

Crinoid Form and Function

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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 pentaradiate 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-

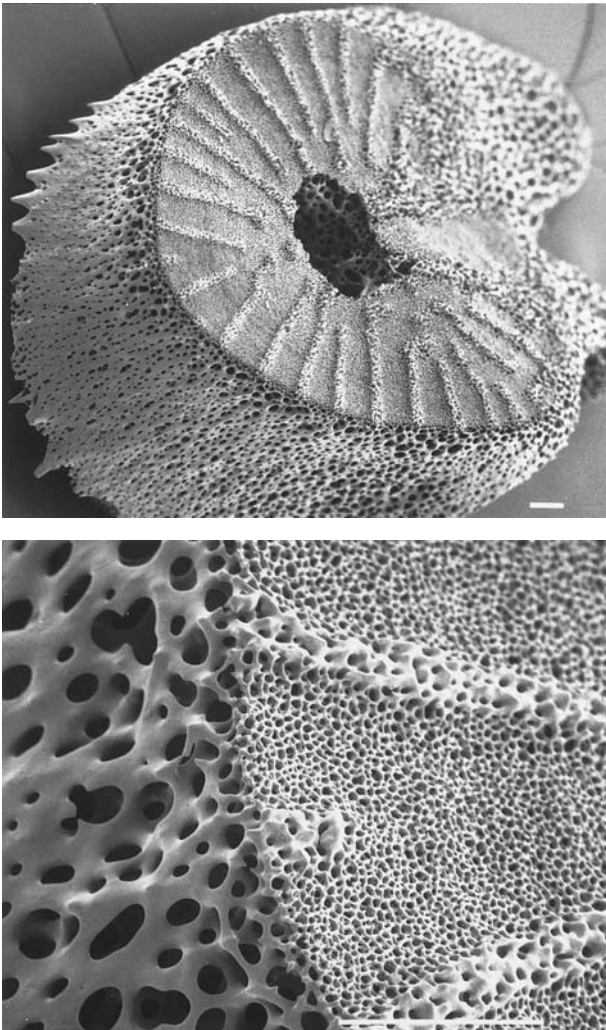


Fig. 4. Scanning electron photomicrographs of a brachial plate from *Promachocrinus kerguelensis* (Recent from the McMurdo Shelf, Antarctica) showing stereomic microstructure. This brachial facet with radiating crenulae is a ligamentary articulation, called syzygy. (Courtesy C. P. Hart and W. I. Ausich.)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

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

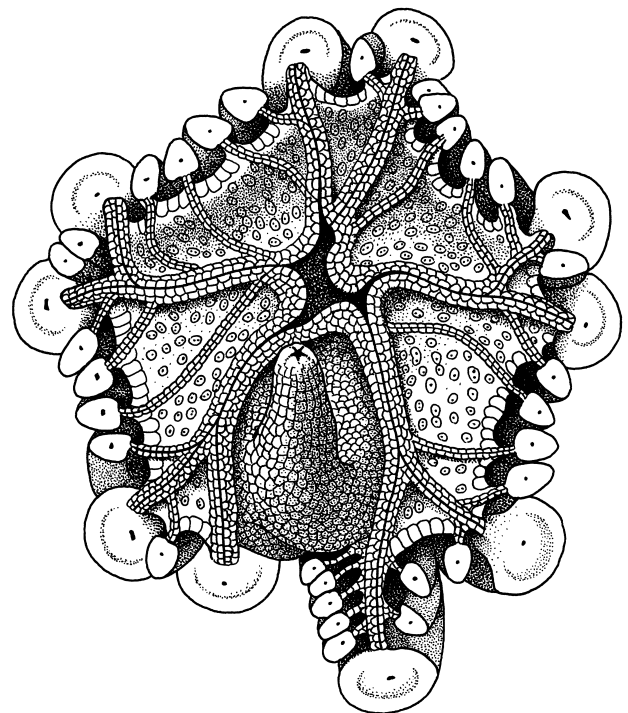


Fig. 5. Oral view of the disc of *Metacrinus angulatus* with tegmen. Food grooves end in the slightly displaced mouth; anal opening at the tip of an eccentric cone. (Redrawn from Carpenter 1884.) $\times 3$.

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 (Bau-
 miller *et al.* 1991). Muscular articulations, allowing

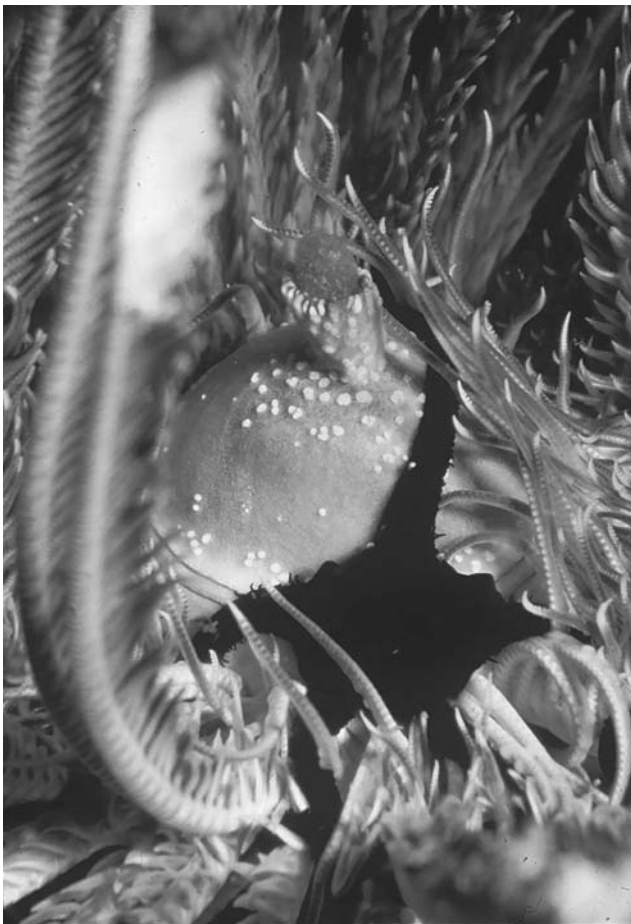


Fig. 6. Close-up of the oral disc (tegmen) of a comasterid comatulid with yellow-tipped oral pinnules; terminal comb teeth show on some of the pinnules. A black ophiuroid is sprawled across the disc, and the crinoid is releasing a bolus of faecal material from the anal tube. (Photograph O. C. Honegger, 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.

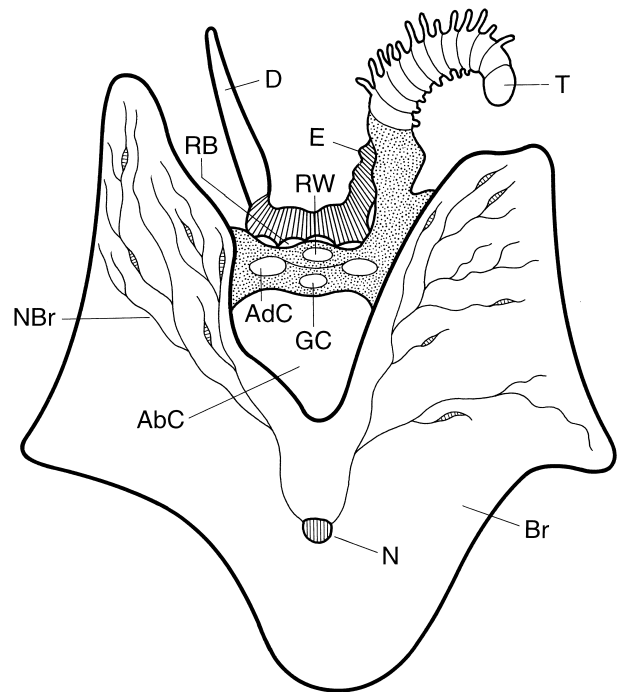


Fig. 7. Section through arm of *Bathycrinus aldrichianus*. Key: T, tentacle or tube foot or podium; D, covering plate of ambulacral groove; E, epidermis of ambulacral groove; Br, brachial ossicle; N, main brachial nerve; NBr, nerve branches; AbC, aboral coelomic canal; AdC, adoral coelomic canal; RW, 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-

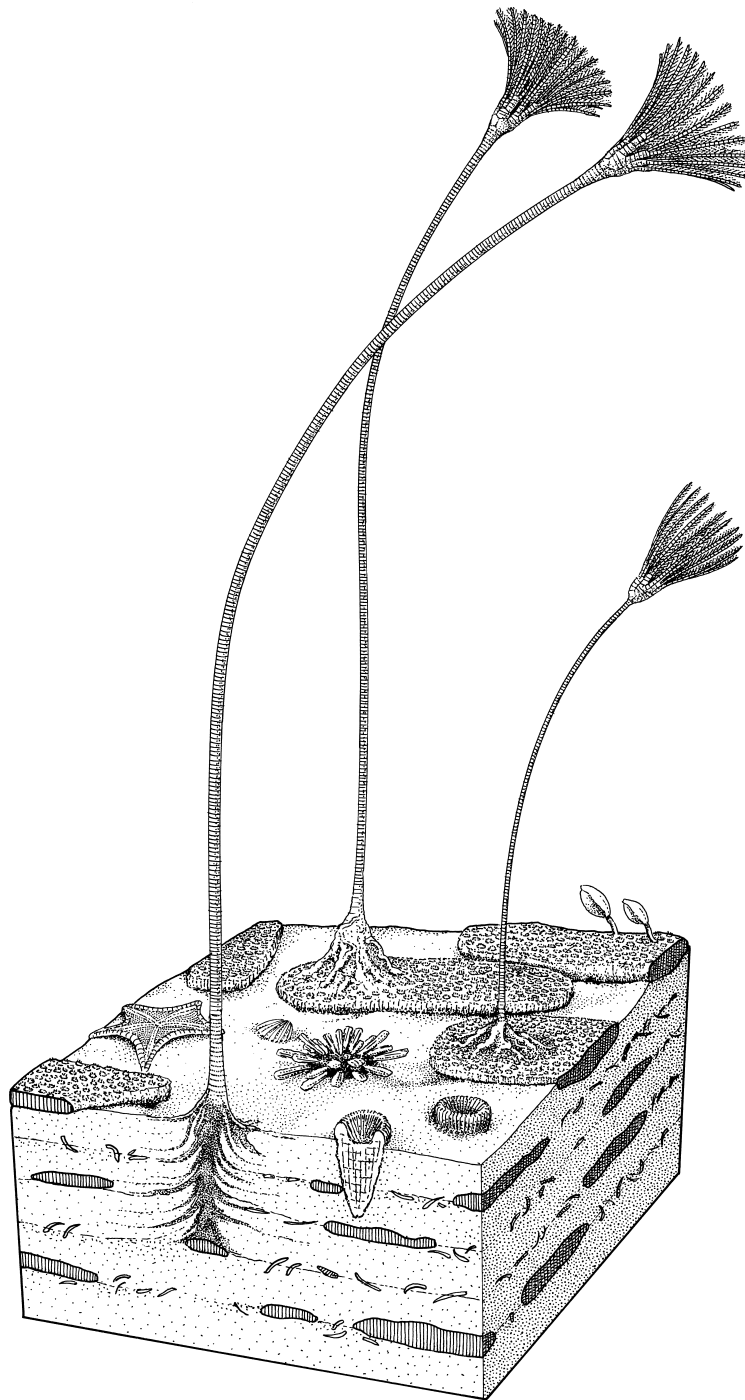


Fig. 8. Reconstruction of the Jurassic sea lily *Liliocrinus munsterianus*. Two individuals attached to dead corals (*Thamnasteria*) by a compact root, another individual anchored in muddy sediment (Liesberg Beds, Middle Oxfordian, Swiss Jura). This environment is comparable to today's lagoon southeast 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 echinoderm stem appears to have originated from an aboral evagination of the body, leading first to hollow tubes that were reinforced with irregular ossicles. Such primitive stems occur in Middle Cambrian pre-crinoidal pelmatozoans like *Gogia* (Fig. 2). In contrast, even in the earliest known crinoid, *Aethocrinus*, the stem is significantly 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

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 columnals 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 below the cup, so the short proximal region is the immature stem. Near the cup, the developing internodals are completely hidden by the nodals (Fig. 11), but internodals are successively introduced between nodals. Proximal columnals are shorter (thinner) than distal ones, so the stem grows or matures by sequentially adding columnals in the proximal region, first by adding nodals, then by intercalating internodals and finally by increasing the diameter of individual columnals.

