



# Fossil Crinoids

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# 1

## Crinoid Form and Function

**WILLIAM I. AUSICH, CARLTON E. BRETT, HANS HESS AND  
MICHAEL J. SIMMS**

### ANCESTORS, ARCHITECTURE AND ADAPTATION

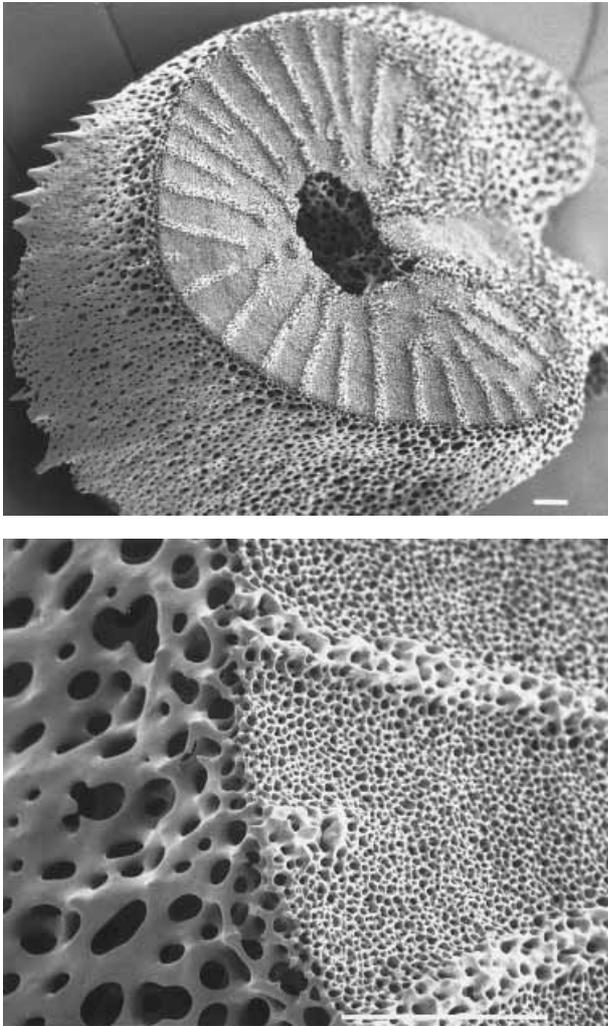
Environmental adaptation accounts for much of the morphological variety within the class Crinoidea, but two other factors also have an important influence on gross morphology. First, crinoid morphology is constrained by the evolutionary history of the group; in other words, much of a crinoid's morphology is inherited from its ancestors. This is particularly evident in the pentaradial symmetry and calcite endoskeleton that dominate echinoderm morphology. Second, the crinoid skeleton and soft tissues have certain physical properties and limits within which the animal must operate. Some aspects of crinoid morphology are strategies for reducing these architectural constraints rather than being direct adaptations to particular environmental factors. For example, the crinoid skeleton is composed largely of discrete ossicles connected by ligaments and other soft tissue. By adopting this multi-element construction, crinoids overcome the inherent inflexibility of individual calcite ossicles.

To understand the functional morphology of crinoids, fundamental constraints of ancestry, constructional materials and ecology must be considered. Crinoids are the most primitive group among extant echinoderms and, typically, retain at least a vestige of the stem that characterizes the largely extinct pelmatozoans. Like all pelmatozoans, crinoids are largely sessile and exclusively suspension-feeding.

### SOFT AND HARD PARTS

The numerous calcareous plates of living crinoids are produced within the body wall, so that they are actually part of an endoskeleton. The bulk of the animal is the skeleton, with only a small percentage of living tissue. Under high magnification, crinoid plates are seen to be highly porous (Fig. 4). In life these pores were filled with tissue. This skeletal microstructure is called stereom, and it is easily recognized in well-preserved fossil ossicles and in thin sections.

The soft parts of crinoids are quite inconspicuous. The digestive tract with mouth, oesophagus, gut, rectum and anus is situated in the aboral cup. The anus and mouth are on the upper surface (Figs. 5, 6), with the anus commonly elevated on a cone or tube (Fig. 6) that is reinforced by platelets (Figs. 37, 38). A system of fluid-filled tubes, called the water-vascular system, is unique and vital for all echinoderms. The central element of the water-vascular system is the ring canal around the oesophagus. Radial canals extend from the ring canal into arms and pinnules, and these extensions underlie the ambulacra (Fig. 7). The water-vascular system canals terminate in the tube feet. This system has a hydrostatic function, as in other echinoderms; it seems to counteract muscular contractions of the tube feet by lengthening them. Tube feet, also called podia or tentacles, are part of the food-gathering ambulacral system, which is made up of ciliated, sensory and mucus-



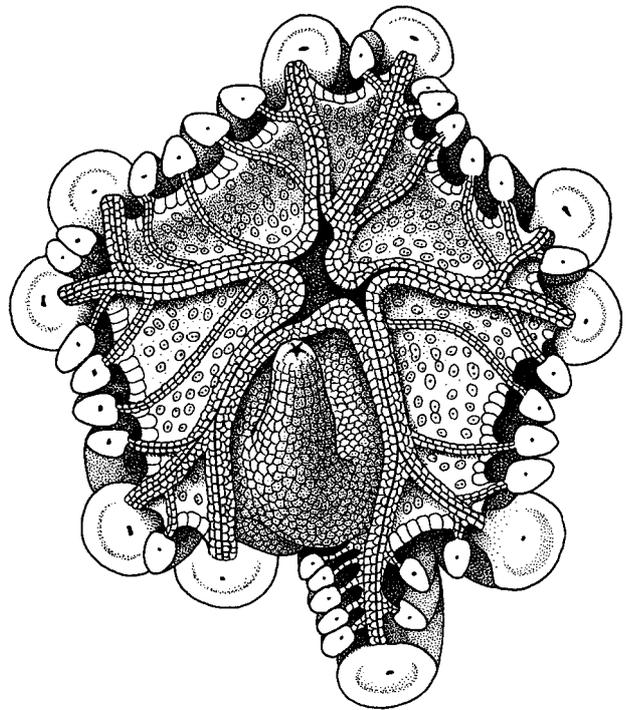
**Fig. 4.** Scanning electron photomicrographs of a brachial plate from *Promachocrinus kerguelensis* (Recent from the McMurdo Shelf, Antarctica) showing stereomic microstructure. This brachial facet with radiating crenulae is a ligamentary articulation, called syzygy. (Courtesy C. P. Hart and W. I. Ausich.)  $\times 50$  and  $\times 300$  (scale bars = 100  $\mu\text{m}$ ).

secreting cells. In living crinoids, food particles are detected on impact by tube foot sensory cells and secured by mucus secretions of the finger-like extensions (papillae) of the tube feet (Fig. 7). Food particles are then passed along the ciliated food grooves to the mouth. The food grooves are commonly protected by platelets (Fig. 50c), or they may be concealed by enrolling the arms (Figs. 31–34). This ambulacral epidermis is underlain by a layer of nerve cells, to which the sensory cells connect. The nervous system is formed by a ring in the cup with extensions into the stem and cirri, as well as into the arms and pinnules. The reproductive system of

living crinoids is situated on specialized pinnules (see the subsection on pinnules). Crinoids also possess a haemal system; this is actually a network of spaces in the connective tissue of the body cavity.

This brief overview would not be complete without mention of the coelom, or body cavity. Adoral coelomic canals underlie the water-vascular and ambulacral systems of the arms and pinnules. The aboral coelomic compartment surrounds the intestine and continues into the arms and pinnules as aboral coelomic canals (Fig. 7). Crinoids do not have special respiratory organs. Respiration commonly occurs on the surface of the tube feet, probably by diffusion of oxygen through the body wall. Oxygen is transported to internal organs through the coelomic fluids rather than by the haemal fluid.

The skeleton of most crinoids is composed of a crown, a stem (also called stalk or column), which elevates the crown above the sea floor, and a holdfast for attachment to the substrate (Fig. 8). The lower part of the crown, the aboral cup (or calyx), contains the bulk of the soft parts, as already described. The food-gathering arms are attached to the cup. The oral (also

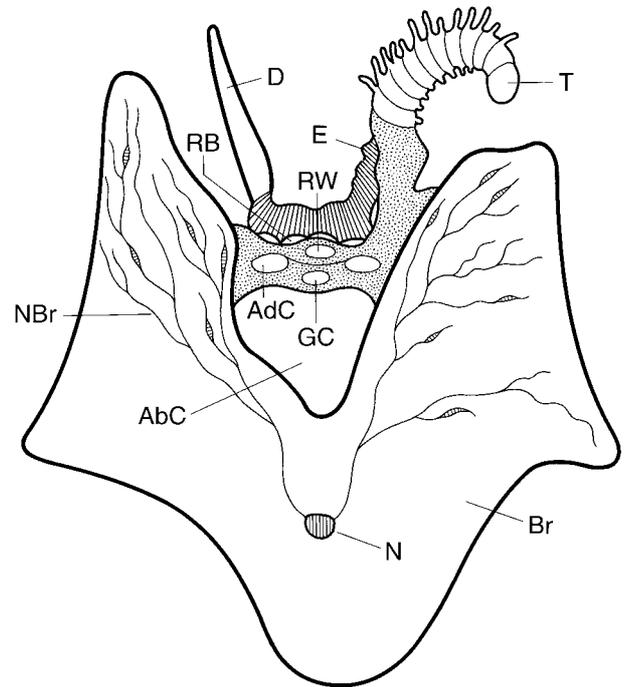


**Fig. 5.** Oral view of the disc of *Metacrinus angulatus* with tegmen. Food grooves end in the slightly displaced mouth; anal opening at the tip of an eccentric cone. (Redrawn from Carpenter 1884.)  $\times 3$ .

called ventral) side of the arms is the site of the food grooves and is always directed upward or downcurrent (Fig. 1), whereas the aboral side (dorsal) is directed toward the bottom (or upcurrent). The parts making up the skeleton usually consist of individual plates or ossicles that are more or less firmly joined together. All articulations between ossicles of the stem (called columnals) are bound by ligamentary connective tissue and allow only passive movements. Innervated epithelial cells along cirri (branches off the stem) of certain groups effect slow movement for these stem appendages (Baumiller *et al.* 1991). Muscular articulations, allowing



**Fig. 6.** Close-up of the oral disc (tegmen) of a comasterid comatulid with yellow-tipped oral pinnules; terminal comb teeth show on some of the pinnules. A black ophiuroid is sprawled across the disc, and the crinoid is releasing a bolus of faecal material from the anal tube. (Photograph O. C. Honegger, taken off Manado, northern tip of Sulawesi, depth around 20 m.) To view this figure in colour, see the colour plate section following page xv.

