27

Uintacrinus Beds of the Upper Cretaceous Niobrara Formation, Kansas, USA

HANS HESS

A LARGE, SHALLOW INLAND SEA

During most of the Cretaceous, the western interior of the North American continent was covered by an epicontinental sea. During the Late Cretaceous, at the peak of the transgression, this shallow sea extended from the Rocky Mountains to close to the Mississippi Valley and from northwestern Canada into the Gulf of Mexico, flooding one-third of North America and covering an area of about 1,500 by 6,000 km (Fig. 224). The Western Interior Seaway was eventually filled with sediments from the rising western highlands, ancestors of the Rocky Mountains. From west to east, the sediments include non-marine lowland sands and silts, littoral marine sands and silts and offshore marine muds. The Cretaceous transgression reached western Kansas by the Late Cretaceous, about 85 million years before present. The sequence, with a total thickness of 450 m, starts here with deltaic sediments, represented by the sands and silts of the Dakota Formation. This interfingers laterally with the finer-grained Graneros Shale, deposited seaward of the delta. With continuing transgression, the eastern margin of the sea moved farther to the east. In western Kansas, shallow-water limestones began to accumulate, followed by laminated chalk (Lower and Upper Greenhorn Limestone). Partial regression of the sea is reflected in the deposition of the Carlile Shale; renewed transgression led to the deposition of the Niobrara Chalk, a fine-grained, rather pure limestone derived from shells, planktonic foraminifera and coccoliths. During this period, the bottom waters became stagnant at times, limiting life on the sea floor. In the lower part of the Niobrara Formation, an occasional increase in salinity led to the precipitation of gypsum. However, at other times, an abundant fauna existed. Finally, the Pierre Shale, a succession of muds resulting from erosion of lands far to the west and to the east, concludes the sequence with the final regression of the Cretaceous Interior Sea (Fig. 225).

THE PROVINCIAL FAUNA OF THE WESTERN INTERIOR SEAWAY

Because of the great distance from the open oceans, the shallow Western Interior Seaway lacked periodic interchange with the Cretaceous oceans of the world. Even at their best, marine assemblages had a low diversity, and many strata lack shelly invertebrates altogether, suggesting hostile conditions at the bottom. The fauna is usually dominated by a few species of planktonic foraminifera, crustaceans, swimming and bottom-dwelling cephalopods (*Baculites* and *Scaphites*) and huge, thin-shelled benthic inoceramid clams. Oyster beds (*Pseudoperna congesta*) are very common in places. Remains of marine vertebrates, such as fishes, reptiles and turtles,

