, the ramification and articulations of the arms follow the same general pattern in all Articulata. Almost all Articulata have arms divided at primibrachs *2* and have nonmuscular articulations at primibrachs *1-2* and secundibrachs *1-2,* and with variable intervals more distal in the arms. The number of further divisions is variable, and the kind of nonmuscular articulations is different in different groups of Articulata.

The presence or absence of nodals with cirri, and the radiate or petaloid pattern of crenellae in symplectial articulations of the column are the two most distinct and permanent differences between the two large orders of sessile Articulata, the Millericrinida and the Isocrinida, but the origin of these two groups may not be far apart. There is a considerable resemblance between the Triassic Dadocrinidae and Holocrinidae, and nodals with cirri are found in several Poteriocrinina. Also, a petaloid pattern of crenellae may be approached in pentalobate proximal columnals of the Dadocrinidae and several Millericrinidae, and simple radiating crenulae are found in the almost noncirriferous column of the recent *Proisocrinus.* We cannot exclude, therefore, that Isocrinida may be derived from Millericrinida near the beginning of the Mesozoic, or that the two groups may have a common origin from the Poteriocrinina.

The origins of the Roveacrinida and Uin-

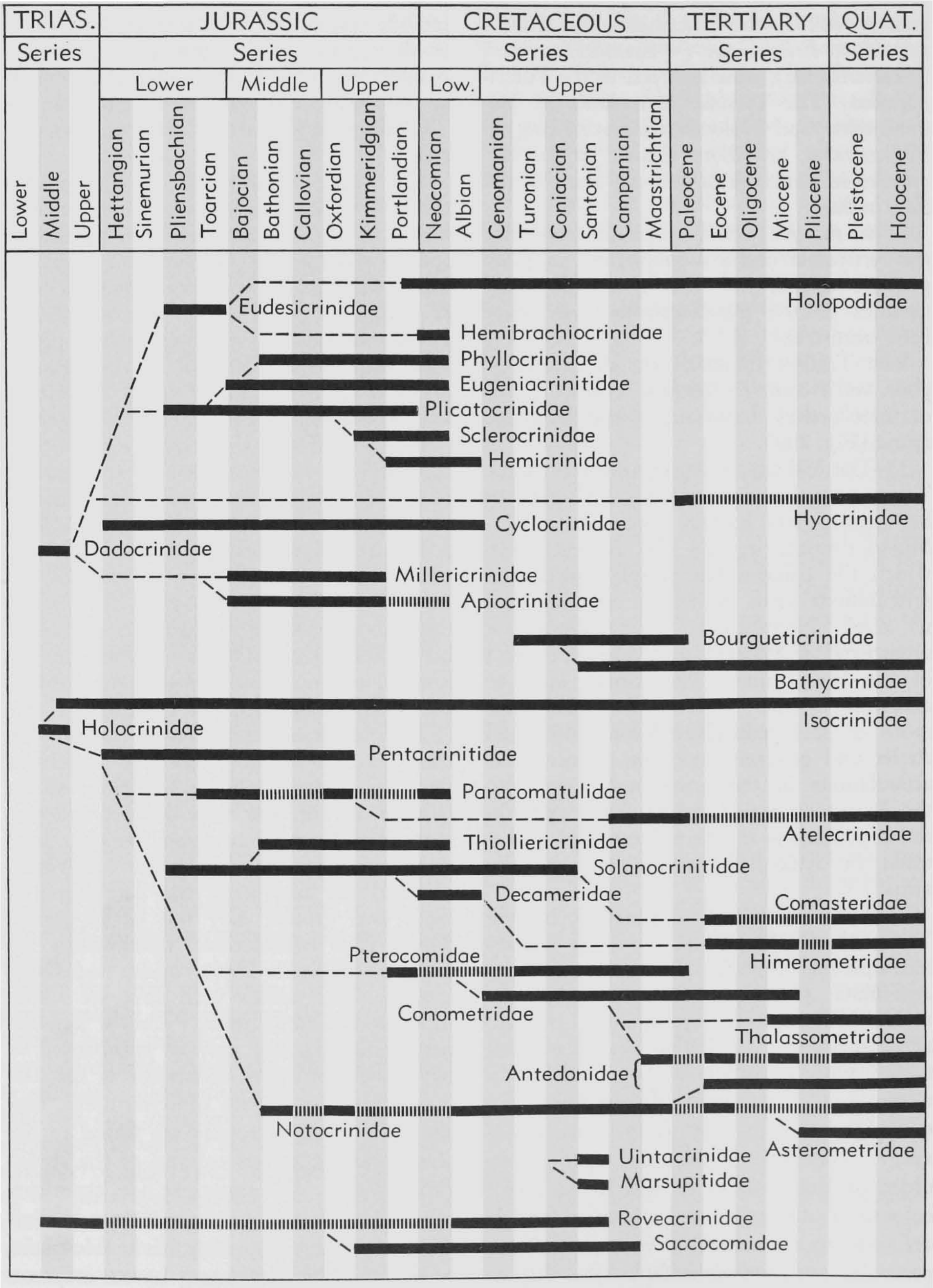

FIG. 209. Diagram showing evolutionary trends of the Articulata (Rasmussen, n). (The lower Paleocene now includes the Danian, which was established in 1846 as uppermost stage of the Cretaceous.)

tacrinida are entirely unknown, although the structure and articulation of the arms of Roveacrinida may have features in common with the Millericrinida, and those of Uintacrinida with the Comatulida.

MILLERICRINIDA

The Dadocrinidae, containing the single genus *Dadocrinus* from the Middle Triassic are the earliest known representatives of the order Millericrinida. According to VON KOENEN (1895a), *Dadocrinus* is related to *Erisocrinus* (Inadunata). Specimens of *Dadocrinus* show considerable individual variation. The column is circular in section, but may be more or less pentagonal in its proximal part as in most of the Millericrinidae. The diameter of the column may be uniform, or it may increase conically in its upper part as in *Apiocrinites* and in some species generally referred to the Millericrinidae. Some specimens of *Dadocrinus* show columnals apparently elliptical in section as in *Bourgueticrinus* although without a fulcral ridge. According to BATHER (1897a), small and low columnals below the conical top of the column may indicate the growth zone below the conical part, thus anticipating the evolution of the uppermost columnals as a proximale similar to that of *Bourgueticrinus*. All of these variations in *Dadocrinus* thus demonstrate features found in the Millericrinidae, Apiocrinitidae, and possibly the Bourgueticrinidae.