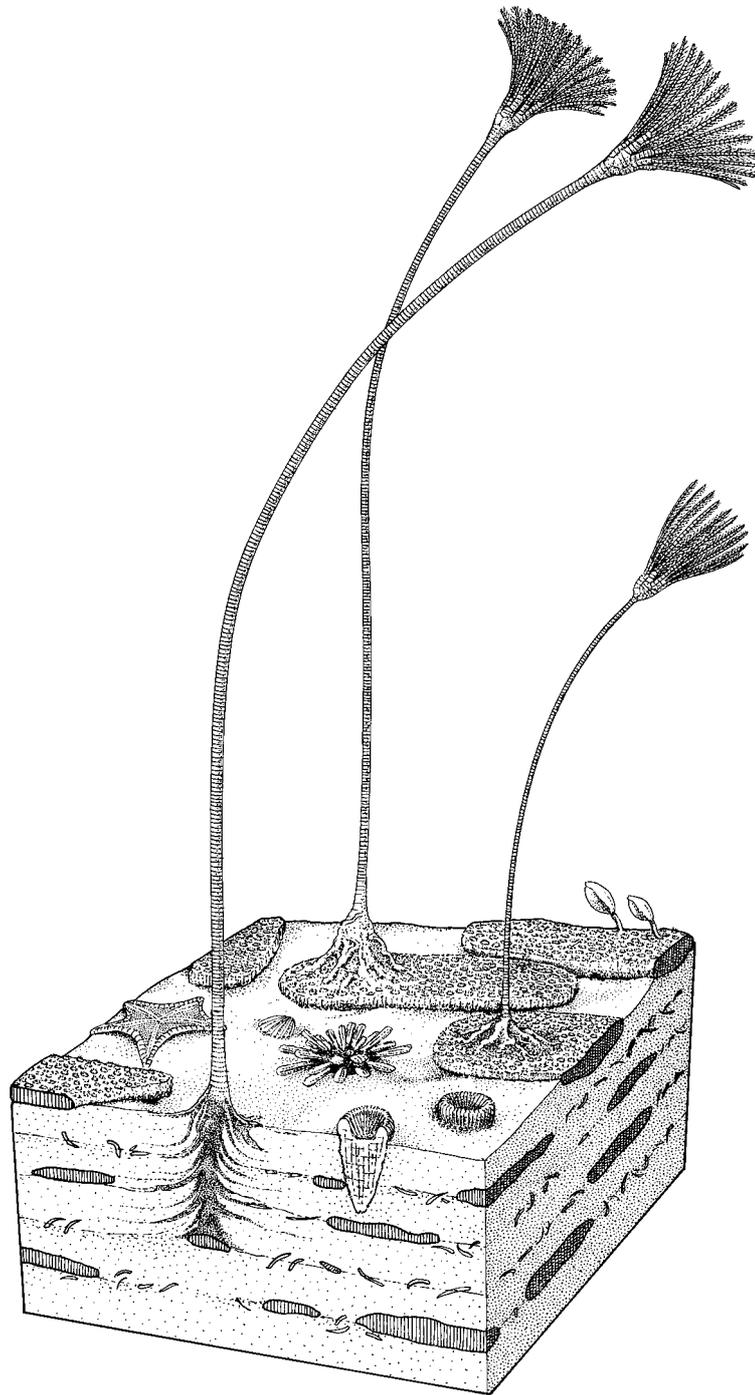


**Fig. 7.** Section through arm of *Bathycrinus aldrichianus*. Key: T, tentacle or tube foot or podium; D, covering plate of ambulacral groove; E, epidermis of ambulacral groove; Br, brachial ossicle; N, main brachial nerve; NBr, nerve branches; AbC, aboral coelomic canal; AdC, adoral coelomic canal; RW, radial water vessel; RB, radial blood vessel; GC, genital cord. (Redrawn from Carpenter 1884.)  $\times 200$ .

movements, have apparently developed only between arm ossicles. Ligament fibres penetrate the interior of plates, producing a specific microscopic (galleried) pattern of stereom. Muscles do not extend into the stereom, so that areas of muscular insertion have a more irregular (labyrinthic) stereom. The structure of articular surfaces between ossicles is one of the keys to understanding crinoid function. For orientation of the different parts, we use the terms 'oral' and 'aboral', as well as 'proximal' (towards the base of the cup) and 'distal' (away from the base of the cup) (Figs. 10, 11).

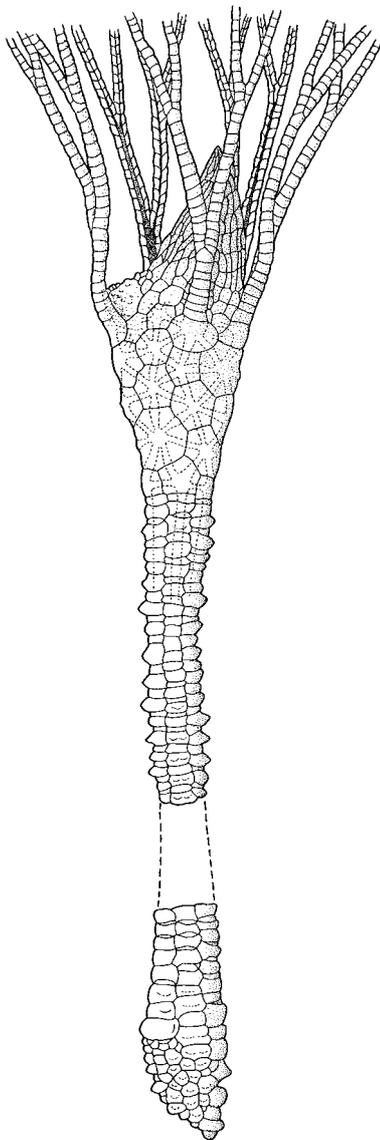
## THE STEM AND ITS APPENDAGES

The crinoid stem can serve several functions. The two most important are attachment to the substrate and elevation of the food-gathering system, represented by the arms, above the sea floor. In the majority of non-crinoid pelmatozoans the stem was short and rather weakly developed, suggesting that attachment or an-



**Fig. 8.** Reconstruction of the Jurassic sea lily *Liliocrinus munsterianus*. Two individuals attached to dead corals (*Thamnasteria*) by a compact root, another individual anchored in muddy sediment (Liesberg Beds, Middle Oxfordian, Swiss Jura). This environment is comparable to today's lagoon southeast of Nouméa (New Caledonia), where flat corals lie loose on a muddy bottom in 35- to 40-m-deep water (L. Hottinger, pers. comm., 1996). *Liliocrinus munsterianus* had a stem with a length of up to 2 m and a crown with a height of 15 cm. The crinoid was fixed to hard substrates by a massive root; alternatively, it was anchored in the soft bottom by roots that became quite long, growing in step with accumulating sediment (Fig. 62). It must be assumed that such roots first attached to some hard object (piece of coral, shell fragment). Also shown are other parts of the fauna such as the echinoid *Paracidaris florigemma*, the asteroid *Tylasteria*, a pectinid bivalve and two terebratulids; the solitary coral *Montlivaltia* (dead specimens) is partly embedded in the mud.

chorage may have been its primary function. The echi-  
noderm stem appears to have originated from an aboral  
evagination of the body, leading first to hollow tubes  
that were reinforced with irregular ossicles. Such primi-  
tive stems occur in Middle Cambrian pre-crinoidal pel-  
matozoans like *Gogia* (Fig. 2). In contrast, even in the  
earliest known crinoid, *Aethocrinus*, the stem is signifi-  
cantly more robust and longer (Fig. 9), a pattern largely  
maintained throughout the history of the group. A stem  
is not required for attachment – the only purpose of a  
stem is elevation off the bottom so that the animal can



**Fig. 9.** Reconstruction of *Aethocrinus moorei*. Lower Ordovi-  
cian, Montagne Noire, France. (Redrawn from Ubachs 1969.)  
×1.

escape the benthic boundary layer for better feeding,  
and perhaps reproduction. It has been suggested that the  
development of true columns in the Early Ordovician  
contributed largely to the huge success of crinoids in the  
Palaeozoic. The comatulids, which flourish today, have  
become detached, with the potential to climb to a  
higher position for feeding or to crawl into cavities to  
avoid predation.

### Stem Morphology and Growth

Stems of modern isocrinids will serve as the starting  
point for our discussion. They are composed of colum-  
nals with a central canal, so that the stem contains a  
central tubular cavity with extensions of the coelom and  
nervous system. Columnals bearing cirri are nodals or  
cirrinodals; those without cirri are internodals (Fig. 10).  
Stems have two distinct regions. In the distal part, away  
from the cup, the arrangement of the columnals remains  
constant, and nodals are separated by a nearly constant  
number of internodals. New nodals are formed just be-  
low the cup, so the short proximal region is the immat-  
ure stem. Near the cup, the developing internodals are  
completely hidden by the nodals (Fig. 11), but intern-  
odals are successively introduced between nodals. Proxi-  
mal columnals are shorter (thinner) than distal ones, so  
the stem grows or matures by sequentially adding col-  
umnals in the proximal region, first by adding nodals,  
then by intercalating internodals and finally by increas-  
ing the diameter of individual columnals.

Columnals are bound together by two types of elastic  
ligament fibres or mutable collagenous tissue,<sup>1</sup> which  
occur in a characteristic pattern (muscles are absent in  
the stem). Short, intercolumnar ligaments connect each  
pair of adjacent columnals. Longer, through-going liga-  
ments connect a set of internodals and one associated  
nodal (Fig. 12). The corresponding articulations are  
called symplexies and are recognized in lateral profile by  
their crenulate appearance: interlocking grooves and  
ridges on adjacent columnals (Figs. 10, 13). The grooves  
and ridges occur commonly as a petaloid pattern (Fig.  
10), which presumably gives the stem a certain flexibil-  
ity in different directions, preventing twisting and al-  
lowing for easy return to the original position. Longer,  
through-going ligaments are limited to the areola of  
each interradianal petal; each ligament extends all the way  
through a series of columnals and terminates at the  
aboral (distal or lower) side of a nodal (Grimmer *et al.*  
1985). Thus, longer ligament fibres are lacking between  
a nodal and the internodal immediately below. At this

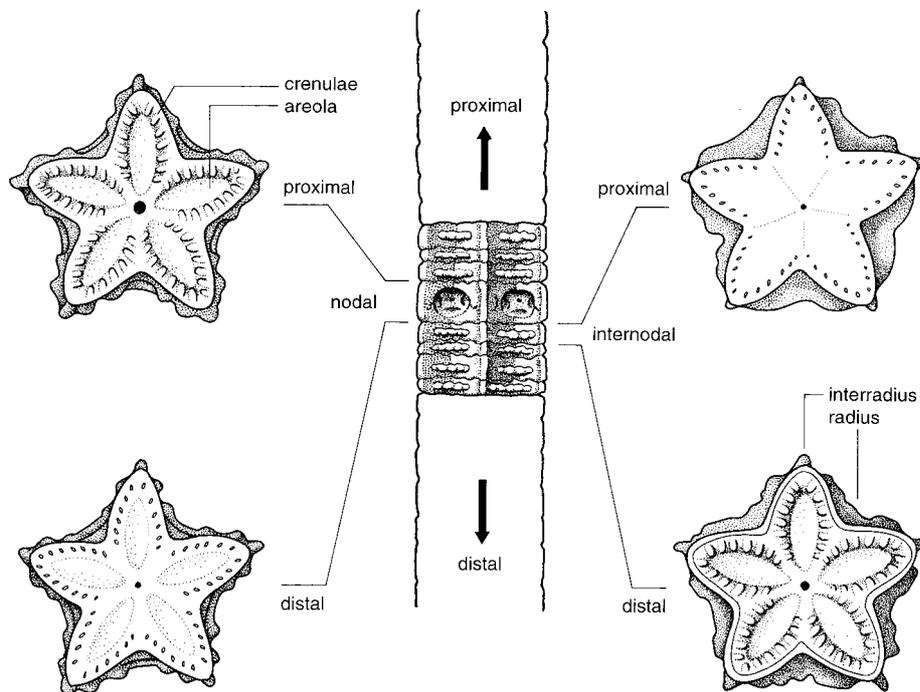


Fig. 10. Part of the stem of the isocrinid *Metacrinus angulatus*, with nodal and internodals, showing the different articular facets. (Redrawn from Carpenter 1884.)  $\times 3$ .

