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Scyphocrinitids from the Silurian–Devonian Boundary of Morocco

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SEA LILIES IN THE DESERT

Slabs with beautifully preserved scyphocrinitids from the Sahara region regularly appear at mineral and fossil fairs; most of these fossils are labelled, 'Erfoud'. Very little work has been undertaken on the detailed stratigraphy of the scyphocrinitid beds of Morocco; hence, the information provided in this chapter is limited. One would hope that future work will increase our knowledge of these remarkable occurrences.

The western Sahara (Fig. 108) underwent several marine transgressions during the Palaeozoic. The extended Silurian transgression started during mid-Llandovery times with the deposition of graptolitic shales. Subsidence increased, so that the thickest part of the succession accumulated during Ludlow times. At the southern edge of the Anti-Atlas in the Dra Plain, in the Tafilalt area near Erfoud and in the Ougarta chains of western Algeria, the Silurian is composed largely of black, sometimes bituminous shales with graptolites. These shales weather on the surface to brighter colours. In the Pridolian part of the series (uppermost Silurian, about 410 million years before present) they contain bands of blue, fossiliferous limestones with *Scyphocrinites*, orthocone nautiloids ('*Orthoceras*'), bivalves (*Cardiola*) and gastropods. Upper Silurian to Lower Devonian argillaceous shales or laminated clays with limestone intercalations or lenses containing scyphocrinitids and orthocone nautiloids are in fact found in a wide area, from the coast near Casablanca and Rabat, across the High Atlas, to the Dra Plain, the Tafilalt, and the Ougarta chains of western Algeria. The limestones commonly occur as nodular concretions in large cushion-like masses that are interbedded in the shales. They appear to be the result of diagenetic accumulations of calcium carbonate by migration of material towards a suitable nucleus in a fairly homogeneous calcareous clay; the beds with calcareous nodules thus represent extremely slow deposition (Destombes *et al.* 1985). The thickness of the Silurian succession decreases from a maximum of 1,500 m in the west to 100–300 m in the Erfoud area (but reaches 500 m in the Ougarta, where strong subsidence occurred). The Silurian is followed without a break by Devonian sediments, mainly shales, which reach a thickness of 5,000 m in southern Morocco.

MINING FOR COLLECTIONS

The following information on the main crinoid site east of Haroum, about 15 km southeast of Erfoud, has been gathered from visitors to the extensive mining operations, performed by local workers who make their living selling fossils (Fig. 109). The horizons that have yielded most of the specimens are made up of a series of lenses of crinoidal limestone that strike northeast–southwest for several kilometres in a barren plane; this plane is fringed by low hills and crossed by mostly dry river beds (called oueds). The sequence is as follows, from bottom to top (B. Imhof, pers. comm., 1993): (1) '*Orthoceras*' limestones that crop out to the north, forming a low ridge; (2) 30 m of mudstone; (3) 10-cm-thick scyphocrinitid bed; (4) 1 m of mudstone with interbedded '*Orthoceras*' limestone; (5) main scyphocrinitid bed; (6) 0.6-m-thick layer of mudstone; (7) '*Orthoceras*' limestone. The scyphocrinitid lenses of the main bed can be located at the soil surface by the occurrence of disarticulated crinoids. In such places the crinoidal limestone, which has a dip of 30–50°S (as the southern part of an eroded anticline), is excavated to considerable depth. When excavations began in the early 1980s, the lenses were close to the surface; in order to reach them now, at 4–5 m below the surface, pits are dug manually. The lenses have a diameter of 0.5–3 m; most have a thickness of about 10 cm in the centre, but some may reach a thickness of 15 or even 20 cm. Intact crowns with attached stems occur on lower bedding planes, whereas the interior and the upper surface contain mainly stem fragments and ossicles. A layer of soft marl covers the fossils. Other fossils, including shells of orthocone nautiloids, small brachiopods, gastropods and bivalves, are also present in lesser abundance. Certain parts of the beds may contain only poorly preserved or recrystallized specimens. Intact plate loboliths (Fig. 21; see the section titled 'Remarkable New Discoveries' for an explanation of lobolith type) occur about 20 km to the east in lenses or fields with a diameter of up to 50 m. Newly discovered beds 80 km to the southwest have loboliths still attached to stems and accompanied by crowns (Fig. 110).