Columnals are bound together by two types of elastic ligament fibres or mutable collagenous tissue,¹ which occur in a characteristic pattern (muscles are absent in the stem). Short, intercolumnar ligaments connect each pair of adjacent columnals. Longer, through-going ligaments 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 flexibility in different directions, preventing twisting and allowing for easy return to the original position. Longer, through-going ligaments are limited to the areola of each interradian 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

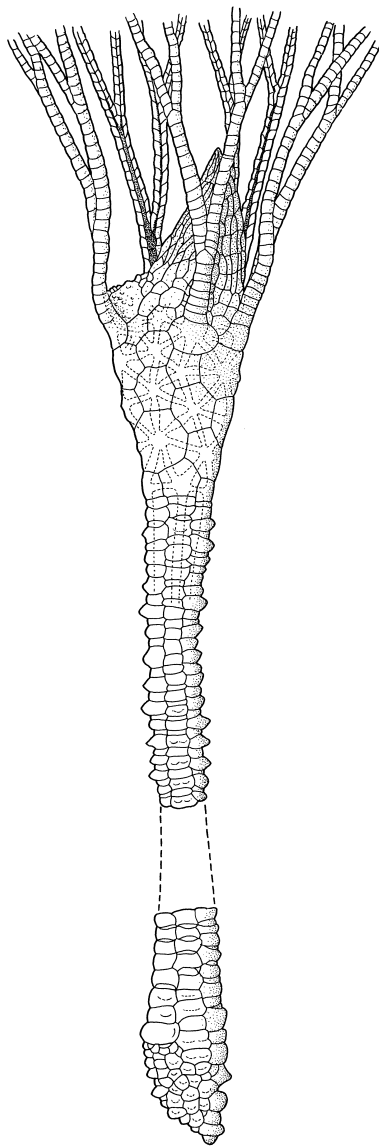


Fig. 9. Reconstruction of *Aethocrinus moorei*. Lower Ordovician, Montagne Noire, France. (Redrawn from Ubaghs 1969.) $\times 1$.

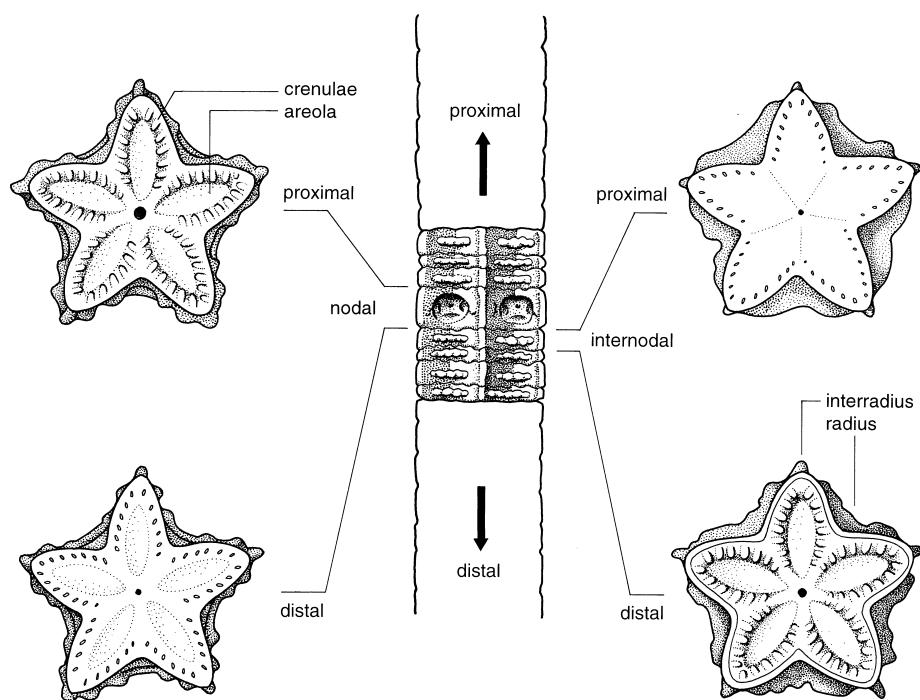


Fig. 10. Part of the stem of the isocrinid *Metacrinus angulatus*, with nodal and internodals, showing the different articular facets. (Redrawn from Carpenter 1884.) $\times 3$.

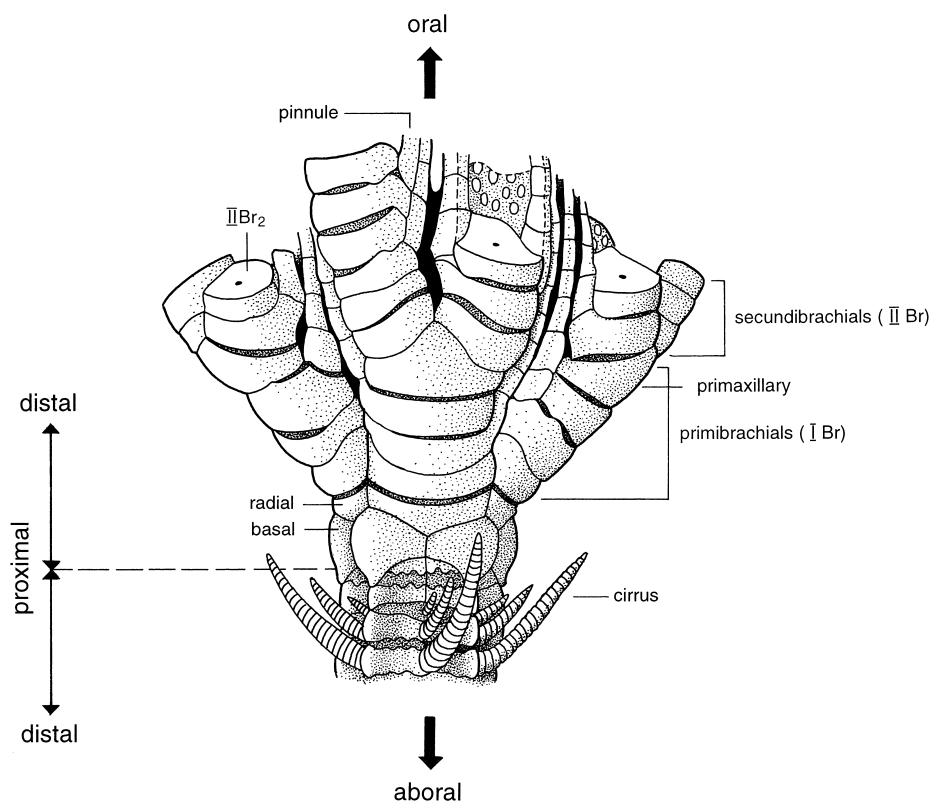


Fig. 11. Proximal stem, cup and base of arms of *Metacrinus angulatus*. (Redrawn from Carpenter 1884.) $\times 3$.

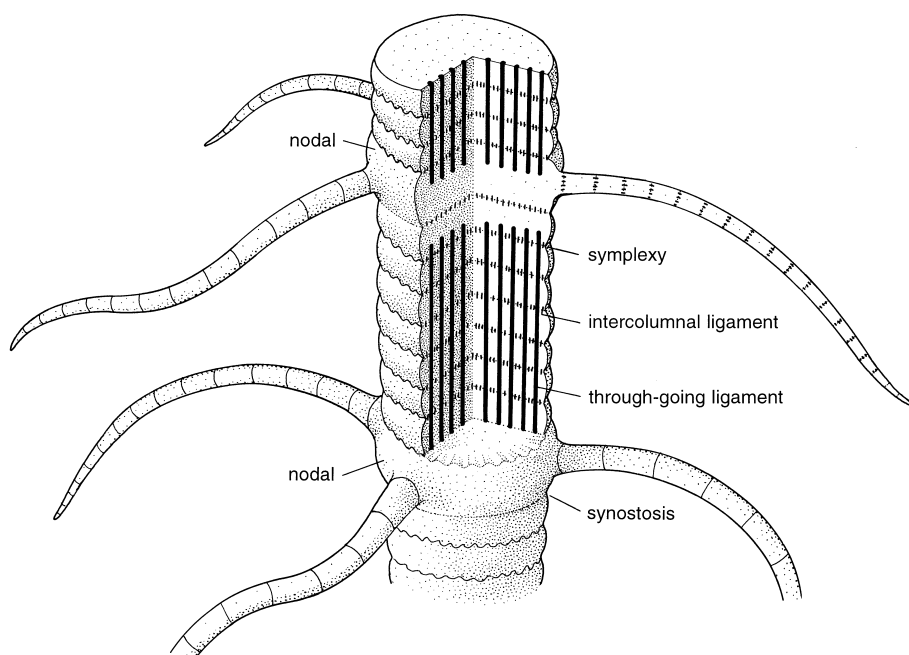


Fig. 12. Ligaments between nodal and internodals of an isocrinid stem. (Adapted from Baumiller & Ausich 1992.)

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-

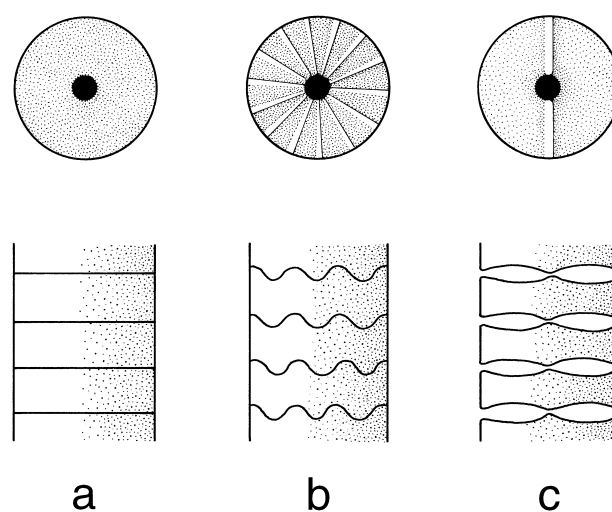


Fig. 13. Typical articular facets and long sections of crinoid stems. (a) Synostosis; (b) symplexy; (c) synarthry. (Redrawn from Donovan 1989a.)

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 bifascial pits are a feature of the Bourguetocrinida, 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-

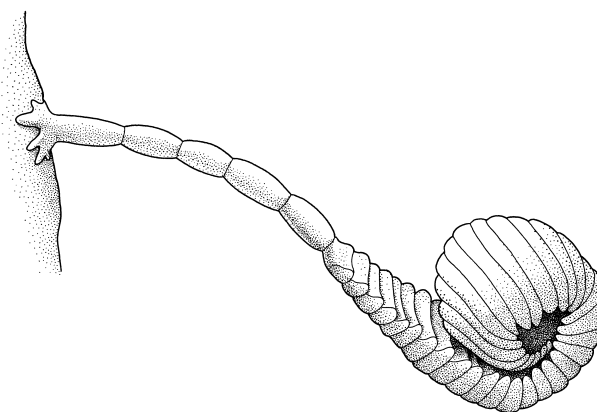


Fig. 14. Reconstruction of *Ammonicrinus doliiformis*, with crown hidden in enrolled stem. Stem is xenomorphic, with abrupt change between distal and middle part. Middle Devonian, Germany. (Redrawn from Ubaghs 1953.) $\times 1.5$.