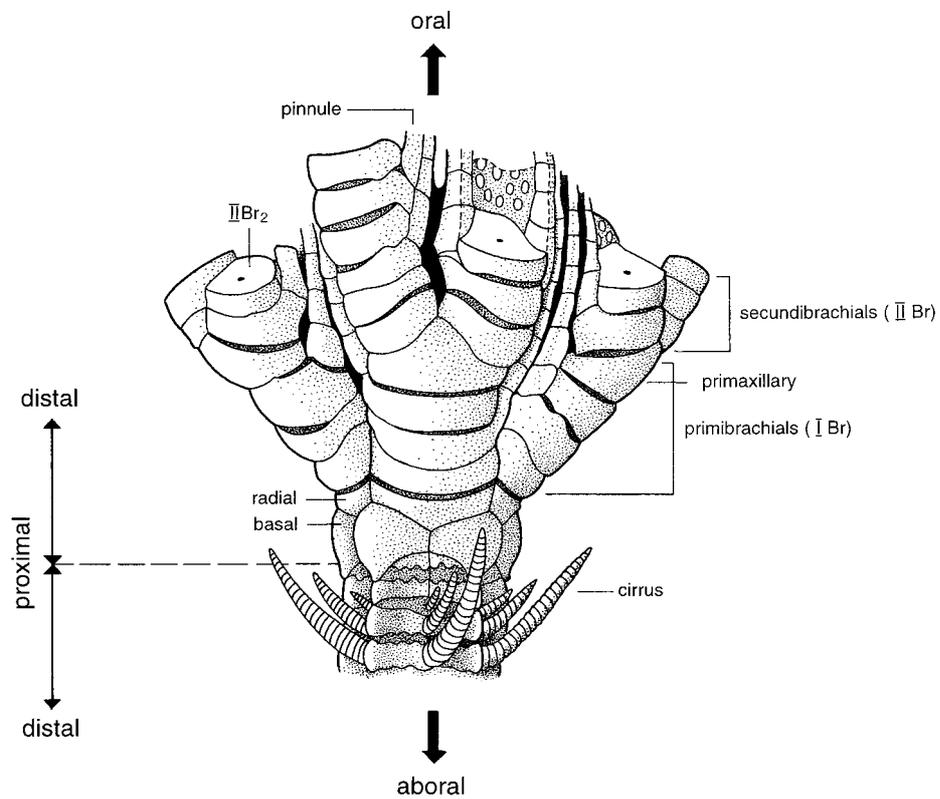


Fig. 11. Proximal stem, cup and base of arms of *Metacrinus angulatus*. (Redrawn from Carpenter 1884.)  $\times 3$ .

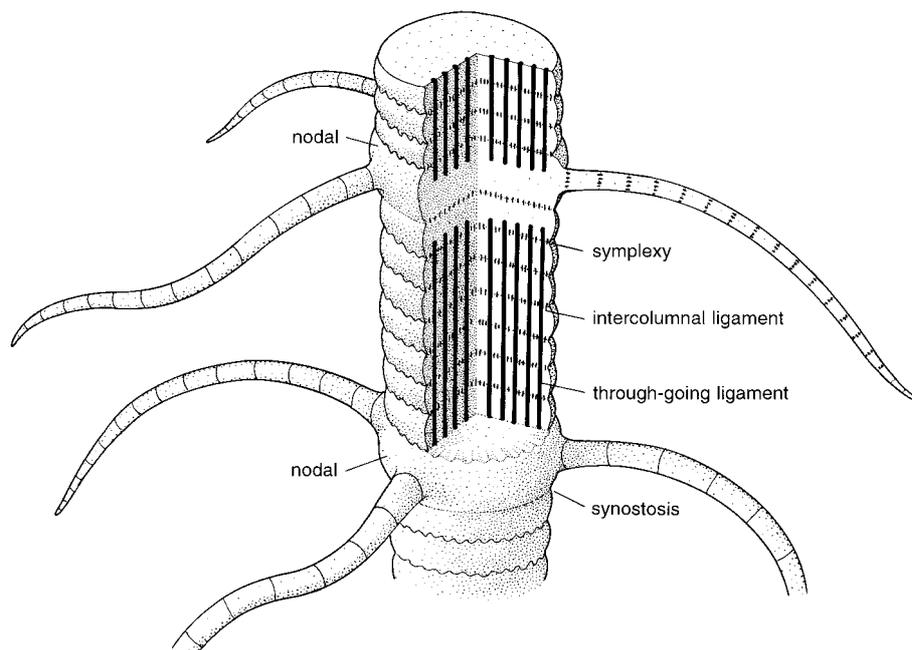


Fig. 12. Ligaments between nodal and internodals of an isocrinid stem. (Adapted from Baumiller & Ausich 1992.)

place, a tight junction, called synostosis, or more properly cryptosymplexy (hidden symplexy), is developed (Fig. 10). Synostoses and cryptosymplexes are easily recognized from the outside by a straight suture between nodal and distal internodal (Figs. 10, 12). These articulations have a simple low-relief topography and are held together only by the short intercolumnar ligaments. Breaking of the stem at this point guarantees that stem segments always end with a whirl of cirri for better attachment. It has been suggested by Hagdorn (1983) that this articulation developed among Middle Triassic isocrinids as a result of a habitat change from hard to soft bottoms. However, in contrast to Middle Jurassic isocrinids that thrived on soft bottoms (see Chapter 25), extant isocrinids prefer hard substrates or cling to pieces of rubble and shell (see Chapter 29). After breakage of the stem, the animal could reanchor itself with the terminal cirri, a possibility that does not exist for crinoids fixed with an attachment disc. Disintegration after death occur more rapidly along cryptosymplexes than along symplexes, and this is the reason for the occurrence of pluricolumnals (several articulated columnals) in sediments. Because such stem segments are common in many sediments from the Palaeozoic onward, it may be assumed that the two types of ligaments were developed early in the history of crinoids (Baumiller & Ausich 1992).

A different type of articulation is characterized by two opposing bundles of long ligaments that are separated by a fulcral ridge (Fig. 13). Such articulations, called synarthries, first evolved during the Middle Ordovician. Synarthries were never a dominant column articulation type, but one or another crinoid group had synarthries from the Middle Ordovician until the pres-

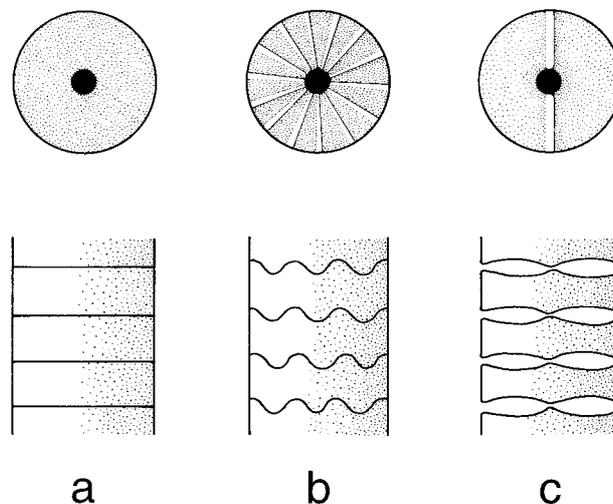


Fig. 13. Typical articular facets and long sections of crinoid stems. (a) Synostosis; (b) symplexy; (c) synarthry. (Redrawn from Donovan 1989a.)

ent. Furthermore, this columnal articulation style developed independently in four subclasses. Synarthrial articulations with fulcra aligned and unequal ligamentary areas on either side of each fulcrum produced a planispirally coiled column. Perhaps this served a protective function; and it evolved in the flexible *Ammonicrinus* (Fig. 14), and in the camerate *Camptocrinus* (Fig. 15). Possibly the most abundant crinoid with synarthrial articulations is *Platycrinites* (Mississippian to Permian) (Fig. 17). More or less circular articular facets with rather deep bifacial pits are a feature of the Bourguetiacrinida, an order of articulate occurring from the Upper Cretaceous to Recent (Fig. 16), and in very young isocrinids and comatulids. Synarthrial-type articulations are also present in the cirri, as discussed later in the subsection on cirri.

Columnals of living crinoids have only a small central canal, but the lumen was very large in some fossil species, such as in the long stems of *Liliocrinus* (Figs. 8, 62) with their sometimes massive holdfasts. A wide canal does not lead to reduced strength.

### Flexibility

Even when the stem serves solely for attachment, it must be either massively robust, as in Recent and fossil cyrtocrinids (Figs. 32–34), or else flexible enough to avoid fracturing due to stresses imposed by currents. The stereomic structure of crinoid ossicles enhances the resistance to fracturing of the calcite, but, nonetheless, the material of the skeleton is inherently inflexible. To overcome this constraint, the crinoid stem is divided into a series of rigid ossicles connected by flexible ligaments. It is interesting that stem flexibilities in Lower Mississippian crinoids are not correlated with hard-part characters such as stem diameter or columnal height (Baumiller & Ausich 1996), and ligament properties have been implied to be the most likely control of flexibility.

In some crinoids, such as the post-Palaeozoic encrinids and the isocrinids, the stem is most flexible a short distance below the crown and stiffer more distally, allowing for optimum positioning of the food-gathering arms in the current (Fig. 1). In other crinoids, such as the Jurassic millericrinids *Apiocrinites* and *Liliocrinus*, enlargement of the proximal columnals greatly reduces the flexibility near the cup. Instead, probably the whole stem, which reached a length of 2 m, was bent over by strong currents (Fig. 8). Seilacher *et al.* (1968) found that in the Lower Jurassic *Seiocrinus*, flexibility in-

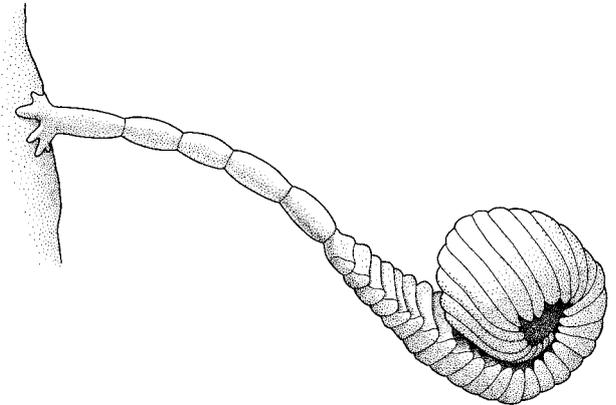


Fig. 14. Reconstruction of *Ammonicrinus doliiformis*, with crown hidden in enrolled stem. Stem is xenomorphic, with abrupt change between distal and middle part. Middle Devonian, Germany. (Redrawn from Ubaghs 1953.)  $\times 1.5$ .