THE ERFOUD SLABS

The largest Erfoud slab or lens on exhibit in a museum, presumably from the horizon with the lenses mentioned earlier, measures about 2 m^2 and contains 75 crowns and stems of *Scyphocrinites* sp.; it can be admired in the museum of the University of Göttingen. This remarkable specimen has been described by Haude *et al.* (1994). As already mentioned, the crowns and attached stems are preserved on the lower surface of a crinoidal limestone. On the surface, a few lobolith fragments of the cirrus type are visible, but no distal part of any of the stems with an attached lobolith is preserved. The stems are mostly bundled together and oriented with the crowns pointing in the same direction. From this preservation, Haude *et al.* (1994) assumed that the crinoid stems, with their length of several metres, were entangled before being embedded. The crinoids are all of similar size. They came to rest on their sides, with the

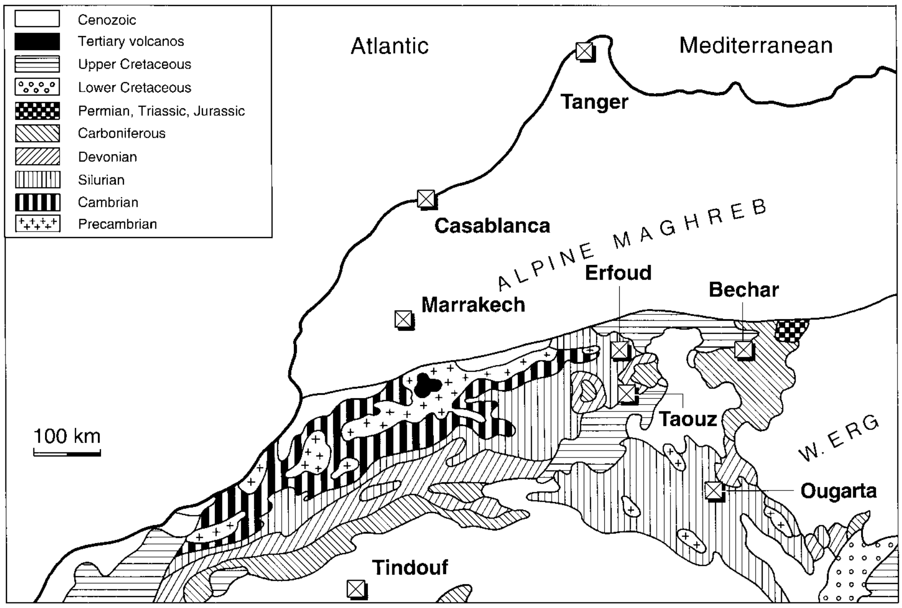

Fig. 108. Geological map of the Anti-Atlas area in southern Morocco and western Algeria. Strata north of the line separating the Anti-Atlas and Sahara regions from the Alpine Maghreb (High Atlas and Rif zones to the north) are omitted. (After Trümpy 1957.)