The genera of the Millericrinidae are distinguished mainly on form of cup and transition between cup and column. *Liliocrinus* and *Angulocrinus,* with their conical cup, show the greatest resemblance to *Dadocrinus,* and also the gradual transition from column to cup in *Liliocrinus* may be an approach to *Apiocrinites. Millericrinus* is more unique in its low, wide cup and flat base, and *Orbignycrinus* with its hemispherical cup may be an approach toward *Pomatocrinus.*

The Apiocrinitidae, separated by JAEKEL (1918), on the family level from the Millericrinidae, include advanced forms derived from the Millericrinidae, but it is uncertain whether the two genera, *Apiocrinites* and *Guettardicrinus,* which are included by most authors, constitute a natural group. They are both advanced in having modified articular faces in radials and proximal brachials, connected with reduced mobility in the proximal parts of the arms, and this is generally considered a decisive feature of the Apiocrinitidae, but the degree of modification in the articular face is rather variable and to some degree dependent on growth and age of the specimen. We may also consider differences in the transition between cup and column, where the Millericrinidae have a modified uppermost columnal or proximale included in the cup, but *Apiocrinites* a very gradual transition from the cup to the conical upper part of the column. In this respect *Apiocrinites* may well be an extreme end member of evolution from *Liliocrinus* or directly from *Dadocrinus,* while *Guettardicrinus* appears much more similar to *Pomatocrinus* and to certain species similar to *Pomatocrinus* but generally referred to *Apiocrinites* (e.g., *A. insignis, A. beltremieuxi, A. magnificus, A. crassus, A. changarnieri,* and *A. murchisonianus*).

The family Cyclocrinidae, based on very large, cylindrical columnals of *Cyclocrinus,* shows some resemblance to the Millericrinidae and Apiocrinitidae in absence of nodals and cirri, in size, and to some degree in the articular face of columnals, and has been placed in the Millericrinida in the absence of further information.

CYRTOCRINIDA

The Cyrtocrinida were considered separately as a group, Coadunata, by MILLER (1821), as suborder Compacta by JAEKEL (1918), and as order Cyrtocrinida by SIEVERTS-DORECK (in UBAGHS, 1953).

The Cyrtocrinida have a stout cup consisting of more or less fused radials, without distinct indication of basals, attached directly to a short column or to a dorsal element variously interpreted as fused basals or as a proximale. The column, when present, is more or less cylindrical without nodals or cirri, the articular face with radiating marginal crenulae. Synostosis may occur at primibrachs *1-2,* but generally all other articulations are muscular.

WACHSMUTH & SPRINGER (1889) referred

Holopus (together with *Hyocrinus* and *Bathycrinus*) to monocyclic Inadunata (Larviformia), due to its large oral plates and absence of infrabasals. WANNER (1916a, 1929) compared *Holopus* with Permian *Palaeoholopus* and *Brachypus* [*Permobrachypus*] among the dicyclic Flexibilia (Lecanocrinidae) having a sessile cup of similar structure, but without muscular articulations and pinnules.

The Cyrtocrinida, generally referred to Articulata, were derived in the Early Jurassic from the Millericrinidae by reduction of the column and basal circlet and by various modifications in relation to currents and hard substrate, mainly in reef sediments.

The least specialization is found in the Plicatocrinidae, which maintain cylindrical columnals and a conical, upright cup, although unique in fusion of pinnules. From the Plicatocrinidae we may have an evolution through Eugeniacrinitidae to Phyllocrinidae. *Proholopus* is still rather similar to *Plicatocrinus,* but with increasingly compact structure of the cup and beginning separation of the arms it may have evolved to *Pilocrinus* and by further development of interradial projections separating the arms to *Remisovicrinus, Eugeniacrinites, Psalidocrinus* and ultimately to *Phyllocrinus.*

Another line of evolution in Cyrtocrinida is characterized by the cup forming an angle with the column and by increasing fusion within cup and column, which can be followed through Sclerocrinidae to Hemicrinidae.

A third group within the evolution of the Cyrtocrinida is formed by the Holopodina, already present in the Lower Jurassic among the earliest Cyrtocrinida known, and also the only one found in the recent. They have a large and wide cup with radials more or less fused with the dorsal element attached to the substrate. It is not really possible to see any sign of the origin of this group, except that they agree with other Cyrtocrinida in the structure of the cup, the stout arms protecting the ventral side, the muscular articulations, and the presence of pinnules. In Eudesicrinidae and juveniles of Hemibrachiocrinidae the radials are still separated by distinct sutures from the dorsal element and there is an increasing difference in form and size of the radials (and arms). In Holopodidae the elements of the cup are completely fused, but the cups are less oblique.

AFFINITIES OF HYOCRINIDAE

The Hyocrinidae have a long column without nodals or cirri, articular face of columnals with radiating crenulae. Cup thin-walled, formed by large radials and by basals, which are often reduced in number or fused. The arms are narrower than the radials and with several synostosial articulations.

Hyocrinus was placed by ZITTEL (1882) in Plicatocrinidae due to resemblance in column, high conical and thin-walled cup, and presumed absence of basal sutures. CARPENTER (1884a) found *Hyocrinus* to differ from *Plicatocrinus* by the presence of distinct basals and undivided arms, and established the Hyocrinidae as a family. JAEKEL (1892) followed ZITTEL considering *Hyocrinus* closely related to *Plicatocrinus,* but also to *Saccocoma,* and considered this group derived from the early dicyclic Inadunata (Cyathocrinidae).

