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PART T, REVISED, VOLUME 1, CHAPTER 19: PALEOECOLOGY OF PELAGIC CRINOIDS

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INTRODUCTION

During their extended history, crinoids have repeatedly freed themselves from the constraints of being tethered to the bottom. They did this first by modifying the distalmost column into a floating device, then by attaching the column to driftwood, and finally, by abandoning the column altogether. The comatulids that flourish in today's oceans have reduced the column to a single, cirri-bearing piece: the centrodorsal. This enables them to climb to a higher position for feeding, to seek protection within the reef infrastructure, to crawl, and even to swim using their arm muscles. Further, a number of comatulids have lost the centrodorsal altogether and use their arms for anchoring. The present chapter concerns pelagic or planktonic forms feeding near the surface or in the water column. The term pelagic is used for passively drifting (planktonic and pseudoplanktonic), as well as for actively swimming (nektonic) forms. Pelagic crinoids are not known today, so their mode of life and food collecting habits must be deduced from evidence based on morphology, occurrence, and taphonomy of the fossils.

Crinoids are passive suspension feeders, so the food-containing water must move past the crown through the filtration fan. Therefore, because crinoids are presumably floating with their food, how can a sufficient flux of water move through their filtration fan? One example is a pseudoplanktonic crinoid attached to a log. Surface currents or wind may move logs at or near the water-air interface. Adult crinoids attached to logs would have hung down beneath the log. A velocity gradient between the surface layer and deeper layers caused the crowns to be dragged through the water (tow-net filtrators), and filtration efficiency is expected to increase with distance from the surface. This will not work with short-stalked crinoids attached to logs, so another mechanism must be assumed in this case. Feeding may also have taken place through interception of zooplankton during diurnal vertical migration (LEVINTON, 2001, p. 162).

SCYPHOCRINITIDS: PLANKTONIC CRINOIDS WITH FLOATS

Members of the family Scyphocrinitidae are known from the Silurian–Devonian boundary beds of Europe, North America, Asia, and Africa. These large, monobathrid camerates are among the most peculiar crinoids, because they have developed a unique, bulbous, chambered organ at the distal end of the column. This organ, called the lobolith (*Camarocrinus*)-type radix, has created much speculation as to its function; examples are a float (SCHUCHERT, 1904), a genital organ (JAEKEL, 1904), a brood pouch (JAHN in SCHUCHERT, 1904), a holdfast on muddy bottoms (SPRINGER, 1917), a bulbous holdfast of an unknown crinoid (RAY, 1980), or a parasitic cyst (EHRENBERG, 1926).

Scyphocrinites elegans was first described by ZENKER (1833) from Bohemia, where it occurs in black mudstones of upper Silurian (Pridolian) and Lower Devonian age. SPRINGER (1917) provided a detailed description of North American material that he assigned to the Bohemian species, but PROKOP and PETR (1986) limited *S. elegans* to Bohemia. Several species and genera of scyphocrinitids have been described from the upper Silurian of England, France, Spain, Russia, Burma, and China. In North America (Tennessee, Missouri, Oklahoma, West Virginia), they range from upper Silurian to Lower Devonian (Bailey Formation). PROKOP and PETR (1987)

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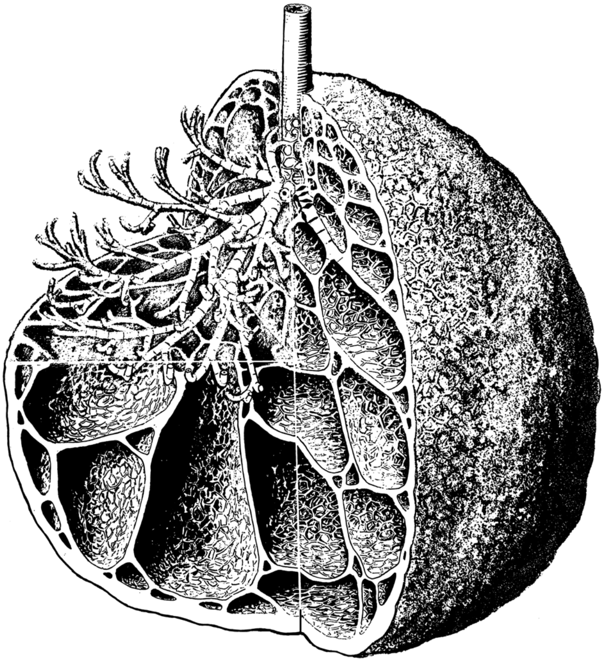

FIG. 1. Reconstruction of a scyphocrinitid cirrus lobolith in presumably inverted life position; late Silurian–Early Devonian, Europe and Africa, approximately ×1 (Haude, 1972).

established *Marhoumacrinus legrandi* for Algerian scyphocrinitids (upper Silurian–Lower Devonian), assigning this genus and *Carolicrinus* WAAGEN & JAHN to the Marhoumacrinidae (PROKOP & PETR, 1994). The morphological similarities among the scyphocrinitids and marhoumacrinids indicate that these amazing crinoids had very similar lifestyles.

The material described by SPRINGER (1917), presumably from the Lower Devonian Bailey Formation, was excavated from the bluffs of the Mississippi River, near Cape Girardeau, Missouri. This occurrence established for the first time the relationship between well-preserved scyphocrinitids and their bulbous radix. At this locality, the crinoids occurred in the lower third of a 15-cm-thick bed of argillaceous limestone overlying a seam of clay. The fossiliferous part of the layer was limited to a small area and considered by SPRINGER (1917) to be "the remnant of a thickly crowded colony, suddenly killed by some change in the water or movement of the sea bottom and embedded in the soft mud without much disturbance by currents" (p. 5). The main slab, 120 by 160 cm, contains 24 crowns, several with more or less broken columns, and a few flattened or fractured loboliths. The bulbs are free of columns, indicating "that they were near the edge of the colony, and when the forest of crinoids went down . . . the stalks fell away from these roots, leaving them imbedded in the mud where they grew" (p. 7). The bulbs were on the lower side of the layer, showing their rounded, nonstalked ends; "hence they stood with the stalked end uppermost, as they naturally would if growing in or resting upon the soft bottom" (p. 8). Springer did not find a single case in which the column was still connected to the bulbous end.

In adult scyphocrinitids, the column ends distally in a large, bulbous, chambered organ that reaches a diameter of 20 cm or more. These curious, bladderlike structures were definitely associated with

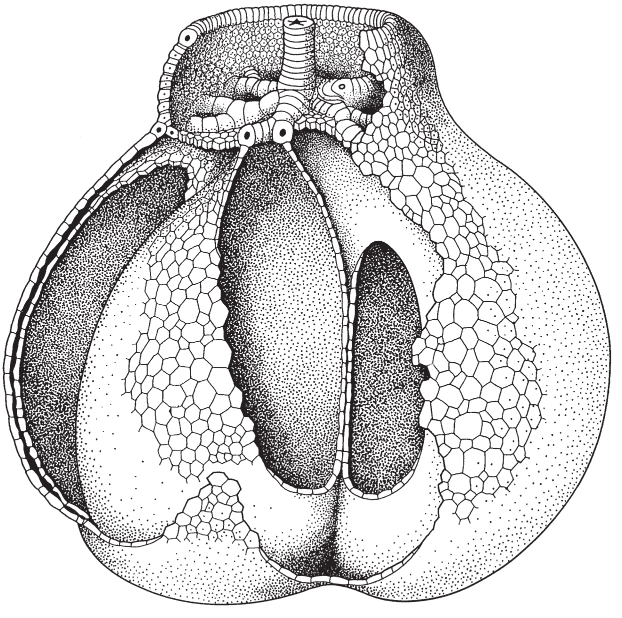

FIG. 2. Reconstruction of plate lobolith (*Camarocrinus*) of scyphocrinitid, Early Devonian, North America; bulb is shown in presumably inverted life position, with stump of broken-off column, contained in a collar, pointing upward, 1 (Hess, 1999a).

the camerate *Scyphocrinites* by SCHUCHERT (1904) and BATHER (1907), when the idea of their function as buoys was first proposed. According to BATHER (1907, p. 192), "... it is . . . believed by many that this swelling was hollow and served as a float from which the crinoid hung, arms downwards. The latter hypothesis explains why it is that in various parts of the world the loboliths occur unassociated with the crowns to which they are supposed to have belonged; upon death and gradual decay of the animal, the crown would naturally drop off and sink to the bottom, while the lobolith floated on."

SCHUCHERT (1904) derived his opinion that the loboliths served as the float of a so-called unknown crinoid, because at that time loboliths in North America had never been found associated with crinoids, and scyphocrinitids were unknown from North American strata. The discovery of well-preserved *Scyphocrinites* by SPRINGER (1917) disproved SCHUCHERT's notion that "the great majority of the bulbs are found in strata with the stalked end downward" (p. 2). As already discussed, the bulbs were embedded in the mud with the stalked end directed upward, into the bed.

Two different types of loboliths are now known: the subspherical, orange-shaped, cirrus lobolith with numerous chambers of unequal size (Fig. 1) and the lobed plate lobolith with a few large chambers, a curved, bilaterally symmetric root trunk, a simplified wall structure, and a characteristic collar (Fig. 2) (HAUDE, 1972, 1992). The smallest plate lobolith known has a diameter of 5 mm (HESS, 1999a, p. 99), while the largest cirrus lobolith reaches a diameter of more than 30 cm (H. HESS, personal observation, 2000). Most plate or cirrus loboliths are between 10 and 20 cm in diameter. According to HAUDE (1992), plate loboliths evolved from Silurian cirrus loboliths at the Silurian–Devonian boundary, and he suggested that lobolith morphology might be useful in biostratigraphy. However, the occurrence of both cirrus and plate loboliths in the same horizon in Bohemia (PROKOP & PETR, 2001) indicates that lobolith evolution may have

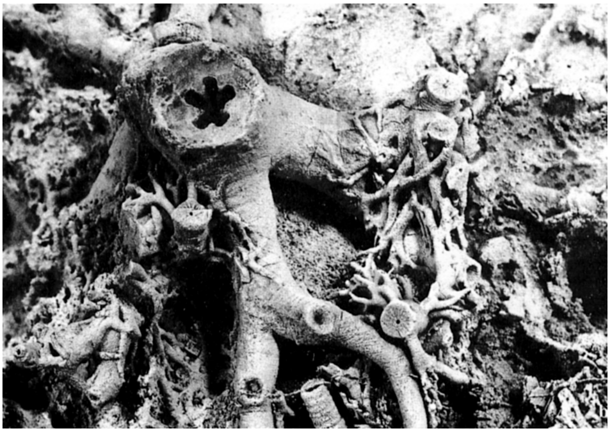

FIG. 3. Proximal part of cirrus lobolith of *Scyphocrinites* with stump of column; roots of juvenile *Scyphocrinites* occurring within protected space of collar (not shown) suggesting some kind of nursery, Pridoli, upper Silurian, Praha-Reporhyje, Czech Republic, Museum of Natural History, National Museum, Praha, L 36533, ×1.6 (Prokop & Petr, 2001).

been more complex. Mainly on morphological grounds, HAUDE (1992) followed and strengthened the conclusion of SCHUCHERT (1904) and BATHER (1907) that the loboliths must have served as buoys. SEILACHER and HAUFF (2004) suggested that the animals drifted between two water layers in a stratified ocean, because the upper part of the buoys would have been exposed to deadly wind and sun. Apertures of the loboliths enabled buoyancy to be actively adjusted to a certain water depth. Evidence from taphonomy is in contrast with this hypothesis.

A cirrus lobolith starts from primary roots at the end of the column; these divide repeatedly into ever finer branches to form innumerable elements (spicules) that build the walls of the inner chambers as well as the outer covering wall. The stronger outer and the thinner inner layers, both of which are composed of small spicules, are supported by a middle layer with larger elements. Calcite crystals may fill the smaller, peripheral chambers, suggesting that these chambers were sealed. Larger chambers around the base of the column were probably open, because they are preserved with a sediment infilling (HAUDE, 1992). It may be hypothesized that the openings at the root bifurcations inside the projecting collar of plate loboliths (Fig. 2) served for gas exchange: for example, to relieve pressure in the case of overproduction of gas or its expansion due to temperature changes. It appears that the columns were easily broken off near the bulbs, leaving plate loboliths typically with a column stump surrounded by a collar (Fig. 2).

The occurrence of small encrusting roots attached to the outer side of mature bulbs (SPRINGER, 1917, fig. 7–10; HAUDE, 1992, fig. 3) indicates that larvae settled on mature bulbs, so that juvenile individuals were anchored by branching radices or roots, as in other crinoids. In Bohemian plate loboliths, the roots of juvenile animals occur within the protected space of the collar (rarely also on the outer side of the collar), suggesting some kind of nursery (Fig. 3; PROKOP & PETR, 2001; see also HAUDE, 1992). From this occurrence, PROKOP and PETR (2001) concluded that the larvae were lecithotrophic with limited swimming capability, as in extant comatulids. STRIMPLE (1963) suggested that larval scyphocrinitids started with roots and formed loboliths after breaking off the mature bulbs. However, no juvenile specimen with roots and a budding lobolith has ever been described, and the early ontogeny of the bulb is not understood. It is hardly conceivable that a cirriferous radix attached to a larger lobolith could somehow turn into an independent lobolith, and no intermediate forms are known. A potential scenario where some larvae settled on loboliths and grew into small individuals until the demise of the carrier, while others used foam floats or nearby plant material as stepping stones for lobolith formation seems more plausible, but this must remain speculative. HAUDE (1992) suggested that the small-rooted scyphocrinitids attached to the bulbs may represent sexual dimorphs, but this would be unique among crinoids.

