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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-

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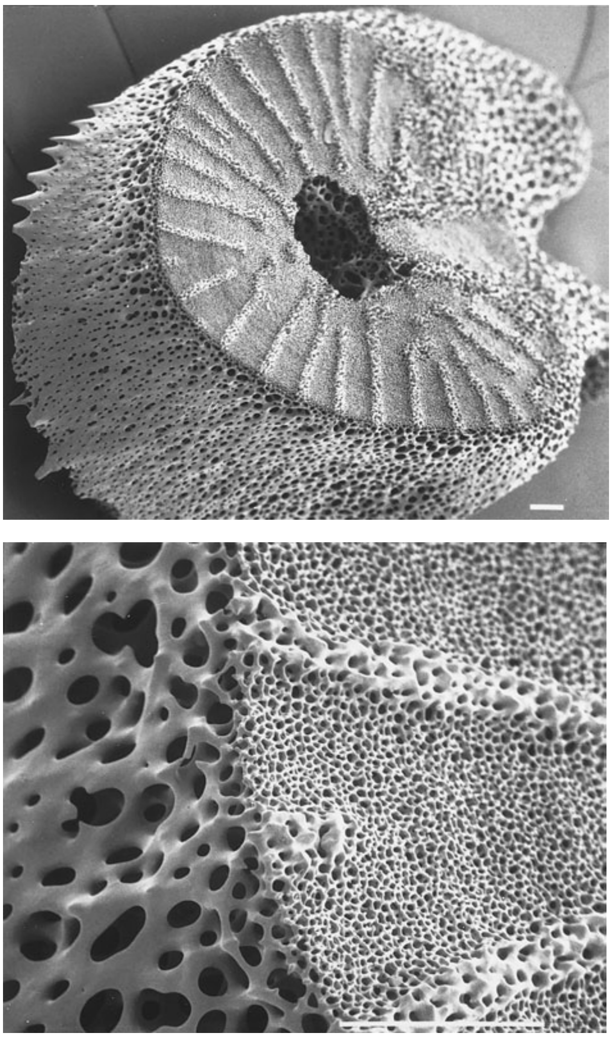

Fig. 4. Scanning electron photomicrographs of a brachial plate from *Promachocrinus kerguelensis* (Recent from the McMurdo Shelf, Antarctica) showing stereomic microstructure. This brachial facet with radiating crenulae is a ligamentary articulation, called syzygy. (Courtesy C. P. Hart and W. I. Ausich.)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

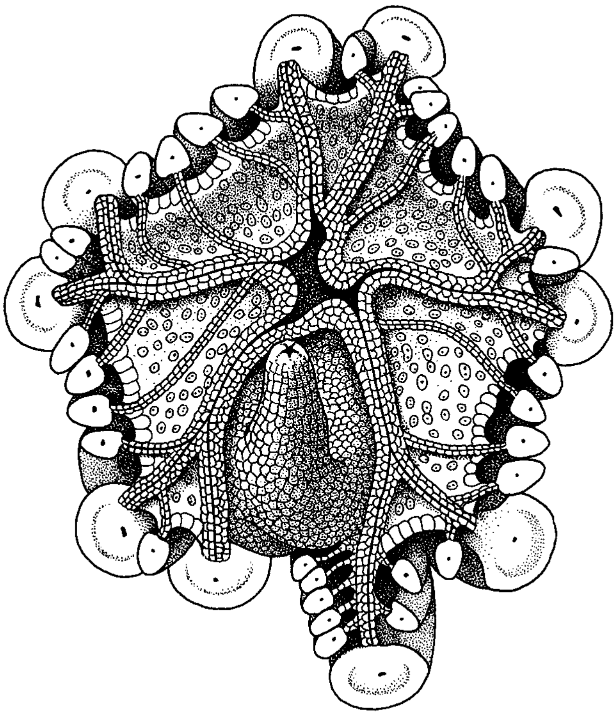

Fig. 5. Oral view of the disc of *Metacrinus angulatus* with tegmen. Food grooves end in the slightly displaced mouth; anal opening at the tip of an eccentric cone. (Redrawn from Carpenter 1884.) ×3.

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 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).