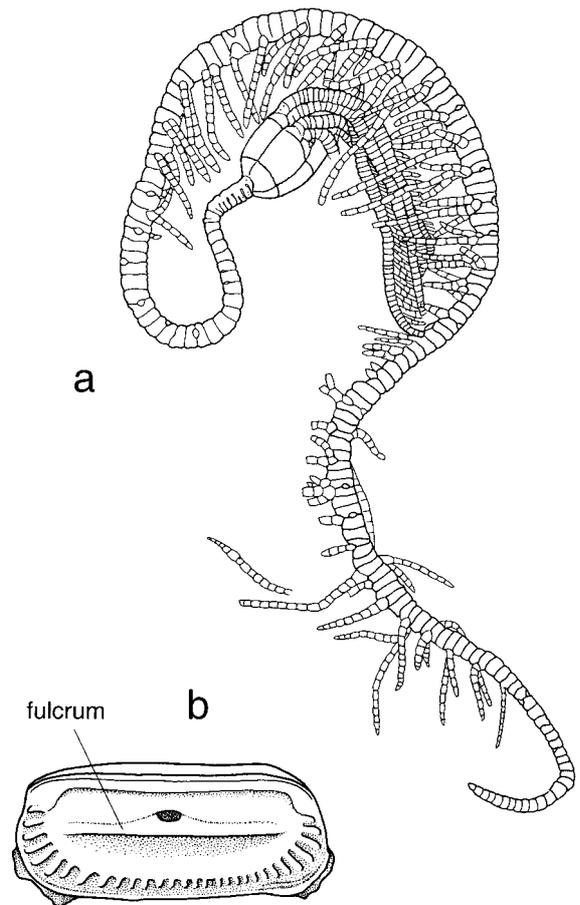
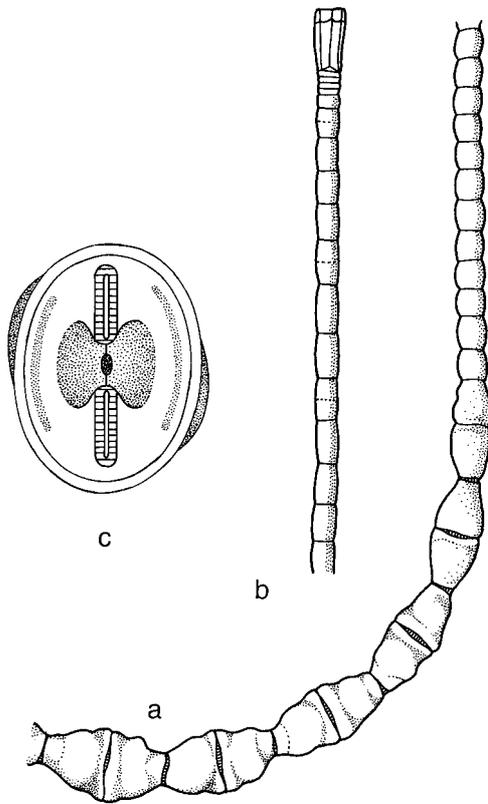


Fig. 15. (a) *Camptocrinus multicirrus*. Mississippian, Illinois. Complete specimen with coiled stem. (Redrawn from Ubaghs 1978.)  $\times 1.5$ . (b) Articular, synarthrial facet of a columnal of *Camptocrinus compressus*. Lower Carboniferous, Scotland. (Redrawn from Ubaghs 1978.)  $\times 5$ .



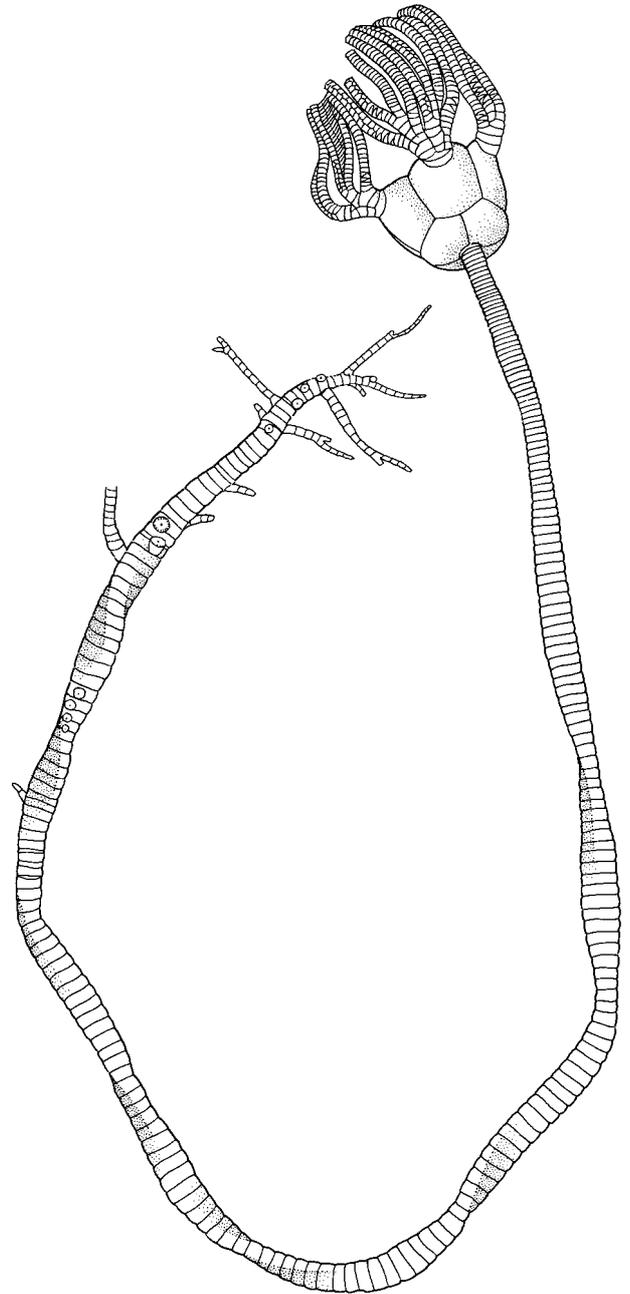
**Fig. 16.** (a, b) *Naumachocrinus hawaiiensis*, a Recent bourgueticrinid with synarthrial stem articulations. (Redrawn from Breimer 1978.) Approx.  $\times 1$ . (a) Distal column with fulcral ridges on alternate pairs of apposed facets rotated by  $180^\circ$ ; (b) proximal column with cup; (c) Articular facet of the bourgueticrinid *Democrinus rawsoni*. (Redrawn from Breimer 1978.)  $\times 18$ .

creased toward the distal end of the stem. They interpreted this as an adaptation to a pseudoplanktonic mode of life (see Chapter 23).

#### Resistance to Tension, Torsion and Shearing

Among crinoids inhabiting environments where there is significant current activity, the stem may be subject to a range of stresses, which can broadly be grouped as tension (stretching), torsion (twisting) and shearing. In fossil stems, torsion is documented by twisted pluricolumnals of the Upper Ordovician *Plicodendrocrinus casei* (Donovan *et al.* 1995). Tensional stresses are resisted largely by the ligaments.

In crinoids with symplectial connections, shearing caused by lateral forces and torsion caused by twisting of the stem are resisted by the crenulae, a series of ridges



**Fig. 17.** *Platycrinites regalis*. Complete specimen with twisted stem carrying root-like radicular cirri (radices) distally. Mississippian (Burlington Limestone), Iowa. (Redrawn after Wachsmuth & Springer 1897.)  $\times 0.7$ .

and grooves on the articulating face of one columnal that interlock with those on the opposing face of the next columnal (Figs. 10, 13). In circular columnals the crenulae are arranged around the margin of the articular facet; hence the number of crenulae is limited by the diameter of the columnal and the size of the crenulae.

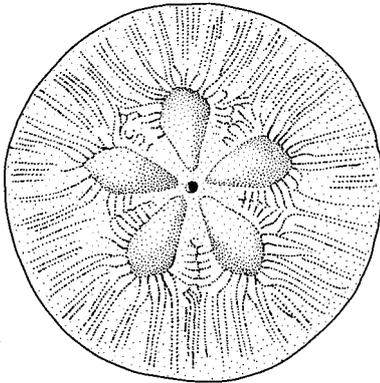


Fig. 18. Articular facet of internodal columnal of *Austinocrinus erckerti*. Senonian of Turkestan. (Redrawn from Rasmussen 1961.)  $\times 2$ .

In pentaradiate columnals, such as those of the isocrinids, the crenularium has radial infoldings that greatly increase its effective length compared with that of circular columnals. This is particularly important in resisting shear stresses. In circular columnals there may be only a few crenulae actually oriented perpendicular to the direction of shear stress, whereas in pentaradiate columnals more than five times as many may have such an orientation. In some rounded columnals that evolved from pentaradiate ones, the crenulae may be greatly elongated in the radii (Fig. 18). This has been carried a stage further in the Early Jurassic *Seirocrinus*, where these radial spaces have developed significant rugosities that interlock with corresponding rugosities on the next columnal (Fig. 197). No such obvious skeletal adaptations exist in synostosial or synarthrial articulations to resist these forces.

#### ATTACHMENT AND SUPPORT

If the stem served only as an attachment structure for the animal, little would be gained by having a long stem. For crinoids, a longer stem confers feeding advantages. It elevates the food-gathering apparatus, the crown, above the sea floor into faster currents. Ausich (1980) and Ausich and Bottjer (1985) have documented tiering among crinoids, with different species having different stem lengths. High-diversity crinoid communities typically have species with various stem lengths, and this places different species at different feeding levels to minimize competition. The maximum number of tiering levels was reached when diversity, and

presumably competition for resources, was also at a maximum (Simms 1990). At first sight it would appear that comatulids, the stemless form that dominates the modern crinoid fauna, might be adaptively disadvantaged. However, loss of the stem conferred much greater mobility on the comatulids. Many are able to clamber on to rocks, coral heads and other high points on the sea floor, using these objects as a surrogate stem. Many shallow-water species hide from predators during the day, and at night they crawl to favourable feeding perches (Magnus 1963). Some comatulids can even swim for short distances.

Attachment by distally tapered coiled stems was widespread during the Early Palaeozoic, particularly among the camerates and certain cladids. Examples are the Upper Ordovician *Pycnocrinus* (Fig. 90) and the Lower Devonian *Acanthocrinus* (Fig. 124). It appears that many of these crinoids either lacked a primary holdfast or possessed such a cemented attachment only during the juvenile stages and then broke free. There are many cases of these crinoids attaching to other objects by what appears to have been initially tapered stems (Fig. 103). Just how the juvenile crinoids were able to move around in order to locate a suitable host and then coil the distal stem around the object is quite enigmatic. One possibility is that crinoid larvae initially settled on upright stalks of bryozoans or other crinoids and then twisted the entire stem gradually around the upright posts, moving their crown in a spiralling motion coordinated with growth. After a point in time the attachment became permanent. This is inferred from the presence, in many of the distal coils, of wedge-shaped columnals that are thicker on the outside of the curving coiled stem.