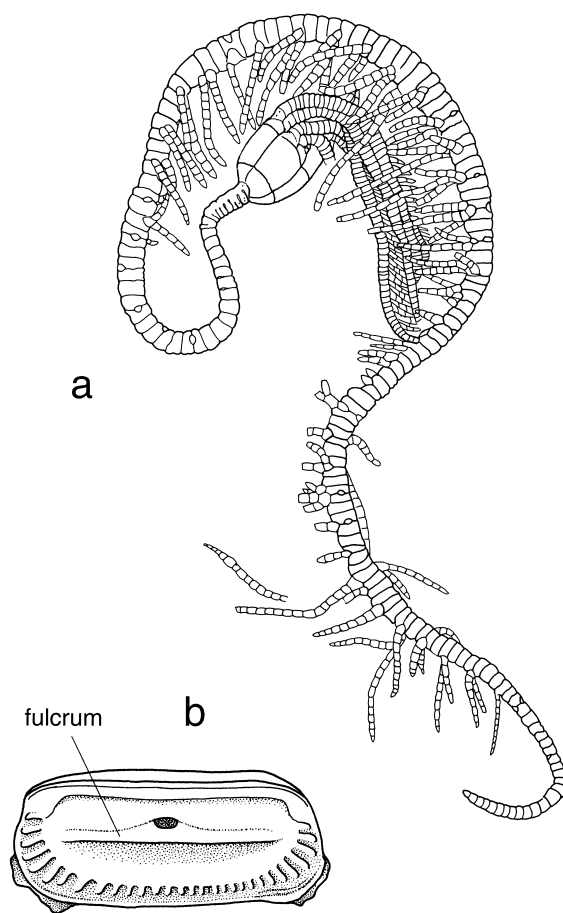


Fig. 15. (a) *Camptocrinus multicirrus*. Mississippian, Illinois. Complete specimen with coiled stem. (Redrawn from Ubaghs 1978.) $\times 1.5$. (b) Articular, synarthrial facet of a columnal of *Camptocrinus compressus*. Lower Carboniferous, Scotland. (Redrawn from Ubaghs 1978.) $\times 5$.

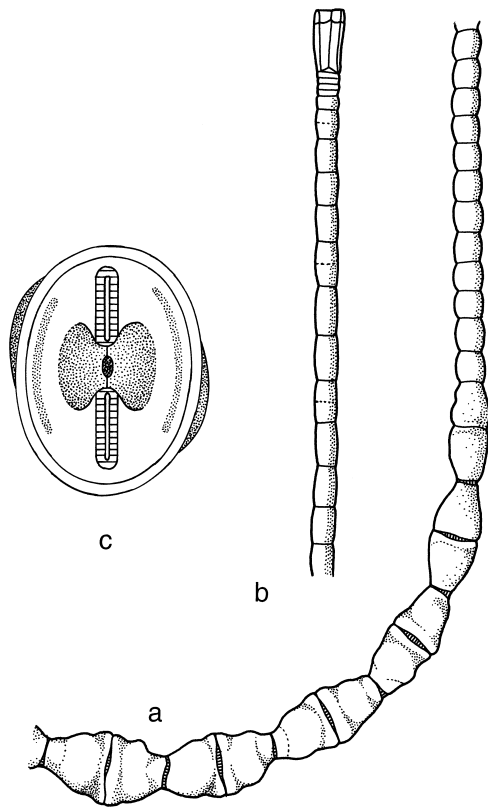


Fig. 16. (a, b) *Naumachocrinus hawaiiensis*, a Recent bourguetocrinid with synarthrial stem articulations. (Redrawn from Breimer 1978.) Approx. $\times 1$. (a) Distal column with fulcral ridges on alternate pairs of apposed facets rotated by 180° ; (b) proximal column with cup; (c) Articular facet of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

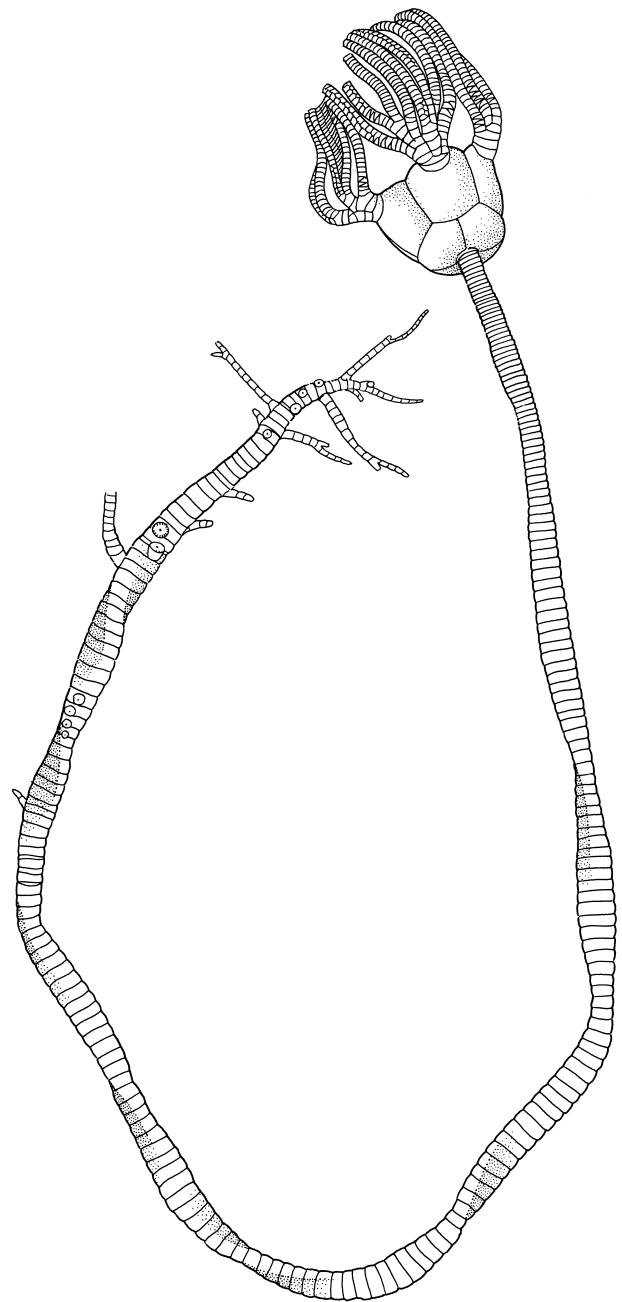


Fig. 17. *Platycrinites regalis*. Complete specimen with twisted stem carrying root-like radicular cirri (radices) distally. Mississippian (Burlington Limestone), Iowa. (Redrawn after Wachs-muth & Springer 1897.) $\times 0.7$.

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.

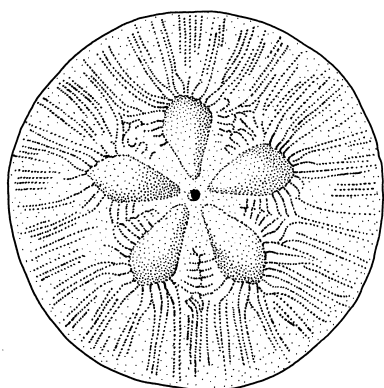


Fig. 18. Articular facet of internodal columnal of *Austinocrinus erckerti*. Senonian of Turkestan. (Redrawn from Rasmussen 1961.) $\times 2$.

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 *Seiocrinus*, 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 synostosomal 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 bourguetocrinid 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 *Liliocrinus*, 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

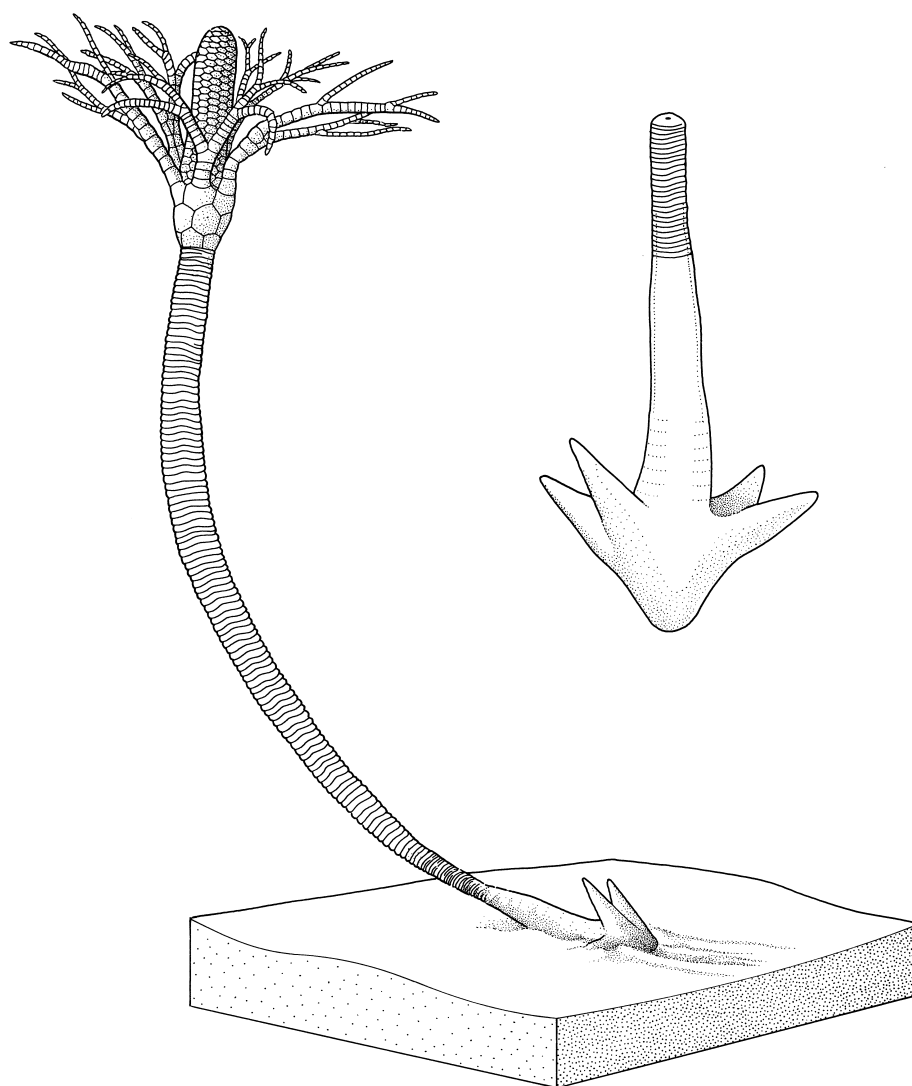


Fig. 20. *Ancyrocrinus bulbosus*. Devonian, New York. Left: complete animal; right, radicular cirri and terminal columnals ankylosed into the anchor-like holdfast. (Redrawn from Ubachs 1953.) Complete animal $\times 2$.