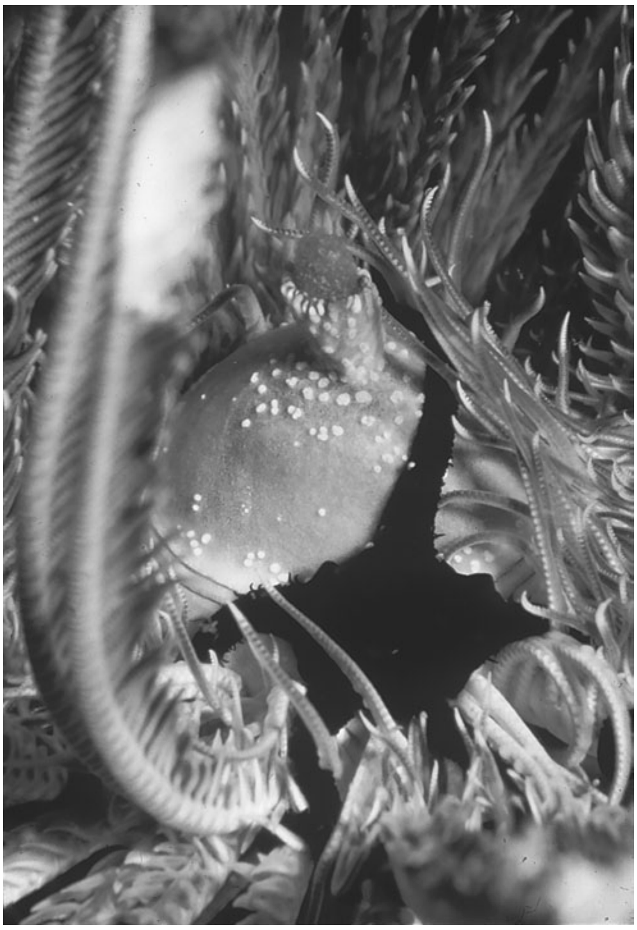

Fig. 6. Close-up of the oral disc (tegmen) of a comasterid comatulid with yellow-tipped oral pinnules; terminal comb teeth show on some of the pinnules. A black ophiuroid is sprawled across the disc, and the crinoid is releasing a bolus of faecal material from the anal tube. (Photograph O. C. Honegger,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

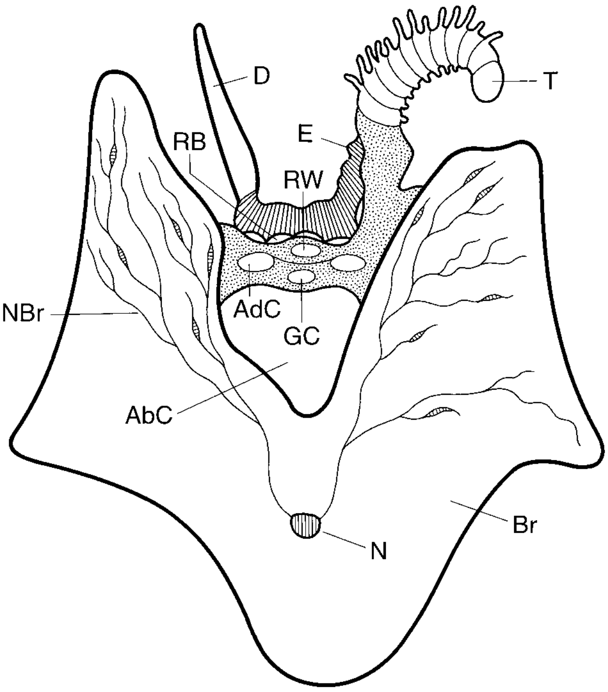

Fig. 7. Section through arm of *Bathycrinus aldrichianus*. Key: T, tentacle or tube foot or podium; D, covering plate of ambulacral groove; E, epidermis of ambulacral groove; Br, brachial ossicle; N, main brachial nerve; NBr, nerve branches; AbC, aboral coelomic canal; AdC, adoral coelomic canal; RW,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