Other crinoids do not appear to have coiled the distal end of the stem around any object, but rather to have laid out loose coils like a rattlesnake on the substrate to provide a base of stability (Fig. 124). Still more curious, but also very common, are many crinoids, including shoal-dwelling species during the Palaeozoic, that appear to have lacked any sort of holdfast whatsoever (Fig. 117). It is amazing that, without any appendages (radicular cirri) and with only a distally tapering stem, such crinoids were able to live in relatively high-energy environments. It seems plausible, but is purely speculative, that they simply dragged the column behind them, particularly if the crown achieved neutral buoyancy and was hence lower in density than the partially recumbent column.

### Holdfasts

In any event, it is clear that certain crinoids had horizontally trailing stems because we find their holdfasts as creeping roots or runners along the substrate. Up to several centimetres of horizontal stem may be anchored to the substrate by small finger- or lobe-like protrusions of the stereom. Such specimens, which are common in many Silurian (Franzén 1977) and Devonian reef settings, typically attached to corals or stromatoporoids. The peculiar calceocrinids combined a stem that lay on the sea floor with an attachment disc (Fig. 29). This must have made them particularly vulnerable to burial and clogging of the ambulacra due to turbidity. However, the presence of a hinged crown, folding on the column, would have sealed the feeding surface; opening of the crown would have disengaged it from accumulated sediment (Brett 1984).

On muddy substrates, creeping stems are also common; these may be anchored to the substrate or attached to each other by strands of stereom. Only the distal parts of these stems were horizontal; the crown was borne by an upright stem. Examples abound in Middle Oxfordian calcareous mudstones of the Swiss and French Jura (Loriol 1877–1879, Pl. 12, Figs. 1–6).

Attachment of the stem may be either permanent or temporary. Attachment may be by a root or holdfast cemented to a hard substrate or by flexible outgrowths from the stem, known as cirri. The bewildering array of holdfasts, roots, accretion discs and so on shows the importance of fixation for benthic crinoids. Brett (1981) gave a comprehensive account of the variety of crinoid attachment structures.

The most primitive type of holdfast, a hollow tube made up of small irregular plates, is restricted to the archaic *Aethocrinus* (Fig. 9), but it was common in primitive blastozoans such as *Gogia* (Fig. 2). Such multi-plated tubes (*Hohlwurzeln*) appear to have grown downward into a muddy bottom to keep the animals upright and to counter-balance the crown. Smaller multi-plated holdfasts, such as *Lichenocrinus* (Figs. 87–89), were commonly cemented by a basal disc to solid substrates (hardgrounds or skeletal material). Many primitive disparids, some cladids and flexibles possessed a simple cone- or volcano-shaped attachment disc that was cemented to shells or hardgrounds. In a more advanced holdfast or radix, the distal end of the stem branches into root- or finger-like extensions. These are usually made up of segments and contain an axial canal; and

again, they serve to anchor crinoids in unconsolidated sediments (Fig. 19). Roots of Jurassic millericrinids are commonly attached to dead corals, but they also occur on soft bottoms, where they reached a considerable length, growing stepwise in parallel with accumulating sediment (Figs. 8, 62).

Many crinoids living in agitated environments, such as reefs or flanks of reefs, were permanently attached. This is especially true of Palaeozoic crinoids that lacked efficient grappling devices for temporary attachment as present in comatulids and the isocrinids. The lack of attachment structures with contractile tissues prevented most Palaeozoic crinoids from actively moving around for better feeding positions or hiding from predators (Donovan 1993).

The cemented holdfast or radix structure of many Early Palaeozoic crinoids and other pelmatozoan echinoderms is by no means uncommon in later taxa. Recent comatulids pass through a sessile stage in early life. The larvae settle on some hard object, where they attach by a small disc and grow a stem during the so-called pentacrinoid stage before breaking away to assume a free-moving life. Among Mesozoic forms, the Triassic encrinids (Figs. 181, 183, 186) and Jurassic mil-



Fig. 19. Radicular cirri of *Rhizocrinus lofotensis*, a bourguetiacrinid living on the muddy bottom. (Redrawn from Breimer 1978.) Approx.  $\times 4$

lericrinids (Fig. 8) had cemented holdfasts, as do fossil and extant cyrtocrinids, including *Holopus* (Fig. 31) and *Gymnocrinus* (Fig. 32). Additional weight may be added to roots by encrustment with secondary stereom. In *Lilioocrinus*, such roots became very large blocks (Fig. 8) that held an animal with a total height reaching 2 m even in stronger currents.

The cemented form of attachment places much greater restriction on crinoids. Not only are the animals committed to that site of attachment during their life, but they are confined to hardground environments or sites where there are numerous hard objects to which they can attach and in which sedimentation rates are very low. The stability of the environment is of prime

importance because crinoids would be unable to escape from any unfavourable change. From the palaeontologist's point of view, this has one considerable advantage: any sudden increase in sedimentation will entomb such faunas where they stand. There are many examples of hardground crinoid faunas preserved at the base of such sediment influxes. In some instances, crinoids with this mode of attachment appear to have broken free of the holdfast yet survived for some time after, as shown by the rounding of the distal end of the stem (Fig. 180). The length of stem remaining attached to the crown may vary from only a few to many columnals, suggesting that detachment occurred as a result of trauma.

Some additional holdfast types are worth mentioning

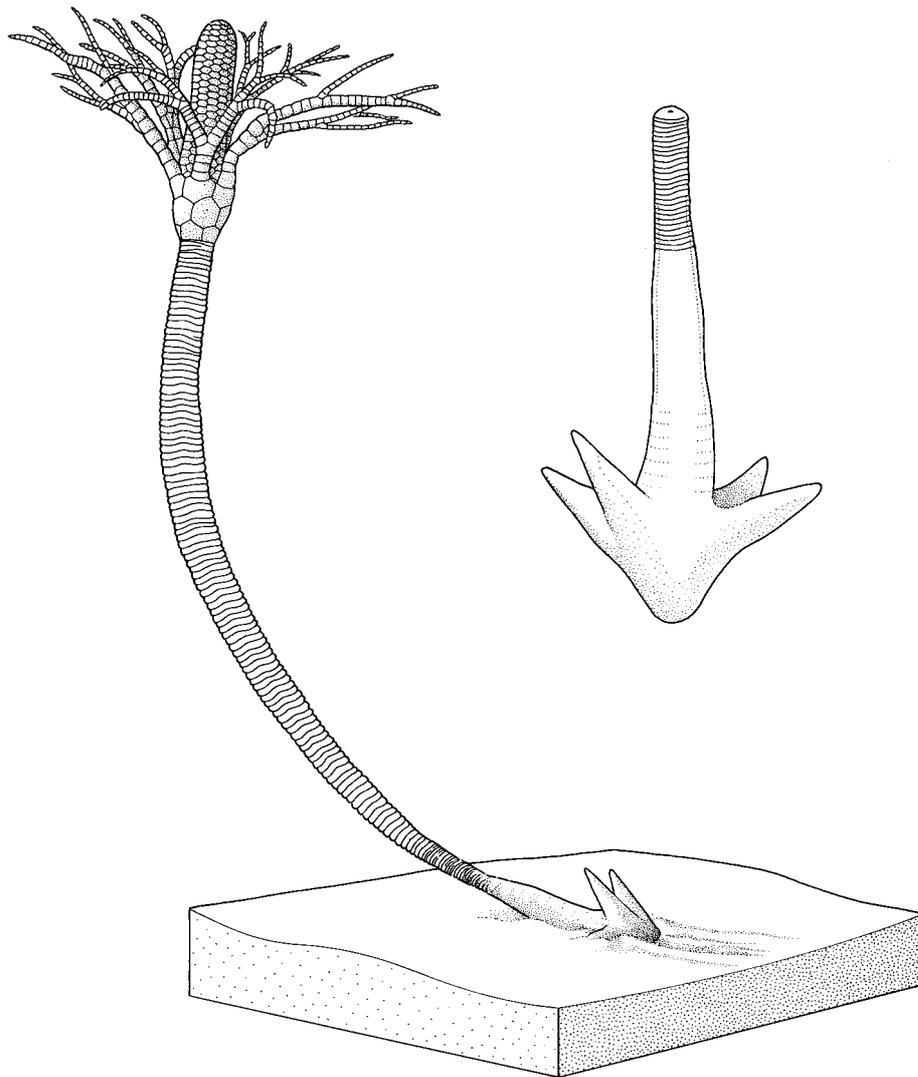


Fig. 20. *Ancyrocrinus bulbosus*. Devonian, New York. Left: complete animal; right, radicular cirri and terminal columnals ankylosed into the anchor-like holdfast. (Redrawn from Ubaghs 1953.) Complete animal  $\times 2$ .

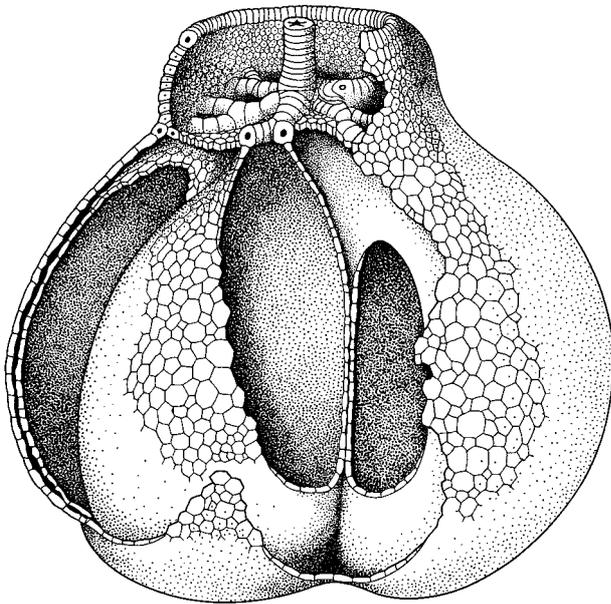


Fig. 21. Reconstruction of a lobolith ('*Camarocrinus*') of a scyphocrinitid. Lower Devonian, North America. The bulb is shown in presumably inverted life position, with the stump of the broken-off stem, contained in a collar, pointing upward (see Chapter 11 for further discussion). (Redrawn from Springer 1917.)  $\times 1$ .

here. The grapnel- or anchor-like holdfasts of *Ancyrocrinus*, composed of fused columnals and their radicular cirri and crusted over with secondary stereom, prevented drag of the animal in moving waters (Fig. 20). Probably the most remarkable 'holdfasts' are the highly specialized chambered bodies or bulbs developed in scyphocrinitids (Fig. 21), large crinoids widely distributed in Silurian–Devonian boundary beds. Whereas some authors have argued that the bulbs (also called loboliths) may simply have provided anchorage on loose or soft substrates (Springer 1917; Brett 1984), others have assumed that these organs served as buoys to sustain a planktonic lifestyle, a theory that is adopted here (see Chapter 11 for further discussion).