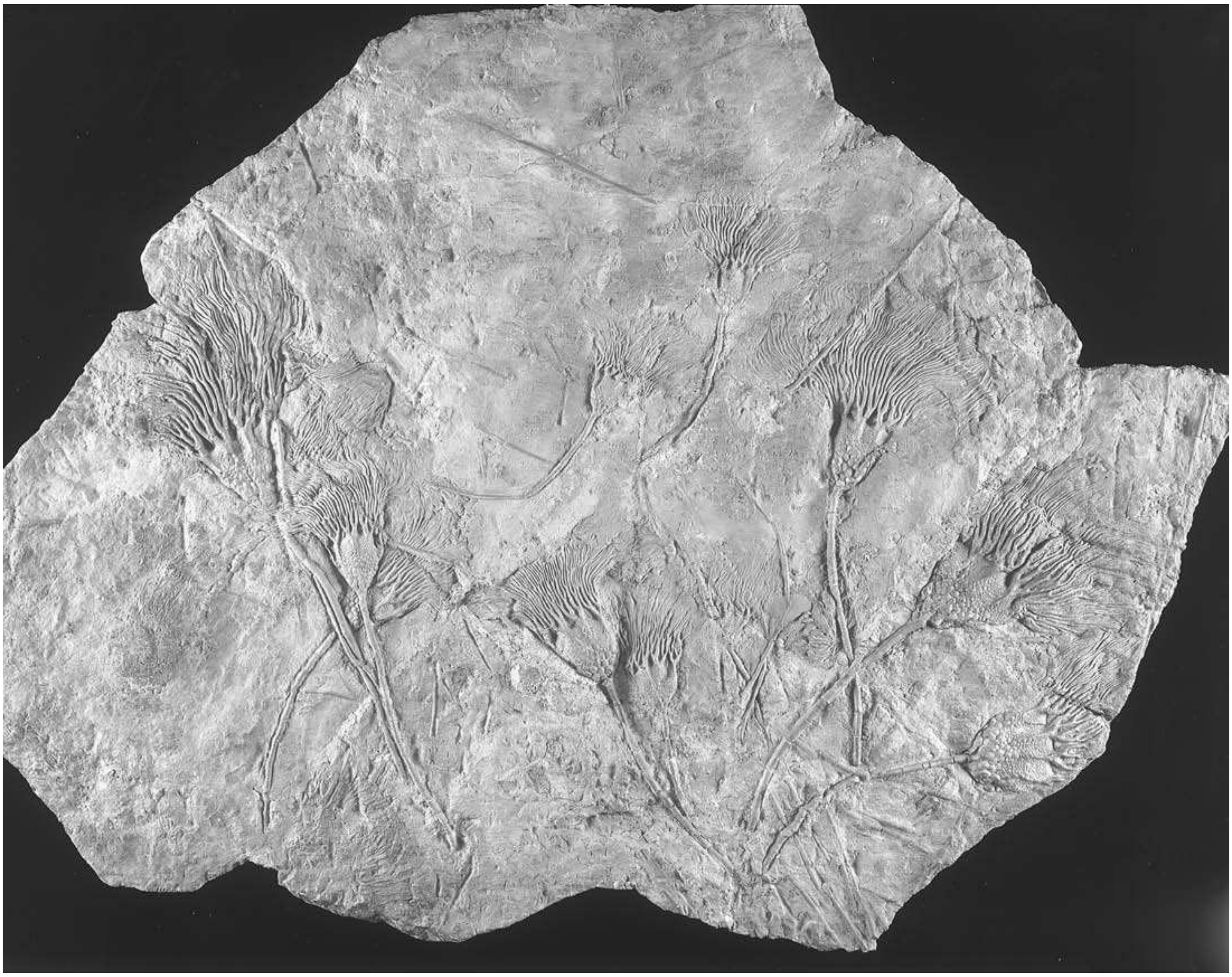

Fig. 109. Lower surface of a slab with *Scyphocrinites* sp. in natural colour. Upper Silurian, from an excavation east of Haroum near wadi of Oued Ziz. (Natural History Museum, Basel; photograph S. Dahint.) ×0.15. To view this figure in colour, see the colour plate section following page xv.

exception of three stemless crowns, which were embedded with the oral side downward and the arms splayed out, so that the aboral side of the calyx disappears in the bed. Similar preservation is shown by some of the 44 crowns on the large slab of the Naturmuseum Senckenberg (Plodowski 1996).