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-

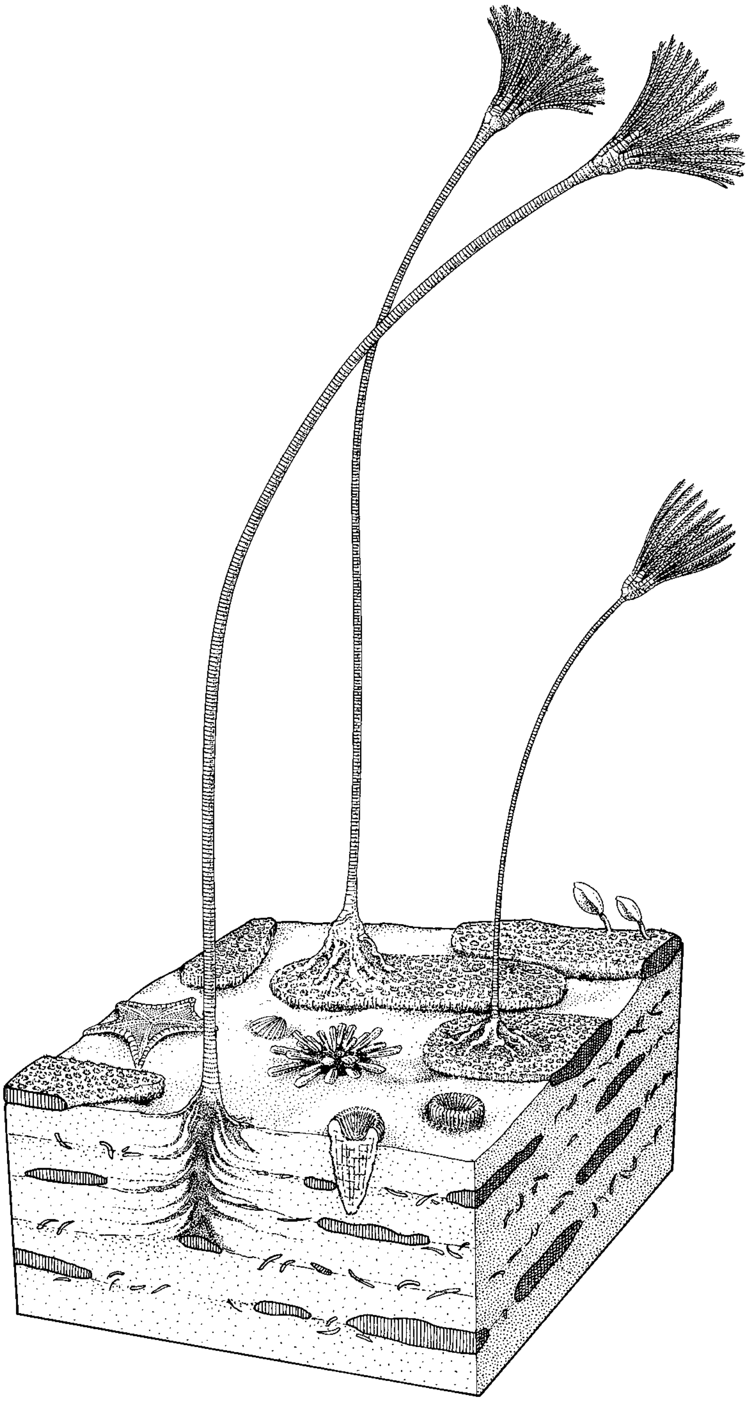

Fig. 8. Reconstruction of the Jurassic sea lily *Liliocrinus munsterianus*. Two individuals attached to dead corals (*Thamnasteria*) by a compact root, another individual anchored in muddy sediment (Liesberg Beds, Middle Oxfordian, Swiss Jura). This environment is comparable to today's lagoon southeast 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.