### Cirri

Cirri, flexible appendages arising at intervals from the stem of certain crinoids, are widespread among post-Palaeozoic crinoids (Figs. 11, 201–203, 210, 213, 214, 235, 236). True cirri, as they occur in isocrinids and comatulids, have synarthrial articulations, in contrast to the appendages of Palaeozoic crinoids with symplectial or synostial articulations (Donovan 1993); these are termed radicular cirri or radices. Cirri have some degree

of variation and almost certainly evolved more than once among the different crinoid taxonomic groups (Brett 1981; Simms & Sevastopulo 1993). For attachment they have considerable advantages over the cemented holdfast. First, they are not permanently attached to the substrate. Crinoids could detach themselves at will and drift with the current in search of food. Second, crinoids with cirri are not necessarily confined to specific substrates. The cirri could be used to anchor in soft bottoms (see, e.g., *Paracomatula helvetica*, Chapter 25) or onto hard objects on the sea floor, such as sunken driftwood, rocks or other benthic organisms (Fig. 234). Finally, because the cirri in many crinoids arise at regular intervals along the stem, loss of its distal part did not entail the complete loss of the attachment structure, as was the case for crinoids with a holdfast or a root. The possibilities of this strategy were carried a step further by the post-Palaeozoic isocrinids, in which pre-formed rupture points (= cryptosymplexes) developed in the stem immediately beneath the nodals. This ensured the optimum positioning of the cirri in the event of the loss of the distal part of the stem. Efficient anchorage is provided by terminal cirri, as demonstrated by isocrinids in the Straits of Florida under quite high current regimes (Fig. 1). The strategy was perhaps carried to its ultimate conclusion in the comatulids, the most common extant group, in which the stem has been lost and cirri arise from the centro-dorsal at the base of the cup (Fig. 22a). In comatulids, cirri show great diversity in form and size, usually correlated with the mode of life and habitat. Cirri are exceptionally closely spaced, long and sturdy in species of *Pentacrinites* (Fig. 201), presumably an adaptation to their lifestyles (see Chapters 22, 23 and 25 for further discussion).

The radicular cirri, or radices, in many Palaeozoic crinoids resembled miniature versions of the stem, with the same overall morphology of circular ossicles with symplectial articulations (Fig. 17). They may serve functions in addition to that of attachment, such as protection of the crown in myelodactylids (Figs. 15, 100) (Donovan & Sevastopulo 1989). By Late Palaeozoic times, the radices became more specialized structures (Simms & Sevastopulo 1993). Proximal ossicles developed a fulcral ridge type of articulation, imparting greater flexibility in a plane parallel to the long axis of the stem. In isocrinids and comatulids, the cirri developed a morphology quite distinct from that of the stem, reflecting the prevailing stresses imposed upon the different parts of each cirrus (Fig. 22b). The ossicles of

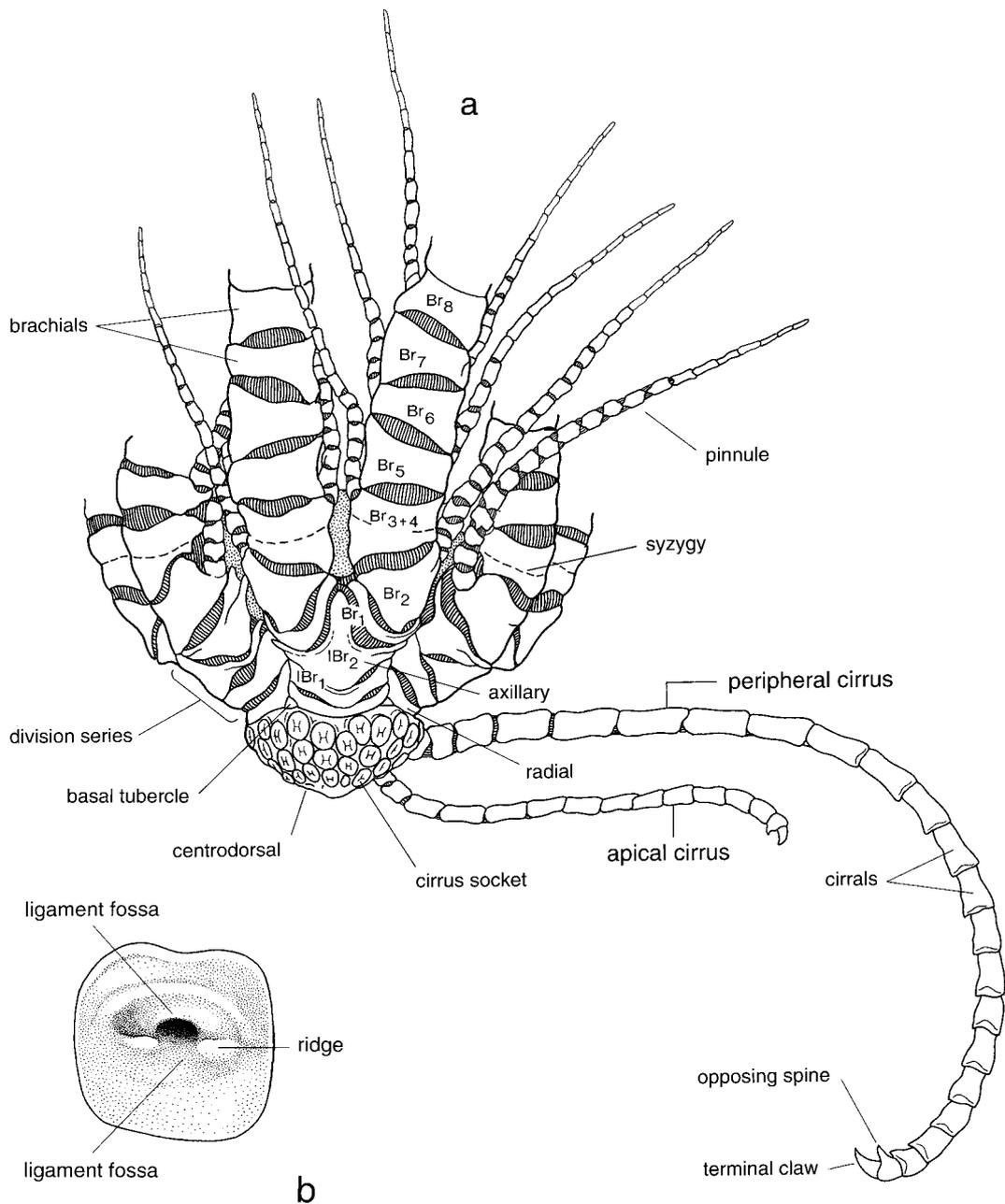


Fig. 22. (a) Lateral view of a comatulid with centrodorsal, two cirri and base of arms. (Redrawn from Messing & Dearborn 1990.) (b) Articular facet of second cirral of *Nemaster rubiginosus*. Recent. (After Donovan 1993.) Approx.  $\times 30$ .

cirri, cirrals, are connected by ligaments composed of collagen fibrils. At each articulation there is an oral and an aboral ligament separated by a fulcral ridge. The cirrals are pierced by a central canal, a branch of the axial canal of the stem with coelomic and nervous extensions. In living isocrinids, distal cirri are used to anchor the stem (Figs. 1, 235, 236). In living comatulids, cirri may grasp the substrate with a terminal claw

or hook, aided by an opposing spine on the penultimate segment (Fig. 22a). Grasping is made possible by very fine contractile filaments within the coelomic epithelial cells of the axial canal (Grimmer *et al.* 1985). Because the axial canal of comatulids is below the synarthrial fulcra (i.e., it is situated aborally), contraction of the filaments curves cirri away from the crown towards the centrodorsal for clasping (Figs. 22, 234). In isocrinids,

contraction of the filaments pulls the cirrus downward towards the stem. Relaxation of the filaments, combined with the elasticity of the upper, orally situated ligament, allows the cirrus to be detached and raised (Donovan 1989a). Cirri help isocrinids to crawl or climb to higher positions; they may also play a role in achieving and maintaining the vertical posture of the stem (Baumiller *et al.* 1991).

### CUP OR CALYX

The aboral cup (or calyx) represents the link between the stem and the arms and is the site of the main organs of the digestive, haemal and nervous systems. It must provide both a rigid base from which the arms can operate efficiently and a protective housing for the vital organs.

In the great majority of cases, the morphology of the crinoid cup represents variations on a common theme – a series of two or three interlocking and offset circlets of five plates. The shape of the calyx may be altered by the addition or elimination of plates or by the modification of the size or shape of existing plates. Ausich (1988) recognized 11 basic calyx designs, some of which are shown in Figs. 23–27. These designs embrace constructional possibilities available to crinoids and have developed in parallel in different taxonomic groups. For example, the multi-plated bowl design, common in camerates (Fig. 38), also evolved in flexibles (*Sagenocrinites* and *Forbesiocrinus*, Fig. 27) and in articulates (*Uintacrinus*, Fig. 24, and *Apiocrinites*, Fig. 204).

The number of plates in each circlet is a consequence of the phylogenetic history of the crinoids. A single circlet of five plates would lack rigidity. The addition of a second circlet interlocking with the first circlet, and with the sutures between the plates offset by 36°, so that the suture in one circlet coincides with the centre of the plate in the other circlet, produces a much more rigid structure. The addition of a third circlet of plates would confer little extra advantage in terms of increased strength. This is perhaps borne out by the evolutionary history of the Crinoidea, in which there has been an increasing prevalence of two-circlet forms in parallel with the decline in diversity of three-circlet, and even four-circlet, forms of Early Palaeozoic faunas (Simms 1994a).

In addition to these basic plate circlets, various other plates may form an integral part of the cup in some crinoids. In most Palaeozoic taxa, the pentaradiate sym-

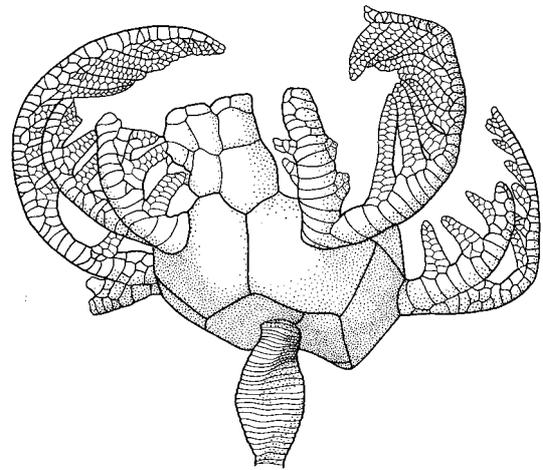


Fig. 23. Hand-shaped cup of the monobathrid *Eucladocrinus pleuroviminus* with elliptical, twisted stem. Early Mississippian (Burlington Limestone), Iowa. (Redrawn from Ausich 1988.)  $\times 0.6$ .

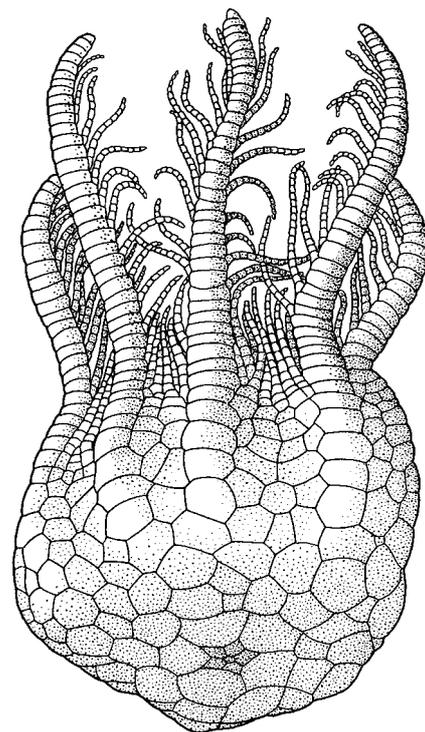


Fig. 24. Calyx of the articulate *Uintacrinus socialis*, a multi-plated bowl design. Upper Cretaceous, North America. (Redrawn from Ausich 1988.)  $\times 1$ .

metry of the cup circlets is disrupted by the addition of one or more so-called anal plates (Fig. 27). The function of these plates is unclear, although they are lost in all post-Palaeozoic crinoids (Simms & Sevastopulo 1993).