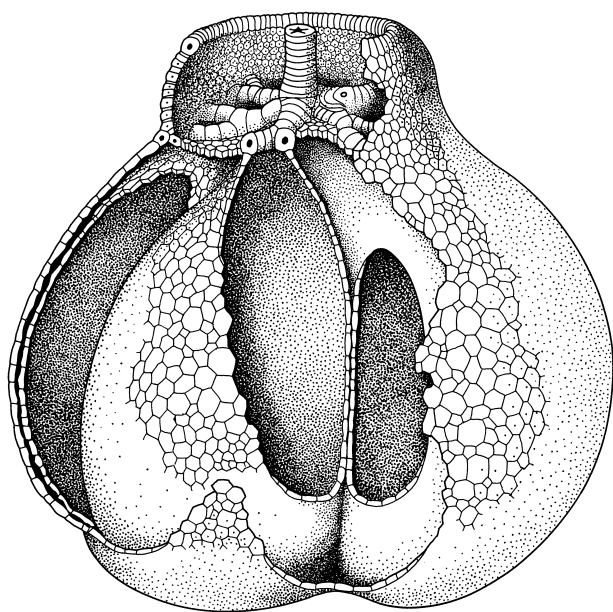


Fig. 21. Reconstruction of a lobolith ('Camarocrinus') of a scyphocrinitid. Lower Devonian, North America. The bulb is shown in presumably inverted life position, with the stump of the broken-off stem, contained in a collar, pointing upward (see Chapter 11 for further discussion). (Redrawn from Springer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

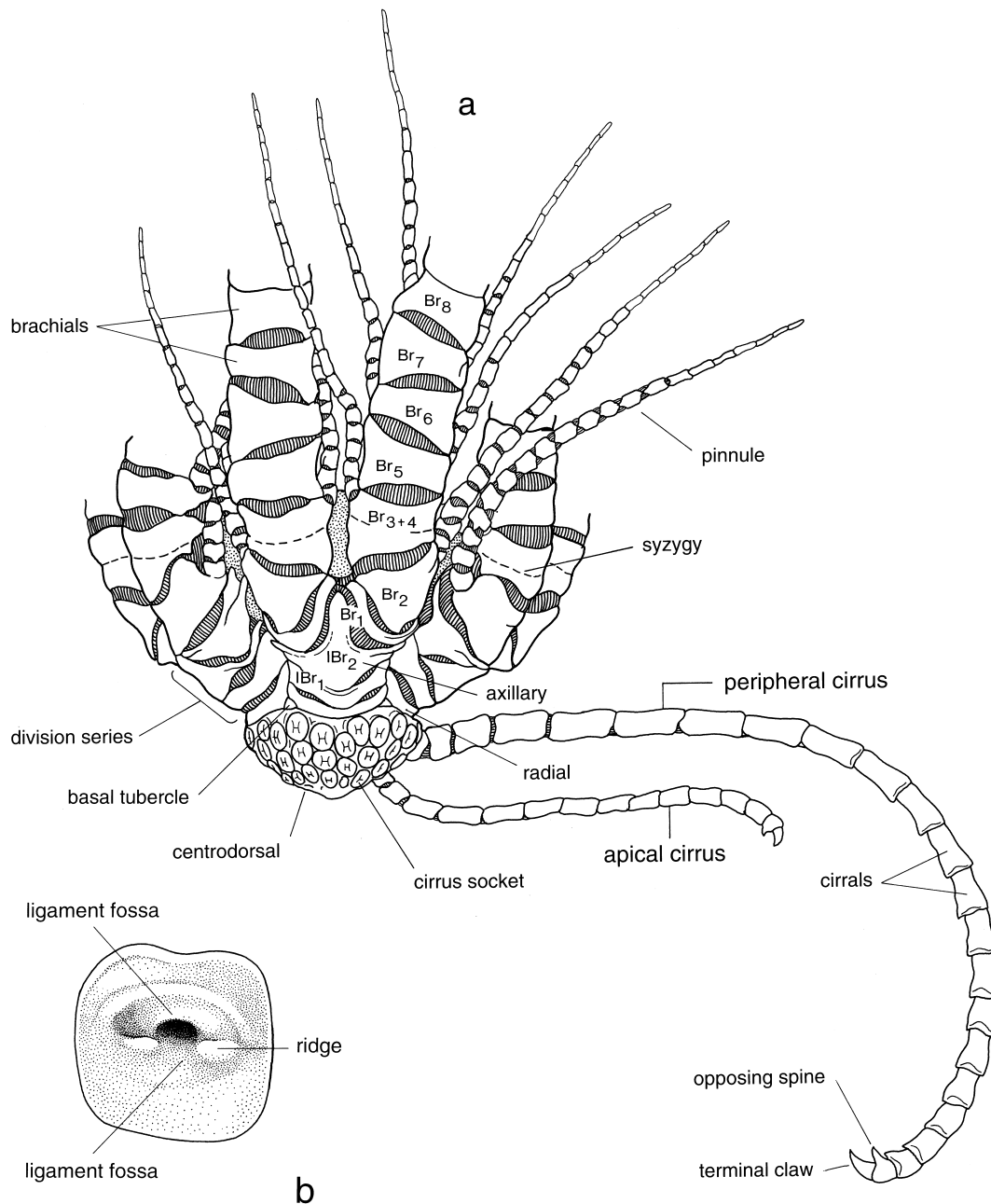


Fig. 22. (a) Lateral view of a comatulid with centrodorsal, two cirri and base of arms. (Redrawn from Messing & Dearborn 1990.) (b) Articular facet of second cirral of *Nemaster rubiginosus*. Recent. (After Donovan 1993.) Approx. $\times 30$.

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-

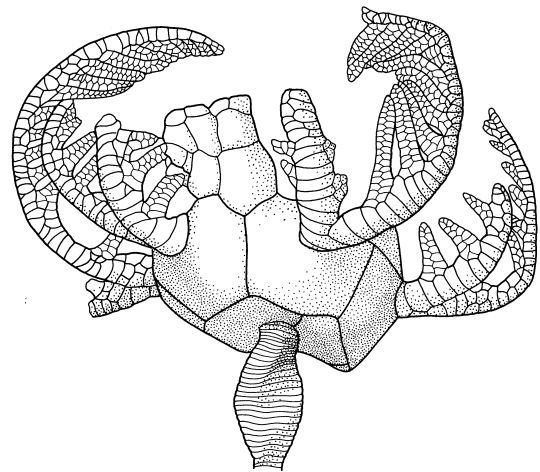


Fig. 23. Hand-shaped cup of the monobathrid *Eucladocrinus pleurovminus* with elliptical, twisted stem. Early Mississippian (Burlington Limestone), Iowa. (Redrawn from Ausich 1988.) $\times 0.6$.

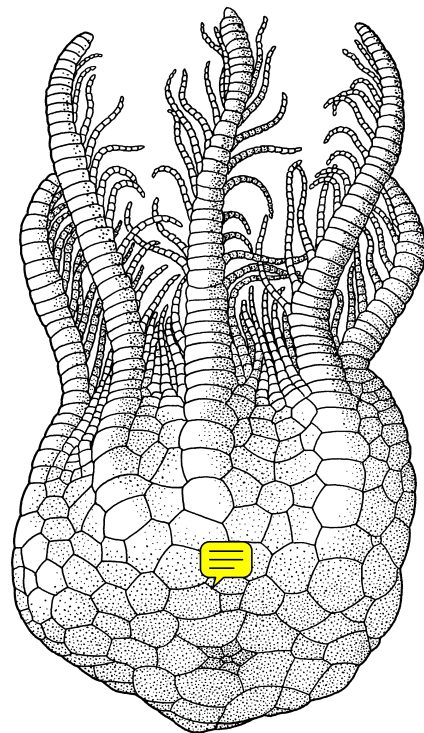


Fig. 24. Calyx of the articulate *Uintacrinus socialis*, a multi-plated bowl design. Upper Cretaceous, North America. (Redrawn from Ausich 1988.) $\times 1$.

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).

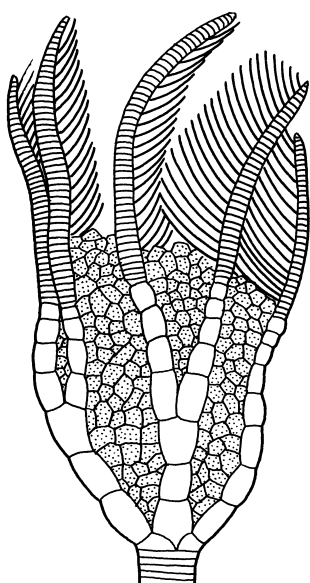


Fig. 25. Conical mosaic calyx of the monobathrid *Xenocrinus penicillus*. Upper Ordovician, Ohio. (Redrawn from Ausich 1988.) $\times 2$.

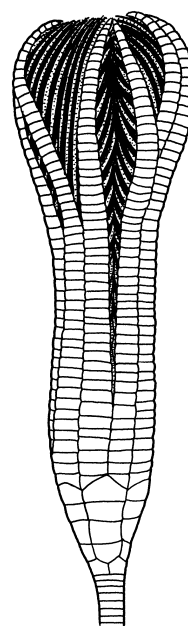


Fig. 26. *Ectenocrinus grandis*, a disparid with cylindric cup. Upper Ordovician, Ohio. (Redrawn from Ausich 1988.) $\times 1$.

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

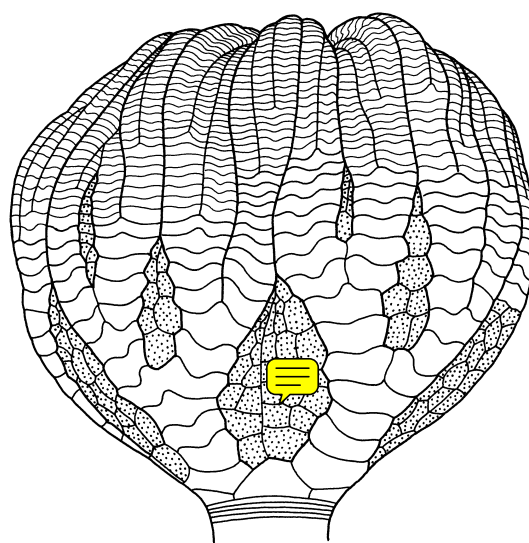


Fig. 27. *Forbesiocrinus wortheni*, a flexible with undifferentiated anal and interbrachial plates (stippled). Mississippian, Indiana. (Redrawn from Ubaghs 1978.) $\times 1$.

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-

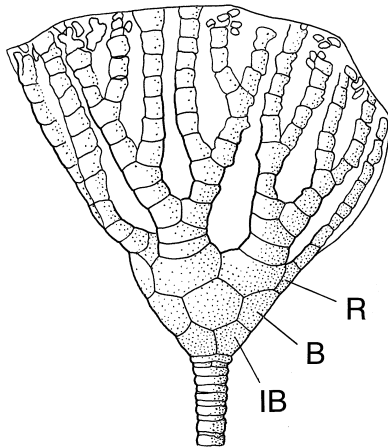


Fig. 28. *Eoparisocrinus siluricus*, a cladid with dicyclic cup. Upper Silurian, Indiana. Key: IB, infrabasal; B, basal; R, radial. (Redrawn from Ubaghs 1978.) $\times 1.5$.