A slab with a surface of approximately 1 m^2 was donated to the Basel Natural History Museum (Fig. 109). It contains 21 complete crowns of different sizes. The largest individuals have a crown height of 25 cm and a proximal stem diameter of 0.7 cm. Five juvenile specimens have crown heights of between 1 and 4.5 cm and a stem diameter of 0.1 cm. Two of the juvenile stems reach a length of 1.2 cm, without being complete. All individuals lie on their side and are to some extent oriented as on the Göttingen slab. The stems are invariably broken. Broken and flattened remains of cirrus loboliths are also preserved on this slab.

REMARKABLE NEW DISCOVERIES: INTACT CROWNS AND STEMS WITH LOBOLITHS

Recently, new excavations have been made by local workers in the Jissoumour area between Tazoulet and Alnif, approximately 80 km southwest of Erfoud, at the

Fig. 110. Lower surface of a slab with mostly juvenile scyphocrinitids and loboliths of corresponding size. Several loboliths (L) (the largest one sideways) are on the bedding plane. The structure of the loboliths, including a wall composed of two layers (see Fig. 21), indicates that they belong to the plate type. Arrows point to the terminal distal stem with radicular cirri and stump. Primary roots disappear here and merge into bulbs (best visible at lower left and right, respectively); attached loboliths are crushed. A platyceratid snail is also exposed. The smallest loboliths (not figured) on the surface of the lens have a diameter of only 5 mm. On the basis of the type of lobolith and slightly elliptical cross section of stem in the median part, the specimens from this locality appear to belong to *Marhoumacrinus legrandi*. However, some characters of calyx and arms (a more or less pronounced biserial arrangement of tertibrachials is restricted to juvenile specimens at this location) make such an assignment doubtful. Silurian–Devonian boundary, Jissoumour area between Alnif and Tazoulait. (Natural History Museum, Basel; photograph S. Dahint.) ×0.85.

foot of hills rich in Devonian horned and giant trilobites. The beds are lenses with a maximum thickness of 15–20 cm. Some of them carry large crowns on the lower surface; locally they are packed with loboliths of the plate type reaching a diameter of 10 cm. Smaller, more or less intact loboliths occur on the lower surface of other lenses, where they are accompanied by complete crowns, many of them juvenile (Fig. 110). This is apparently the first report of loboliths still attached to the stem. A few of the smaller specimens have strongly sculptured calyx plates and a heteromorphic proximal stem, with nodals and internodals, a unique feature of scyphocrinitids (Fig. 111). The reason for this aberrant morphology is not known. The exact age of the bed has not been determined yet, but the trilobite faunas in the following strata are Early Devonian.

WIDE DISTRIBUTION OF SCYPHOCRINITIDS

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 American material that he assigned to the Bohemian species. According to Prokop and Petr (1986), *S. elegans* is limited 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) proposed for the Algerian scyphocrinitids (Upper Silurian to Lower Devonian) a new genus and species, *Marhoumacrinus legrandi*. The Erfoud specimens (Fig. 109) are assigned here to *Scyphocrinites* on the basis of the type of lobolith (see the next section).

The material described by Springer (1917) presumably from Lower Devonian strata, and now in the National Museum of Natural History, was excavated from the bluffs of the Mississippi River, near Cape Girardeau, Missouri. This occurrence is worth mentioning because it established for the first time the connection between well-preserved scyphocrinitids and their bulbous roots. At this locality, the crinoids occur 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 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'. The main slab, 120 by 160 cm, contains 24 crowns, several with more or less broken stems, as well as a few flattened or fractured bulbs (loboliths, *Camarocrinus*; see the next section). The bulbs are free of stems, 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.' The bulbs were on the lower side of the layer, showing their rounded, non-stalked ends; 'hence they stood with the stalked end uppermost, as they naturally would if growing in or resting upon the soft bottom.' Springer did not find a single case in which the stem was still connected to the bulbous end.