HAUDE (1992) proposed a hypothetical model for lobolith evolution, starting from a dense, tangled, cirrus network of a crinoid rooted in muddy sediment. Small, open spaces in the network swelled into soap-bubble–like chambers (with the possibility of floating) and eventually into the large, diving-bell–like chambers of the plated loboliths. However, this sequence, starting from a crinoid rooted at the bottom and ending as a pelagic lobolith, is purely conjectural. The crinoid's generation of gas to fill the bulb has so far not been explained in a satisfactory way. HAUDE (1972) assumed that gas accumulated from the surrounding water by diffusion, as in floating algae, but failed to define the mechanism. In a later paper, HAUDE (1998) suggested that larval or juvenile scyphocrinitids were attached by their root cirri to some plant material (algae) drifting at the air-water interface. Closure of the cirrus network to form a bulb could have entrapped photosynthetic organisms that were the real gas producers. Again, this is conjecture, and both the evolution and the ontogeny of the bulb require further study.

The North African scyphocrinitid lenses occur in pelagic sediments that were deposited at moderate depth, possibly on a submarine ridge or platform in a basin with limited sedimentation (JAEGER & MASSA, 1965). The wide distribution of scyphocrinitids in such sediments, as well as the peculiar transformation of the root cirri into chambered bulbs, has been taken by a number of authors as an indication of a pelagic lifestyle. Scyphocrinitids invite comparison with the Lower Jurassic *Seirocrinus* with similarly developed crowns and even longer columns. The presence of long columns in scyphocrinitids may indicate that the chances of food collection increased with depth, as in today's oceans, where plankton-rich zones are well below the surface. Columns are not preserved bent near the crown, so that the crown formed a funnel that may have captured zooplankton moving vertically; in case of drifting, the crowns were dragged through the water, adding to food collecting efficiency (Fig. 4). This is in stark contrast to the Triassic *Traumatocrinus* with its bent proximal column and its crown perpendicular to the surface, but similar to the crowns of the Jurassic *Seirocrinus*.

Scyphocrinitids appear to have formed dense aggregations. Perhaps breakage in stormy weather led to numerous individuals sinking to the bottom together. As a rule, the waterlogged bulbs became detached from the columns, breaking off at a weak point close to the collar (where column diameter is reduced). The bulbs eventually sank to the bottom, with their collar upward (as seen in Fig. 2), like short-necked, water-filled bottles. HAUDE, JAHNKE, and WALLISER (1994) concluded that the isolated crowns on some of the North African slabs reached the bottom first, oral side downward. They were followed by a group of more intact crinoids with entangled columns, which sank in a horizontal position, and then more broken columns finally settled. Differences in transport by currents led to the deposition of crowns with attached columns in one place, whereas the loboliths usually accumulated elsewhere, sometimes in huge numbers. Preservation of articulated crowns with columns on the lower side of a bed, disarticulated ossicles, and some column fragments on the top surface suggests that the crinoids were exposed on the sea floor some time after death, before final burial.

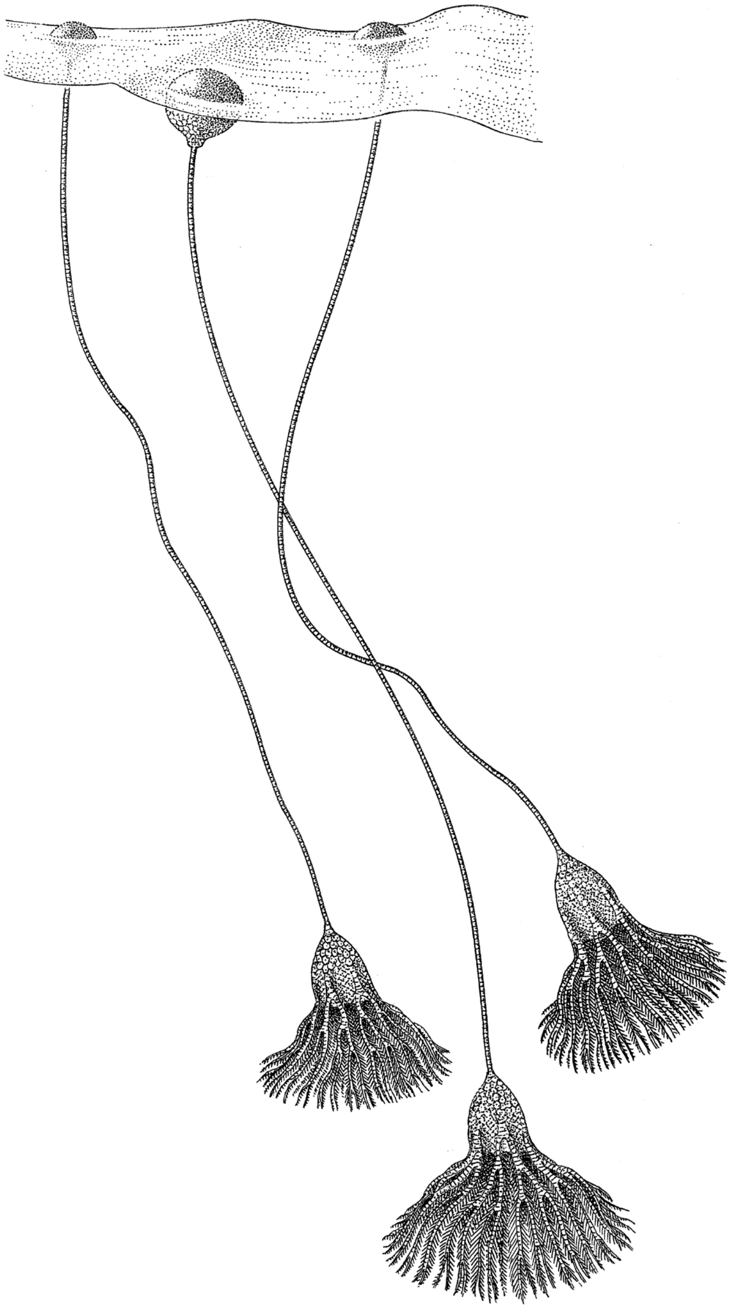

FIG. 4. Reconstruction of scyphocrinitids as pelagic, floating sea lilies, approximately ×0.1 (Hess, 1999a).

PSEUDOPLANKTONIC CRINOIDS ATTACHED TO DRIFTWOOD

During geological history, the number of crinoid species clearly attached to driftwood is very limited, but this unusual habit occurred at different times. The earliest occurrences are reported from the Upper Devonian. Klug and others (2003) described large numbers of small, discoidal, crustose holdfasts of indeterminate crinoids on pieces of wood (*Archaeopteris*) in dark-colored mudstones and limestones of lower Famennian age in the eastern Anti-Atlas (Morocco). This black shale Kellwasser Facies with layers of fossiliferous limestone nodules is rich in nektonic and planktonic organisms but sparse in benthos. Mytiloid bivalves were also attached to wood, a bivalve group not known otherwise from these sediments. One specimen, possibly belonging to a different species, was anchored by radices to a log. Webster, Becker, and Maples (2005) described two new Famennian crinoid species from Morocco that occur in several stratigraphic levels and localities (*Mrakibocrinus bockwinkeli*, *Moroccocrinus ebbighauseni;* descriptions were based on complete crowns, but the columns are incomplete). Although associated with driftwood, the authors were not entirely convinced of the pseudoplanktonic nature of these crinoids. The latest discovery of a colony of *Mrakibocrinus bockwinkeli* is also associated with driftwood (C. Klug, personal communication, 2008). This wood lies directly on disarticulated crinoid ossicles. This repeated association of crinoid colonies with logs in a paleoenvironment extremely poor in benthos can be interpreted as another example of pseudoplanktonic life mode in Devonian crinoids. Similar occurrences are known from upper Frasnian to lower Famennian strata of North America, where the crinoids (assigned to *Melocrinites*) were also attached by radices to logs (Wickwire, 1936; Wells, 1942, 1947; McIntosh, 1978).

Driftwood with attached complete crinoids are also known from the Mesozoic (Middle Triassic–Lower Jurassic). They include species of the Triassic order Encrinida (*Traumatocrinus caudex*, *T. hsui,* and possibly *Vostocavocrinus boreus*) and species of the order Isocrinida, suborder Pentacrinitina (*Pentacrinites fossilis*, *P. dichotomus*, and *Seirocrinus subangularis*) from the Lower Jurassic, as well as *Seirocrinus klikushini* and an undescribed find of *Pentacrinites* from the Upper Triassic (Norian) of northern Siberia.

Common to all Mesozoic crinoids that are associated with driftwood is their occurrence in black shale environments and their excellent preservation on the lower side of the bedding plane. The side of the animal exposed on the upper bedding plane is commonly disarticulated. In many occurrences, the specimens are partly pyritized. All forms have large to very large crowns with arms branching endotomously, yielding a very dense filtration fan. However, the forms differ in column morphology. Columns of *Traumatocrinus* species are thickened and commonly bent proximally, so that the opened filtration fan is nearly vertical, and they are rather long and lack cirri, except in the distalmost part where anchoring cirri occur. Column length of adult specimens of Pentacrinitidae varies between being extremely long in adult *Seirocrinus subangularis*, medium to short in *Pentacrinites fossilis*, and very short in *P. dichotomus*. Columns of *Seirocrinus* and *Pentacrinites* were attached by cirri and are not thickened or bent proximally. The possible reasons for these differences are discussed in the following sections.

The pseudoplanktonic lifestyle is not known after the Early Jurassic. Wood-boring bivalves appeared toward the end of the Early Jurassic. These bivalves began to destroy floating logs relatively rapidly, making drifting logs unsuitable for colonization. Thus, Mesozoic pseudoplanktonic crinoids occupied a niche ranging from the Middle Triassic (upper Ladinian–lower Carnian) to the Lower Jurassic (Toarcian) (Fig. 5).

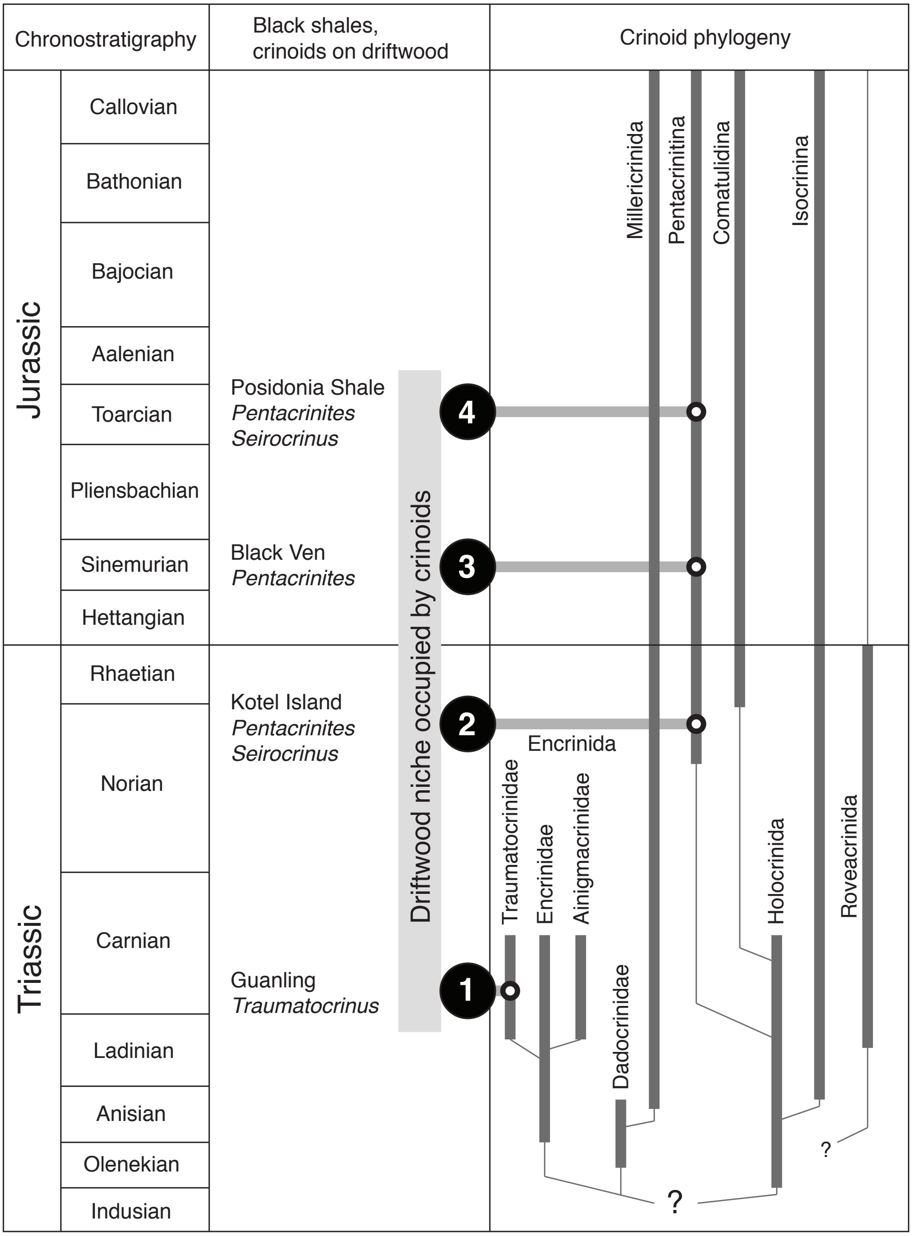

FIG. 5. Occurrence of pelagic crinoids in Triassic–Lower Jurassic strata (adapted from Hagdorn, Wang, & Wang, 2006).

ENCRINIDS FROM THE TRIASSIC

Traumatocrinus has a worldwide occurrence from upper Ladinian to lower Carnian (KRISTAN-TOLLMANN & TOLLMANN, 1983; HAGDORN, WANG, & WANG, 2006). Articulated specimens that may belong to *T. hsui* MU are known from the Upper Triassic of southern China (MU, 1949; HAGDORN, 2001; HAGDORN, WANG, & WANG, 2006; WANG & others, 2008) and are from the lower Carnian Xiaowa Formation (formerly Falang Formation), exposed in Guanling

County, Guizhou Province. In the lower part of the Xiaowa Formation, *Traumatocrinus* colonies are preserved attached to driftwood at several stratigraphic levels in black mudstones and shales (HAGDORN, WANG, & WANG, 2006; WANG & others, 2008). The intact specimens occur with the crowns on their side or with splayed arms with the aboral side on the bedding plane (Fig. 6*a*). The upper bedding planes contain individuals that are partly or completely disarticulated. Sedimentary structures are absent in this setting, thus there is no indication of bottom currents in the black mudstone and shale facies. Specimens of *Traumatocrinus* still attached to driftwood (HAGDORN, WANG, & WANG, 2006) prove a pseudoplanktonic mode of life for this species (Fig. 7), and the same lifestyle may be assumed for *Vostocovacrinus*. Thus, the Chinese crinoid Lagerstätte is comparable to the Lower Jurassic Posidonia Shale discussed in the next section (herein, p. 11). The remainder of the invertebrate fauna consists of pelagic somphocrinids that are restricted to a few layers, pseudoplanktonic bivalves (*Daonella*), and nektonic animals, such as ammonites (*Protachyceras*). Fishes occur rarely, and reptiles (ichthyosaurs and thalattosaurs) are more common (WANG & others, 2008).