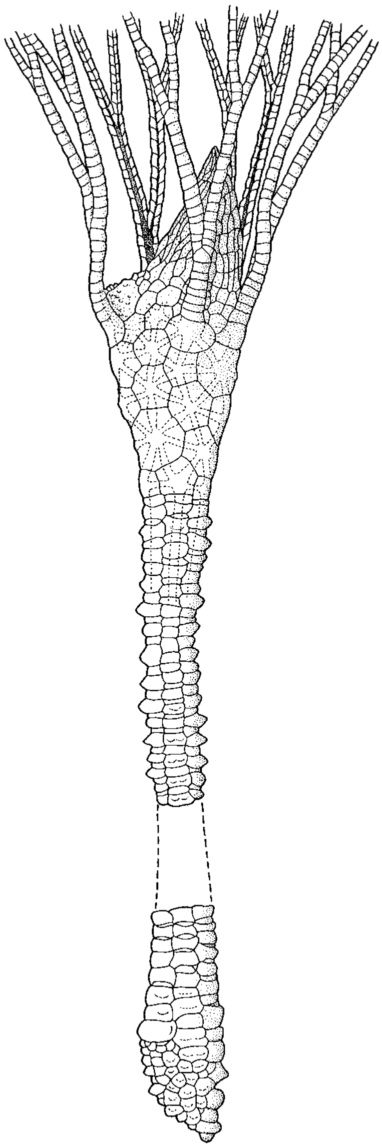

Fig. 9. Reconstruction of *Aethocrinus moorei*. Lower Ordovician, Montagne Noire, France. (Redrawn from Ubaghs 1969.) ×1.

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 interradial 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

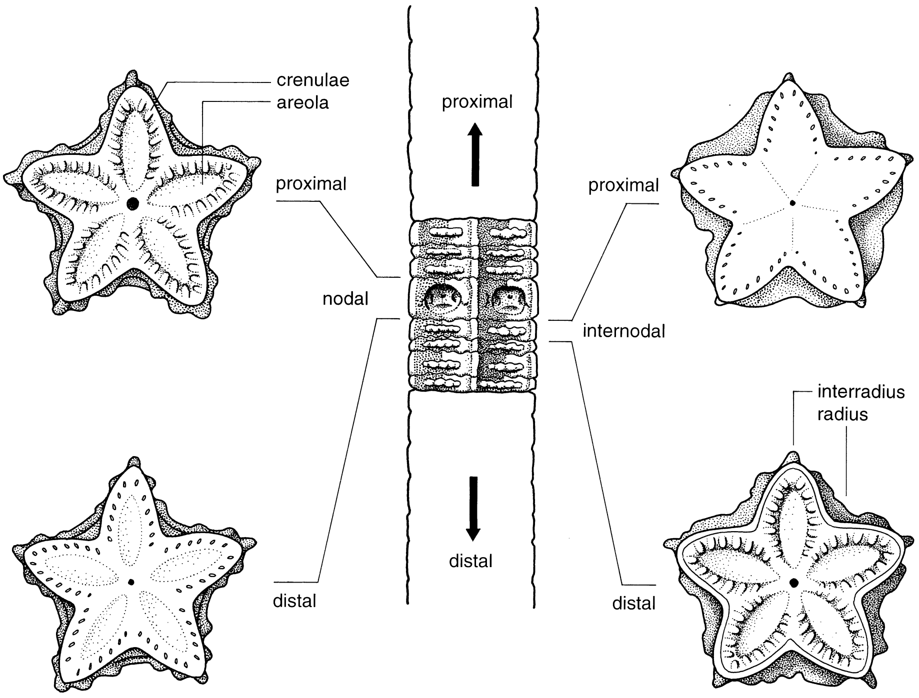

Fig. 10. Part of the stem of the isocrinid *Metacrinus angulatus*, with nodal and internodals, showing the different articular facets. (Redrawn from Carpenter 1884.) ×3.