The genus *Calamocrinus* described by AGASSIZ (1890; 1892) was first considered closely related to *Apiocrinites, Millericrinus,* and *Hyocrinus,* and was referred by BATHER (1900a) to the Apiocrinidae, and by JAEKEL (1918) to the Millericrinidae, far removed from *Hyocrinus,* which was placed among monocyclic Inadunata.

GISLÉN (1939) gave a review of the Hyocrinidae and a discussion of their affinities. He clearly demonstrated *Calamocrinus* with its five distinctly separated basals, high tegmen, and inconspicuous orals as the most primitive member of the family and also the one least similar to the Inadunata. He considered the Hyocrinidae related to the Plicatocrinidae and other Cyrtocrinida but with distinct and well-preserved basals. Moreover, these recent deep-sea crinoids have none of the specializations or adaptations characteristic to the reef-dwelling Cyrtocrinida. SIEVERTS-DORECK (in UBAGHS, 1953) separated the Cyrtocrinida as an order from the Millericrinida without comment on the classification of the Hyocrinidae. So, Hyocrinidae are maintained herein within the Millericrinida, believed to be derived probably from the same or a closely related form as the Plicatocrinidae but following an entirely different line of evolution.

BOURGUETICRINIDA

The Bourgueticrinidae and the Bathycrinidae have generally been classified as belonging to Millericrinida, and agree with that order in possessing a long column without nodals or cirri. Furthermore, in the earliest and most common fossil genus, *Bourgueticrinus,* the uppermost columnals fuse to a large proximale, often compared to the conical proximal part of the column in *Apiocrinites* and a few other Millericrinida. The cup is simple, with exposed circlets of basals and radials, but no trace of infrabasals. The frequent nonmuscular brachial articulations are either synostosial or synarthrial to trifascial.

The Bourgueticrinida, however, did not appear until the Upper Cretaceous after the Millericrinidae and the Apiocrinitidae had disappeared, and they do not share the advanced characters in the modified articular face of radials and proximal brachials found in the Apiocrinitidae, nor is there any close resemblance in the column.

The column of all Bourgueticrinida typically consists of elongate, twisted columnals with elliptical section and synarthrial articulations. This character is also found in the Platycrinitidae among Paleozoic Camerata, but is unique among Articulata except for the larval column of comatulids, discarded by the adults of all comatulids except the Thiolliericrinidae. Synarthrial articulations may also be anticipated in proximal columnals of very small, juvenile specimens of some Isocrinidae (Clark, 1908d, p. 88).

Synarthrial columnals are unknown in the Millericrinida, the only approach being a few, apparently elliptical columnals found in some specimens of *Dadocrinus,* and no intermediate forms between Triassic *Dadocrinus* and Upper Cretaceous *Bourgueticrinus* have been found. On the other hand, it should be mentioned that columnals with simple radiating crenulae similar to the Millericrinida are found in recent *Proisocrinus* and in a few distal columnal articulations of *Porphyrocrinus.*

The identical form of the column in the Bourgueticrinida and in larval Comatulida may indicate a possible relationship between these two orders. The possibility that *Bourgueticrinus* may be ancestral to the Thiolliericrinidae and maybe other comatulids, as proposed by Kirk (1911), can hardly be accepted, since there was a rich evolution of comatulids, including the Thiolliericrinidae, before the first arrival of the Bourgueticrinidae, and furthermore, all comatulids, including the Thiolliericrinidae, have a centrodorsal with cirri derived by evolution from the Isocrinida.

Gislén (1924) considered Bourgueticrinida to be closely related to the Thiolliericrinidae and derived, together with Comatulida, from the Isocrinida (Pentacrinitidae), but in 1937 he postulated Bourgueticrinida to be derived from the Apiocrinitidae or their predecessor, the Dadocrinidae. Although synarthrial columnals are unknown in the Millericrinida, they might, according to Gislén, have been characteristic of juvenile specimens of the Apiocrinitidae as they are of juveniles of comatulids and to some degree isocrinids, thus explaining evolution of the Bourgueticrinida by "neoteny." The larval growth and early ontogeny of stalked crinoids, except *Rhizocrinus,* is, however, virtually unknown.

The "pentacrinoid" larval stage of comatulids, before the development of cirri, has a remarkable resemblance to the Bourgueticrinida, not only in the high and slender, twisted, synarthrial columnals, but also in the disc-shaped, generally enlarged, proximal columnals and the cup with large basal circlet. This may strongly indicate a possible proterogenetic evolution of Bourgueticrinida from the comatulids. The absence of syzygial articulations in the arms is shared not only with the Millericrinida, but also with many early comatulids.

Among late species of the Bourgueticrinida, near the end of the Cretaceous, we find specimens with high basals and a small proximale, indicating a transition from *Bourgueticrinus* toward *Democrinus* and its more specialized aberrant, *Conocrinus,* and also occasionally specimens without a proximale, showing affinity to other Bathycrinidae.

Considering the distinct and unique common features of the column and the ambiguous origin of the group, Rasmussen

(1969) removed the Bourgueticrinidae from the Millericrinida and classified the Bourgueticrinida as an order.

ISOCRINIDA

The origin of the Isocrinida from the Triassic Millericrinida or from unknown Inadunata has never been traced. The Middle Triassic Holocrinidae are considered the most primitive members of this order, and are the only Articulata with exposed infrabasal circlet, but we also find columnals of typical Isocrinidae in the Middle Triassic and uncertain records from the Lower Triassic.

The most obvious feature common to all Isocrinida is the column with nodals and cirri and a petaloid pattern of crenulae.

It is not likely that the Holocrinidae with their exposed infrabasals are closely related to monocyclic Inadunata (Belemnocrinidae) as proposed by WACHSMUTH and SPRINGER (1886), but columns with nodals and cirri are found among several dicyclic Inadunata (Poteriocrinina) such as the Ampelocrinidae and some Botryocrinidae with five exposed or concealed infrabasals and with uniserial, pinnulate arms undivided or divided at primibrachs *2*. It may be possible, perhaps, that the Holocrinidae have evolved from similar forms by reduction of the anal plates and the large anal sac.