Traumatocrinus has a large crown, with the diameter being more than 40 cm. *Traumatocrinus*, similar to the related *Vostocovacrinus* that is restricted to the Borean realm, has endotomous arm branching and aboral spines on the axillaries above the arm trunk (Fig. 6*a*); but in contrast to the Early Jurassic *Seirocrinus* and *Pentacrinites*, it achieved almost complete pinnulation through the elimination of all brachial muscular articulations and the development of exclusively syzygial articulations. The minor branches continued to branch, so that pinnules of neighboring arms are fastened in Velcro-like manner. The crown, if flattened, did not fit into a planar fan (Fig. 8; SEILACHER & HAUFF, 2004). Therefore, the filtration fan of *Traumatocrinus* had to be corrugated or plicate, resembling a half-opened umbrella. The arm spines may have helped to stabilize the filtration fan (SEILACHER & HAUFF, 2004). The cup and arm base are broadened by the intercalation of polygonal interradials (Fig. 6*a*). Such ossicles also make up the tegmen and the short anal cone (Fig. 6*b*). Proximally, the column is thickened and commonly bent. The columns of both *Traumatocrinus* and *Vostocovacrinus* are composed of very low columnals, and cirri are absent. Columnal facets have crenulae folded into complex loops with pore canals (fossulae) between. The fossulae are expressed on the columnal side as pores; most of the fossulae do not reach the narrow central canal but end in equally narrow vertical canals (tubuli) that run parallel to the central canal (Fig. 9*a–b*). Thus, the column has numerous canals. HAGDORN, WANG, and WANG (2006) suggested that the tubuli contained fibers of mutable collagenous tissue that could stiffen or loosen the column, thereby resisting torsion and adjusting the crown to an optimum feeding position. In fact, columns of some individuals are embedded ropelike, whereas others resemble walking sticks with a bent proximal part near the crown (Fig. 6*a* and Fig. 7). The distalmost column lacks tubuli, perhaps indicating that it was always stiff, so that neighboring individuals did not become entangled at the attachment site. Column length of adult individuals varies between 1 or 2 m and 11 m. Column length is not correlated with columnal diameter; columns of 11 m length may have a diameter of only 7 mm. In contrast, short columns of 1 to 2 m may reach a diameter of 12 mm. Columns were attached by branching and encrusting radices irregularly distributed over the distalmost part of the column (Fig. 9*d*). A driftwood with a length of 330 cm and a diameter of 27 cm described by HAGDORN, WANG, and WANG (2006) contains approximately 60 intact crinoids with different column lengths, but the crowns are all of similar size (Fig. 7). The crinoids are concentrated at both ends of the driftwood, perhaps an indication that wood was a better substrate for colonization

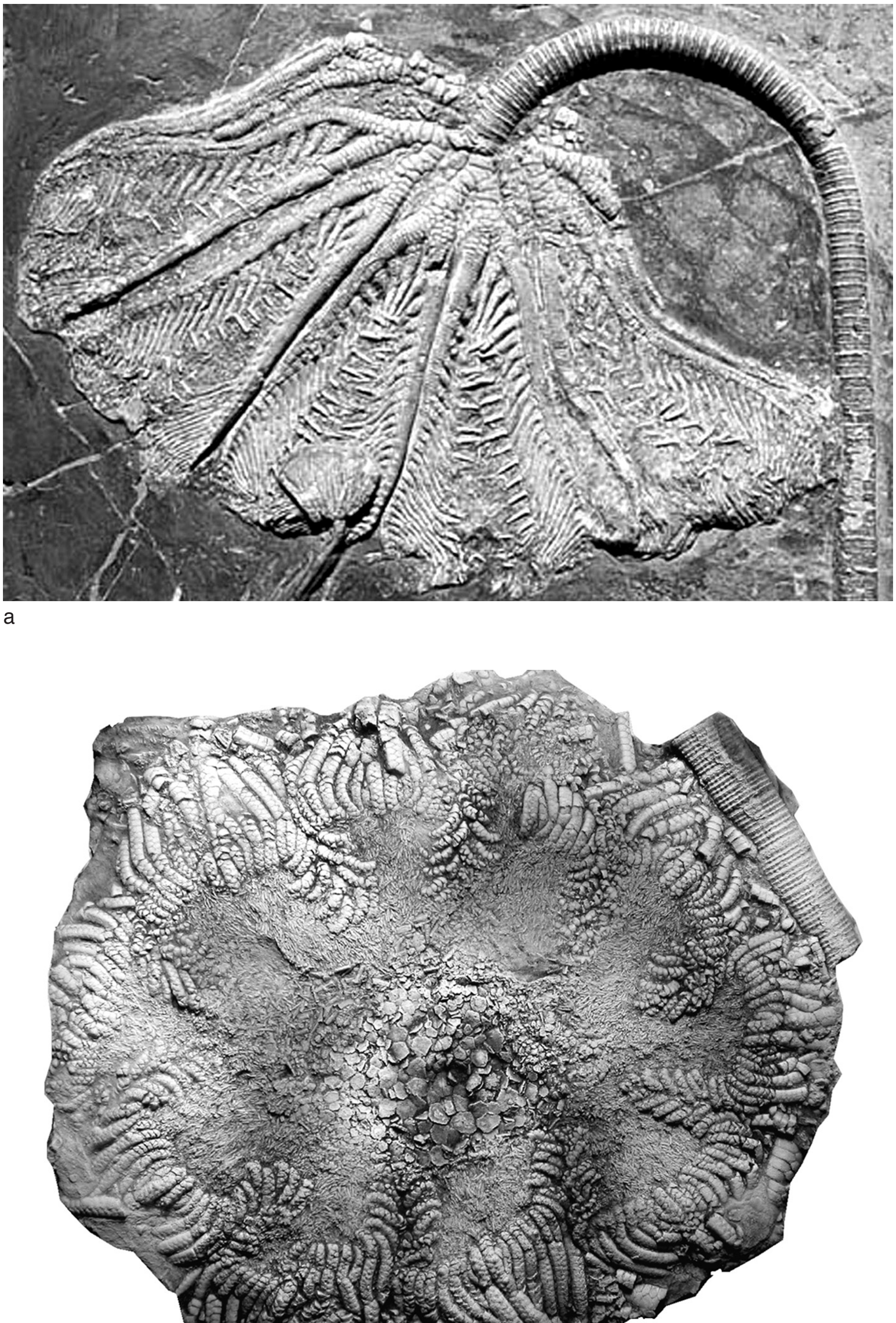

FIG. 6. *Traumatocrinus hsui* Mu, Carnian, China; *a,* crown and proximal column, Yichang Institute of Geology and Mineral Resources, Yichang, China, XT3xH-10, ×0.35; *b,* adoral view of semiadult crown with tegmen, anal cone, and distal arms, Muschelkalkmuseum Hagdorn, Ingelfingen, Germany 1882/3, ×1.5 (Hagdorn, new).

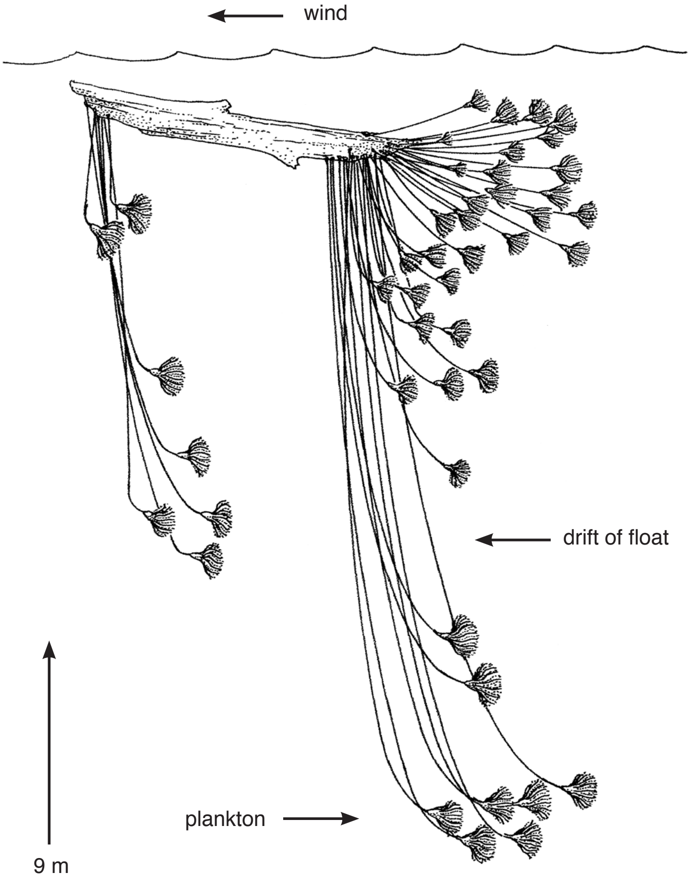

FIG. 7. Colony of *Traumatocrinus hsui* attached to driftwood, drawn after *in situ* occurrence; the crinoids preferentially attached to tips of log; crowns of similar size, but columns differ in length to reach different depths, length of driftwood 3.3 m, Xiaowa Formation, Ladinian-Carnian boundary, Guanling, China (adapted from Hagdorn & others, 2004).

than bark. In longer-stalked individuals, the proximal part of the column is bent so that the crown was displayed at nearly a right angle to filter the plankton beneath the moving driftwood raft. Short-stalked individuals were spread bouquetlike at one end of the log, possibly making use of eddying currents for feeding.

PENTACRINITIDS FROM THE LOWER JURASSIC OF SOUTHERN ENGLAND AND SOUTHERN GERMANY

Nearly all specimens of *Pentacrinites fossilis* from the Dorset coast of southern England are from a 2 m interval of dark, well-laminated, oil-rich mudstones within the *obtusum* Zone of the Lower Jurassic (Sinemurian) Black Ven Marls. The crinoids are the only large organisms in these mudstones. The remainder of the fauna is dominated by pelagic or nektonic organisms, particularly ammonites. As early as 1836, WILLIAM BUCKLAND noted that groups of *Pentacrinites fossilis* were commonly associated with thin lenses of coalified driftwood that occur in this part of the succession. More importantly, he noted that these pieces of fossil driftwood invariably lay above the crinoid lenses rather than beneath them. From this he concluded that they had lived attached

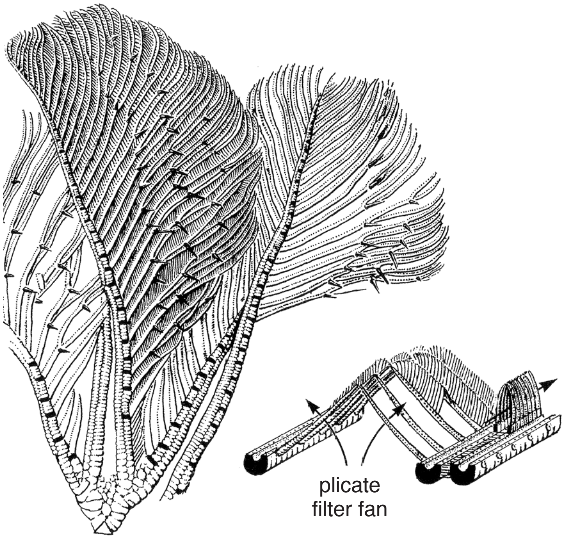

FIG. 8. *Traumatocrinus hsui* MU; at left, part of crown with aboral spines at branching points; at right, model of ramules and pinnules forming plicate filtration fan, Yale Peabody Museum, YPM 202269, approximately ×0.5 (Seilacher & Hauff, 2004).

to pieces of driftwood floating at the surface of the sea and that they died when the driftwood and its crinoid cargo sank to the sea floor. This idea was not universally accepted, although its cause was championed elsewhere in relation to the similar occurrences of the giant crinoid *Seirocrinus* in the German Posidonia Shale, and it remained a contentious issue, with *Pentacrinites fossilis* usually depicted in reconstructions as a benthic crinoid (RASMUSSEN, 1977).