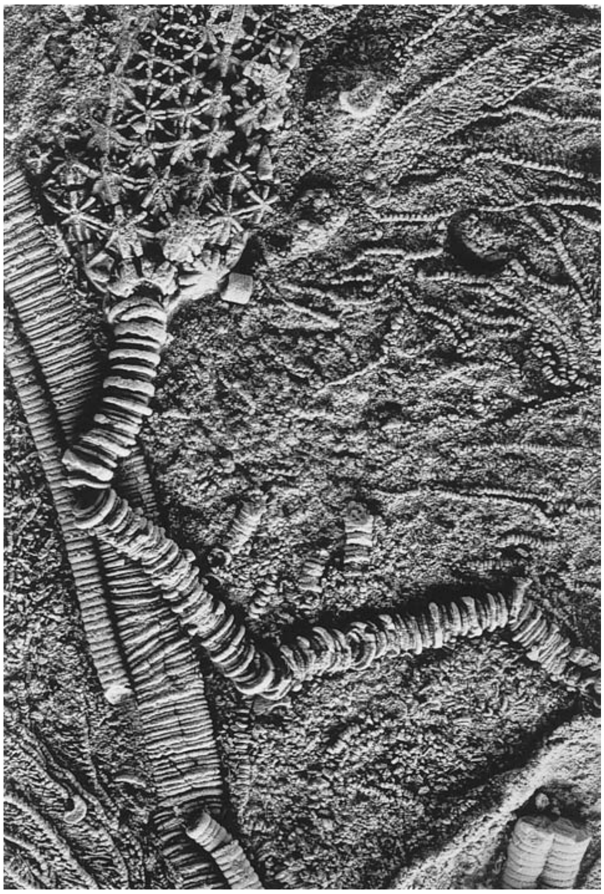

Fig. 111. Small scyphocrinitid with heteromorphic stem and strongly sculptured calyx. Lower bedding plane of a thin lens. Note part of the wall of a plate lobolith at lower right. Silurian–Devonian boundary, Jissoumour area between Alnif and Tazoulait. (Hess Collection; photograph S. Dahint.) ×2.

SOLUTION TO THE LOBOLITH ENIGMA: KEY TO THE LIFESTYLE OF SCYPHOCRINITIDS

In adult individuals, the column ends distally in a large, bulbous, chambered organ, which reaches a diameter of 20 cm. These bulbs were described, from U.S. material, by Hall in 1869 as *Camarocrinus*. Around the same time, Barrande (working on material from Bohemia) called them *Lobolithus*. Originally they were of unknown affinity. These curious, bladder-like structures were definitely associated with the camerate *Scyphocrinites* by both Jaekel and Bather around the turn of the century when the idea of their function as buoys was first proposed. According to Bather (1907), 'It is . . . believed by many that this swelling was hollow and served as a float from which the crinoid hung, arms downward. 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; following death, the gradual decay of the animal would cause the crown to drop off and sink to the bottom, while the lobolith floated on.' Schuchert (1904) derived his opinion that *Camarocrinus* served as the float of an 'unknown crinoid' from the fact that at that time loboliths in the United States had never been found associated with crinoids, and scyphocrinitids were unknown from U.S. strata. The discovery of well-preserved *Scyphocrinites* in the Bailey Formation at Cape Girardeau, Missouri, on which Springer's monograph (1917) was based, disproved Schuchert's notion that 'the great majority of the bulbs are found in strata with the stalked end downward.' As already discussed, the bulbs were embedded in the mud with the stalked end directed upward, into the bed.

Haude (1972, 1992) reanalyzed the loboliths. He recognized two types – orange-shaped cirrus loboliths with numerous chambers of unequal size, and lobed plate loboliths with a few large chambers, a curved, bilaterally symmetric root trunk, a simplified wall structure and a characteristic collar (Fig. 21). Both types are cosmopolitan. According to Haude, plate loboliths evolved from Silurian cirrus loboliths at the 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 (R. J. Prokop, pers. comm., 1995) suggests that lobolith evolution may have been more complex. Mainly on morphological grounds, Haude followed and strengthened the conclusion of Schuchert and Bather that the loboliths must have served as buoys. In spite of the excellent preservation of the Erfoud scyphocrinitids, stems with attached loboliths have been found only at one locality so far.