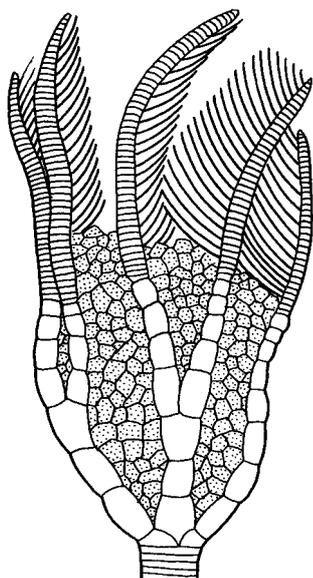


Fig. 25. Conical mosaic calyx of the monobathrid *Xenocrinus penicillus*. Upper Ordovician, Ohio. (Redrawn from Ausich 1988.)  $\times 2$ .

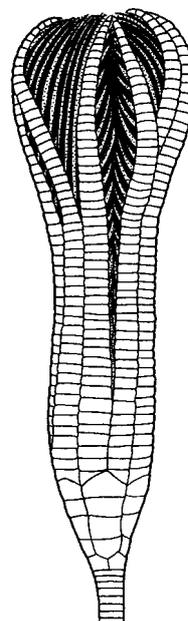


Fig. 26. *Ectenocrinus grandis*, a disparid with cylindric cup. Upper Ordovician, Ohio. (Redrawn from Ausich 1988.)  $\times 1$ .

Technically, the aboral cup encompasses the radial plates and all other plates beneath the radials and above the stem, whereas the calyx includes all of the plates above the stem and beneath the point where the arms become free. In its simplest form, the cup is composed of two circlets of five plates each. The uppermost plates of the cup are radial plates. Radials typically define the five-part symmetry of crinoids and give rise to the arms. Interradially below the radials are the basal plates, which may form the base of the cup and articulate with the column (Fig. 11). In comatulids, basals may be only partly visible (basal tubercle, Fig. 22a) or hidden. In other crinoids, an additional circlet of plates, called infrabasal plates, is present between the basals and the stem. An aboral cup composed of radials and basals is termed 'monocyclic' (Figs. 11, 26), and a dicyclic cup (Figs. 20, 28, 35) is one that also has infrabasals ('mono'- and 'dicyclic' refer to the one or two circlets of plates, respectively, beneath the radials). Cladids, disparids, articulates and some flexibles typically have this construction. All of these plates are immovably joined to each other, with only rare exceptions, such as the calceocrinids (Fig. 29).

If the arms become free above the radials, the cup is equivalent to the calyx (Figs. 22, 23, 28, 30). Alternatively, proximal arm plates (brachials) may be sutured directly into the body wall of the crinoid rather than being part of the free, feeding arms. These brachials are

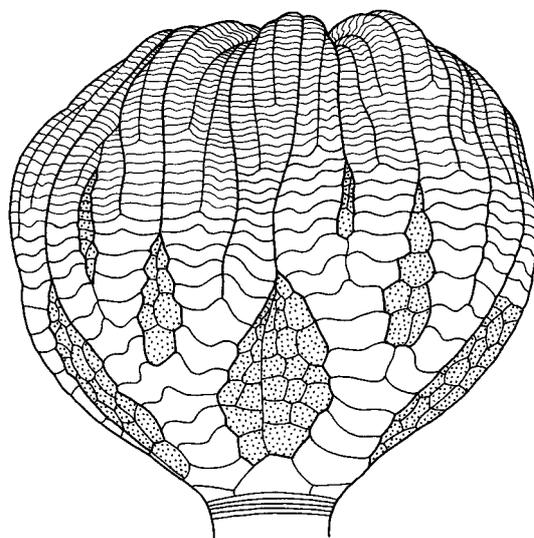


Fig. 27. *Forbesiocrinus wortheni*, a flexible with undifferentiated anal and interbrachial plates (stippled). Mississippian, Indiana. (Redrawn from Ubaghs 1978.)  $\times 1$ .

called fixed brachials; where fixed brachials are present, the cup is only the lower part of the calyx. The fixed brachials greatly expanded the size and volume of the calyx. Crinoids with this construction may also be either monocyclic or dicyclic. This type of calyx is characteristic of most camerates (Figs. 38, 112, 161), many flexi-

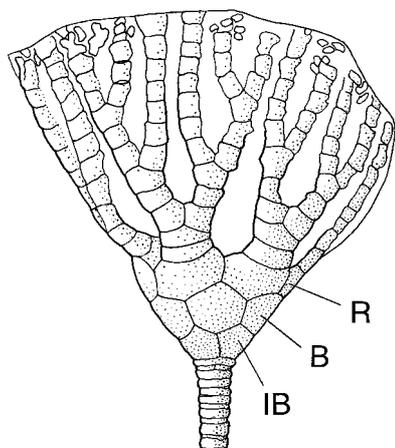


Fig. 28. *Eoparisocrinus siluricus*, a cladid with dicyclic cup. Upper Silurian, Indiana. Key: IB, infrabasal; B, basal; R, radial. (Redrawn from Ubaghs 1978.)  $\times 1.5$ .

bles (Fig. 27) and also some articulates (Fig. 24). Calyxes with fixed brachials typically require extra plates (interradials or interbrachials) to fill in the area between adjacent rays (Figs. 27, 38). Extra plates are also typically present in the posterior interradius<sup>2</sup> and the reader is referred to the *Treatise* (Ubaghs 1978) for further details about these plates or about modifications from the standard plating described here.

Calyx shapes such as bowls, urns, cones and hands appear to be sensible constructions for food processing, but the very specialized bilateral recumbent constructions and the fists merit special attention and a short discussion. Bilateral recumbent designs evolved in a single, highly specialized family, the disparid Calceocrinidae, which lasted from the Middle Ordovician to Late Permian. These bent-down crinoids with well-developed hinges within the cup have engendered much interest in the function of this unique morphology. Most workers now agree that these crinoids lived with the stem along the bottom. In a resting posture, the arms folded

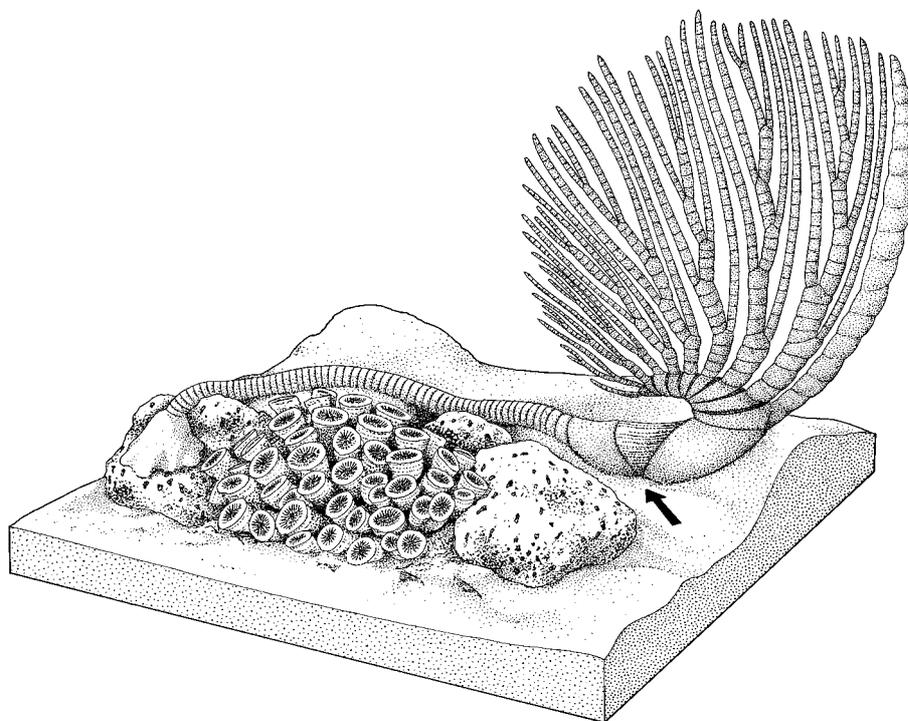
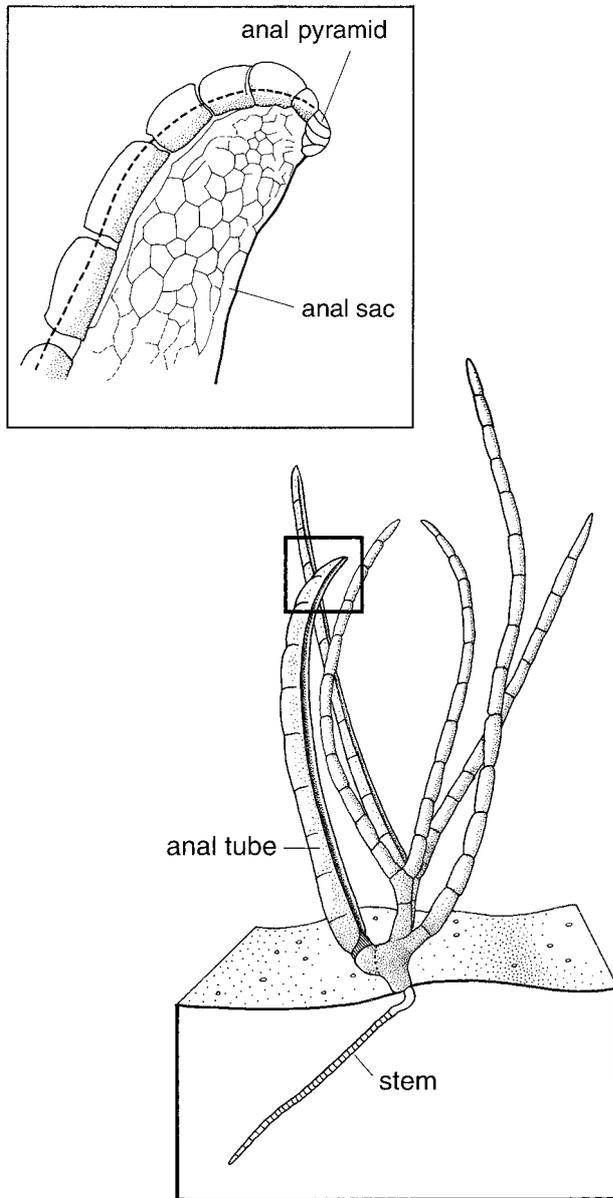


Fig. 29. Reconstruction of the feeding posture of a calceocrinid with opened crown on a coral reef (current from right). Radial circlet and arms are elevated above the substrate by opening above a hinge (arrow) between the basal and radial circlet. One lateral arm of this bilaterally symmetrical crinoid is shown; the second lateral arm behind is not shown. (Combined after Jaekel 1918; Harvey & Ausich 1997.)