Pentacrinites fossilis occurs as thin lenses composed almost entirely of crinoid ossicles cemented together with a syntaxial calcite overgrowth. Virtually no sediment occurs within these crinoid lenses, and the lithology above and below crinoid lenses is typically identical. Furthermore, although the lower surface is commonly exquisitely preserved with every ossicle intact (Fig. 10), the upper surface invariably has some dissociation of the ossicles, with clear evidence of size-sorting by currents. This preservational mode of life is not indicative of rapid burial in sediment. In fact, the animals' remains must have lain exposed on the sea floor for some time before burial. It would appear that the softness of the sea floor muds, holding the ossicles in their original positions, and the absence of disruptive benthic organisms in this anoxic environment, resulted in the remarkable preservation of these crinoids. Other aspects of the driftwood-crinoid relationship support the pseudoplanktonic model. Preserved driftwood may or may not have crinoids attached, and benthic crinoids do occur associated with driftwood. The largest examples of *Pentacrinites* are confined to large pieces of driftwood, as might be expected; but in the case of benthic crinoids, even large individuals may be associated with quite small pieces of driftwood. Another feature of *P. fossilis*, and of its sister genus, *Seirocrinus*, is what has been termed the all or nothing rule (WIGNALL & SIMMS, 1990). Where these crinoids are present on a piece of driftwood, they occur in great abundance and with a range of sizes; whereas other pieces are entirely devoid of crinoids. This is consistent with the pseudoplanktonic model, in which most larvae settled among their parents on an increasingly overloaded ark. Constant recruitment to the same piece of driftwood was clearly unsustainable and hastened the demise of the colony. In

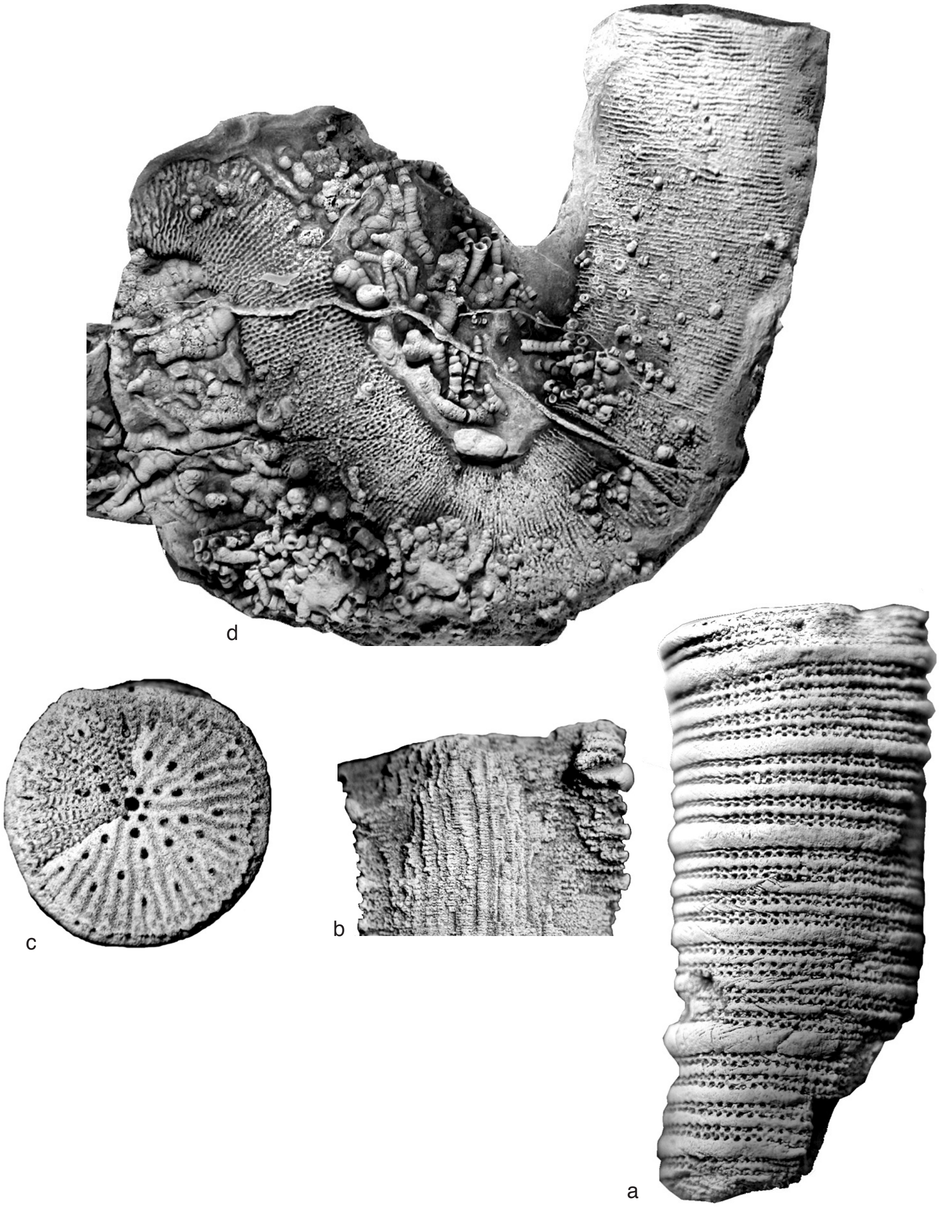

FIG. 9. *Traumatocrinus hsui Mu*, Carnian, China; *a–b,* proximal column; *a,* lateral with nodal-internodal sequence, ×3; *b,* interior view of weathered side with tubuli, Muschelkalkmuseum Hagdorn, Ingelfingen, Germany (MHI) 1880/2, ×5; *c,* facet of immature internodal with fossulae overlying mature nodal with crenulate loops, MHI 1880/4, ×5; *d,* terminal column with radicular cirri, MHI 1882/1, ×1.75 (Hagdorn, new).

effect, each assemblage was committing slow, inadvertent suicide.

The relationship between *P. fossilis* and the associated driftwood is not, in itself, sufficient to convince everyone that these crinoids were pseudoplanktonic, living suspended beneath floating objects. The first *in situ* observations of living isocrinids, during the early 1970s, convinced some that the longer-stalked pentacrinitids raised their

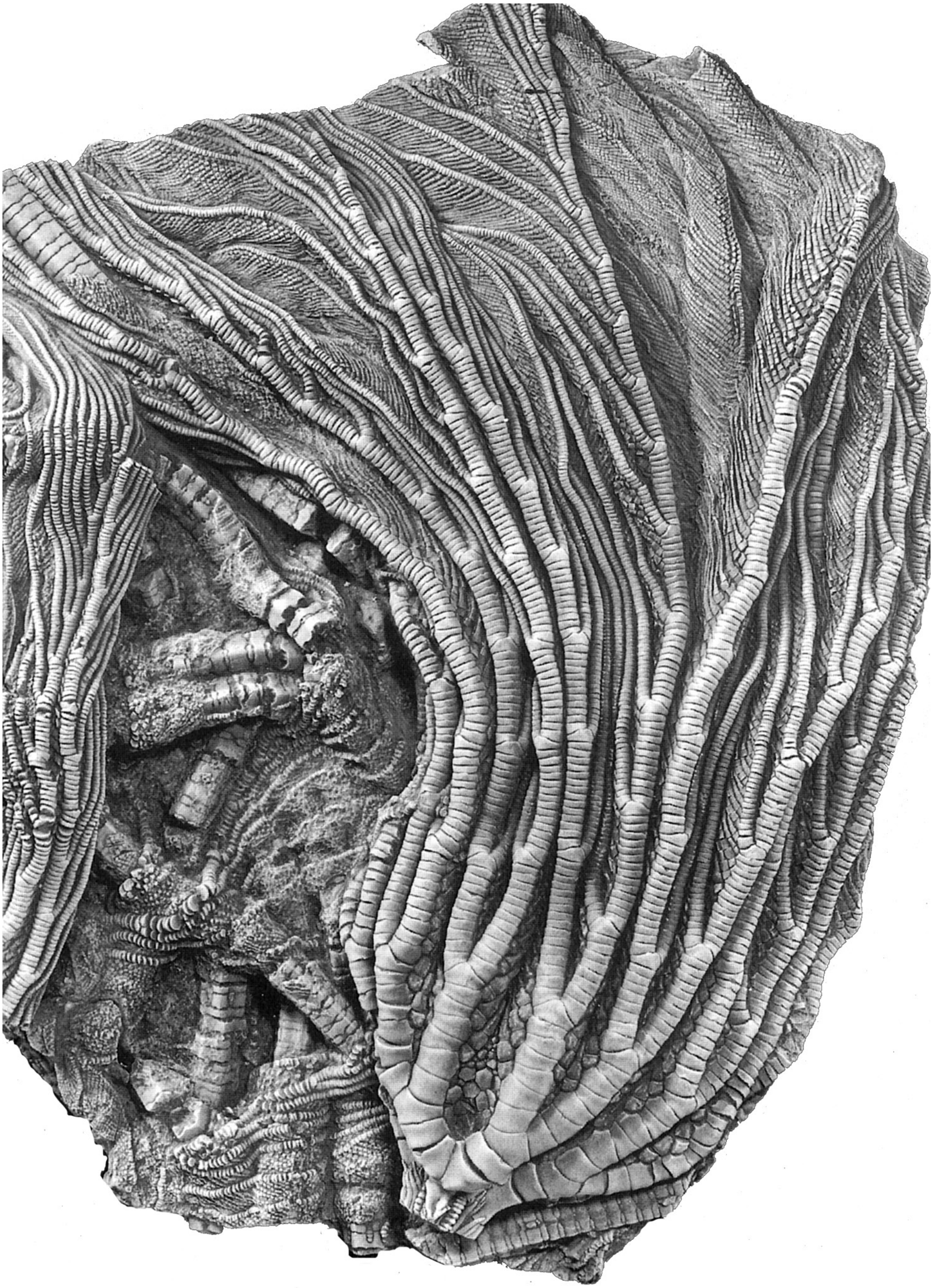

FIG. 10. *Pentacrinites fossilis* BLUMENBACH; crown, Sinemurian, England, The Natural History Museum, London E35056, ×1 (Simms, 1999).

crowns above the anoxic conditions close to the sea floor (RASMUSSEN, 1977; BREIMER & LANE, 1978, p. 339; RASMUSSEN, 1978, p. 863). In this interpretation, *Pentacrinites fossilis* inhabited the area during brief times of oxygenated bottom water and was killed as anoxia returned. However, as discussed above, evidence from the associated pieces

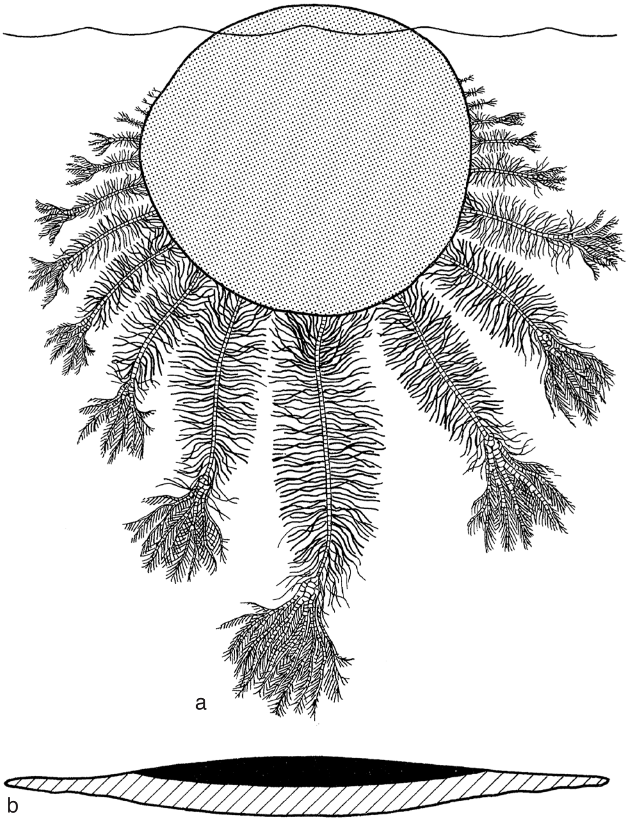

FIG. 11. *a,* Reconstruction of distribution of short-stalked *Pentacrinites fossilis* BLUMENBACH on floating driftwood reflecting colonization by successive generations of larvae on progressively higher parts of log; *b,* cross-sectional appearance of coalified driftwood (black) after burial and compression; larger crinoids seen as a layer (hatched) extending from beneath coalified driftwood, 0.2 (Simms, 1999).

of driftwood establishes quite unequivocally that *P. fossilis* must have been pseudoplanktonic. Benthic crinoids are known to use sunken pieces of driftwood as an anchorage, and it is conceivable that current activity rolled a piece of driftwood so that it came to lie on top of the crinoids. However, a remarkable discovery in 1985 showed that *P. fossilis* must have colonized pieces of wood while floating at the surface and that this species was unable to survive in the anoxic conditions on the sea floor (SIMMS, 1986). The specimen in question is a fragment of highly compressed, coalified driftwood. The fragment is only 12 cm wide and 18 cm long, but it was clearly part of a much larger log at least 20 cm in diameter. Mature specimens of *P. fossilis* are preserved as a thin layer on the underside of the driftwood and extend a short way beyond its margin. The upper surface appeared to be devoid of any crinoid remains until examined closely. Along the one remaining original edge of the log, a band approximately 2 cm wide was covered with innumerable tiny attachment discs from the column of a larval crinoid less than 1 mm across. A single, slightly larger attachment disc was present at one end of the driftwood fragment. The larval attachment discs were confined almost entirely to this marginal band, with only one small group farther toward the center. Their distribution coincides almost perfectly with a scenario in which *P. fossilis* colonized floating logs. The optimum position for the crinoids would have been on the underside of the log, a position that would have been occupied first (Fig. 11). As the log sank lower in the water, higher parts of it would have become accessible to and colonized by new larvae. However, as the log sunk into the anoxic zone at the sea floor, death occurred for all the inhabitants of the log, from the earliest colonizers on the underside to the latest recruits along the upper edge. The virtual absence of new attachment discs from the upper part of the log shows that when it was on the sea floor, none of the original inhabitants of the log survived to grow larger, and no new recruits were able to occupy the vacant space. The position of the mature crinoids on the lower side of the log and the presence of larval attachment discs above them proves that this stand of crinoids was not established during an interval with aerobic conditions at the bottom.

Living attached to floating driftwood must have presented many hazards to these crinoids. Even though the larval crinoids were attached by a cemented disc, this was abandoned when the crinoids were only 2 to 3 cm high, and cirri were used for attachment throughout the remainder of their life. Considering how crucial this was to their existence, there does not seem to have been a standard strategy for ensuring firm attachment by the cirri. Cirri development in *Pentacrinites fossilis* is variable, with two distinct types even within single colonies. Some individuals have columns no more than 20 cm long, along with cirri densely crowded and very long. In contrast, others have columns perhaps as much as 1 m in length, along which the cirri are, except in the proximal region of the column, widely spaced and very short. Commonly, these longer columns occur tangled together into large bundles; and occasionally, at their distal end, there is a second region of long, closely spaced cirri like those in the proximal region of the column. Presumably these long cirri were used to grasp irregularities in the surface of the driftwood or, particularly in the case of the short-stalked individuals, to attach to other individuals. Attachment was not always entirely successful, as demonstrated by isolated specimens or groups of *Pentacrinites* that became detached and sank to the sea floor. Even for those that did not suffer this fate, there was no certainty that the driftwood would stay afloat for long under its increasing burden of crinoids and other organisms.