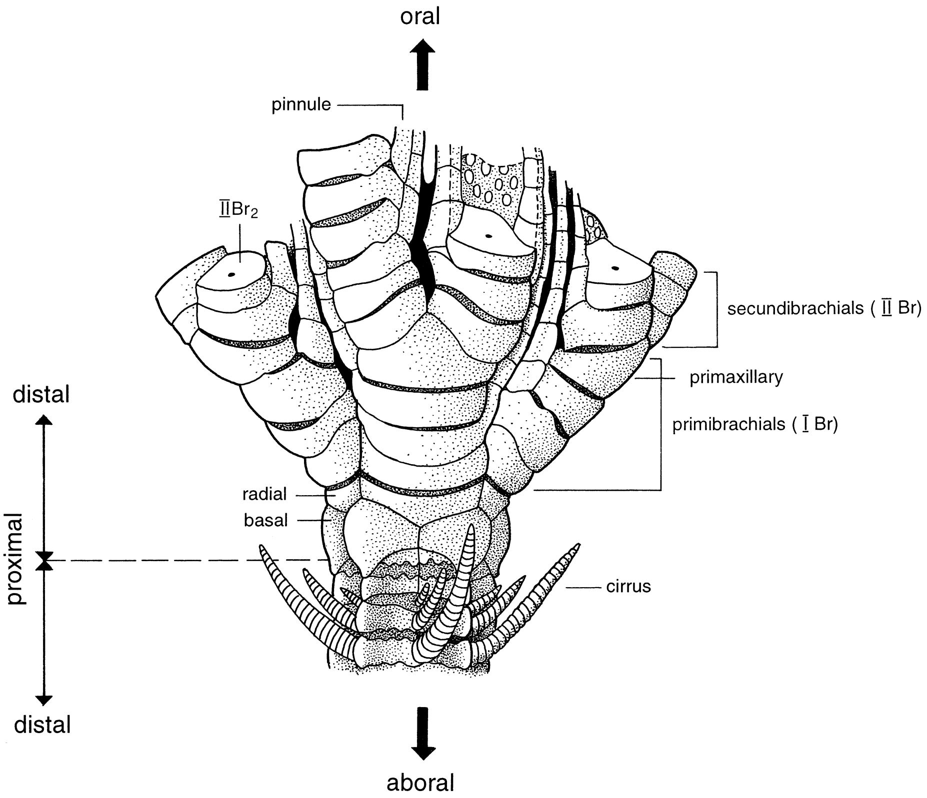

Fig. 11. Proximal stem, cup and base of arms of *Metacrinus angulatus*. (Redrawn from Carpenter 1884.) ×3.

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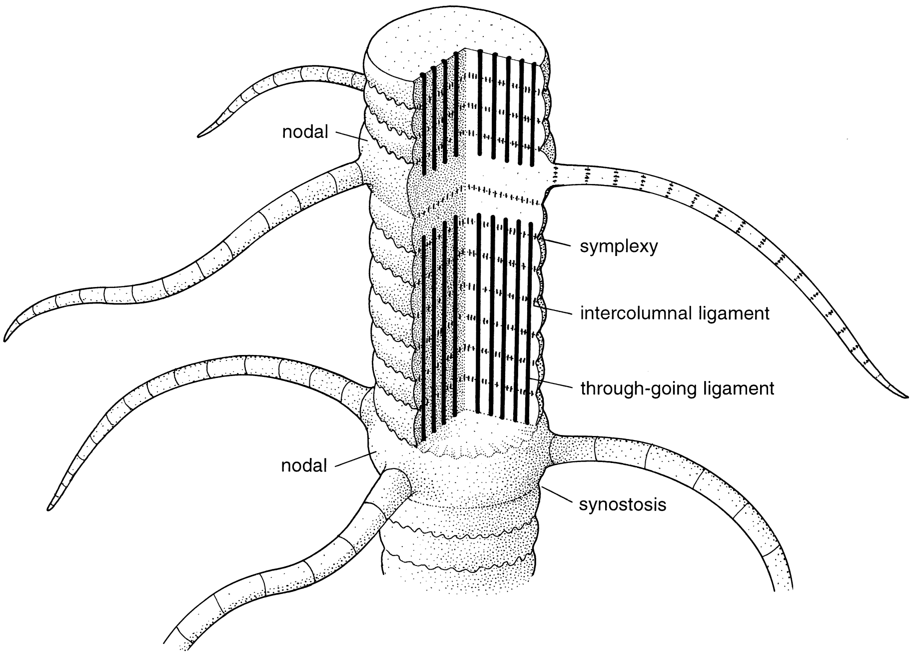

Fig. 12. Ligaments between nodal and internodals of an isocrinid stem. (Adapted from Baumiller & Ausich 1992.)

place, a tight junction, called synostosis, or more properly cryptosymplexy (hidden symplexy), is developed (Fig. 10). Synostoses and cryptosymplexies 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 cryptosymplexies than along symplexies, 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-