HILDEBRAND (1926) considered the Holocrinidae closely related to or even derived from *Dadocrinus* by evolution of cirri and increasement of infrabasals and basals. The greatest resemblance, however, in the column with cirri as well as in the crown is found between the Isocrinidae and the Middle Triassic *Encrinus pentactinus* BRONN, 1837, except for the biserial structure of the arms.

According to VON KOENEN (1895a), the mouth of *Holocrinus wagneri* appears excentric as in the Comasteridae and *Uintacrinus*.

Considerable variation among the Isocrinidae is seen in the articular pattern of columnals, arrangement of cirrus sockets, ramification of arms, and in kind and distribution of nonmuscular brachial articulations. All of these features have been used in separation of the many genera. In fossil identifications, this is inconvenient since numerous distinct species are known from columnals only, and their assignment to genus, therefore, uncertain.

A subdivision of the large family Isocrinidae above the genus-level has never been made, because we cannot demonstrate which characters will unite natural phylogenetic groups. The old division into three genera, *Pentacrinus, Isocrinus,* and *Balanocrinus* (partly under other names), was based on a pattern of columnal articulations. The three fossil genera *Austinocrinus, Isselicrinus,* and *Doreckicrinus* are distinguished by columnal articulations and arrangement of cirrus sockets, but their mutual relationship or relation to other Isocrinidae is unknown, and a similar pattern of columnal articulations may occur among Triassic Isocrinidae as well as in recent *Annacrinus.*

SIEVERTS-DORECK (1944) considered *Balanocrinus* (including *Isselicrinus*) to be derived from early *Isocrinus* through change of columnal articular pattern and by development of cryptosyzygial instead of synarthrial articulation at primibrachs *1-2,* and *Austinocrinus* to be derived from *Balanocrinus* by evolution of a marginal zone of crenellae in the columnals.

CARPENTER (1884a) divided the recent Isocrinidae into what he considered "two very natural groups," those with synarthrial articulation and those with cryptosyzygial articulation at primibrachs *1-2*. If the many genera of Isocrinidae, now accepted, are divided according to this criterion, we find in the first group: *Isocrinus, Chladocrinus, Chariocrinus, Hypalocrinus,* and apparently *Balanocrinus* (with different columnal articulation), and in the second group: *Nielsenicrinus, Cainocrinus, Teliocrinus, Cenocrinus,* and *Endoxocrinus* as well as *Metacrinus* (with greater number of primibrachs) and the four genera *Austinocrinus, Isselicrinus, Doreckicrinus,* and *Annacrinus* (with different columnal articulations). According to CARPENTER (1879a) and CLARK (1908e), the articulations primibrachs *1-2* and secundibrachs *1-2* are homologous and identical, but any synarthrial articulation may be replaced by other kinds of nonmuscular articulation ("syzygy"). In *Cainocrinus, Nielsenicrinus,* and *Teliocrinus* we find primibrachs *1-2* cryptosyzygial and secundibrachs *1-2* synarthrial. So it is uncertain in which group these three genera belong. Also, it is clear that subdivision based on columnal articulations differs from subdivision based on brachial articulation.

The very few Lower Triassic columnals referred to Isocrinidae are dubious and indeterminable, but in the Middle Triassic there is a rich fauna of columnals showing remarkable variation. Although described by BATHER as *Isocrinus,* there are also columnals with an articular face similar to *Balanocrinus* as well as some with very long crenellae in the radial areas as in recent *Annacrinus,* and cylindrical columnals rather similar to *Austinocrinus.* The first species with some resemblance to *Pentacrinites* seem to be *"Isocrinus" gravinae* from the Upper Triassic of Alaska and *P. versistellatus* from the Alpine Upper Triassic. The Pentacrinitidae, or at least certain species, are very different from the Isocrinidae in columnal articulations, basal circlet, and endotomous branching of arms after the second division. They may be derived from early Isocrinidae or more likely from their predecessors.

COMATULIDA

By the beginning of this century about 188 species of recent comatulids had been described and were referred to six generally accepted genera and about 127 fossil species referred to nine fossil and some of the recent genera. The distinction of modern genera was based mainly on the central or excentric position of the mouth, the size of basals and the arms undivided or divided; further informal grouping of species was based on pattern of division and articulation in arms.

Since A. H. CLARK (1907) began his studies of recent comatulids, the number has increased to 530 accepted species, 138 genera, and 17 families, synonyms and fossils excluded. Of these new forms, CLARK himself established 310 species, 124 genera, and 14 families, most of them during the years 1908 to 1915. He developed an entirely new scheme of classification on the basis of recent forms alone, and this was done explicitly and quite regardless of their fossil relatives: "The palaeontological succession of crinoid types is not at all to be trusted in matters of crinoid phylogeny, except possibly on the basis of broad averages. Phylogenetic facts must be acquired through the study of comparative anatomy of the group, combined with the study of the embryology and later development; later they may be tested in the light of the palaeontological record if one so desires" (CLARK, 1915a, p. 183). A discussion of the geological history of recent crinoids and relationship to their fossil representatives was, according to CLARK (1915a, p. 15), planned to end his monograph on the existing crinoids. The first volume of this large and valuable monograph, including introduction and comatulids, was started in 1915, and the fifth and last part of the volume, although more or less completed before 1924, was published in 1967 in collaboration with A. M. CLARK after the death of A. H. CLARK. A section on the phylogeny of crinoids was never written, except for a small note by CLARK (1910b) and scattered remarks on primitive or advanced and specialized groups or features in his monograph do not reveal any phylogenetic pattern of comatulid groups except that the two suborders, Oligophreata and Macrophreata, into which he divided the comatulids are considered as "two rather independent groups."