In the Toarcian Posidonia Shale of southern Germany, *Pentacrinites dichotomus* occurs in the *falciferum* and *bifrons* Zones; and it is more rare than the famous *Seirocrinus subangularis* from the *tenuicostatum* Zone. In contrast to the British occurrences of *Pentacrinites fossilis* in the Sinemurian, the species from the Posidonia Shale is invariably very short stalked. The largest specimens known have columns approximately 20 cm long and an arm length of approximately 15 cm. Only the nodals are visible from the outside, being mostly covered by the closely spaced, compressed cirri with a length comparable to that of the arms (Fig. 12). A slab with 153 individuals of *P. dichotomus*, with a diameter of 1.15 m, is exhibited in the Stuttgart Museum (Urlichs, Wild, & Ziegler, 1994, fig. 68). Most of the crinoids on this slab are of a similar size, but some small juveniles also occur. The crinoids appear to have colonized radially from a central area, where the thickness suggests two layers of crinoids. Individuals on this slab are primarily preserved on their side, but approximately a dozen specimens have the oral side exposed. Another slab from Ohmden, preserved in the Stuttgart collection, contains a group measuring 55 by 40 cm, with approximately a dozen individuals, as well as two *Pseudomytiloides* (Hess, 1999b, fig. 202). Its preservation is quite similar to that of the large Stuttgart slab. These *Pentacrinites* were not preserved together with wood or with other remains of plants. The preserved positioning of these crinoids has the appearance that they may have floated as a more or less spherical body, with their long cirri intertwined for mutual support and grouped around some unfossilized material. This, of course, is very speculative, because it is questionable

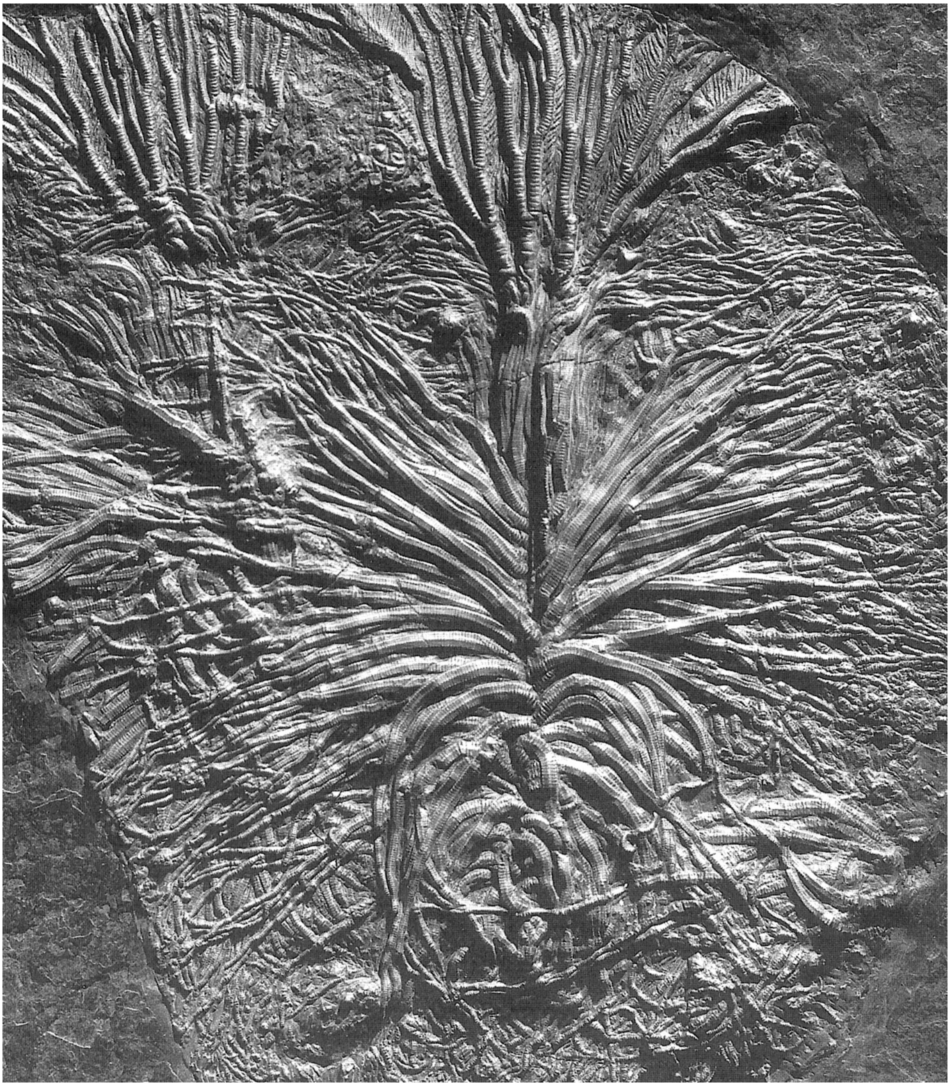

FIG. 12. *Pentacrinites dichotomus* (M'COY); intact columns and base of crowns, Toarcian, Germany, Staatliches Museum für Naturkunde, Stuttgart, Germany 7389, ×0.45 (Hess, 1999a).

whether a material comparable to today's seaweeds would be buoyant enough to support such crinoid large groups. It may well be that the crinoids were separated from their buoyant support before burial. The two slabs in the Stuttgart Museum with a group of *P. dichotomus* preserved without supporting wood seem exceptional. A group of *P. dichotomus* approximately 3 m long is preserved in the Dotternhausen Werkforum (JÄGER, 1993, fig. 13). It is attached to a log of similar length, proving a pseudoplanktonic lifestyle for this species also. The group contains approximately 45 densely spaced individuals, which are inserted on one side (presumably the lower side) of a now-flattened log, with a diameter of 10 cm. The crowns point away from the log. The Dotternhausen collection also includes another group of *P. dichotomus* attached to wood, and recent collecting indicates that such occurrences are not uncommon (B. HOSTETTLER, personal communication, 2009).

Therefore, the Dotternhausen specimens are similar to the Dorset crinoids, which are regularly preserved underneath the lignitized driftwood to which they were attached. However, the Dorset *Pentacrinites fossilis* developed longer columns, similar to *Seirocrinus*. The stratigraphically younger *P. dichotomus* may have evolved from *P. fossilis* by an increase in the number of brachials and the development of syzygies between secundibrachials 6 and 7, as well as by a shortening of the column. These differences are presumably the result of a somewhat different lifestyle, allowing mutual support of the animals clinging to the log.

The pride of the Toarcian Posidonia Shale of southern Germany are splendid articulated specimens of *Seirocrinus subangularis*, mostly attached to logs (Fig. 13). Crinoids tend to be grouped around the ends of the logs, similar to the Triassic *Traumatocrinus*. Large groups are restricted to logs and typically also contain small individuals, commonly attached to the columns of the adult specimens (HESS, 1999b, fig. 195). Isolated specimens appear to have been broken from driftwood, because their columns are rarely complete. The showpiece of the Hauff Museum in Holzmaden is a slab measuring 18 by 6 m. It contains a 13 m-long piece of driftwood completely covered with bivalves (*Pseudomytiloides dubius*), a giant group of approximately 280 large and small individuals of *Seirocrinus subangularis,* with bundles of columns partly wound around the log (Fig. 14; SEILACHER, DROZDZEWSKI, & HAUDE, 1968).

Small individuals of *Seirocrinus* are superficially similar to *Pentacrinites dichotomus* with a column length of only a few centimeters. The columnals of large specimens are rounded subpentagonal to circular in cross section and typically vary in height. The articular facets have large, strongly granulated radial areas separating the crenulate, narrow pyriform petals (Fig. 15). With increasing distance from the cup, the diameter of the column is reduced, making it much more flexible. The length of the internodes gradually increases and may reach more than a thousand columnals near the end of a 20 m-long column (SEILACHER, DROZDZEWSKI, & HAUDE, 1968). The total length of the largest column is more than 26 m (SIMMS, 1989). Columns of such extreme length indicate fast growth. In contrast to isocrinids, the articulation between nodals and infranodals in *Seirocrinus* is symplectial. Cryptosymplectial or synostosial autotomy planes are lacking. Elimination of column autotomy on synostosial articulations would have been an advantage for a crinoid hanging from a raft above an anoxic bottom zone, where a detached crown would be rapidly killed. The cirri are closely spaced in both the proximalmost and distal column regions, with a dense tuft of cirri forming the attachment to the driftwood. The cirri vary from small to large individuals and from the proximal to the distal part of the column. In small individuals, cirri are rhomboidal in outline and resemble those of *Pentacrinites*, whereas in large individuals, cirrals are rounded, short, and slender. The primaxil and the secundaxil have an isotomous division, but succeeding divisions are all endotomous.

A pseudoplanktonic mode of life for *Seirocrinus* is supported by a number of facts (HAUDE, 1980; SIMMS, 1986). As observed in living crinoids, a filtration fan held into the current by crinoids anchored to the bottom would need columns that were stiff near the bottom but flexible beneath the crown. In *Seirocrinus*, the reverse is true, and such a morphology is quite exceptional in fossil crinoids. As noted by HAUFF and HAUFF (1981), the size of the crinoids is proportional to that of the driftwood on which they are anchored (Fig. 14). The loading capacity of floating trunks has been discussed by HAUDE (1980). He calculated that the log in the Senckenberg Museum, measuring 190 cm by 8 to 12 cm (Fig. 16) had a load

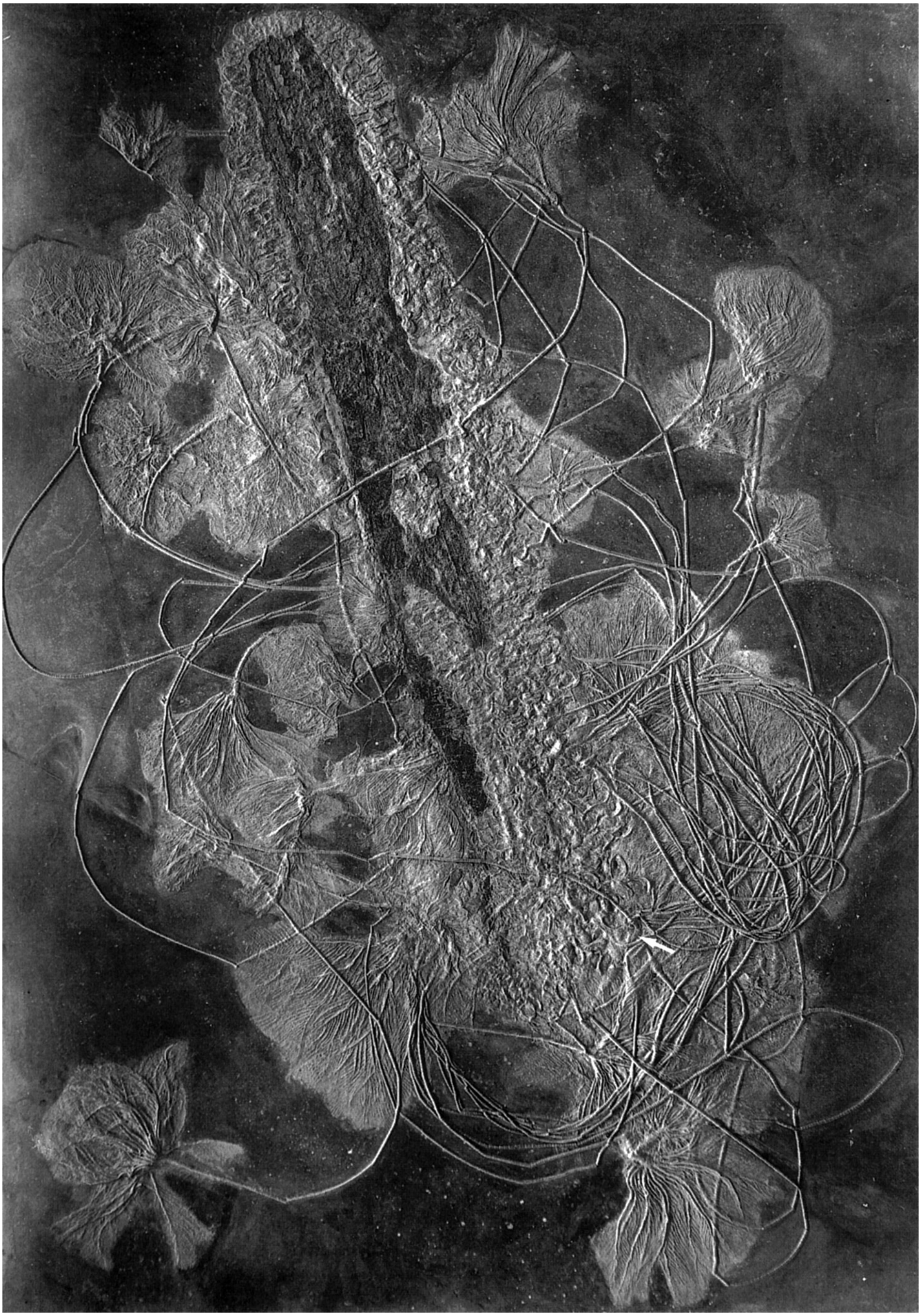

FIG. 13. *Seirocrinus subangularis*; colony with entangled columns on driftwood mostly covered with *Pseudomytiloides*, Toarcian, Posidonia Shale, Holzmaden; slab was prepared from lower side; one specimen, whose attachment is close to upper end of log (*arrow* in lower right), has a column that crosses log twice, proving that log settled on the bottom, on top of the crinoid, SMNS 64854, size of slab: 2.5 by 3.5 m (Hess, 1999b).