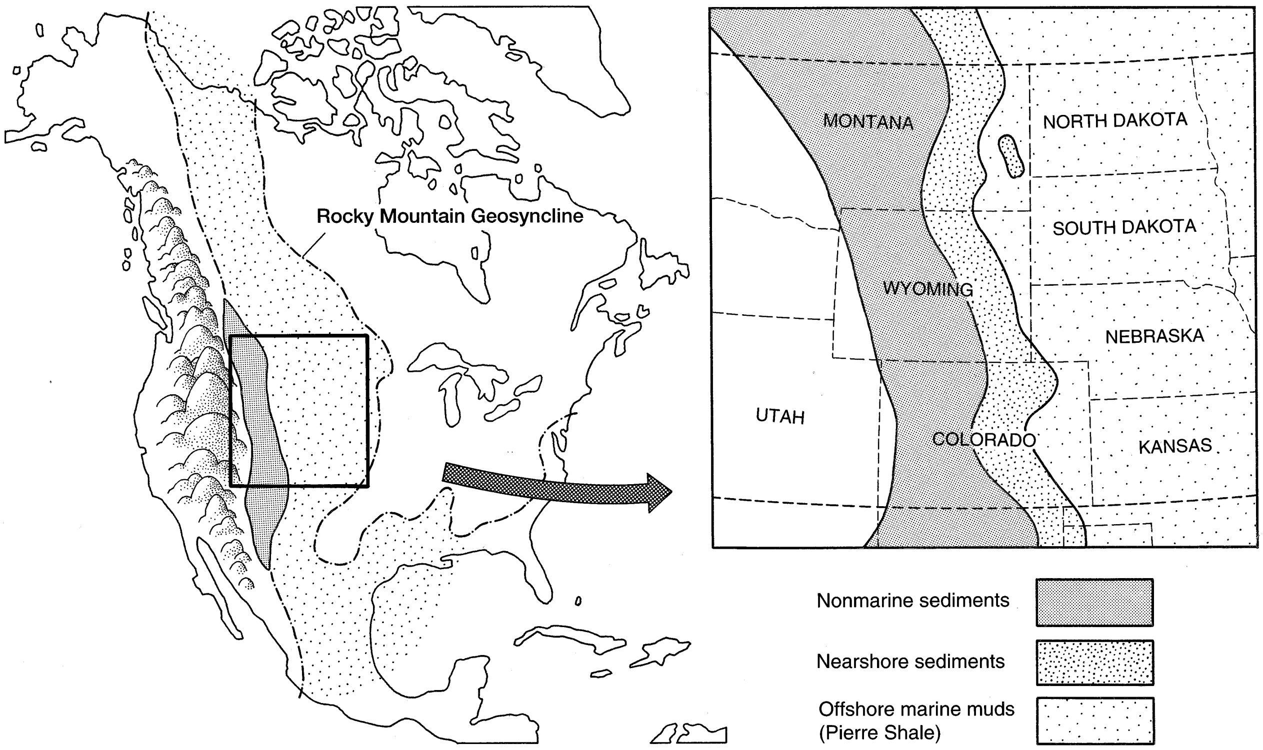

Fig. 224. Palaeogeography of the Western Interior in the Late Cretaceous. (Redrawn from Laporte 1968.)

weather out of the soft strata that lie exposed to summer heat and winter snows on the barren plains. *Uintacrinus*, but even more so reptiles and the diving bird *Hesperornis regalis*, have contributed to the fame of these sediments. The reptiles include the powerful mosasaurs, the long-necked plesiosaurs and the flying *Pteranodon*. Small and large fishes, as well as ammonites, provided the base for a substantial reptilian food chain. Some animals were of extraordinary size, such as the fishes *Portheus* and *Xiphactinus*, which reached lengths of more than 5 m. On land, emerging from the receding Late Cretaceous seas, an abundant fauna and flora developed, dominated by the widely publicized dinosaurs. However, remains of land animals and plants are rare in the Niobrara Chalk, and the same is true of stalked crinoids and echinoids.

THE LARGEST STEMLESS CRINOIDS

The first specimens of a large, stemless crinoid were discovered by Professor Marsh of dinosaur fame in 1870 in the Santonian of the Uinta Mountains, Utah – hence the name of this crinoid. Large slabs containing complete specimens were later collected from the Niobrara Chalk of western Kansas over a considerable geographic range. Well-known localities are near Martin and Elkader in Kansas, and in recent years complete specimens have been uncovered from the same strata in Colorado. Isolated ossicles have been recorded from the Santonian of England, France and Germany, as well as from Italy and even from Australia (Rasmussen 1961).

The Niobrara Chalk specimens are the best known and are exhibited in many museums. More or less complete individuals occur on the lower surface of thin lenticular limestone slabs that are interbedded with chalk. The localities near Elkader (Logan County, Kansas) furnished the large slabs so suitable for museum exhibits. As described by Springer (1901), several lenses were found within a radius of 10–15 km. At the most productive locality (Springer's No. 1), crinoidal remains formed a bed of about 15 by 6 m, with a thickness of 1.5 cm at the centre and thinning on all sides 'to the thinness of cardboard'. Springer stressed the fact that the crinoids could not be separated easily from the underlying chalk, so that in many cases only moulds of calyces were collected. The crinoids in this large colony were mostly adults with an uncrushed cup diameter of 2–5 cm. They are preserved in all positions, but most