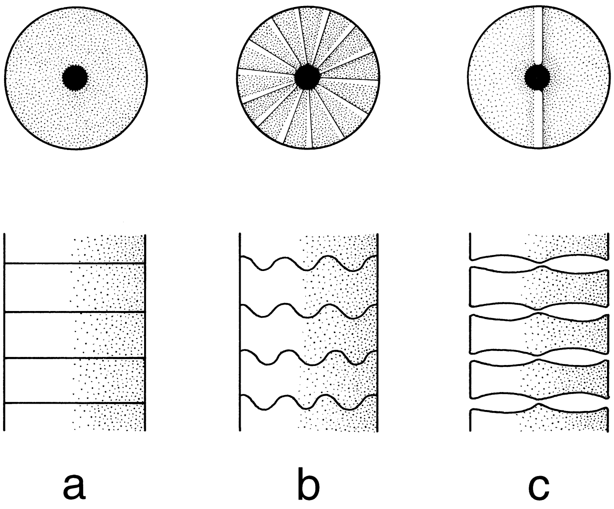

Fig. 13. Typical articular facets and long sections of crinoid stems. (a) Synostosis; (b) symplexy; (c) synarthry. (Redrawn from Donovan 1989a.)

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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 Bourgueticrinida, an order of articulates 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 *Seirocrinus*, flexibility in-

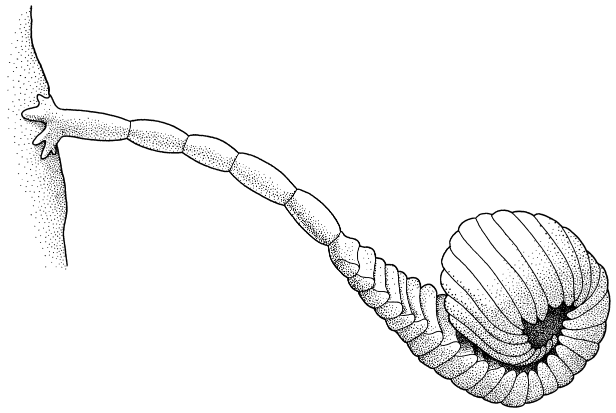

Fig. 14. Reconstruction of *Ammonicrinus doliiformis*, with crown hidden in enrolled stem. Stem is xenomorphic, with abrupt change between distal and middle part. Middle Devonian, Germany. (Redrawn from Ubaghs 1953.) ×1.5.

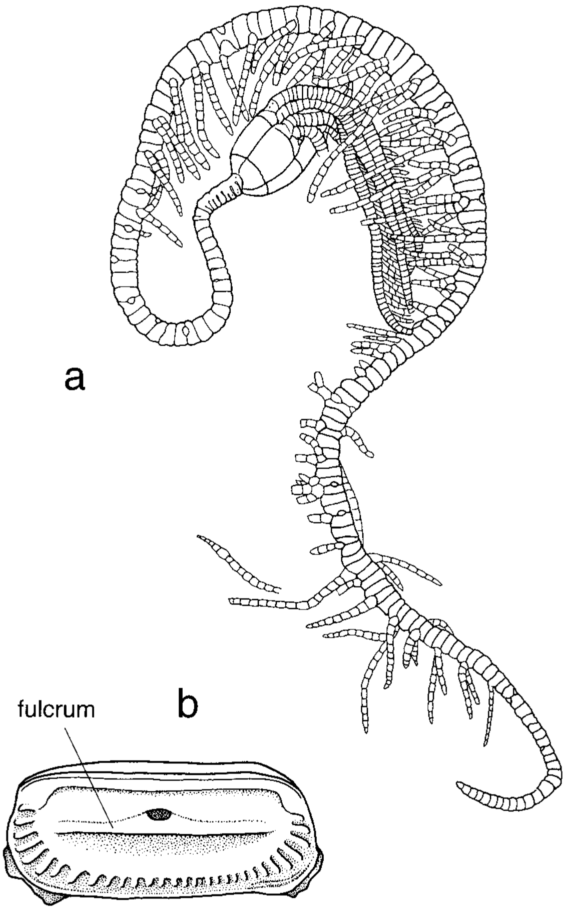

Fig. 15. (a) *Camptocrinus multicirrus*. Mississippian, Illinois. Complete specimen with coiled stem. (Redrawn from Ubaghs 1978.) ×1.5. (b) Articular, synarthrial facet of a columnal of *Camptocrinus compressus*. Lower Carboniferous, Scotland. (Redrawn from Ubaghs 1978.)×5.