The Bohemian *Scyphocrinites elegans* of Upper Pridolian and Lower Devonian age appears to be associated with cirrus loboliths only. Prokop and Petr (1987) reported plate loboliths from the Tafilalt (Erfoud) area and such loboliths are also on the Jissoumour slab (Fig. 110). However, according to Haude *et al.* (1994), the loboliths on the Göttingen slab from Erfoud are of the cirrus type, and this is also true of those on the Haroum slab (Fig. 109). A cirrus lobolith starts from primary roots at the end of the stem; these divide repeatedly into ever finer branches to form innumerable elements (spicules) that build up the walls of the inner chambers as well as the outer covering wall. The stronger outer and the thinner inner layers, which are composed of small spicules, are supported by a middle layer with larger elements. Crystallized calcite may fill the smaller, peripheral chambers (also in loboliths from Erfoud), suggesting that these chambers were sealed. Larger chambers around the base of the stem were probably open, as shown by infilled sediment (Haude 1992). Haude 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 then swelled into soap-bubble-like chambers (with the possibility of floating) and eventually into the large diving-bell-like chambers of the plated loboliths. As noted later, this sequence, starting from a rooted crinoid and ending as a planktonic one, is purely conjectural. The generation of gas to fill the bulb has so far not been explained in a satisfactory way and the issue of whether it actually occurred appears unresolvable at present. Haude (1972) assumed that gas accumulated from the surrounding water by diffusional process, as in floating algae, but failed to define the driving force. It may be speculated that the openings at the root bifurcations inside the projecting collar (see Fig. 21) served for gas exchange – for example, to relieve pressure in the case of overproduction of gas or its expansion due to temperature changes. How the smaller, presumably sealed chambers of the cirrus loboliths became filled with gas from the outside is an enigma, unless one assumes that gas formed from symbiotic cells growing in the chambers, one of many possibilities in the absence of evidence.

It appears that the stems were easily broken off near the bulbs, leaving plate loboliths with a typical stump that may be surrounded by a collar (Fig. 21). The occurrence of small encrusting roots, attached to mature bulbs (Springer 1917, Figs. 7–10; Haude 1992, Fig. 3), shows that larvae settled on mature bulbs so that juvenile individuals were anchored by branching roots, as in other crinoids. Aggregative larval attachment is very characteristic of abundant solitary animals (such as mussels), and loboliths must have presented a suitable environment for juveniles to grow. Larvae settling on loboliths may have started the aggregation of large numbers so typical of these crinoids, which include – on the Erfoud slabs – individuals of all age-classes. In Bohemian plate loboliths, 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 (R. J. Prokop & V. Petr, in prep.; see also Haude 1992). 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. On the other hand, a small lobolith, with a diameter of only 5 mm, occurs on the slab of Fig. 110. For Haude (1992), the small rooted scyphocrinitids may represent sexual dimorphs, but this would be unique among crinoids. In any case, the formation and development of loboliths offer a fascinating area for future research.

LONG STEM AND LARGE CROWN WITH PAVED CALYX

Scyphocrinitids are large crinoids. Stems that may have reached 3 m in adult individuals supported a calyx 10 cm high and arms more than 30 cm long. The primibrachials and secundibrachials, as well as their pinnules, are all fixed in the calyx, forming a network of similar plates through surface sculpturing; the arms become free above some tertibrachials (Fig. 112). There are up to four more bifurcations above the tertibrachials; and because the free brachials are all very low, with a biserial tendency, the effective food-gathering surface of this magnificent crinoid was very large indeed. The multi-plated tegmen and the distinct anal tube are usually not visible in the Moroccan specimens, but occasionally platyceratid snails are attached to the tegmen (Fig. 110). The proximal stem is cylindrical, composed of extremely low columnals and thus very flexible. It tapers gradually from the cup until its diameter is reduced to about half at the distal end; through this length, the columnals gradually increase in height. The axial canal is obtusely pentagonal in the proximal and middle part of the stem, where it becomes very large. It diminishes to a sharply stellate opening distally. Although several scyphocrinitid species and genera have been distinguished in the literature, the clear morphological similarities between them indicate that these amazing crinoids had very similar lifestyles.