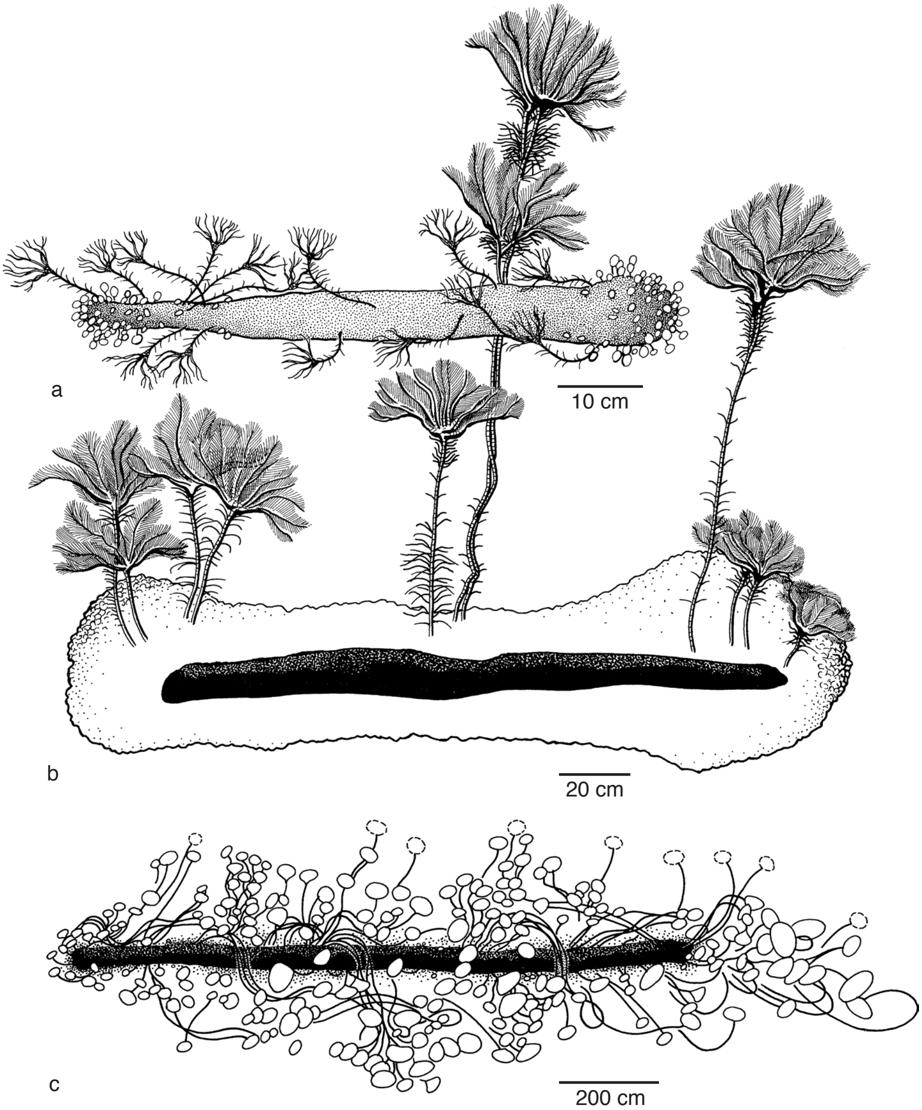

FIG. 14. Completely preserved colonies of *Seirocrinus subangularis* on logs of different size; *a,* colony of juvenile individuals (Göttingen Museum); *b,* colony of subadult individuals (Senckenberg Museum; see also Fig. 16); *c,* giant colony, Hauff Museum, Holzmaden (Hess, 1999b).

capacity of approximately 12 kg. The weight in seawater of all *Seirocrinus* specimens on this log was estimated to be only around 0.5 kg, compared with a total weight of as much as 10 kg for as many as 5000 *Pseudomytiloides dubius* bivalves. These figures are in agreement with a pseudoplanktonic life for *Seirocrinus*. Doubts have also been raised as to whether the trunks could have floated long enough to allow *Seirocrinus* individuals to colonize and grow to such size. According to HAUDE (1980), unloaded trunks of modern conifers (a type of tree common in the Early Jurassic) remain buoyant for two years, at the most. Therefore, he assumed that either the crinoids grew rapidly or the wood remained floating for longer periods, possibly because of its resin content or some other unknown feature that prevented decay and saturation of the pores. However, the trunks could have remained floating for much longer (SIMMS, 1986).

On the large trunks floating near the surface, large *Seirocrinus* individuals must have been hanging down (Fig. 16 gives an impression of this). Once the buoyancy fell below a certain point, large logs sank. The eventual preservational relationships between the crinoids and the log depended on the speed with which the log sank and the density of the crinoids, including any attached epizoans. If the log sank quickly, the crowns would have been dragged along like parachutes. After the trunk settled, the crowns would have tilted over and sunk to the bottom, resulting, in most cases, in preservation of crowns on their side (Fig. 13 and Fig. 14*a–b;* HESS, 1999b, fig. 195, 199; HAUFF & HAUFF, 1981, fig. 113–119). In contrast, if the logs sank slowly, or if large individuals with very long columns were heavy, the crowns may have reached the bottom in their natural, hanging position with the oral side downward, as suggested by a very large group in the Tübingen Museum (Fig. 17; HAUDE, 1980). Another example is a trunk with a length of approximately 3 m in the Stuttgart Museum (Fig. 13). It has a heavy overgrowth of *Pseudomytiloides dubius* and crinoids with twisted columns that lie partly over the log. Because this slab is the lower bedding surface, the log must have settled only after some of the crinoids

FIG. 15. *Seirocrinus. subangularis* (MILLER); columns with facet, Toarcian, Germany, Werkforum Dotternhausen, ×0.9 (Hess, 1999a).

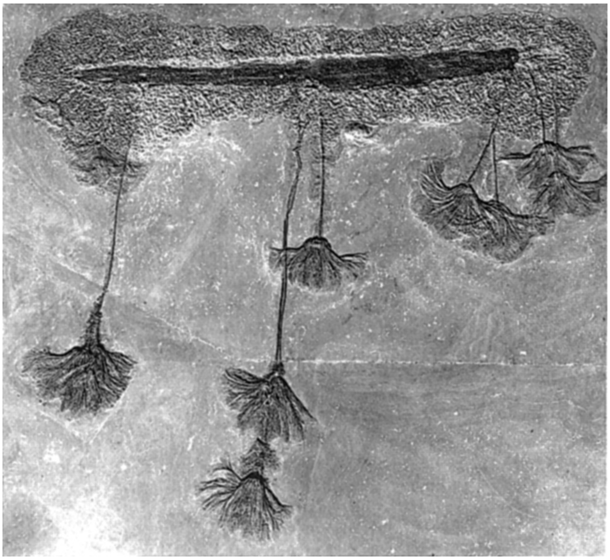

FIG. 16. *Seirocrinus subangularis* (MILLER), with crowns hanging down to show presumed life position, Posidonia Shale, Toarcian, Holzmaden, Naturmuseum Senckenberg, Frankfurt, size of slab: 250 × 260 cm (Hess, 1999b).

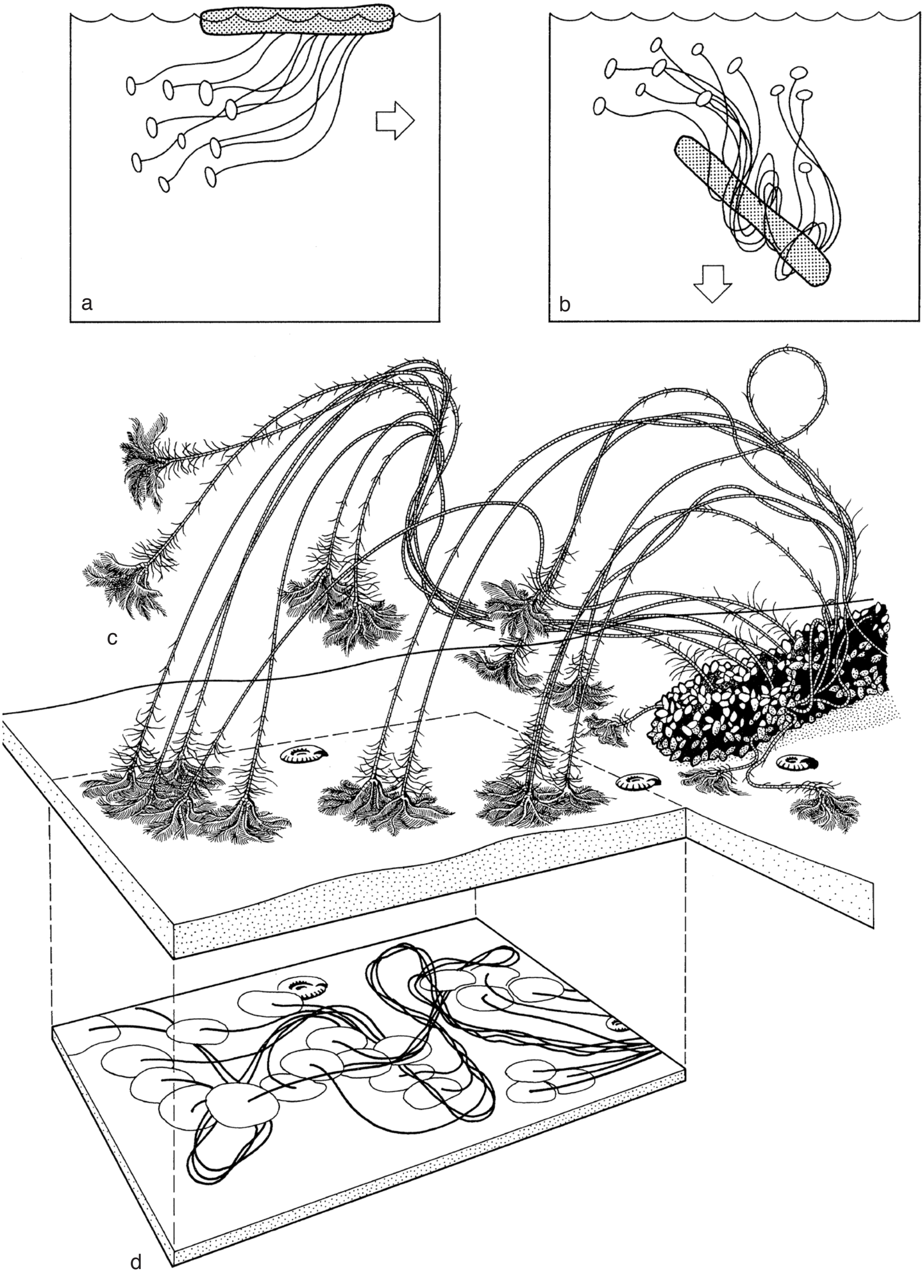

FIG. 17. Reconstruction of the sinking process of a large *Seirocrinus subangularis* colony, exhibited in the Museum of the University of Tübingen; length of slab: approximately 10 m; *a,* floating log; *b,* log at beginning of sinking process; *c,* log reaching bottom; *d,* slab with fossils (Hess, 1999b).

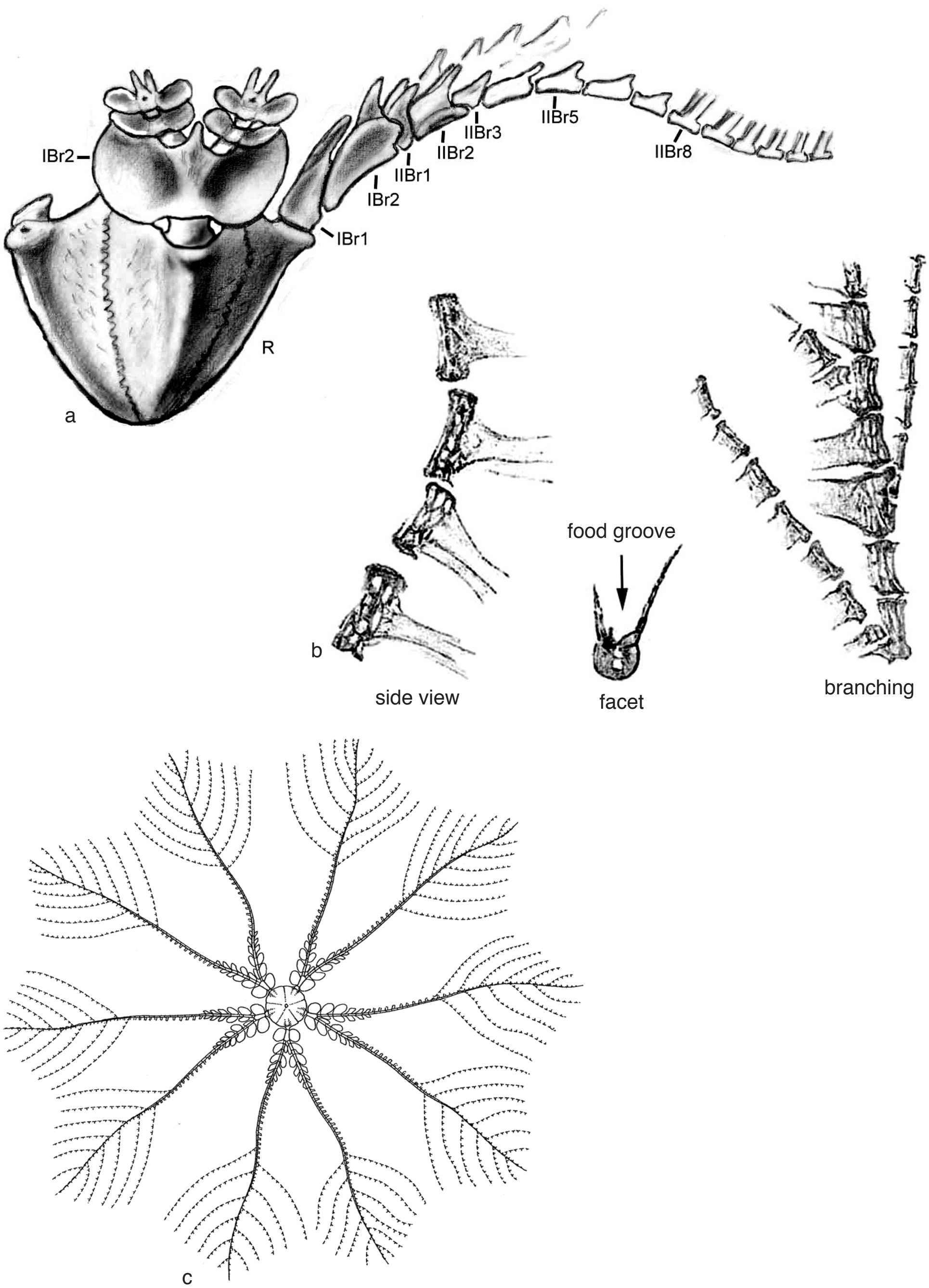

Fig. 18. *Saccocoma tenella* (Goldfuss), Tithonian, Germany; *a,* reconstruction, sculpturing omitted, *R,* radial, *IBr,* primibrachial, *IIBr,* secundibrachial, approximately ×8 (Hess & Etter, 2011); *b,* brachials with oral processes, ×15 (facet, ×20) (Jaekel, 1892); *c,* aboral projection, ×1.6 (Hess, 1999c; after Jaekel, 1918).

touched the bottom: an indication of slower settlement.