The main features used by CLARK for identification and classification of comatulids are size and structure of proximal pinnules, size, structure and number of cirri and cirrals, and division of arms. Such features are, with few exceptions, unknown in fossil comatulids. Other features such as form of centrodorsal, arrangement of cirrus sockets, ventral face of centrodorsal, form and reduction of basals, and form of articular face of radials, which are seen in most fossil comatulids, are less considered in the classification by CLARK, and to some degree undescribed in many modern species and genera. To bring fossil and recent comatulids together in a common classification is therefore at present a most difficult task. Moreover, it is not certain that present subdivision of recent comatulids reflects a natural classification in agreement with phylogeny. GISLÉN (1922) expressed his reservation to the validity of species and genera based on very small differences in length of pinnules and other features.

E. Kirk (1911) made the first important contribution to the origin of comatulids. He considered the comatulids to be a probable polyphyletic group representing a number of convergent lines of evolution, derived at different times in the Mesozoic from one or more groups of crinoids by a reduction of the columnal and fusion of columnals to form a centrodorsal. The dicyclic origin according to the law of Wachsmuth & Springer is demonstrated by the radial orientation of the first verticil of cirri in larval comatulids. In several groups of stalked Mesozoic crinoids, we find the tendency to stop the permanent formation of new columnals immediately below the cup, and thus a permanently uppermost columnal, which may be enlarged and differentiated, is obtained, forming a proximale. This may be indicated in *Millericrinus charpyi* and *M. beaumonti* and is characteristic of *Bourgueticrinus,* where the proximale is intimately connected with the thecal structure and infrabasals have disappeared or fused with the proximale. The column in such forms has a tendency to break immediately below the proximale, where the small and new columnals are placed. Such a break and detachment, at first only in the adult, may in later forms take place earlier in the ontogeny. By acquisition of cirri on the proximale, a true centrodorsal is formed and the comatulid stage is reached. The centrodorsal in such comatulids consists of a single enlarged columnal and is low, with few and irregularly arranged cirrus sockets. This transition from *Bourgueticrinus* or forms related to the comatulids is illustrated, according to Kirk, by the Lower Cretaceous (U.Jur.-L. Cret.) *Thiolliericrinus,* which maintains a column similar to *Bourgueticrinus* in the adult stage, and a centrodorsal with only few and small, irregularly placed cirrus sockets in some species *(T. heberti),* but larger sockets in other presumed later species. *Thiolliericrinus* was therefore considered as the start of one line of comatulid evolution, leading to comatulids with a low centrodorsal and few, irregularly placed cirrus sockets.

Other comatulids, according to Kirk, have a centrodorsal formed by fusion of several columnals, as may be indicated by larval development of some species *(Koehlermetra porrecta)* in which a number of proximal columnals are enlarged and the first cirri are formed from a single verticil of radially placed sockets.

Contemporary with *Thiolliericrinus,* we find "highly specialized" comatulids which may be traced far back in the Jurassic, mainly forms with large centrodorsal and stout arms. The extremely variable degree of specialization among contemporary comatulids was taken by Kirk to indicate different lines of comatulids developed at different times from stemmed crinoids, and the ancestors may be looked for among the Apiocrinitidae and the Bourgueticrinidae as well as the Pentacrinitidae.

The pentagonal section of the centrodorsal in many comatulids, the stellate scar from the larval column in juvenile centrodorsals of many comatulids, and the petaloid, crenulate basals in some Jurassic comatulids *(Archaeometra scrobiculata)* extremely similar to *Pentacrinites dargniesi,* indicate comatulids derived not from *Bourgueticrinus* but from forms with a pentagonal column, i.e., the Pentacrinitidae (Isocrinida). Also, the tendency to abbreviation and modification of the column, resembling an articulated centrodorsal in *Pentacrinites collenoti* and *P. sorlinensis,* indicates that some comatulid lines may have evolved from Pentacrinitidae.

Among the Millericrinida we may also find species with columns resembling the Pentacrinitidae in a more or less petaloid articular pattern such as *Millericrinus charpyi* and species with an abbreviated column such as *Millericrinus partti,* although without cirri. Kirk did not exclude an evolution also from such forms to the comatulid stage.

Clark (1915a, p. 16, 17, 222) followed the concept of Kirk with some modification, deriving not only comatulids but also Isocrinida by evolution in opposite directions from *Thiolliericrinus* or closely related Thiolliericrinidae. In comatulids the formation of columnals stops after the formation of the first and only nodal, and this nodal remains attached to the cup as a centrodorsal when the larval column is discarded. In the Isocrinida, the column is strongly elongated by a continuous formation of proximal columnals and by repeated formation of cirriferous nodals, each of which corresponds to a centrodorsal.

GISLÉN (1924) slightly modified the arrangement of recent comatulids given by CLARK to agree better with their fossil representatives. He based the groups mainly on features in the centrodorsal and radials that are present also in fossil species. From the study of early (Jurassic) comatulids he concluded, as did KIRK, that there are such considerable differences between Jurassic comatulids that a polyphyletic origin is most likely. He found that most primitive fossil comatulids have a conical or columnar centrodorsal with cirrus sockets arranged in two columns on each radial side and with a distinct fulcral ridge on the cirrus sockets as in the Isocrinida. He therefore rejected an evolution from species with a noncirriferous column and proximale by subsequent evolution of cirri in forms like *Thiolliericinus,* and he accepted only the Pentacrinitidae (Isocrinida) as ancestors to the different lines of comatulid evolution. The more or less five-sided centrodorsal and the presence in some recent and fossil specimens of five interradial impressions in the dorsal side of the centrodorsal, resembling the petaloid pattern of columnals in *Pentacrinites,* and formed presumably as remains of a petaloid articulation in the uppermost larval columnals, were taken as indication that comatulids evolved from species with a pentagonal column. He concluded that the origin of comatulids should be searched among stalked Triassic or Jurassic crinoids with a pentagonal column and with verticils of five cirri attached to nodal columnals. The greatest resemblance to the primitive centrodorsal he found in Pentacrinitidae with closely placed nodals and almost no internodals in the proximal part of the column. In species with very low nodals such as *Pentacrinites dargniesi* the cirrus sockets of successive nodals may be displaced alternating right and left of the midradial line, thus forming two columns of sockets on each radial side of the column. He also found that the retarded evolution of the most proximal pinnules in comatulids indicated that comatulids evolved from crinoids with reduced proximal pinnules due to extension of the disc up between the arms as described for *Seirocrinus* among the Pentacrinitidae, but also found in several other groups of the Articulata. He excluded the Thiolliericrinidae from the comatulids and rejected this group as ancestral to other comatulids, but considered the Thiolliericrinidae as a separate line of evolution, in most of their characters so similar to the Solanocrinitidae that most likely they came from the same ancestral form among Pentacrinitidae.