**Fig. 30.** Reconstruction of the calceocrinid *Senariocrinus maucheri*. Crown with strong bilateral symmetry, single dichotomous division of two arms and long unbranched arm; short, vermiform stem attached at extremity of single triangular basal plate.  $\times 3$ . *Inset*: Enlarged distal part of anal sac attached to anal 'tube', with small anal pyramid at tip. Lower Devonian Hunsrück Slate, Bundenbach. (After Schmidt 1934; Moore 1962.)

back onto the stem, but the crown bent upward for feeding (Fig. 29). This interpretation was rejected by Schmidt (1934), who favoured an upright stem with a bent-down crown during times of rest. The crown would have been raised at a right angle into the current for feeding. Schmidt even thought that *Senariocrinus*

*maucheri* (Fig. 30), a calceocrinid from the Lower Devonian Hunsrück Slate with a rudimentary, tapering stem and a long anal sac, was free-living; and he proposed that this peculiar crinoid used its short stem not only for temporary attachment but also for swimming, in conjunction with the arms and hinge. Muscle or other contractile fibres may have moved the hinges,<sup>3</sup> but we think it more likely that *Senariocrinus maucheri* lived on the muddy bottom, used the stem for attachment, folded the crown to protect the ambulacral furrows against predators and clogging by sediment and raised the arms for feeding, just as other calceocrinids did.

Fists include cyrtocrinids with a few commonly short arms. The cup may be asymmetric (hence the name for these crooked crinoids), and it is cemented to a substrate or borne by a short stem. Such a structure has been explained as an adaptation to wave action (reef forms), but these crinoids occur mainly in deeper waters (see Chapters 3 and 29). A recently discovered species from the Pacific is *Holopus alidis* (Fig. 31). The discovery of a living species of *Gymnocrinus* (Fig. 32) at depths of 300–500 m on seamounts off New Caledonia confirms that most cyrtocrinids were restricted to hard substrates



**Fig. 31.** *Holopus alidis*. Side view of complete individual with closed arms, dredged from a depth of 460–470 m off the Loyauté Islands. (Courtesy J.-P. Bourseau; from Bourseau *et al.* 1991.)  $\times 3$ .



Fig. 32. *Gymnocrinus richeri*, dredged from 470 m off New Caledonia. Side view of individual with enrolled arms and pinnules. (Courtesy J.-P. Bourseau; from Bourseau *et al.* 1991.)  $\times 1$ .

in rather sheltered environments. These living fossils have been observed coiling their asymmetric arms quite slowly, which may be an adaptation for protection against predators. For additional protection of the food grooves, the pinnules can be enrolled between projections of the brachials. Tegmen and soft parts within the cup are completely covered by lid-like oral extensions of the first primibrachials (Fig. 238). The food grooves are thus completely hidden in a tunnel if the arms are enrolled and the soft parts are inaccessible to predators. Similar cyrtocrinids with a short stem and a crown with arms that could be enrolled were widely distributed in the Jurassic and Lower Cretaceous of Europe. They have furnished a number of extraordinary forms. In some of these, the small arms could be hidden in a cavity formed by large median prolongation of the second primibrachials (*Eugeniocrinites*, *Lonchocrinus*) or by interradial processes of the radials (Fig. 33). Others (*Hemicrinus*, Fig. 34) are extremely asymmetric with a spoon-like cup and fused proximal stem, presumably adapted to constant unidirectional current. Possibly due to local conditions, individual species (e.g., *Cyrtocrinus nutans*; see Chapter 3) may vary considerably in degree of asymmetry. It is interesting that many individuals of the living *Gymnocrinus richeri* were in the course of regeneration when collected. Deformations, which may have been caused by a parasite, are common in some fossil cyrtocrinids

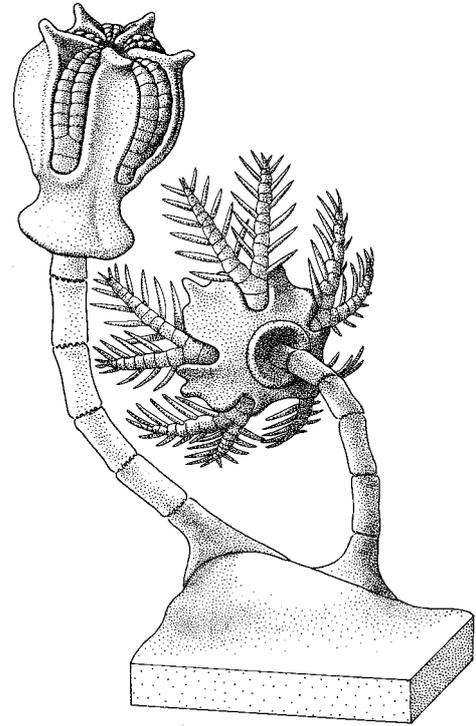


Fig. 33. Reconstruction of *Apsidocrinus moeschi*. Tithonian, Rogoznik (Poland) and Switzerland. (Redrawn from Pisera & Dzik 1979.)  $\times 4$ .

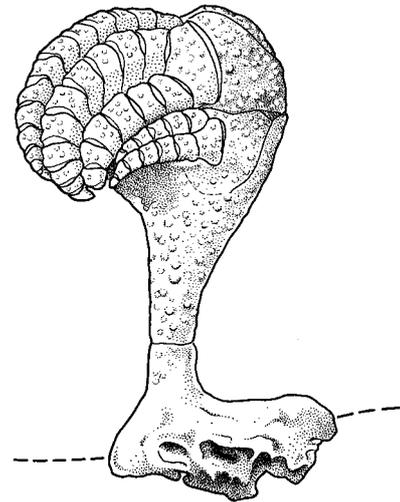


Fig. 34. Reconstruction of *Hemicrinus astierianus*. Lower Cretaceous, Var, France. (Redrawn from Jaekel 1918.)  $\times 3$ .

(see Chapter 3). The advantage of protective morphology appears to have outweighed the reduced surface area for catching food, perhaps because of the small size of these crinoids, which occupied and still occupy a low tier, feeding on larger-sized particles. In Cretaceous and extant *Cyathidium*, the small arms may be completely

sheltered underneath the closely fitting proximal arm pieces, so that these forms resemble a barnacle (Fig. 237; see also Chapter 29).

The cups of the stemless, pelagic Roveacrinida are, as a rule, composed of only thin radials that commonly have spines, ridges or wings to facilitate floating. In the somphocrinids, the cups may be prolonged into aboral spines, and long or short spine-like projections may have served to stabilize the animals in an upright position. The best-known representative of this group is *Saccocoma*, which is described in Chapter 26.

The oral surface of the cup may be covered by a variety of types of plates, in each case presumably serving to house and protect the vital organs. Five large oral plates are present in larval crinoids and persist into the adult stage of neotenous microcrinoids,<sup>4</sup> disparids and cladids (Fig. 35). In cladids and the post-Palaeozoic articulates, there is a tegmen (also called disc) composed of small tessellate plates or a membrane studded with calcareous granules (Fig. 6). In living crinoids, the tegmen is typically divided into five interambulacral areas by narrow ambulacral grooves passing into the arms (Fig.

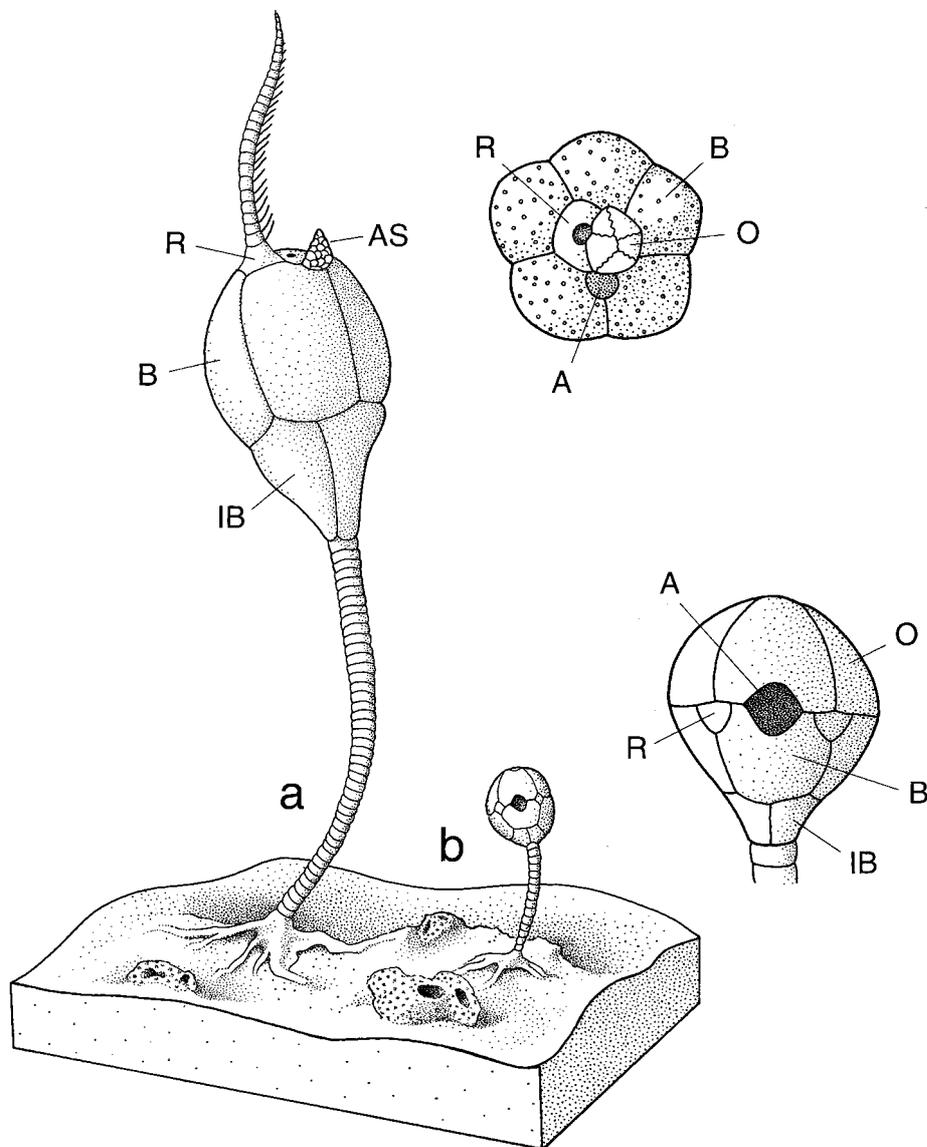


Fig. 35. Reconstruction of (a) *Monobrachiocrinus ficiformis granulatus* with single arm, with enlarged oral view of cup; and (b) armless *Embryocrinus hanieli*, with enlarged anal side view. Permian Basleo (also called Besleo) Beds, Timor. Key: A, anal opening; AS, anal sac; B, basal; IB, infrabasal; R, radial; O, oral plate. (Redrawn from Wanner 1920.)  $\times 1$ .