For the long-stalked crinoids attached to driftwood, SEILACHER and HAUFF (2004) coined the term tow-net filtrators, a group they thought would also include the scyphocrinitids. Attached to long, flexible columns, the crowns of *Seirocrinus* would have been dragged along parachute-like, and the columns were not bent in their proximalmost part. The velocity gradient between the log and the crown would not work for the short-stalked pentacrinitids, so that these authors suggested that *Pentacrinites dichotomus* was an active filtrator, using its long, flattened cirri to create a current. This idea is rejected herein because cirri lack active muscles. In addition, it does not explain how the juvenile specimens of *Seirocrinus* fed before becoming long-stalked adults. It also does not explain why the earlier *Pentacrinites fossilis* had both short and long columns. Therefore, it appears that the pelagic crinoids fed by several mechanisms that include tow-net filtration, but also capture of (phyto-) plankton concentrating (or reproducing) around the logs or zooplankton moving vertically during diurnal migration. Because *Seirocrinus subangularis* and *Pentacrinites dichotomus* do not occur on the same logs, one or the other of the mechanisms may have been preferred by either species.

NEKTONIC ROVEACRINIDA

Roveacrinids are diminutive, stalkless crinoids. They are interpreted as mostly pelagic and display adaptations consistent with this mode of life, such as a thin, delicate skeleton, cups ornamented by spines, ridges, wings, and flanges to increase frictional drag. Similar sculpturing also occurs on brachials. Whether roveacrinids developed directly from planktonic larvae or used foam floats (e.g., on siphonophores, as suggested by SEILACHER & HAUFF, 2004) as steppingstones to pelagic life is not known.

Roveacrinida occurred during the Middle and Late Triassic (Somphocrinidae and Axicrinidae), during the Jurassic (Saccocomidae, also known from the Cretaceous) and during the Cretaceous (Roveacrinidae). No extant species are known. These families are linked by the synapomorphy of strongly sloping, immovable cryptosynarthries in the proximal part of the arms, a feature unique among articulated crinoids. Whereas the roveacrinids were mostly pelagic, some forms appear to have been benthic during at least part of their lives (HESS, 2002), suggesting that sloping cryptosynarthries were not exclusively for a pelagic lifestyle. Most of the brachials are joined by muscular articulations. It should be mentioned that the Saccocomidae also include *Applinocrinus*, an armless form widely distributed during the Late Cretaceous. Because it lacks arms, it is assumed to have lived mostly on the bottom.

The characteristic sloping cryptosynarthries common to all roveacrinids must have served an important function for their mode of life. The corresponding ossicles are imbricated, and this would have stabilized the lowermost part of the arms of these small and mostly fragile animals, preventing easy breakage and, thus, protecting the area of the cup with exposed soft parts (Fig. 18*a*). Nonsloping synostoses only occur between higher secundibrachials (the first between secundibrachials 3 and 4) where the arms of roveacrinids could break due to stress, a situation known also from other articulates.

The best known and most numerous roveacrinid is the fascinating *Saccocoma tenella* from the Tithonian Plattenkalk facies of Bavaria. Its taphonomy and morphology, unique among crinoids, is discussed in the next section.

SACCOCOMA TENELLA FROM THE UPPER JURASSIC SOLNHOFEN PLATTENKALK OF BAVARIA, GERMANY

Saccocoma tenella is preserved primarily as complete specimens, so the morphology and taphonomy are well known. The lower

Tithonian Solnhofen Plattenkalk facies is characterized by extremely fine-grained, even-layered carbonate mudstones. By far the most dense occurrences of *Saccocoma tenella* in the Plattenkalk facies are known from the Schernfeld area near Eichstätt. In a sequence of only 7 m, Röper, Rothgaenger, and Rothgaenger (2000, p. 123) reported approximately 300 horizons with *Saccocoma* at densities of more than 30 individuals per square meter. In the Solnhofen area, *Saccocoma* occurs mainly on bedding planes of dense, thick limestone beds (Flinz); and in the Eichstätt area, on thin, somewhat marly beds (Fäule or Blätterflinz). In comparison to the Solnhofen basin with thicker limestone beds, the Eichstätt basin contains approximately seven times more *Saccocoma*, although there are differences between the very rich, western part near Schernfeld and the somewhat less rich, eastern part near Wintershof. This distinction correlates well with the number of sedimentation breaks, or marly intervals, between limestone formations (Röper, Rothgaenger, & Rothgaenger, 2000, p. 50). The aboral side of the cup typically stands out from the surface on the underside of the beds, and the arms are distally mostly coiled or crumpled. Röper, Rothgaenger, and Rothgaenger (2000) suggested that the animals accumulated after mass death on beds lithified by microbial mats and were later covered by sediment. This theory of slow accumulation of dead animals on the bottom during long periods of nonsedimentation, followed by rapid deposition of the limestone beds that preserved the organisms at the lower surface, is essentially from Barthel (1978, p. 77). However, in actualistic experiments, dead crinoids begin to disarticulate within a few days of exposure on the sea floor (Meyer, 1971; Liddell, 1975). In contrast, Hess (2002) suggested that the animals were immobilized by an influx of fine sediment that clogged the food grooves, impairing feeding and preventing further movement; the curled-up animals settled, by virtue of size and density, before the bulk of the sediment. The orally enrolled arms (Fig. 19) are a trauma posture resulting from muscular contractions of the brachials before death. Such events produced the compact Flinz limestone beds of the Solnhofen area. In more marly (Fäule) and thinner beds (Blätterflinz), as they commonly occur in the Schernfeld area, the animals appear to have perished mainly from lack of oxygen or increased salinity (Röper, Rothgaenger, & Rothgaenger, 2000, p. 122). The arms may also be detached from the cup, a further indication of trauma. This preservational state is known as *Saccocoma schwertschlageri* (Manni & Nicosia, 1986). The uncommon specimens with outstretched, occasionally aborally flexed arms (Hess, 1999c, fig. 219) may have perished from other natural causes, and current-oriented specimens indicate weak currents on the bottom before final burial (Röper, Rothgaenger, & Rothgaenger, 1998, fig. 35, 38). The available data suggests that conditions for death and preservation may have varied. The common occurrence of coprolites (*Lumbricaria*) composed entirely of remains of *Saccocoma* (Müller, 1969) on the same bedding planes as *Saccocoma* specimens leaves no doubt that the crinoids lived and were preyed on in the upper, oxygen-rich, water layers of the Plattenkalk basins (Röper, Rothgaenger, & Rothgaenger, 1998, 2000; Hess, 1999c, 2002). The coiled coprolites must have descended to the anoxic sea floor from an animal living and feeding in the water above (Fig. 20; Hess, 2002). *Saccocoma* presumably fed on the photosynthetic coccolithophorids and was preyed upon by teuthoid cephalopods (Fig. 19; Janicke, 1970) and ammonites (Schweigert & Dietl, 1999).

Saccocoma tenella is large by roveacrinid standards. The cup is a hemispherical or slightly conical, open bowl with a diameter reaching 5 mm, composed of five very thin radials. Tegminal plates are absent. The surface of the radials is covered with a network of anastomizing ribs, and a median ridge is thickened on top to reinforce the area beneath the radial articular facet. This

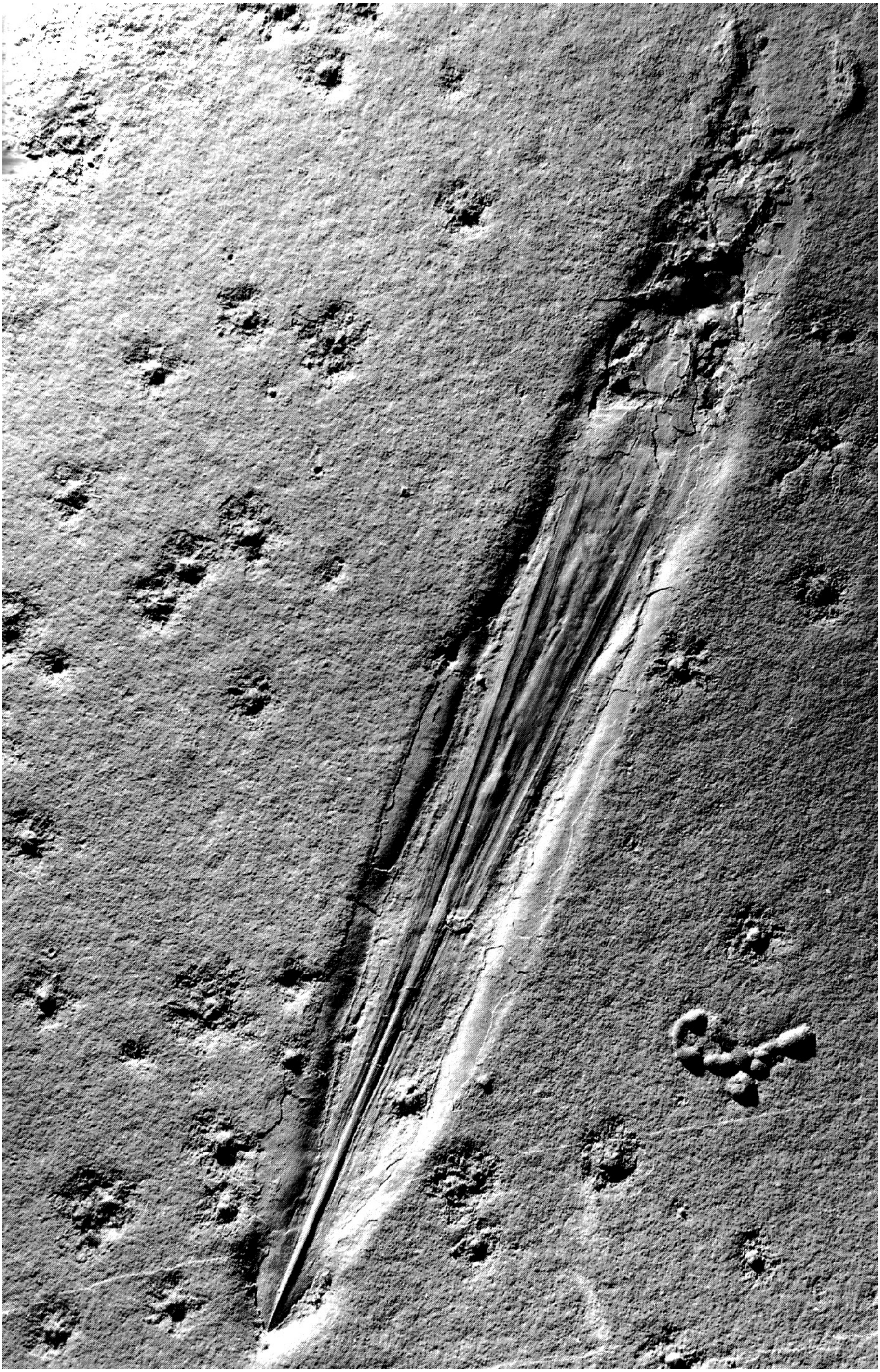

FIG. 19. Underside of slab from Tithonian Plattenkalk, Schernfeld, with *Plesioteuthis prisca* RUEPPELL, *Saccocoma tenella* (GOLDFUSS) with coiled arms, and a coprolite (*Lumbricaria*); slab unites prey, possible predator, and excretion product, Museum Bergér, Eichstätt, ×0.75 (Röper, Rothgaenger, & Rothgaenger, 2000).

facet has a small aboral part and elongate muscle fossae articulating with V-shaped muscle fossae on the first primibrachial. The exposed aboral surface of the first primibrachial is low, and the distal surface is a sloping cryptosynarthry that is hidden by the aboral surface of the axillary second primibrachial. Thus, the two primibrachials are connected by rather large ligamentary, immovable facets. The same type of articulation is developed between the first and second secundibrachials. In contrast, the wingless third and the winged fourth secundibrachials are connected by a synostosial articulation perpendicular to the axis of the arm. All subsequent articulations are muscular, with a pronounced aboral ligament fossa. The ten main arms rising from the second primibrachial (primaxil) bear a number of side arms or ramules. These originate in some sort of pinnule socket, but their elements are essentially comparable to the elements of the main arms and, thus, cannot be classified as true pinnules. The primaxil, the second secundibrachial, and fourth to seventh secundibrachials bear conspicuous, symmetric, dishlike lateral wings or flanges and weak oral processes (Fig. 18*a*). The first and third secundibrachials lack wings. The lateral wings have a dense, porcelain-like, nonreticulate structure. The two distal articular facets of the primaxil slope outward at an angle of approximately 45°, and the arm attitude is nearly horizontal around the fourth or fifth secundibrachials (BRODACKI, 2006). Away from the cup, the lateral wings are progressively reduced in size, and, in contrast, paired vertical processes or baffles are present to the very tips of the arms. On the proximal (oldest) brachials, the height of the processes exceeds the length of the corresponding arm ossicle (Fig. 18*a*); near the arm tips they are lower but occupy the whole length of the needlelike brachials. The processes commonly are compacted and lie parallel to the bedding planes, but they were vertical during life, so that the food grooves were in a deep trough (Fig. 21). On proximal elements, the processes are extensions of the arm ossicle with the same reticular structure at the base, and their sides are stiffened by rods. The ten main arms are unbranched for approximately twelve brachials, after which ramules are attached to every second brachial (Fig. 18*b–c*). The brachials of the side arms have essentially the same structure as the main brachials, although the processes are lower. The ramules replace the pinnules of ordinary articulated crinoids, so SEILACHER and HAUFF's (2004) speculation that the pinnules simply lost their calcareous armor and were supported by an organic axis seems redundant. In JAEKEL's famous reconstruction (1892, pl. 30), approximately three times as many ossicles are on the side ramules, as compared to the main arm; the living animal efficiently covered the area within its reach.