One line of evolution among comatulids, according to GISLÉN, is formed by the Comasteridae, to which he referred the fossil *Palaeocomaster,* which is the oldest comatulid known. It has a large, discoidal centrodorsal with rather few and small, closely placed, almost smooth cirrus sockets arranged in a few irregular circles. The centrodorsal cavity is small. The basals are rod shaped. The articular face of radials is steep to vertical, generally with small and low ventral muscular fossae except in the oldest forms, and with a large radial cavity. This group, according to GISLÉN, shows resemblance to *Seirocrinus* among the Pentacrinitidae in the commonly reduced cirri.

Archaeometra and other Solanocrinitidae with a large discoidal to columnar centrodorsal, large cirrus sockets with distinct fulcral ridge, generally arranged in distinct columns and with very stout basals at least in the oldest forms *(Archaeometra)* constitute another line of comatulid evolution, probably derived (together with Thiolliericrinidae) a little later in the Jurassic from forms more similar to *Pentacrinites.* The radial articular face is steep to vertical with very low muscular fossae, and the radial cavity is large. The presence of coelomic furrows in the ventral face of the centrodorsal, found in many Solanocrinitacea, indicates evolution toward recent Mariametracea by reduction of basals and of sculpture on cirrus sockets.

A third group comprising two lines of evolution are, according to GISLÉN, the Notocrinacea (including Asterometridae) and the Conometridae (succeeded by the Thalassometridae), both lines characterized by a conical to discoidal centrodorsal and often somewhat sculptured cirrus sockets more or less columnar in arrangement. The centrodorsal cavity is moderate. Basals are rod shaped. Articular face of radials display rather large muscular fossae. The radial cavity is moderate to small. Pinnulars are generally carinate. The Notocrinacea are represented in the Cretaceous by *Loriolometra* and *Glenotremites,* which have large, crenulate cirrus sockets in 10 to 20 more or less distinct columns and deep coelomic canals forming radial pits in the centrodorsal. Later forms such as *Semiometra* and the recent *Notocrinus* have smooth cirrus sockets, which are in *Semiometra* small and numerous. The Conometridae represented in the Cretaceous by *Amphorometra* and in the Tertiary by *Conometra* also include, according to GISLÉN, the Cretaceous genera *Placometra* and *Jaekelometra.* Although there are great similarities to the Jurassic *Archaeometra,* GISLÉN found that the Conometridae and the recent Thalassometridae may be related to the Upper Jurassic *Pterocoma,* and together with Notocrinacea these groups may have evolved from the Pentacrinitidae.

The Macrophreata (Antedonacea) also, according to GISLÉN, are a polyphyletic group. One line of evolution may lead from the Notocrinacea through fossil Paleantedonidae to the Antedoninae, Thysanometrinae and perhaps other Antedonacea with more or less hemispherical centrodorsal, moderate centrodorsal cavity, numerous small, closely alternating cirrus sockets, reduced basals, moderately embayed synarthrial articulations, and in some cases with coelomic radial pits in the centrodorsal. A second line of evolution may lead from the Conometridae to the Thalassometridae and to groups of the Antedonacea including the Zenometrinae, Bathymetrinae, Heliometrinae, Isometrinae, and also to the Atelecrinidae and Pentametrocrinidae, all characterized more or less by a conical or columnar centrodorsal, large to very large centrodorsal cavity, cirrus sockets arranged in columns, rod-shaped basals commonly present, and synarthrial articulations generally deeply embayed. The Perometrinae may belong to the same line of evolution as the Antedoninae or may have evolved from the Colobometridae (Mariametracea).

Few of the modifications made by GISLÉN to the classification by A. H. CLARK were accepted by CLARK in his great monograph on all recent comatulids, and no attempts at new classifications of comatulids have been published since.

Apart from the description of several recent and fossil comatulids, the most important new contribution to the evolution of comatulids is the discovery by H. HESS (1951) of the Middle Jurassic *Paracomatula. Paracomatula* has an articulated "centrodorsal" consisting of a few nodals and resembling a very short column of *Pentacrinites.* The stellate basal ring has a petaloid pattern of crenellae toward the centrodorsal. Primibrachs *1-2* and secundibrachs *1-2* are synarthrial and rather flat. The arms divide at primibrachs *2* only. Secundibrachs *3-4* are syzygial, more distal syzygies with very few, radiating ridges. This species shows the most perfect transition from the Jurassic Isocrinida such as the Middle Jurassic *Pentacrinites dargniesi* to early comatulids such as the Middle to Upper Jurassic *Archaeometra,* and supports the theory of KIRK and GISLÉN on evolution of comatulids from Pentacrinitidae. However, the long, slender arms and the large, muscular fossae of the radials are not similar to Comasteridae but rather to *Archaeometra* or to the Atelecrinidae.

Since this discovery another two genera and three species of the Paracomatulidae with articulated "centrodorsal" have been found, although not yet described. These new forms show a beautifully preserved, conical, articulated centrodorsal, and one of them shows a most remarkable resemblance to the Atelecrinidae in form of the centrodorsal and cirrus sockets but still with a stellate ring of basals with a petaloid pattern of crenellae. The variation in the centrodorsal cavity in *Jaekelometra* and in the Antedonacea indicates that the division of comatulids into Oligophreata and Macrophreata is more problematic than considered by A. H. CLARK.