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 interradius² 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

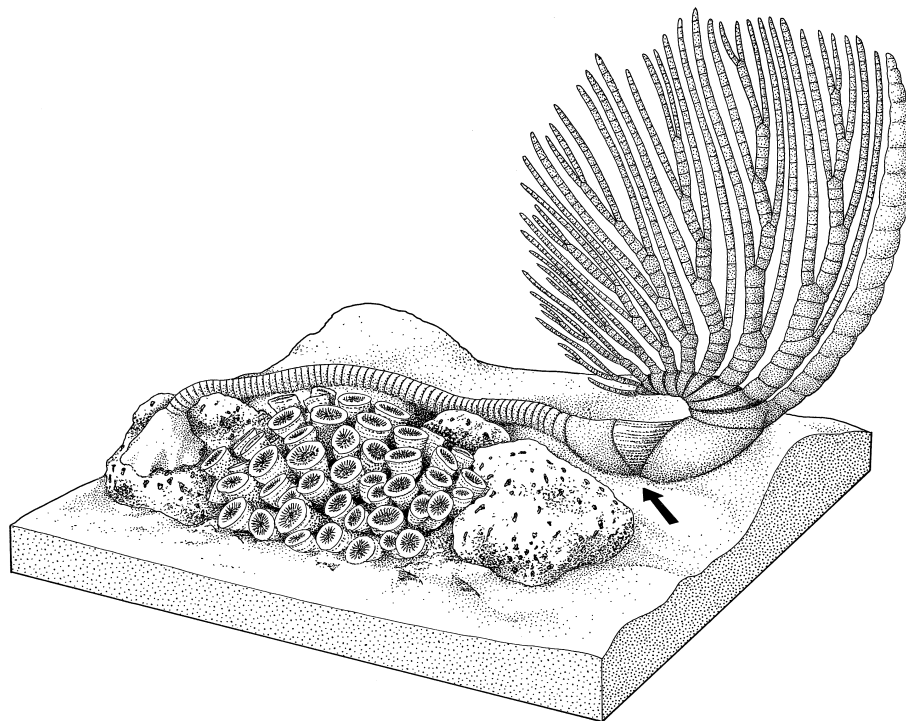


Fig. 29. Reconstruction of the feeding posture of a calceocrinid with opened crown on a coral reef (current from right). Radial circlet and arms are elevated above the substrate by opening above a hinge (arrow) between the basal and radial circlet. One lateral arm of this bilaterally symmetrical crinoid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

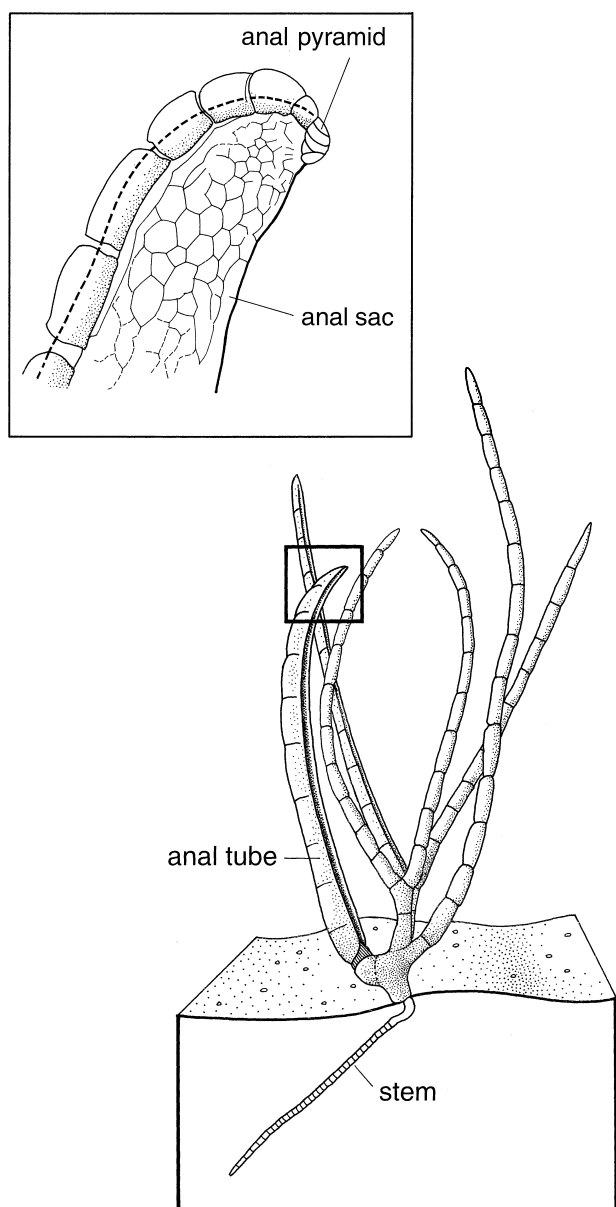


Fig. 30. Reconstruction of the calceocrinid *Senariocrinus maucheri*. Crown with strong bilateral symmetry, single dichotomous division of two arms and long unbranched arm; short, vermiform stem attached at extremity of single triangular basal plate. $\times 3$. Inset: Enlarged distal part of anal sac 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,³ 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 interradian 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

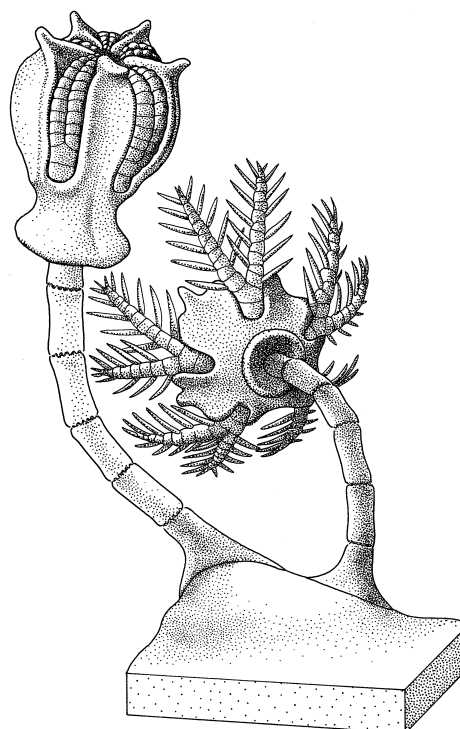


Fig. 33. Reconstruction of *Apsidocrinus moeschi*. Tithonian, Rogoznik (Poland) and Switzerland. (Redrawn from Pisera & Dzik 1979.) $\times 4$.

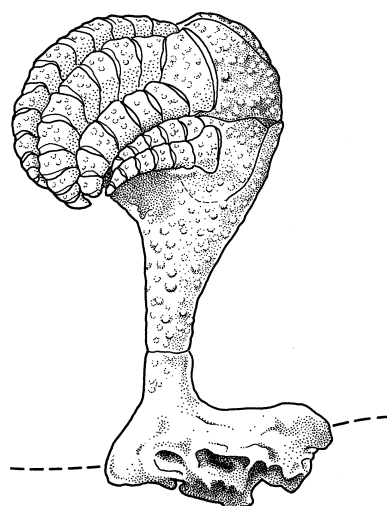


Fig. 34. Reconstruction of *Hemicrinus astierianus*. Lower Cretaceous, Var, France. (Redrawn from Jaekel 1918.) $\times 3$.

(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,⁴ 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.

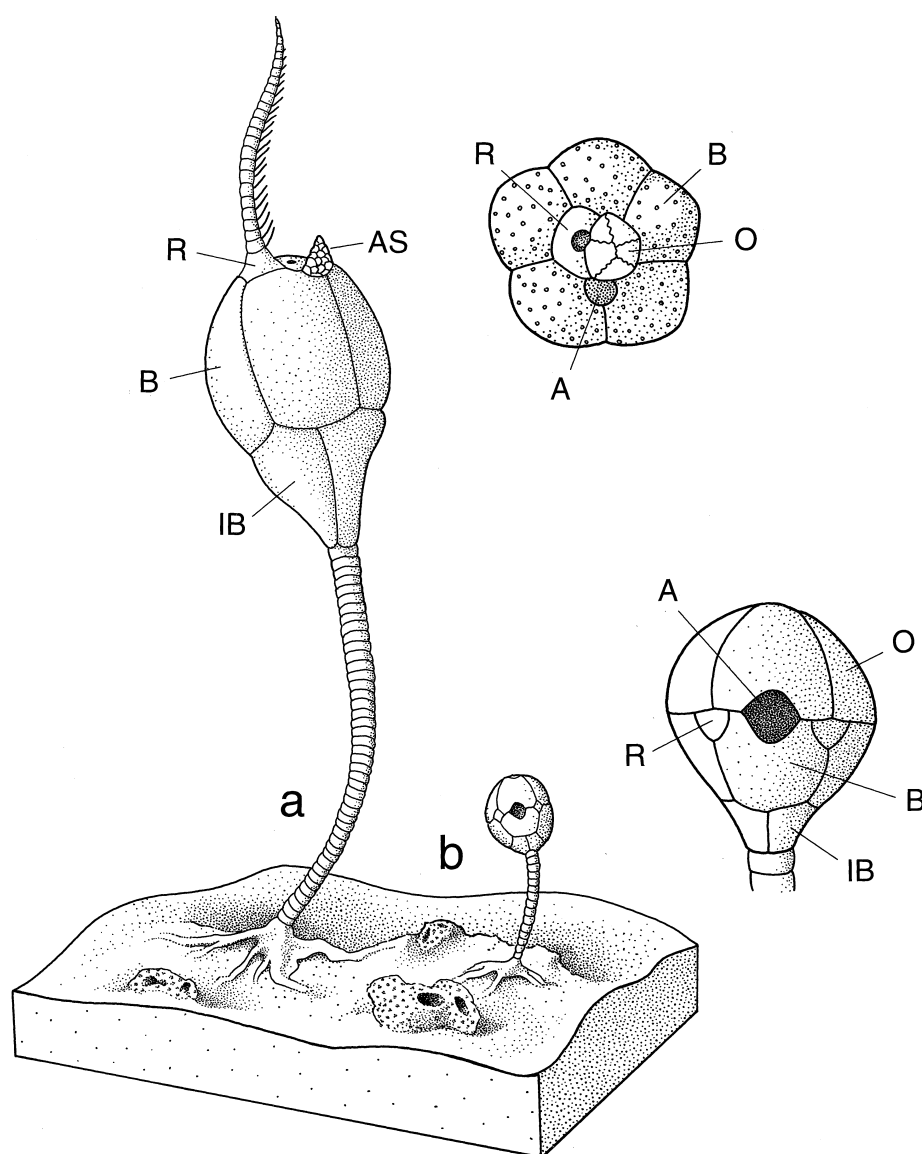


Fig. 35. Reconstruction of (a) *Monobrachiocrinus ficiformis granulatus* with single arm, with enlarged oral view of cup; and (b) armless *Embryocrinus hanieli*, with enlarged anal side view. Permian Basleo (also called Besleo) Beds, Timor. Key: A, anal opening; AS, anal sac; B, basal; IB, infrabasal;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

5). The ambulacral grooves are commonly protected by covering plates. In the Upper Carboniferous camerate genus *Pterotocrinus*, the ambulacrals located at the points of bifurcation of the ambulacra are developed into conspicuous appendages, reaching a size similar to that of the whole crown. These wing plates may assume an extraordinary variety of shapes, from thin, knife-like wings to massive clubs and spines. Their function has been a matter of much speculation. According to a recent hydrodynamic analysis, they may have served as stabilizing fins or rudders, allowing the passive maintenance of an efficient feeding position in moving water (Baumiller & Plotnick 1989).

Many crinoids have an elongate anal sac or tube with the anal opening at the summit. The function of this sometimes highly ornate structure may have been to avoid faecal contamination by ingested food, because the anus and the mouth otherwise lie close together on the tegmen. Although both camerates and inadunates (cladids and disparids) have the anus on tubular extensions above the tegmen, different names are applied, because the anal tube and anal sac had independent evolutionary origins. The most extensive modifications of anal structure occur among inadunates (disparids and cladids), in which the structure is termed an anal sac. An example of a crinoid with an anal sac is the bilaterally symmetric calceocrinid *Senariocrinus*, which has an arm-like series of U-shaped anal plates, supporting a fine-plated sac with the anal pyramid at its tip (Fig. 30). The hinged anal sac may have been moved to direct the anal opening away from the arms and mouth of this crinoid, a helpful function in the more quiet waters of the Devonian Hunsrück facies. Late Palaeozoic inadunates developed elaborate, sometimes spinose anal sacs (Figs. 36, 141). Some authors have thought that spines were an anti-predatory adaptation, whereas Lane (1984) suggested that the entire anal sac, rising from the crown, may have been an offering to predators so that predatory attacks would be non-lethal.