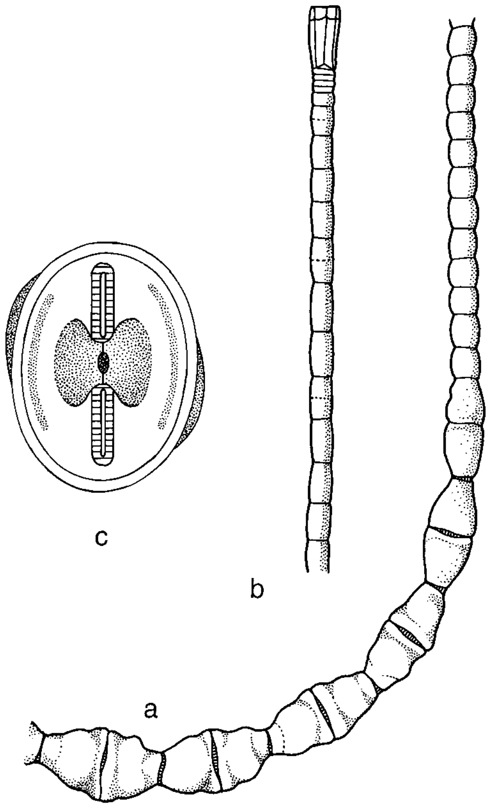

Fig. 16. (a, b) *Naumachocrinus hawaiiensis*, a Recent bourgueticrinid with synarthrial stem articulations. (Redrawn from Breimer 1978.) Approx. ×1. (a) Distal column with fulcral ridges on alternate pairs of apposed facets rotated by 180°; (b) proximal column with cup; (c) Articular facet of the bourgueticrinid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

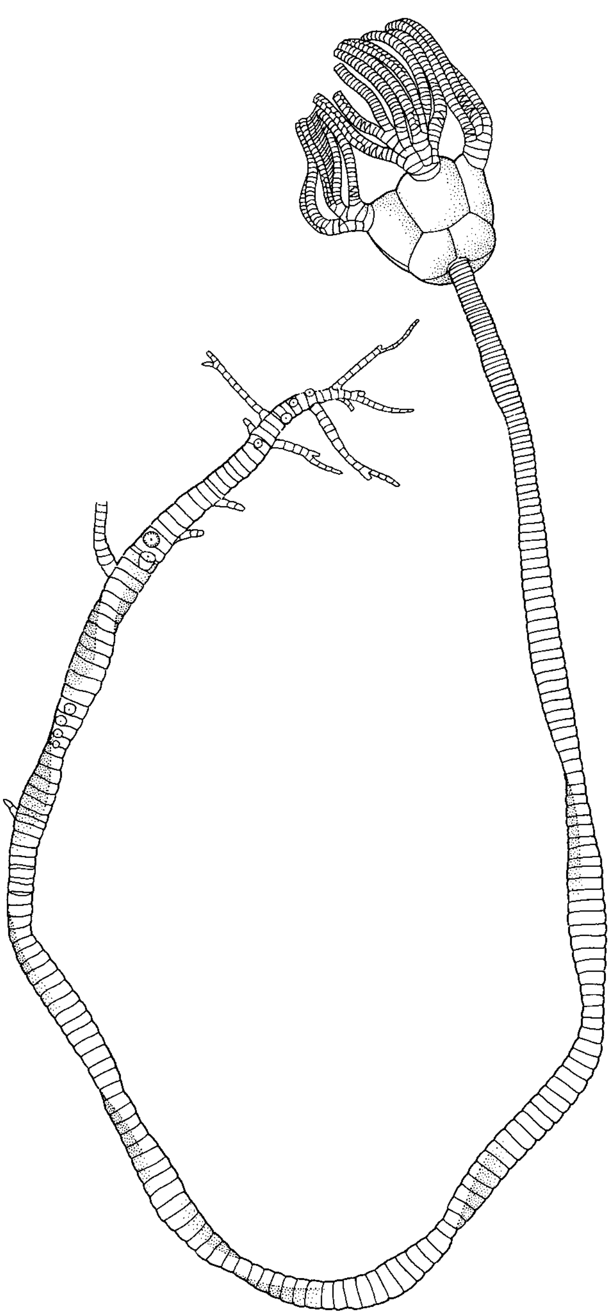

Fig. 17. *Platycrinites regalis*. Complete specimen with twisted stem carrying root-like radicular cirri (radices) distally. Mississippian (Burlington Limestone), Iowa. (Redrawn after Wachsmuth & Springer 1897.) ×0.7.