Evolutionary tendencies among comatulids are now seen as a gradual modification of the primitive ancestral or juvenile features in different parts of the crinoid skeleton. The conical or columnar centrodorsal dominating in the Jurassic and expected from presumed ancestors among the Isocrinida may modify to hemispherical or discoidal. The arrangement of cirrus sockets in 10 columns is modified ontogenetically and presumably phylogenetically by intercalation of new sockets in the midradial areas, the number thus increasing to 15 or 20 less distinct columns, and may proceed to a more irregular pattern of verticils or "circles." The cirrus sockets are commonly large and with more or less distinct fulcral ridge or tubercles in most Mesozoic comatulids, but are almost smooth in most Tertiary and recent species. The centrodorsal cavity, which is small and narrow in most early comatulids, becomes extremely small and shallow in the Decameridae, very variable in *Jaekelometra,* and in *Microcrinus,* and large to very large and deep in most Atelecrinidae and some Antedonidae. The basals, which form a rather stout, stellate ring of plates similar to the Isocrinida in *Paracomatula* and *Archaeometra,* become narrow and rod shaped with few or no crenellae and are centrally almost separated in most comatulids and may be further reduced to a delicate, perforate central plate, the rosette, in the Mariametracea and most Antedonacea. A special evolution of large polygonal basals surrounded by the radial ring is found in Decameridae and a circlet of large basal plates is maintained from the larval stage by a proterogenetic evolution in most Atelecrinidae. Coelomic furrows or depressions in the ventral face of the centrodorsal are characteristic of the Decameridae and most Mariametracea. Coelomic canals are seen as radial pits in the centrodorsal of most Notocrinacea, Asterometridae, and in some *Jaekelometra, Microcrinus,* and *Antedon.* The radial articular face is rather high and steep in the Paracomatulacea and *Archaeometra,* but may change in different directions, being very high with large muscular fossae on thin and steep ventral flanges and with a narrow radial cavity in most Atelecrinidae, Antedonidae, and Thalassometridae, whereas the radials are low and compact with small muscular fossae and a large radial cavity in most Solanocrinitacea, Comasteracea, and Mariametracea. The arms are almost always divided at primibrachs 2 and often further divided, and there is a synarthrial articulation at primibrachs *1-2* and generally also in succeeding brachials *1-2.* A syzygial articulation at primibrachs *1-2* is found in the Zygometridae and *Eudiocrinus* among the Mariametracea and in a few Comasteracea. Arms divided at primibrachs *1* are found in some Solanocrinitacea, and undivided arms are found in some Solanocrinitacea, in *Atopocrinus, Eudiocrinus,* and in the Pentametrocrinidae. The synarthrial articulations are rather flat in the Solanocrinitacea, Comasteracea, Mariametracea, and Notocrinacea, but may be more or less embayed in some Atelecrinidae, Tropiometracea, and Antedonacea. Syzygial articulations are almost always present at brachials *3-4* and with variable intervals more distal, but are missing in some Solanocrinitacea. Syzygy with very few radiating ridges are found in some Paracomatulidae, Atelecrinidae, and Solanocrinitacea. Very special features in the Comasteridae are the excentric mouth and the pinnular comb, although the mouth may also be slightly excentric in *Atelecrinus.*

A phylogenetic classification of comatulids should be based on further studies of the evolution in several features such as described above, and of the distribution of such characters especially in fossil species, as well as on more detailed studies of early comatulids and especially the structure and affinities of Paracomatulacea.

The new, partly unpublished observations on fossil crinoids support that comatulids evolved from the Isocrinida through the Paracomatulidae, and we find within this family a considerable variation including species similar to the Atelecrinidae and *Archaeometra* in several features. A polyphyletic origin of comatulids is no longer certain. The interpretation by A. H. Clark of the centrodorsal as a modified single columnal is not supported by the study of fossils, nor is the interpretation of the basal rays (rod-shaped basals) as secondary calcifications independent of the basals. The continuous growth and formation of new cirrus sockets and cirri at the ventral edge of the centrodorsal does not support the general opinion that columnal growth is stopped by a fusion of one columnal with the infrabasals to form a centrodorsal. It is possible, therefore, that only columnals are included in the centrodorsal, and that infrabasals, if present in early larval stage, are resorbed. The Thiollieririnidae appear to be a proterogenetic evolution from the Solanocrinitacea. The origin of the Comasteridae is uncertain. The excentric mouth often associated with reduction in posterior arms, the specialized proximal pinnules, and the common reduction of centrodorsal and cirri indicate that this is a specialized group, hardly ancestral to other groups of comatulids. Most of these special features are not seen in fossils, and there is no certain indication of the Mesozoic Comasteridae. The origin of the Comasteridae is therefore uncertain. A more or less excentric mouth may be found in some Atelecrinidae, and cannot be excluded in some Paracomatulacea resembling the Atelecrinidae in other characters. The centrodorsal and the radial ring of the Comasteridae are more similar to those of *Palaeocomaster* and other Solanocrinitacea.

The classification of comatulids used in the *Treatise* follows, with very few modifications, the classification used by A. H. Clark in his great monograph on the existing crinoids (1915-67), not because this classification is considered final or satisfactory, but in order to facilitate comparison between fossil and recent comatulids and thus encourage future reconsideration of comatulid evolution. For this reason, also, the text includes a record of all genera, also when unknown as fossil, and a description of all groups above the genus level with special reference to features relevant in the study of fossils, even if these characters have not been used in classification of modern species, and are described only for some of the species or genera of each group. The use of superfamilies by A. H. Clark has been followed with change of endings in order to agree with other sections of this *Treatise* volume.

UINTACRINIDA

The two families included, each with a single genus restricted to the Upper Cretaceous (Santon.), are both characterized by a large, ovate cup and thin plates including a centrale without trace of any column or attachment. The arms are long, pinnulate, divided at primibrachs 2 only, and with muscular and syzygial articulations. There is a variable number of fixed brachials, fixed pinnulars, and interbrachial plates.