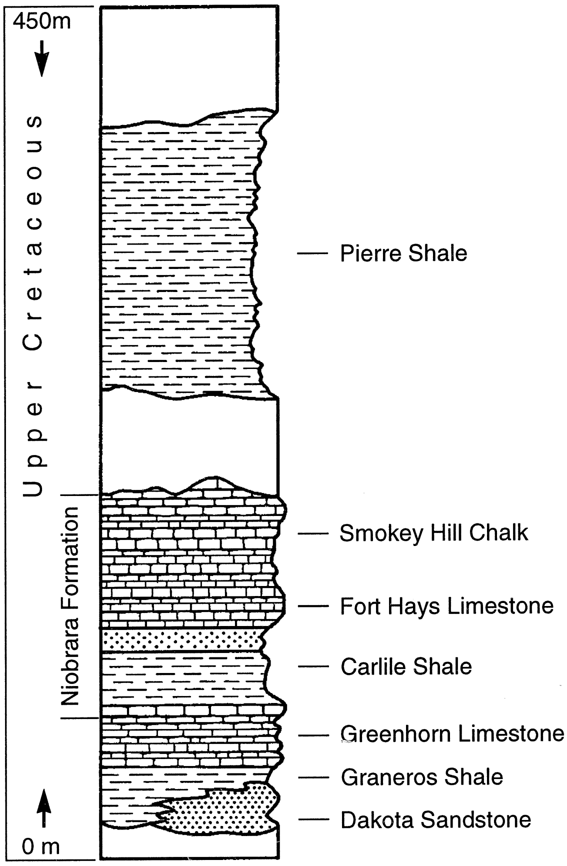

Fig. 225. Stratigraphy of the Upper Cretaceous in western Kansas. (Redrawn from Laporte 1968.)

are lying on their sides with the arms opened out. Many were embedded with the curvature of the cup downward, which presents an aboral view. In such cases the arms can rarely be observed because they penetrate into the slab and lie in another plane. Only a few animals were buried with their oral side down, showing the tegmen with the anal tube. A small colony (Springer's locality No. 2 and situated only about 800 m from locality 1), covering about 1.5 m^2, consisted of only very small crinoids. At another locality (Springer's No. 3, about 20 km from No. 1) the crinoids were preserved with arms closely folded together, resembling bundles of parallel rods. The lenses described by Springer from this area did not all belong to exactly the same stratigraphic horizon. The crinoids were never found as single, detached specimens, but were always more or less entangled with others (Figs. 226, 227). Densities of 25–50 animals per square metre were common. Quite generally, these crinoids are almost completely flattened, with only the cups standing out in some relief.

FLEXIBLE CALYX AND LONG ARMS WITH THIN BRACHIALS

The calyx of *Uintacrinus socialis* is globose and flexible. It may reach a diameter of 7.5 cm and is composed of numerous smooth, thin, closely fitting plates. The elements making up the calyx belong to three categories (Bather 1896): (1) the base with a central piece, five infrabasals, five interradial basals and five radials; (2) the fixed brachial elements with two primibrachials (the second one axillary) and about eight secundibrachials, which become gradually modified from the flat ossicles to the low, free brachials; and (3) the supplementary, interbrachial interradial plates. In adult individuals, up to four pairs of pinnules are fixed into the calyx. The transition from the plates of the calyx to those of the arms is gradual. The large body size, obviously connected to the lifestyle of this crinoid, is thus the result of the incorporation of many brachials, the proximal pinnules and a number of interradials into the calyx (Fig. 24).