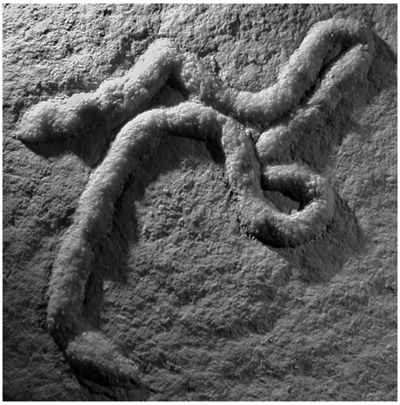

FIG. 20. *Lumbricaria intestinum* MÜNSTER, coprolite composed of remains of *Saccocoma tenella* (GOLDFUSS), Tithonian, Mühlheim, Natural History Museum, Basel, Switzerland, NMB M 10526, ×1 (Hess, new).

Thus, the crown of *Saccocoma* may be divided into three parts, a proximal part with horizontal wings on the brachials, a median part with paired vertical processes on the brachials, and a distal part with arms branching (Fig. 18*c*). By virtue of the porous nature of the plates, the wings on the proximal brachials, and the ramulate distal arms, *Saccocoma* was well adapted to a pelagic way of life. As in other roveacrinids, *Saccocoma tenella* has well-developed, high muscle fossae between radials and first

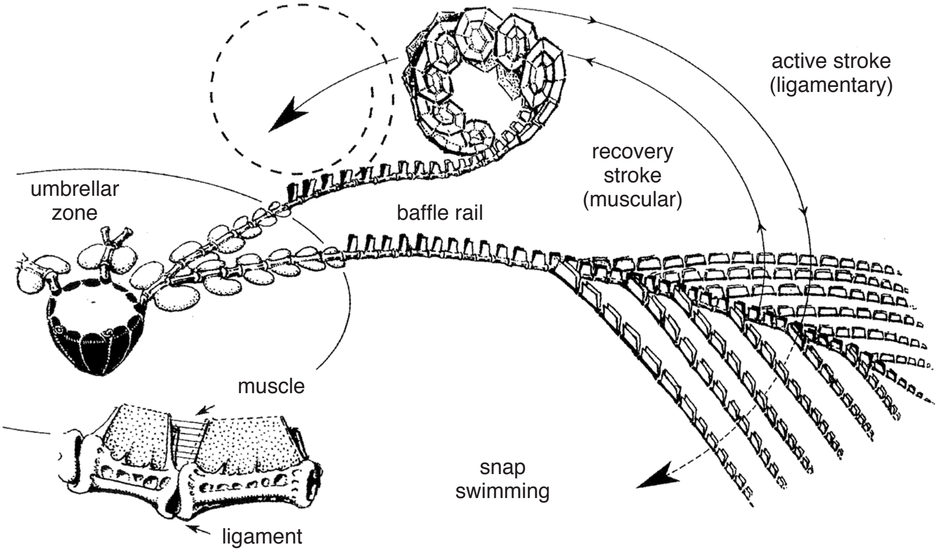

FIG. 21. Snap swimming model of *Saccocoma tenella* (SEILACHER & HAUFF, 2004).

primibrachials (BRODACKI, 2006, fig. 3-E4; HESS, 2002, pl. 1), indicating powerful movement of the arms. Because the proximal lateral wings, although concave downward, were not horizontal, but at an angle of approximately 45°, their role as parachutes to prevent sinking has been questioned by BRODACKI (2006, p. 264), who suggested that they may have increased the animal's surface or friction drag to reduce the sinking rate. The paired vertical processes are somewhat enigmatic. JAEKEL (1892) thought that processes of adjacent brachials were connected by soft membranes, an assumption that cannot be proven. An alternative explanation for their function was offered by SEILACHER and HAUFF (2004), who proposed that they were connected by muscles and, thus, used in the swimming process. They considered the commonly observed coiling of the arms not as a taphonomic artifact but as a frozen snapshot of swimming activity. In this model, the vertical processes were connected by muscles that, upon contraction, loaded the elastic aboral ligament spring. Upon release of the energy thus stored, the arm snapped back in an active stroke. However, it seems highly unlikely that large numbers of *Saccocoma tenella* were frozen in a swimming mode on the bedding planes. On articulations of more or less intact arms, the aboral ligament pit is quite distinct; but the adoral part is very rarely exposed, difficult to observe, and has been properly described only recently (HESS & ETTER, 2011). Compared with the aboral ligament pit, the adoral muscle fossae are rather small, are restricted to the main body of the brachials, and do not extend onto the vertical processes that are at some distance from the facets, except on the small distal brachials (Fig. 18*b;* HESS & ETTER, 2011, fig. 4–5). Thus, there is no evidence that the thin and high vertical processes were connected by muscles, making SEILACHER and HAUFF's (2004) snap-swimming model obsolete (Fig. 21). Therefore, a taphonomic explanation for the coiled arms, as already proposed by JAEKEL (1892, p. 679), is preferred. Life on the bottom as advocated by MILSOM (1994) and MANNI, NICOSIA, and TAGLIACOZZO (1997) is not supported by the evidence from sedimentology, taphonomy, paleoecology (KEUPP and MATYSZKIEWICZ, 1997; VIOHL, 1998), and morphology (HESS, 2002; HESS & ETTER, 2011).

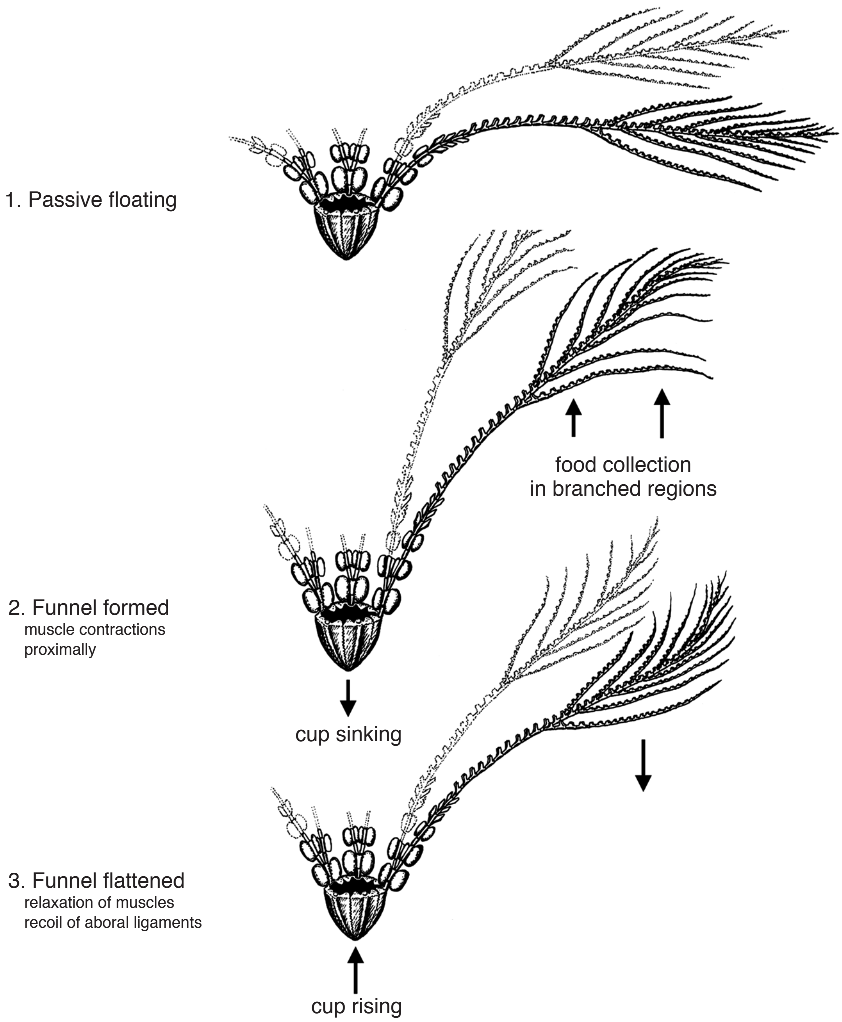

FIG. 22. Pulsating funnel model of *Saccocoma tenella* (Hess & Etter, in press).

Living crinoids deploy filtration fans into the current, whereby the plankton is caught by tube feet (podia) extended between the pinnules (BAUMILLER, 1997). Pelagic roveacrinids must have caught food while moving actively through the water. Similar to living forms, the arms of *S. tenella* displayed a filtration fan to increase the food-collecting surface. Position of the oral processes flanking the food grooves suggests involvement in food collection. For this purpose, HESS and ETTER (2011) proposed the pulsating funnel model (Fig. 22). Muscle contraction of proximal brachials flexed the arms inward and upward, so that a funnel was formed. The middle, and especially the distal, branched region formed a fan, whose upward movement scooped plankton between the vertical processes. How the particles were actually captured is conjectural, but it may be assumed that tube feet with adhesive surface were present along the food grooves. Relaxation of the muscles caused elastic recoil of the antagonistic

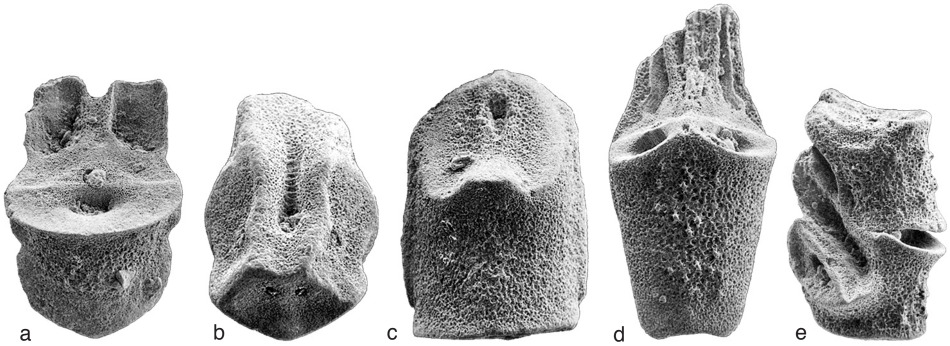

Fig. 23. *Axicrinus alexandri* Kristan-Tollmann, Carnian, Italy, Collection Kristan-Tollmann, Senckenberg Museum, Frankfurt, Germany; *a,* oblique aboral/distal view of radial, holotype, V 79, ×15; *b,* oblique adoral/proximal view of radial, ×15; *c,* aboral view of primibrachial 1, ×15; *d,* aboral view of primibrachial 2, ×15; *e,* lateral view of two secundibrachials with pinnule socket, ×20 (Kristan-Tollmann, 1977).

aboral ligaments, and the downward-concave wings of the widened funnel acted as paddles, pushing the cup upward. In this model, the animals floated mouth-up, a position supported by the biostratinomy. In common with living crinoids, *S. tenella* deployed a filtration fan, but food was not collected downstream by tube feet extended between the pinnules, but by active upward movement of the arms. In such upstream feeding, *Saccocoma tenella* may have differed from other, diminutive roveacrinids feeding downstream while sinking.

TRIASSIC ROVEACRINIDS

In the Somphocrinidae, the cup is composed of five radials that rest on a central piece, commonly prolonged aborally into a spinelike projection whose function is unclear. In the Axicrinidae (with the single species *Axicrinus alexandri* known only from isolated ossicles), the cup consists of five well-developed basals, radials, and brachials that lack processes or flanges (some had side branches). The form appears to have been stalkless (Fig. 23*a–e*). With its large basals and the absence of floating aids, the early Carnian *Axicrinus* appears to be the most primitive roveacrinid (Hess, 2002). The compact nature suggests that *Axicrinus* was essentially benthic, but the presence of articulations with strongly developed muscle fossae indicates that it may at times have been an active swimmer. Despite a wide stratigraphic gap, *Axicrinus* may be ancestral to the Late Jurassic *Crassicoma schattenbergi* with similar characteristics (Hess, 2002). Somphocrinids reached their greatest abundance during the Carnian and declined rapidly during the earliest Norian. Some species are known from the whole Tethys area, ranging from Mexico across Europe to China and Indonesia.

Triassic Somphocrinidae were first described by Peck (1948) from Mexico. *Somphocrinus mexicanus* has also been recorded from the Alpine region and from Timor (Kristan-Tollmann, 1988). The crinoids occur most abundantly in limestones and marls of the Upper Triassic (*Osteocrinus* facies, Carnian), which were deposited in shallow basins and on swells, but they are never preserved in reef settings (Kristan-Tollmann, 1970, 1977). *Osteocrinus rectus* occurs from the Middle Triassic (Anisian) to Upper Triassic (Rhaetian); it is widespread in the Tethys realm from the northern and southern Alps to Greece, Turkey, Iran, the Himalayas, southern China, and Timor. Because of their widespread occurrence and their value as guide fossils, Triassic somphocrinids have been compared to Upper Jurassic saccocomids.

CRETACEOUS ROVEACRINIDS

Roveacrinids occur in great profusion and with a variety of shapes in Cretaceous sediments. The rich material of Lower Cretaceous Roveacrinidae from Texas formed the basis of Peck's (1943) detailed description of these pelagic crinoids with highly ornamental cups. The cups may have vertical (*Plotocrinus*, *Roveacrinus*) or horizontal flanges (*Roveacrinus, Poecilocrinus*). Flanges also occur on brachials to facilitate floating (Scott, Tenery, & Nestell, 1977). Scott, Tenery, and Nestell (1977) were undecided as to whether *Poecilocrinus* was benthic or planktonic. By virtue of their morphology, they are considered herein to have been pelagic.

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