SCYPHOCRINITIDS: THE ONLY TRULY PELAGIC SEA LILIES?

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 meagre sedimentation. This basin was open to the north and northeast and probably also to the southwest (Destombes *et al.* 1985). 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 planktonic lifestyle. The similarity between the long-stemmed scyphocrinitids with their well-developed arms (branching isotomously in scyphocrinitids) and the pseudoplanktonic Lower Jurassic *Seirocrinus* with similarly developed crowns and even longer stems is another point in favor of a floating lifestyle. Both crinoids appear to have grown rapidly to a large size, suggesting an ample supply of nutrients and a lack of other filter feeders in the oxygenated zone above the black shale environment. The presence of long stems indicates that the chances of food collection increased with depth, as in today's oceans, where plankton-rich zones are well below the surface. The fan or funnel formed by the crown possibly captured plankton moving to or from the surface. The huge number and wide occurrence of these crinoids suggest that efficient predators were lacking.

The planktonic lifestyle of scyphocrinitids was made possible by the development of the extraordinary gas-filled bulbs. The animals appear to have formed dense mats, presumably as a consequence of the preference of larvae for settling on adults. In the case of damage to some of the bulbs in such a colony or after water penetrated into the chambers in stormy weather, the gas would escape and the mat would sink to the bottom, perhaps like the great mats of sea grass found on the deep sea bottom in today's oceans. As a rule, the waterlogged bulbs became detached from the stem, breaking off at the weakest point close to the collar (where stem

Fig. 112 Scyphocrinitid, Upper Silurian, Erfoud (exact locality unknown). Specimen with calyx and arm structure well exposed by arid weathering. (Hess Collection; photograph S. Dahint.) ×1.

diameter is reduced). The bulbs eventually sank to the bottom with their collar upward, like short-necked, water-filled bottles. Haude *et al.* (1994) concluded that the isolated crowns observed on some of the Erfoud slabs reached the bottom first, oral side downward. They were followed by the group of more intact crinoids with entangled stems, which had sunk in a horizontal position, and then by more broken stems. According to this view, differences in transport by currents led to the deposition of crowns with attached stems in one place, whereas the loboliths usually accumulated elsewhere, sometimes in huge numbers. Preservation of the scyphocrinitids – articulated crowns with stems on the lower side, disarticulated ossicles and some stem fragments on the top surface – suggests that burial occurred some time after death.

The hypothesis of a planktonic lifestyle for scyphocrinitids (Fig. 113) is consistent with the morphological