The mouth lies close to one of the margins, and a large, conical anal tube is located in the centre of the tegmen (Fig. 228). The tegmen is commonly preserved as a jet-black, carbonized membrane with small, irregular granules. The ambulacral grooves are not covered by any plates. There is no trace of an attachment structure such as stem, cirri or holdfast. The 10 arms, resulting from a single division at the second primibrachials, may reach a length of 125 cm (Fig. 229). Springer (1901, p. 15) mentioned an individual with a cup width of 6.2 cm and an incomplete arm of 100 cm. Muscular articulations alternate with scattered syzygial articulations. In adult individuals, the syzygies occur at regular intervals of three to six brachials and, more distally, the intervals become much more irregular and commonly longer. The syzygies with their prominent ridges resemble those of comatulids. In spite of the rather large number of syzygies, broken or regenerated arms are quite exceptional. The brachials are thin or low; their height near the calyx is about 1.5 mm in large specimens, with a width of 8 mm. Distally the height is nearly the same and the width diminishes to 1.5 mm. The oral muscular fossae on brachials are rather small. The pinnules, which reach a length of 20 mm near the cup, alternate from one side to the other, leading to a wedge-shaped appearance of the brachials, especially the fixed and more distal brachials. Distally the pinnules become extremely fine, almost thread-like. The low and, therefore, very numerous brachials with pinnules constitute a very dense food-

Fig. 226. Large slab of *Uintacrinus socialis*. Niobrara Chalk, Elkader (Logan County), Kansas. As judged from its preservation, this slab comes from Springer's original locality; it shows the lower surface and is exhibited in the Museum für Geologie und Paläontologie, University of Tübingen. (Photograph W. Gerber; courtesy H. P. Luterbacher.) ×0.3.