A tegmen of a very different nature is present on the Palaeozoic camerates. Here, the multi-plated tegmen and the calyx plates are united into a rigid, commonly globose structure that rises above the arms (Figs. 37, 38). It resists disarticulation following death and, presumably, also resisted predator attacks just as effectively. The anal tube of camerates is typically a distal extension of the central tegmen. It has been suggested that such anal tubes, directed downcurrent, not only served to dispose of waste, but also helped to stabilize crowns deployed as a filtration fan (Baumiller 1990a). A long

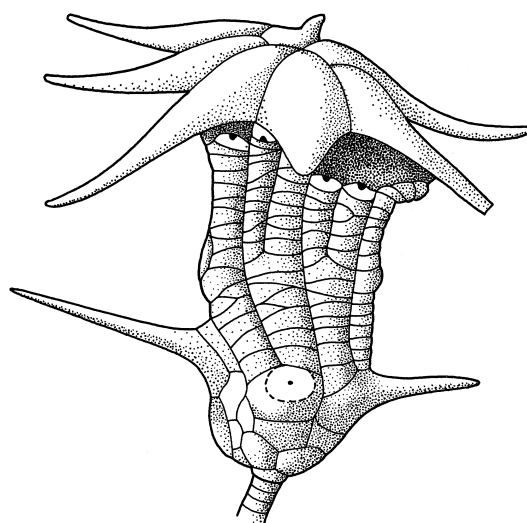


Fig. 36. *Bicidiocrinus wetherbyi*. The mushroom-shaped anal sac of this cladid is concealed by arms, except the distal spiniferous canopy of the sac. Note the large spiniferous axillary primibrachials. Mississippian, Kentucky. (Redrawn from Ubaghs 1978.) $\times 1.5$.

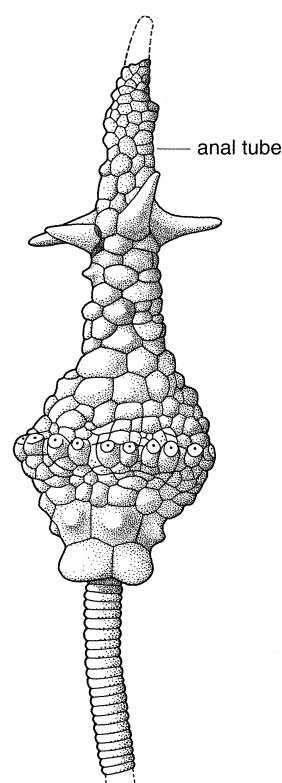


Fig. 37. *Uperocrinus nashvillae*, a camerate with large anal tube (distal end of anal tube and arms lacking); interbrachials are stippled. Mississippian, North America. (Redrawn from Wachsmuth & Springer 1897.) $\times 0.5$.

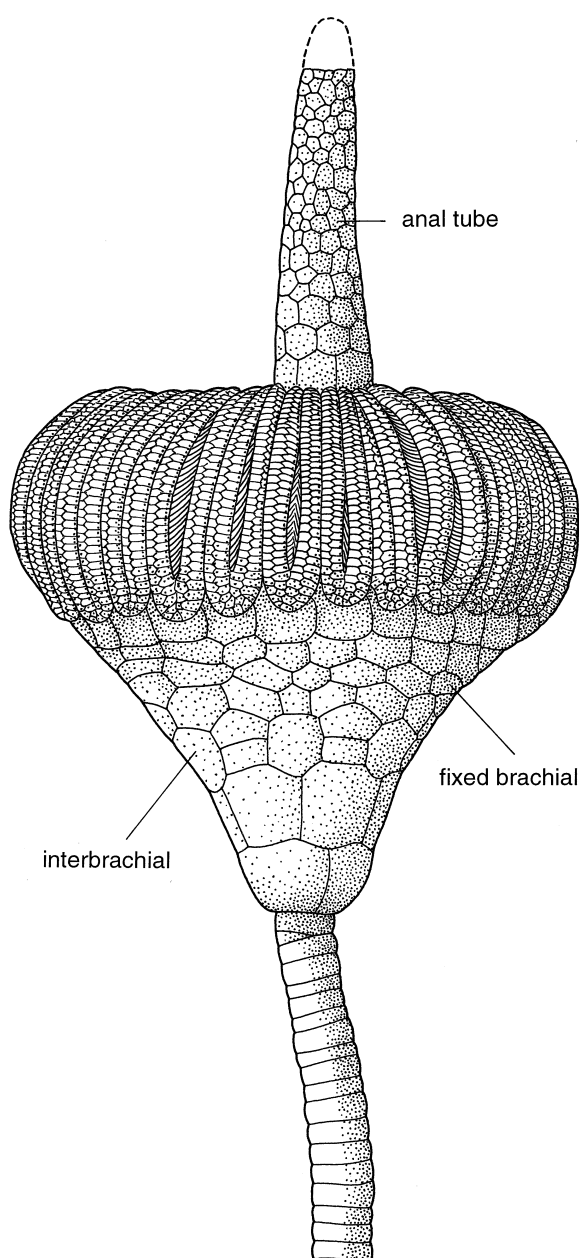


Fig. 38. *Eutrochocrinus christyi*, a camerate with fixed interbrachials and brachials; distal end of anal tube lacking. Mississippian (Burlington Limestone), Iowa. (Redrawn from Wachs-muth & Springer 1897.) $\times 1$.

anal tube would have been ineffective for crinoids living in still water or where currents were very weak.

The size of the cup in many articulates is greatly reduced in comparison to typical Palaeozoic forms, thereby reducing the level of protection afforded to the vital organs. This may be compensated for in part by the relocation of the gonads onto the proximal pinnules, but also by the remarkable regenerative powers that

have been documented in extant crinoids. D. L. Meyer (1988) found that comatulids can regenerate the entire visceral mass in only a few weeks, whereas Amemiya and Oji (1992) have documented even more remarkable instances where isocrinids have regenerated the entire crown from just the basal circlet of the cup. According to Donovan and Pawson (1998) the stem of Recent bourgueticrinids continued to survive following the loss of the crown and proximal column, presumably by absorbing dissolved nutrients through the ectoderm.

THE ARMS

The arms represent the food-gathering parts of the crinoid. The ultimate food-collecting structures are the tube feet; hence some crinoids can function quite effectively despite the presence of only one arm or in the absence of any arms (Fig. 35).

Although food gathering is the primary function of crinoid arms, it is by no means their only function. Arms are important for respiration and locomotion in some taxa, either swimming as in some comatulids or crawling as in comatulids and even in some stalked isocrinids (Messing 1985; Baumiller *et al.* 1991). Attachment is also an important function, particularly in multi-armed taxa such as comasterid comatulids.

Brachials and Their Articulations

The crinoid arm consists of a series of ossicles, called brachials, united by ligaments and/or muscles. A groove along the oral side of the arm is lined with tube feet (Fig. 7), which pass food particles down to the mouth. In most crinoids, the arm must retain both flexibility and mobility so that it can be deployed to maximum advantage in filtering food particles from the water. Flexibility is inherent in the multi-element construction, and mobility is achieved by antagonistic series of ligaments and muscles. Arm flexibility is to an extent controlled by brachial width. Hence, to maintain relative flexibility during growth, brachial height increases much more slowly than brachial width.

In Palaeozoic forms, ligamentary articulations are the most common mode of union between radials and arms and between arm plates. Articulations may be movable to some extent; they may also be immovable, permitting at the most slight movements. Movable articulations typically have three bundles of ligament separated by more or less well-defined elevations. In contrast to the

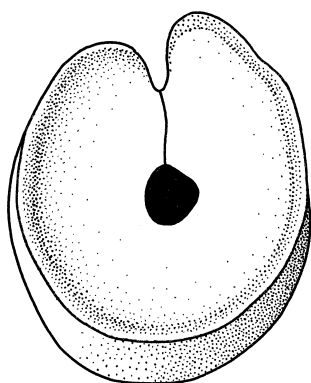
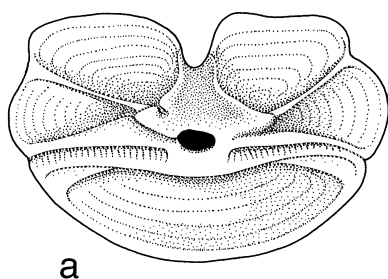
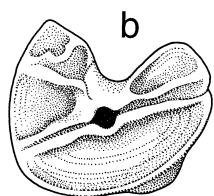


Fig. 39. Synostosal articulation on distal facet of third primibrachial of *Barycrinus rhombiferus*. Mississippian, Indiana. (Redrawn from Ubaghs 1978.) $\times 3$.



a



b

Fig. 40. Muscular articulations of *Marsupites testudinarius*. Upper Cretaceous, Europe. (a) Radial facet with straight articulation; (b) oblique muscular articulation of distal secundibrachial with pinnule facet. (After Ubaghs 1978.) $\times 6$.

bifascial synarthry discussed later in this section, such articulations did not act as a fulcrum. More or less immovable synostosal-like articulations are very common in Palaeozoic crinoids (Fig. 39). The reader is referred to the *Treatise* (Ubaghs 1978) for further details.

Post-Palaeozoic articulate crinoids have brachials with several types of articulations, with muscular articulations (Fig. 40) the most common. These articulations combine ligament fibres with muscles. They possess a transverse fulcral ridge, to the aboral side of which is a large ligament pit for the attachment of the aboral ligament. Immediately to the oral side of the fulcral ridge are two smaller pits for the interarticular ligaments, and

still further orally are two flanges for the attachment of the adoral muscle. The aboral ligaments serve to hold the arms flexed aborally, as is common in parabolic filtration fans, whereas the muscles are antagonistic to these ligaments and are used to draw the arms back in towards the oral surface of the disc. In crinoids such as comatulids that occupy changeable environments or that are highly mobile, the muscular fields on the brachials are large and well developed. In contrast, in taxa such as the pseudoplanktonic *Pentacrinites* and *Seirocrinus* that occupied very stable environments and did not need a great degree of arm mobility, the muscular fields are quite small, and the aboral ligament pit is greatly enlarged, occupying more than half of the total area of the brachial articulum (Fig. 41). Whether muscles existed in the arms of many Palaeozoic crinoids remains a topic of debate (Simms & Sevastopulo 1993). It appears that muscular arm articulations first evolved during the Middle Palaeozoic among cladid inadunates (Ausich & Baumiller 1993).

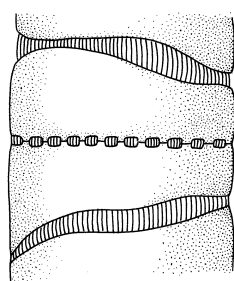
Immovable articulations, connected by short ligament fibres only, are synostoses with smooth surfaces



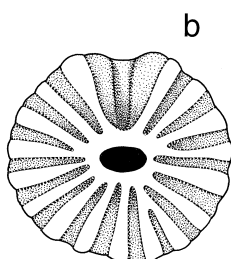
Fig. 41. Muscular articulation on brachials of *Pentacrinites fossilis*. Note comparatively small muscular fields (arrows); a rhomboid cirral is visible at lower left. Sinemurian, *obtusum* Subzone, Black Ven, Charmouth, Dorset. (Also figured by Simms 1989.) $\times 4$.

and syzygies with radiating ridges and furrows on otherwise flat surfaces (Figs. 4, 42). Instead of interlocking as in stem symplexies so that the suture is crenulate (see Fig. 13), the ridges of one face oppose the ridges of the other. Syzygies are irregularly spaced along the proximal part of the arms of articulates and are preferred breaking points (similar to the cryptosymplexy between the nodal and infranodal of the stem). In this way, the optimum position for rupture of the arm, following a predator attack or other trauma, can be determined in advance, thereby limiting the damage to the filtration fan as a whole.