In *Uintacrinus,* the fixed proximal brachials are thin and flat like plates of the cup, and there is a considerable number of fixed brachials, pinnulars, and interbrachial plates. The structure of the base in *Uintacrinus* is very confusing and has been much discussed. Apparently about half of the specimens are dicyclic with small but distinct infrabasals and half are without trace of infrabasals. Furthermore, there is always a centrale, variously interpreted as a rudiment of the column or a secondary additional plate like the interbrachials. Since the infrabasals are by no means reduced or vestigial when present, this appears to be a unique species of crinoid with both monocyclic and dicyclic specimens. It has never occurred to the many specialists discussing this paradox that if the centrale is a secondary additional plate filling up the space inside the basal circlet, then the same explanation may as well be given to the presumed infrabasals. The latter explanation is consistent also with the presence of a few specimens with different composition of the dorsal area (see Fig. 609,*1f-j*) including two or three plates of similar size, or one large and three to five smaller plates of different size. It is a general rule to the secondary plates that a stellate outline or a re-entrant angle or a meeting of more than three plates in a point never occur. Therefore, a centrale is never stellate; if the dorsal area inside the basal circlet is stellate, then a smaller plate is formed in each re-entrant angle, and these are the plates generally interpreted as infrabasals.

The flexible tegmen of *Uintacrinus* shows a central anal tube and excentric mouth as in most Comasteridae and, according to von Koenen (1895a), maybe also in *Holocrinus.*

Marsupites has five large infrabasals, basals, radials, and a large centrale. The arms are narrow, widely separated and not flattened as plates of the cup, although the arms and most proximal pinnules may be connected by a few thin interbrachial plates. Provided the infrabasals are true primary plates of the cup, this is the only genus of the Articulata with large exposed infrabasals, except for the Triassic Holocrinidae (and maybe *Uintacrinus*).

Several authors have classified *Uintacrinus* with the Flexibilia or compared it with *Forbesiocrinus* and the Icthyocrinidae (Schlüter, 1878; Neumayr, 1889; Zittel, 1895), many of which show interbrachial plates, a flexible tegmen, and uniserial arms, but have anal plates in the cup, three infrabasals, a column, no syzygy, and no pinnules.

Jaekel (1894) placed *Marsupites* in dicyclic Inadunata and *Uintacrinus* in dicyclic Camerata.

Bather (1896b) considered all resemblance between *Marsupites* and *Uintacrinus* secondary as results of adaptation to a pelagic life. He found that primary structures such as absence of anal plates in the cup, uniserial pinnulate arms with axial canal, muscular and syzygial articulations, arms divided at primibrachs *2*, and primibrachials connected by interbrachial plates, indicate affinity with Articulata and especially with *Dadocrinus,* although differing in all those characters interpreted as adaptation to the pelagic habit.

Springer (1901) observed the structure of tegmen with excentric mouth and exposed ambulacra. He emphasized the resemblance to the Comasteridae not only in tegmen and mouth, but also in syzygial articulations.

Clark (1909h) included the Uintacrinidae and the Marsupitidae as pelagic comatulids with unmetamorphosed basals and infrabasals under the name "Comatulides Innatantes." Also, Gislén (1924) considered *Uintacrinus* to be probably derived from the same ancestral form as the comatulids.

Kirk (1911) considered the flexible tegmen and excentric mouth of *Uintacrinus* as secondary characters, and that *Uintacrinus* was derived from the same dicyclic Inadunata as *Dadocrinus* and other Articulata.

ROVEACRINIDA

The small, planktonic, stemless Roveacrinida, including the Roveacrinidae and the Saccocomidae, have a generally thin-walled cup of large, thin radials, with or without small basals, and in the Saccocomidae a small centrale and in the Somphocrininae a large, conical or rod-shaped dorsal element variously interpreted as a centrale, a centrodorsal, or a fused basal circlet. Arms generally divided at primibrachs *2* and with a proximal pinnule gap. Muscular brachial articulations alternate with cryptosynarthrial or synostosial articulations.

Goldfuss (1831) described species of *Saccocoma* under the genus *Comatula.*

Neumayr (1889) considered *Saccocoma* to be juvenile specimens of an unknown stemless crinoid similar to *Plicatocrinus.*

Jaekel (1893) compared *Saccocoma* with *Plicatocrinus* and *Hyocrinus,* all having a thin-walled cup with large, thin radials, reduced or fused basals and narrow arms, in *Saccocoma* and *Hyocrinus* with many nonmuscular articulations and a proximal pinnule gap, but in *Hyocrinus* with undivided arms. He considered *Saccocoma* closely related to *Hyocrinus* and *Plicatocrinus,* and these groups derived not from the Articulata or the Poteriocrinitidae but from primitive, dicyclic Inadunata, the Cyathocrinoidea.

Douglas (1908) described *Roveacrinus* and considered it related to *"Extracrinus" (= Pentacrinites)* due to the downward prolongation of the radials.

In 1918 Jaekel placed the Saccocomidae and the Hyocrinidae, together with the Plicatocrinidae and the Eudesicrinidae, in his monocyclic order Costata, also including families now referred to the Inadunata and the Camerata, but *Roveacrinus* (under the name of *Drepanocrinus*) was placed in the Rhizocrinidae (= Bathycrinidae).

Bather (1928) considered *Roveacrinus* allied to *Phyllocrinus,* due to ventral projections from the cup separating the arms.

Sieverts (1932a, 1933b), following Jaekel, considered *Roveacrinus* probably related to the Bathycrinidae due to similar structure of arms, but in 1943 she included the genus in Saccocomidae.

Peck (1943) established the family Roveacrinidae as a group of monocyclic Inadunata, but at the same time as derived from Jurassic or Cretaceous comatulids. In 1948, after a description of Triassic Roveacrinidae with a spine-formed dorsal element, he declared all previously suggested relationships improbable, and the derivation of the Roveacrinidae unclear. In 1955, he classified the family in the Articulata.

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

ECOLOGY AND PALEOECOLOGY

By ALBERT BREIMER and N. GARY LANE

[Instituut voor Aardwetenschappen der Vrije Universiteit, Amsterdam; University of Indiana]

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 physio-