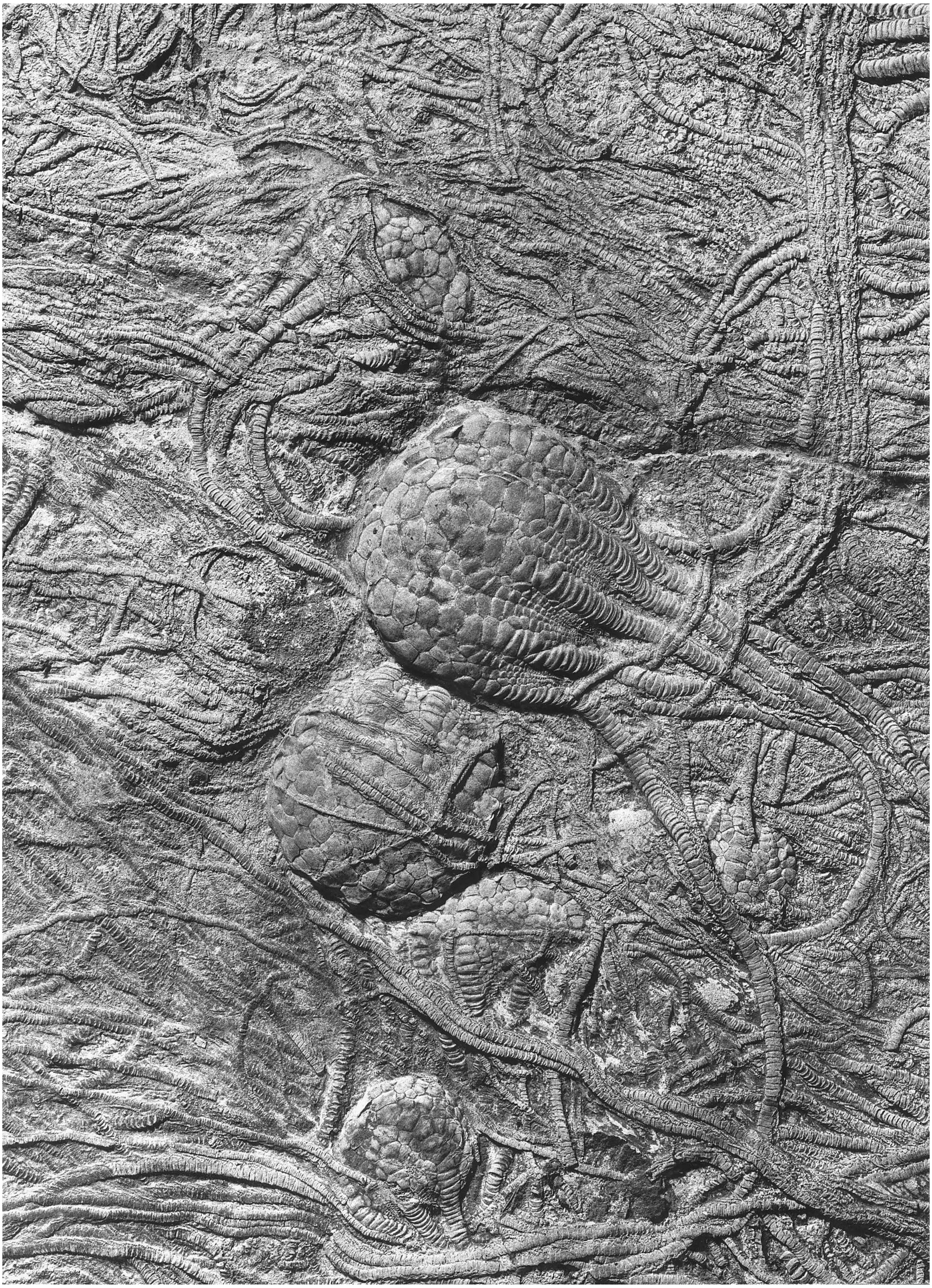

Fig. 227. Detail from the slab of Fig. 226. ×1.

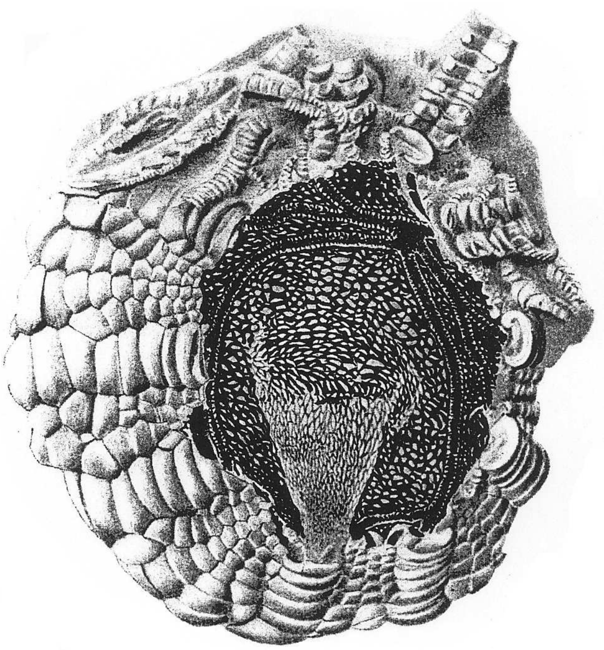

Fig. 228. Close-up of a specimen of *Uintacrinus socialis* with tegmen (note eccentric mouth with food grooves) and central anal cone. Niobrara Chalk, Elkader (Logan County), Kansas. (From Springer 1901.) ×2.

collecting apparatus. The muscular articulations suggest that *Uintacrinus* could move its arms actively to collect food and possibly also to disentangle them from neighboring animals.

UINTACRINUS: A PELAGIC CRINOID?

Most authors dealing with this peculiar crinoid have described it as having floated. Springer (1901) explained the excellent preservation of the fossils by 'the presence of the soft, muddy bottom of a quiet Mediterranean sea, or lagoon. Those crinoids that were at the time at the lowest part of the floating mass rested directly upon the soft mud, and settled into it, in the position in which they happened to be. . . . The others piled on top of them, and not having any such soft or plastic bed to receive and preserve them, were crushed out of shape, disarticulated, and their cup plates and brachials were indiscriminately mixed up.' Bather (1896, Pl. 55) figured *Uintacrinus socialis* 'as swimming, five alternate arms raised, and five in the act of depression.' Abel (1927) assumed that *Uintacrinus socialis* had a pelagic lifestyle on the high seas and was swept into the shallow Niobrara Sea, becoming stranded near the shore. In view of the excellent preservation of the Niobrara specimens, Kirk (1911) suggested that the large swarms of *Uintacrinus* aggregated in the shallow waters near the shore for spawning. Hyman (1955) thought that these crinoids 'lived in floating swarms, in which the long arms were inextricably intermingled'; she illustrated a specimen with the cup uppermost, the long arms hanging down.