Synarthries are superficially similar to those in the stem. They have a fulcral ridge running orally-aborally and two separate bundles of ligaments (Fig. 43). This



a



b

Fig. 42. (a) Schematic representation of two brachials united by syzygy; (b) syzygial articular facet. (Redrawn from Ubaghs 1978.)

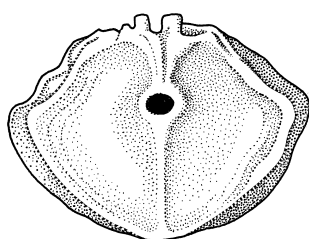


Fig. 43. Synarthrial articular facet of first primibrachial of *Himerometra bassleri*. Eocene, South Carolina. (Redrawn from Ubaghs 1978.) $\times 6$.

structure allows limited movement. Synarthries are confined to the proximal parts of the arms in articulates and have been shown to represent modified syzygial articulations (Simms & Sevastopulo 1993).

Feeding Strategies and Arm Structure

Crinoids are passive suspension feeders, which means that they must rely exclusively on currents to bring suspended food particles to their food-gathering apparatus. In their pioneering work, Macurda and Meyer (1974) showed that living crinoids feed via a parabolic filtration fan with the oral surface downcurrent (Figs. 1, 236). This mode of feeding on fine particles was probably approximated in ancient crinoids, such as the strongly pinnulate camerates. However, because of lack of evidence for muscular articulations in most Palaeozoic crinoids, it is questionable whether the relatively flexible filtration fans of modern crinoids were developed in these ancient forms.

Dense filtration fans appear to be a highly specialized feature that became most successful in advanced cladids and modern articulates. Most of the early crinoids and nearly all of the disparids possess only atomous or slightly branched, stick-like arms that lack pinnules and have relatively broad food grooves. This indicates that the earliest crinoids may have possessed large, fleshy tube feet. These could not have trapped small particles in turbulent downcurrent eddies the way modern crinoids do with their filtration fans. Rather, they may have fed by means of very elongated tube feet. Other crinoids with permanently fused arm plates, such as *Petalocrinus*, could again not possibly have formed a filtration fan. Another example of crinoid that may have fed in an alternative way is the Silurian cladid *Crotalocrinites* with laterally united brachials. The resulting box-like structures may be interpreted as pumping chambers. It seems possible to surmise that these crinoids used a type of ciliary pumping mechanism to draw currents inside the enclosed chambers for feeding in much the way sponges and other chamber-feeding-filter feeders do. Likewise, certain other crinoids such as *Eucalyptocrinites*, with arms that could be only partially withdrawn from large tegmental plates, may also have been able to generate their own feeding currents and hence survived well in an environment of low turbulence (Brett 1984). The same is true of another camerate Silurian reef dweller, the highly specialized *Barrandeocrinus* (Fig. 99). Confirming the existence of these alternative feeding styles requires further research.

Flexibles must have had still other feeding strategies. These crinoids never developed pinnules, but instead had arms that ranged from extremely broad, petal-like appendages to highly ramulate arms that branched out to tendril-like endings (Fig. 56). The arms are strongly incurved at the summit of the crown (Figs. 27, 158). Some of the forms have short, rather stubby arms with extremely broad food grooves, suggesting the presence of large, fleshy tube feet. These may have been able to capture relatively large prey, which could be enrolled within the arms to form a kind of digestive chamber overlying the mouth. These types of flexibles are reminiscent of cyrtocrinids such as *Holopus* (Fig. 31) and *Gymnocrinus* (Fig. 32). Living *Cyathidium* and *Holopus* may use their arms to pass food to the mouth (Grimmer & Holland 1990; Heinzeller & Fechter 1995), but *Gymnocrinus* appears to enroll its arms for protection only (Heinzeller *et al.* 1994); see Chapter 29. Reasoning by analogy, Meyer and Lane (1976) suggested that the feeding strategies of taxocrinid flexibles and cyathocrine cladids with highly branched, non-pinnulate arms were similar to that of basket stars (gorgonocephalid ophiuroids), but this appears unlikely in view of the absence of muscles in the arms of these Palaeozoic forms. Basket stars seize their prey by wrapping the tendril-like endings of the arms around passing macroscopic objects of 10–30 mm size; this catch is eventually moved towards the mouth by enrolling the arms.

Arm Branching

The arms are inserted on the radials, which form the base of a ray. Each ray consists of a series of brachials. In its simplest form, a single unbranched arm is inserted on each ray.

A primary function of the stem is to elevate the filtration fan above frictional effects at the sea floor and into zones of higher current velocity, where the fan can filter larger volumes of water per unit time. From the simple non-branching arms, finer-meshed fans are produced by arm branching. Different filters result from the vast array of brachial types and arm branching styles. If other features remain constant, the progression from non-pinnulate to uniserially pinnulate to biserially pinnulate (see next subsection) results in increasingly more dense filtration fans. Many different patterns of arm branching have developed among the Crinoidea, each of which may have its advantages and disadvantages. Increased filtration fan density is achieved through the following sequence of arm branching styles (Fig. 44):

unbranched or atomous (Fig. 45), simple isotomous/heterotomous branching (Figs. 25, 26), complex isotomous/heterotomous branching (Fig. 46), uniserial pinnulation (Figs. 22a, 33) and biserial pinnulation (Figs. 47, 48). In heterotomous arms the main branch, or ramus, carries smaller branches, called armlets or ramules (ramuli).

Increased density of branching does not increase the efficiency of crinoid feeding. Instead, filtration fans with different densities optimally capture different-sized food particles (Ausich 1980). Crinoids living together, but with contrasting filtration fans, capture different-sized populations of food particles and, therefore, do not com-

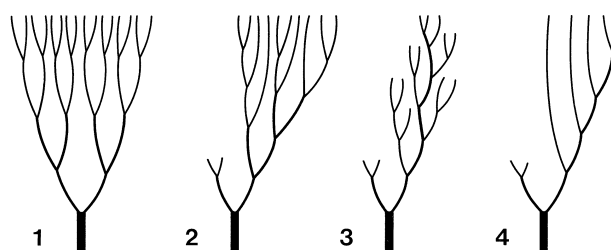


Fig. 44. Various types of arm branching: (1) isotomy; (2 and 3) heterotomy; (4) endotomy. (Redrawn from Ubaghs 1978.)

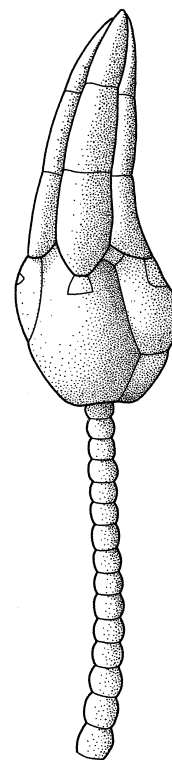


Fig. 45. *Parapisocrinus quinquelobus* with unbranched (atomous) arms. Silurian, Indiana. (After Springer 1926.) $\times 2$.

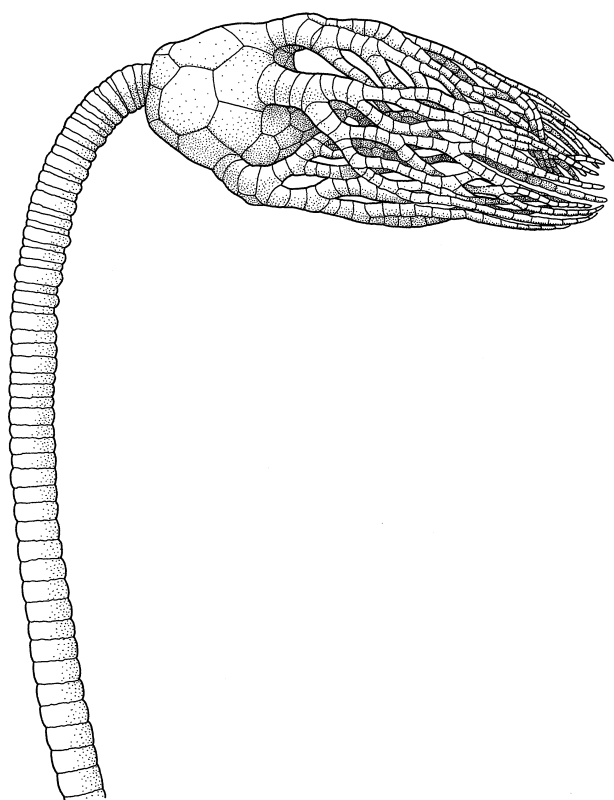


Fig. 46. *Cyathocrinites multibrachiatus* with complex arm branching. (Redrawn from Bather 1900.) $\times 1.2$.

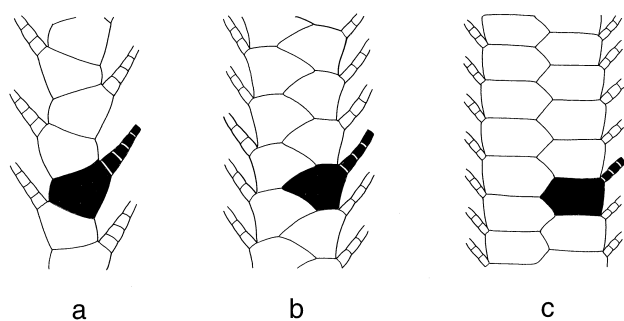


Fig. 47. Comparison of pinnule spacing on uniserial and biserial arms; one pinnule-bearing brachial is in black. (After Ubaghs 1953.)

pete for the same resources. In terms of filtration fan efficiency, if applicable, an endotomous pattern (Figs. 51, 189) has been considered to represent the optimum for transporting food to the mouth (Cowen 1981; Simms 1986), yet this configuration is encountered only under circumstances in which a parabolic or planar filtration fan may have been of limited use (see Chapters 22 and 25). The most common branching is simple

isotomous branching, commonly repeated several times (Fig. 214), suggesting that this configuration, although far from the optimum for total filtration surface, is quite adequate for most crinoids.

In rays with arm branching, each series of brachials leading either from the radial to the first branch point or from a subsequent branch point to another is called a division series or brachitaxis. Such a division series terminates in an axillary with two distal articular facets, but it may also remain undivided to its distal extremity. In most extant and many fossil crinoids, the first brachitaxis (the primibrachials, or IBr) is composed of two brachials. Brachials that immediately precede an arm division are known as axillaries. The second primibrachial is usually an axillary (Fig. 22a, in Fig. 11 it is the fourth) and carries the secundibrachials (IIBr), followed by tertibrachials (IIIr) after the next axillary, and so on.

Pinnules

One type of arm branching deserves further mention – that of pinnulation. Pinnules are small, usually unbranched offshoots of the arm that arise from each brachial plate (Fig. 49). Pinnulation produces the most dense filtration fans. The success of this strategy is evident from the fact that pinnulation arose independently at least three times – in the camerates, cladids and disparids. In Late Palaeozoic cladids and the post-Palaeozoic articulate, pinnules developed on alternative sides of successive brachials (Fig. 50a,b), except axillary brachials, or the distal brachial of a syzygial or synarthrial pair (Fig. 49). Hence, gaps exist in the rows of pinnules along each side of an arm – regular gaps on every alternate brachial and less regular gaps caused by the presence of syzygial articulations and axillary brachials. In a rather bizarre evolutionary twist, the Triassic encrinids *Traumatocrinus* and *Vostocovacrinus*, which have an endotomous pattern of arm branching, achieved almost complete pinnulation through the elimination of all muscular articulations and the development of exclusively syzygial articulations in the arms!