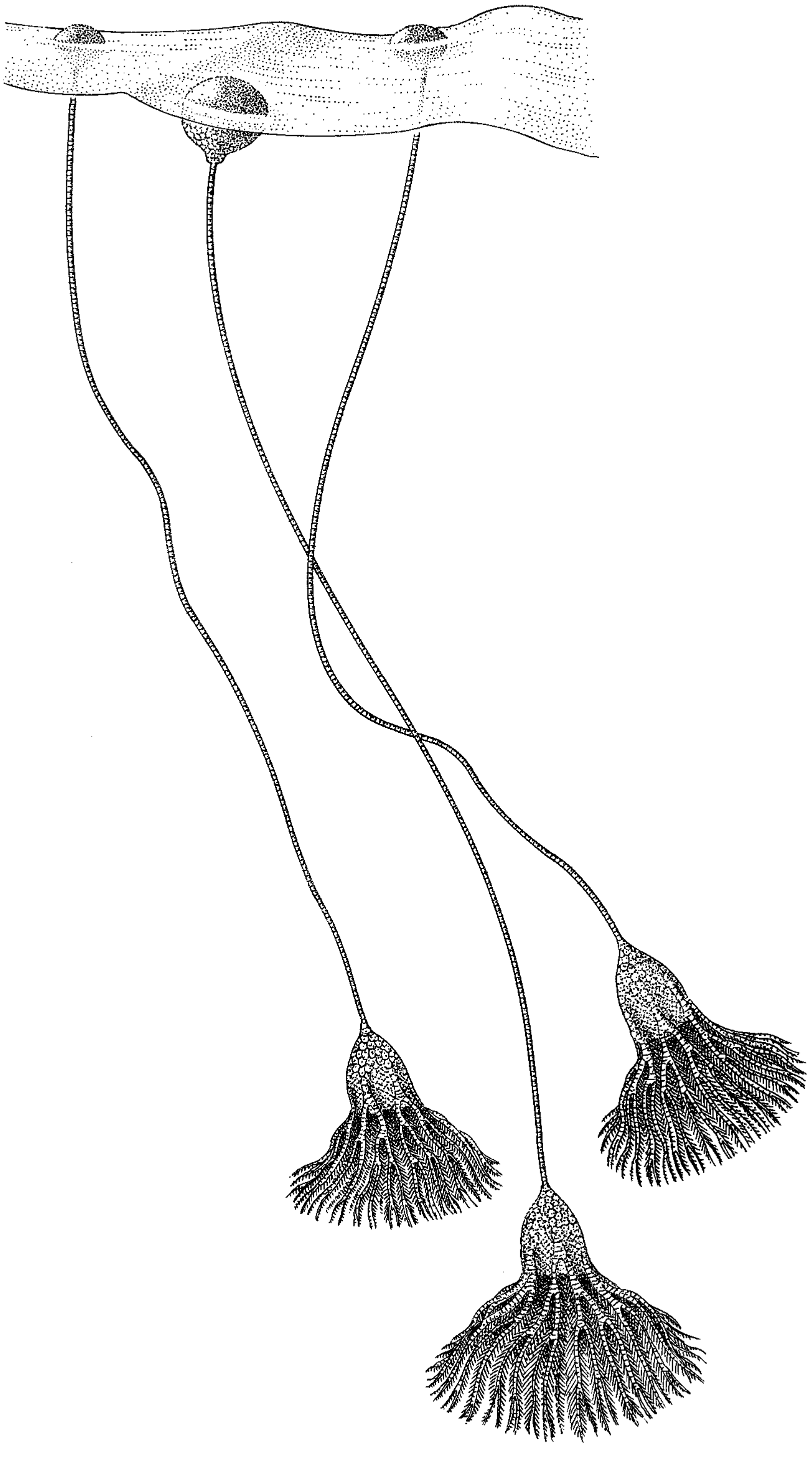

Fig. 113. Reconstruction of scyphocrinitids as pelagic, floating sea lilies. (After Haude *et al.* 1994.)

characteristics of the chambered bulbs, with their presumed buoyancy, as well as with their distribution, including the separate occurrence of crowns with broken stems and loboliths. Because it offers the most plausible explanation, it is widely accepted. The occurrence, at Haroum, of a large number of discrete lenses at the same stratigraphic horizon is difficult to explain by this paradigm. The lenses are separated from their neighbours by 2–10 m of marly clay and may have been formed by diagenetic processes (see section titled 'Sea Lilies in the Desert' above). A storm would not normally deposit floating animals neatly into lenses that thin out into clays or shales. However, such an occurrence seems more likely if the crinoids formed mats, possibly held together by their intermingled stems, or perhaps by some plant material contained in the crinoid colonies. This also explains the rarity of loboliths occurring *in situ* on most of the slabs, whereas one would expect the bulbs to be commonly preserved and attached to stems in bioherms growing from the bottom.

IMPORTANT COLLECTIONS IN EUROPE

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