As discussed by Struve (1957), a few authors assumed that *Uintacrinus* lived on the bottom, and one even considered that this crinoid could creep starfish-like along the bottom, oral face downward. Others thought it could have used its arms for locomotion, similar to today's comatulids (Milsom *et al.*, 1994). Struve favoured a life on the firm bottom for *Uintacrinus*. He rejected a life in dense colonies and burial at the place of living. He thought that each animal must have occupied a space corresponding to its diameter with outstretched arms, that is, 2 m across. For Jaekel (1918) the skeleton was too heavy for a free-swimming lifestyle, and he considered that the animals lived in groups on the bottom, with outstretched arms.

It is interesting to compare here the two supposedly pelagic crinoids, *Uintacrinus* and *Saccocoma* (see Chapter 26). Both crinoids have a wide geographic distribution, which supports the notion of a pelagic life for these animals. *Uintacrinus socialis*, with its exceedingly long arms, is very different from the tiny *Saccocoma*. The very long, pinnulate and flexible arms of *Uintacrinus*, with their muscular and syzygial articulations, are not very different from those of benthic crinoids, and contrast with the highly specialized and branched arms of *Saccocoma*. The conspicuous, central anal cone and the eccentric mouth are reminiscent of modern comatulids, such as *Comatula*, a fact already recognized by Springer. One gets the impression that the large *Uintacrinus* could have had a pelagic lifestyle only by virtue of a buoyant calyx with entrapped gas. Breimer and Lane (1978) have suggested that *Uintacrinus* might have modified the body cavity by developing special oil or gas compartments in its expanded, thin-walled calyx, but such structures have not been found. In the case of a pelagic, floating lifestyle, the buoyant calyx would have been uppermost, with the arms more or less hanging down (as figured by Hyman and contrary to the restoration of Bather), similar to a jellyfish, but unique for a crinoid.

Following this reconstruction one would expect stranded communities to have touched the bottom with their arms first, followed by the calyx. This view is not supported by the position of the fossils, with the calyx normally standing out in some relief from the lower surface of the slabs. The arms usually lie sideways and extend into the slabs. Milsom *et al.* (1994) proposed that *Uintacrinus* lay on the sea floor with the calyx embedded in the sediment. In their reconstruction, the proximal sections of the arms were on the sediment surface, stabilizing the crinoid, and the distal ends curved upward to form a feeding bowl. This view is not supported by the high density and the taphonomy of these crinoids with their arms stretched out to one side (Fig. 226). Moreover, a collecting bowl as proposed by these authors would appear to have been of limited use in the soupy substrate, which would also have been unsuitable for moving across the bottom. In our view, *Uintacrinus socialis* lived gregariously on the soft bottom and was buried in life position; its colonies may have resembled dense patches of tall eel grass.