A second strategy for increasing the number of pinnules along a given stretch of crinoid arm is the reduction in height of the brachials. Such a strategy was adopted by the scyphocrinitids (Fig. 112), and it perhaps reached its acme in the bizarre Triassic genera *Vostocovacrinus* (Fig. 51) and *Traumatocrinus*. Brachials generally have a wedge-shaped section, with the pinnules arising from the high side of the brachial (Fig. 50a,b). Hence,

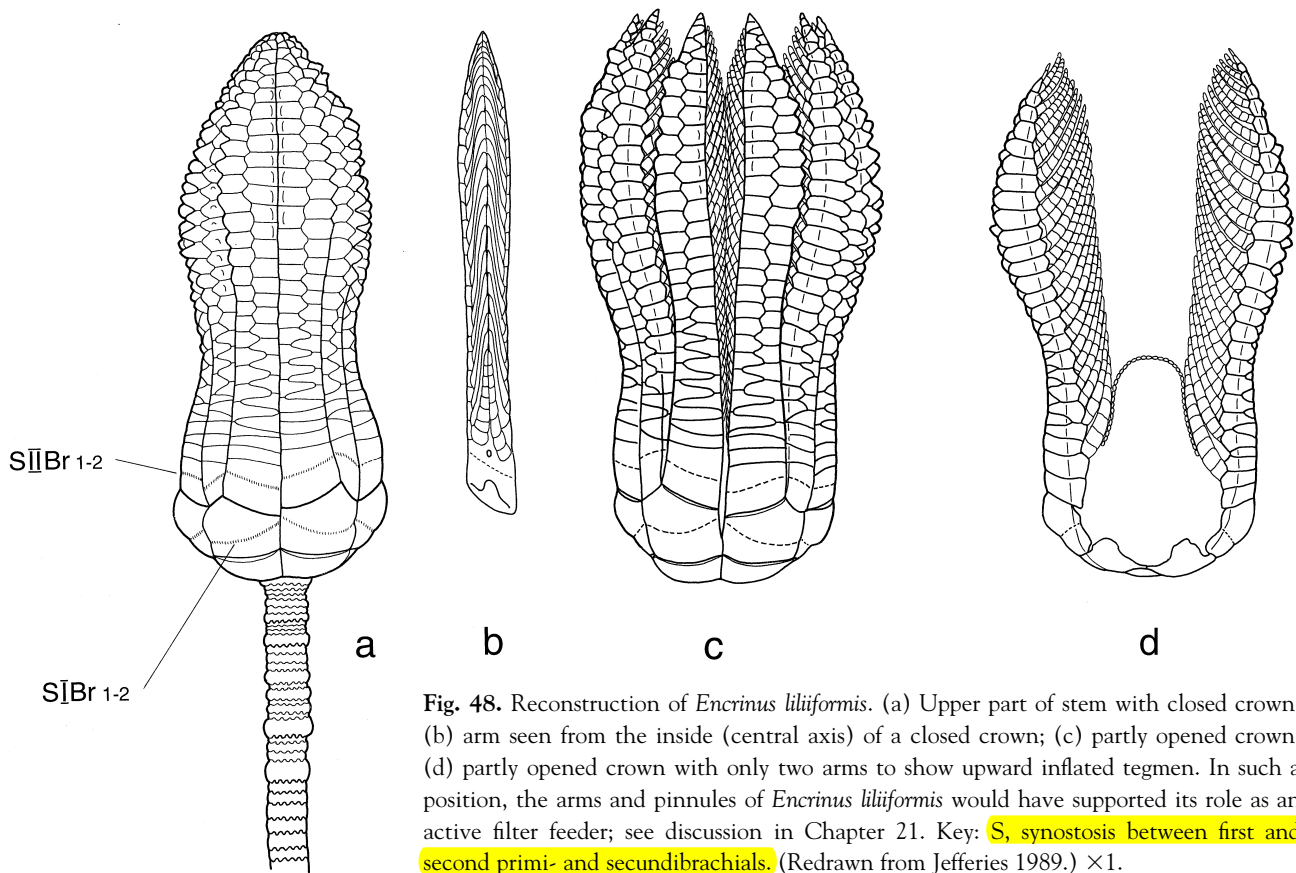


Fig. 48. Reconstruction of *Encrinurus liliiformis*. (a) Upper part of stem with closed crown; (b) arm seen from the inside (central axis) of a closed crown; (c) partly opened crown; (d) partly opened crown with only two arms to show upward inflated tegmen. In such a position, the arms and pinnules of *Encrinurus liliiformis* would have supported its role as an active filter feeder; see discussion in Chapter 21. Key: S, synostosis between first and second primi- and secundibrachials. (Redrawn from Jefferies 1989.) $\times 1$.

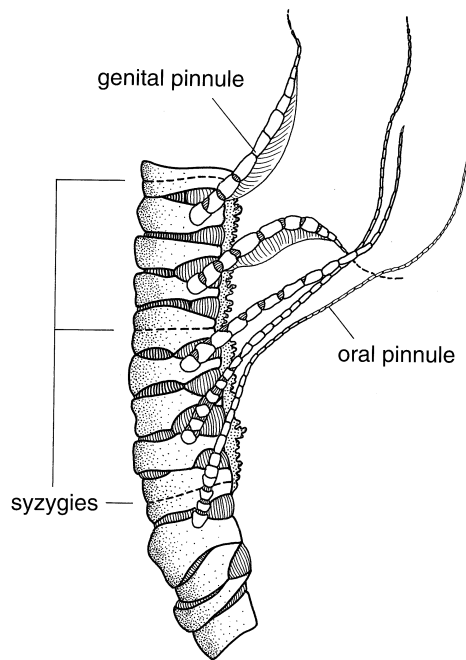


Fig. 49. Oral and genital pinnules on proximal arm of the Recent comatulid *Promachocrinus*. (Redrawn from Breimer 1978.) Approx. $\times 5$.

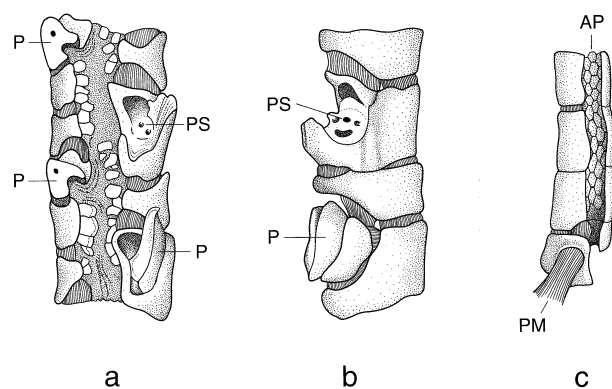


Fig. 50. Pinnular structures in the Recent *Neocrinus decorus*. (a) Oral side showing insertion of first pinnular ossicle on alternating arm ossicle; (b) side view of same; (c) four proximal pinnulars with ambulacral covering plates. Key: P, pinnular; PS, pinnule socket on brachial; PM, pinnular muscle; AP, ambulacral plates. (Redrawn from Breimer 1978.) Approx. $\times 5$.

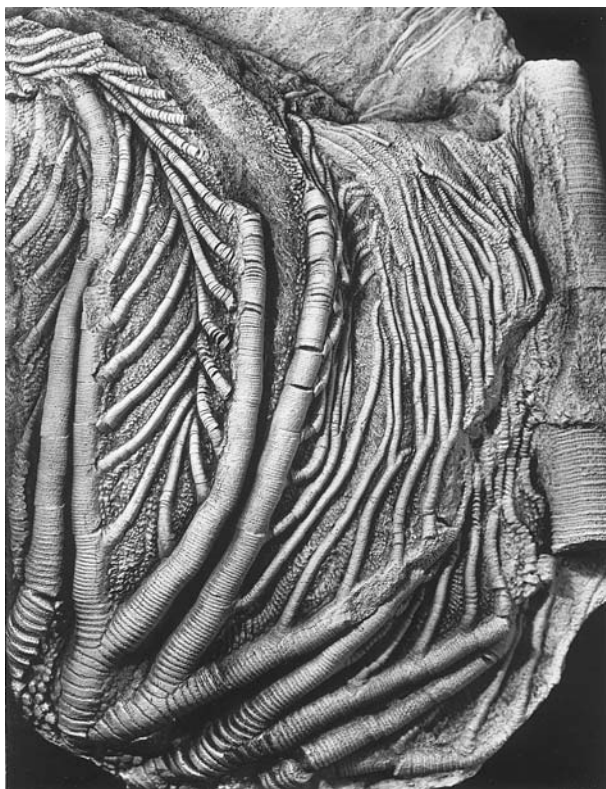


Fig. 51. Extremely low brachials with syzygial articula and complete pinnulation in the endotomously branched uniserial arms of the Triassic (Ladinian) encrinid *Vostocovacrinus boreus*. Kotel Island, Novosibirsk, Russia. (From Yeltisheva & Polyarnaya 1986.) $\times 0.65$.

lowering the height of the opposite side of the brachial significantly reduces the spacing of the pinnules (Fig. 47). The inevitable development from this, present in many camerates and cladids as well as in the Triassic encrinids, is a biserial arrangement of brachials (Fig. 48). Biserial arms are formed as a result of the reduction in thickness, ultimately to zero, of the thin, non-pinnulate side of alternate brachials. Hence, the thicker, pinnulate sides of alternate brachials become juxtaposed in a single column. The overall effect of this is to form two parallel, offset columns of interdigitating, wedge-shaped brachials with a pinnule arising from each along either side of the arm (Fig. 47). Clearly this represents the most dense deployment of pinnules, but at the expense of arm mobility and flexibility as a consequence of the interlocking of the brachials between the adjacent offset columns. Again, the disadvantages associated with this strategy may have restricted it to taxa occupying specific niches (Simms 1990).

In articulate crinoids, one or more pair of pinnules near the arm base may be modified into oral pinnules

(Figs. 6, 49). These lack an ambulacral groove and obviously serve to protect and sweep the oral surface. In a large number of Palaeozoic forms such as the scyphocrinitids (Fig. 11) as well as in some articulates (e.g., *Uintacrinus*, Fig. 24), the calyx includes pinnulate brachials that are firmly articulated with other plates of the calyx. Therefore, the calyx contains not only fixed brachials and interradians but also fixed pinnulars.

The arms form a framework for the support of the radiating extensions of the water-vascular and ambulacral systems used for feeding (Fig. 7). In addition, the arms of living crinoids carry the reproductive system. This is usually confined to the specialized genital pinnules in the lower part of the arms (Fig. 49). These pinnules contain the gonads, which are simply masses of sex cells filling the corresponding cavity. Crinoids are dioecious, but the sexes are usually indistinguishable.

The soft structures of the arms with the podia are lodged in a deep depression in the oral surface of brachials and pinnules; they may be protected by covering plates (Fig. 50c). Nichols (1994) suggested that parts of the arms with the gonads may have been sacrificed to predators to distract them from the more vulnerable organs within the cup. In support of this, he found that in *Antedon bifida* the gonads are maintained in ripe condition virtually all year round rather than just during the spawning season. This suggests that the gonads themselves have taken on this secondary function of predator distraction.

NOTES

1. Mutable collagenous tissues, unique to echinoderms, have variable tensile strength – i.e., the capacity to undergo rapid changes in mechanical properties. These tissues can, within less than a second to a few minutes, switch (e.g., at symplexes) between stiff and compliant conditions. In their compliant state, they allow movements without much force, for example, to attain a feeding posture; in their stiff state, they allow the animal to maintain the feeding posture even under strong currents. They can even disintegrate irreversibly to permit complete detachment of body parts during autotomy, e.g., at synostoses (Wilkie & Emson 1988).
2. 'Posterior' refers to interradius with anus or anal plates, generally wider than other interradii; see *Treatise* (Ubaghs 1978, p. T61) for a discussion of orientation.
3. To date, evidence for ligamentary tissue has been found only in the hinge structure of calceocrinids; and, at least in living echinoderms, ligaments lack active contractile ability.
4. The term 'microcrinoid' has also been used by several authors for post-Palaeozoic articulate crinoids (see Chapter 3).