Undoubtedly, the bulbous, hollow calyx prevented *Uintacrinus* from sinking into the soupy ground of the chalk, at the same time anchoring the animal. As pointed out by Jablonski and Bottjer (1983), the inoceramids, dominant clams of the Niobrara Chalk, adopted two strategies for living on the soupy substrate. The huge, flattened, thin-shelled *Inoceramus (Platyceramus) platinus* (reaching the incredible length of 2 m) floated snowshoe-like on the soft muds; and *Volviceramus grandis* (reaching 30 cm in size) and similar forms chose an iceberg strategy, with their highly inflated bowl-shaped left valve buried in the bottom and their flattened right valve exposed. *Uintacrinus*, with its large, bowl-shaped calyx, was well suited to an iceberg strategy. It is true that inoceramids and *Uintacrinus* do not occur together, but the large size and numbers of the inoceramids and of *Uintacrinus* indicate excellent conditions for benthic animals that could adapt to the muddy chalk. The rich supply of nannoplankton in the water and making up the chalk helped *Uintacrinus* to reach such a large size. Current-oriented specimens are uncommon, indicating weak currents before burial. Death may have been caused by events similar to those that killed other dense colonies, discussed in Chapter 25 (planktonic blooms, with corresponding poisoning, even though there are no indications of anoxic conditions in the *Uintacrinus* beds; perhaps also a sharply increased rate of sedimentation, leading to suffocation). The example of the Jurassic co-

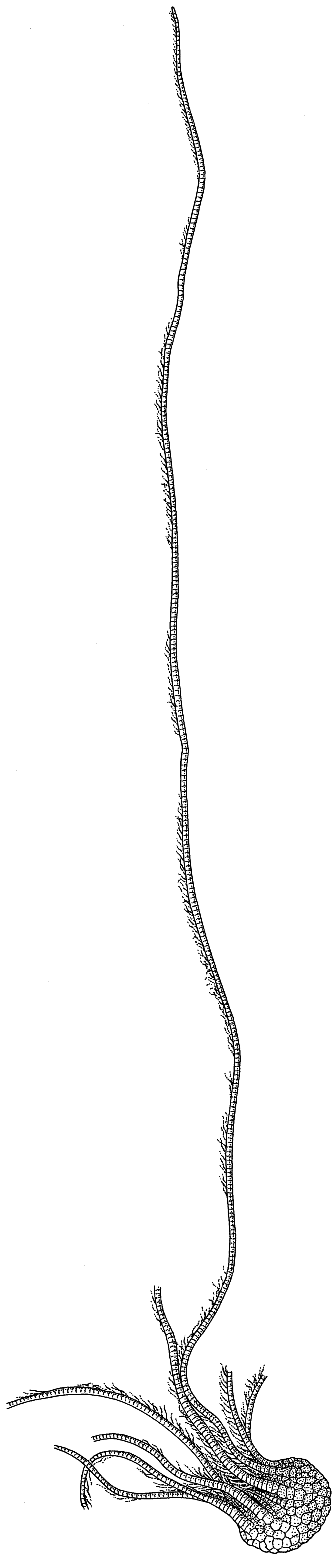

Fig. 229. Arm length of *Uintacrinus socialis* in relation to cup size. (Redrawn from Springer 1901.) ×0.2.

matulid *Paracomatula helvetica* (see Chapter 25) demonstrates that unattached forms could easily have formed very dense aggregations. This gregarious form also has unusually long arms, and the position of the individuals (which lie mostly on their sides) is comparable to the present one.

The related *Marsupites testudinarius* from the English Chalk has a cup of similar size, but with fewer and larger plates, the arms being shorter. This species of worldwide distribution (Sieverts 1927) has also been assumed to be probably pelagic (Breimer & Lane 1978), but we consider it a benthic form, too, populating soft bottoms. As pointed out by Milsom *et al.* (1994), who came to the same conclusion, the widespread distribution of *Marsupites* and *Uintacrinus* may reflect a planktonic juvenile stage of unusual duration among crinoids.

IMPORTANT COLLECTIONS IN THE UNITED STATES

Museums with Slabs on Display

Denver Museum of Natural History, Denver, Colorado
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
Kansas Museum of Natural History, Lawrence
Sternberg Museum at Ft. Hayes State Museum, Hayes, Kansas
Fick Fossil Museum, Oakley, Kansas

Significant Collections

National Museum of Natural History, Smithsonian Institution, Washington, D.C.
Yale Peabody Museum, New Haven, Connecticut