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Lower Jurassic Posidonia Shale of Southern Germany

HANS HESS

ICHTHYOSAURS AND THE LARGEST SEA LILIES EVER FOUND

The Swabian Posidonienschiefer is named after the occurrence of the bivalves *Bositra buchi* and the very abundant *Steinmannia radiata*, both species being formerly assigned to *Posidonia*. The Posidonienschiefer have furnished to museums all over the world some of the most spectacular fossils, including ichthyosaurs, fishes, rare plesiosaurs, crocodiles, flying reptiles (pterosaurs) and the magnificent crinoid *Seirocrinus subangularis*. This sea lily, with its beautiful flower-like crowns and stems reaching more than 20 m in length, has been known for a long time. As early as 1742 Hiemer, a clergyman who wrote in Latin, described a slab from Ohmden with several individuals as *Caput Medusae* (head of medusa), comparing it to the ophiuroid with branched arms already known at that time. Hiemer was convinced that the animals were transported by the Flood from the Black Sea to the Stuttgart area, and this created considerable excitement at the time.

The Posidonienschiefer, which occur at the foot of the Swabian and Franconian Alb between the rivers Rhine and Main, belong to the Lower Jurassic (Lower Toarcian, Lias Epsilon, 185 million years before present) and are part of a facies widely distributed in Europe at that time (Fig. 192). They were laid down during three ammonite zones (*tenuicostatum*, but especially during the *falciferum* and *bifrons* Zones) (Fig. 193); a duration of about 0.5 million years has been estimated for the entire period of black shale deposition (Littke *et al.* 1991). The fossils from the communities of Holzmaden, Ohmden, Bad Boll and Dotternhausen, east and south of Stuttgart, are the best known. A few quarries are still in use and furnish highly priced fossils.

OIL SHALES, STILL QUARRIED

The finely layered Posidonia Shales were compressed from muddy sediments due to burial and the weight of the overlying strata. The black shales are rich in organic matter and in former times were burned for their oil. Some beds are more solid than others. For example, a single slab of 18-cm thickness (*Fleins*), which can be split into four parts, is still quarried, mainly for use in building tables. Directly underneath the *Fleins* is the thin *Hainzen* that overlies the *Koblenzer*, another solid bed with a thickness of 15 cm. The thickness of the Posidonienschiefer varies from about 1 m to about 40 m between the Rhine and the upper Main, and in the Holzmaden area it is between 5 and 14 m.

Similar to other bituminous black shales, the Posidonienschiefer contains many extremely well-preserved fossils, including soft parts. However, the majority of the fossils are not preserved intact. According to B. Hauff

Hans Hess, William I. Ausich, Carlton E. Brett, and Michael J. Simms, eds., *Fossil Crinoids*.

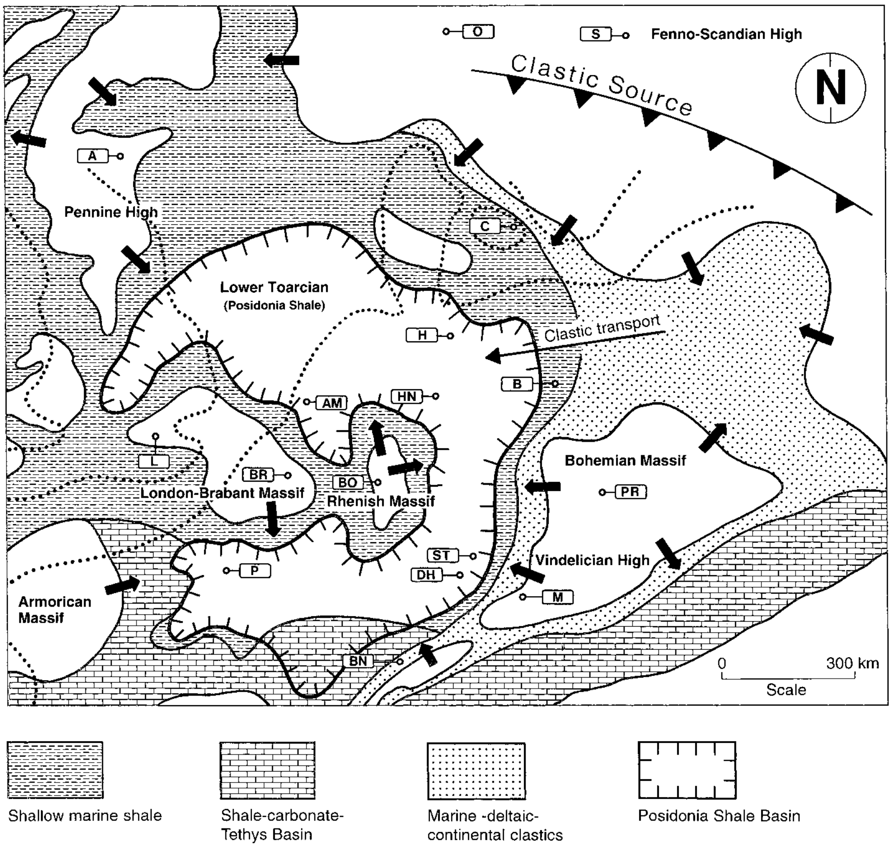

Fig. 192. Distribution of the Posidonia Shale facies in western Europe. Key: A, Aberdeen; O, Oslo; S, Stockholm; C, Copenhagen; H, Hamburg; B, Berlin; AM, Amsterdam, HN, Hanover; PR, Prague; BO, Bonn; BR, Brussels; P, Paris; ST, Stuttgart (Holzmaden area); DH, Dotternhausen; M, Munich; BN, Berne. (After Littke *et al.* 1991.)

(Hauff & Hauff 1981), about 30 quarries were exploited during 1939, and during that year only 8 complete ichthyosaurs were discovered, whereas about 100 ichthyosaurs were found disarticulated or incomplete.

These strata have become famous for their vertebrates, especially the attractive ichthyosaurs. The invertebrates include numerous, thin-shelled and compressed ammonites (*Dactylioceras, Harpoceras* and others), belemnites and squids, bivalves (*Steinmannia, Oxytoma* and *Pseudomytiloides* – formerly *Inoceramus*) and rare arthropods. Pieces of driftwood and remains of plants have also been found, but microfossils (foraminifera and ostracodes) are rare in the bituminous facies. Examples of all of these fossils are illustrated in Hauff and Hauff (1981) and Urlichs *et al.* (1994). The wood has been transformed into fossil hydrocarbon jet (*Gagat*), which can be carved and polished into jewellery; human ice-age relics of jet have been discovered near Stuttgart, apparently made from material found in the Posidonia Shale.

FLOWERING LOGS

The Posidonienschiefer have furnished splendid specimens of *Seirocrinus subangularis*, mostly attached to logs (Fig. 194). These crinoids are concentrated in the lower (*tenuicostatum* Zone) part of the Posidonienschiefer, where they occur in the *Koblenzer* but mainly in the *Fleins* bituminous marly limestones composed partly of coccoliths (Fig. 193). Crinoids tend to be grouped around the ends of the logs; the food supply may have been more abundant in these regions when the logs were drifting. Almost all specimens have been prepared from the lower surface of the slabs, where they are better preserved and are partially pyritized. Large groups are restricted to logs and usually also contain small individuals, commonly attached to the stems of the adult specimens (Fig. 195). Isolated specimens appear to have been broken from driftwood, because their stems are rarely complete. The show-piece of the Hauff Museum in Holzmaden is a slab measuring 18 by 6 m. It contains

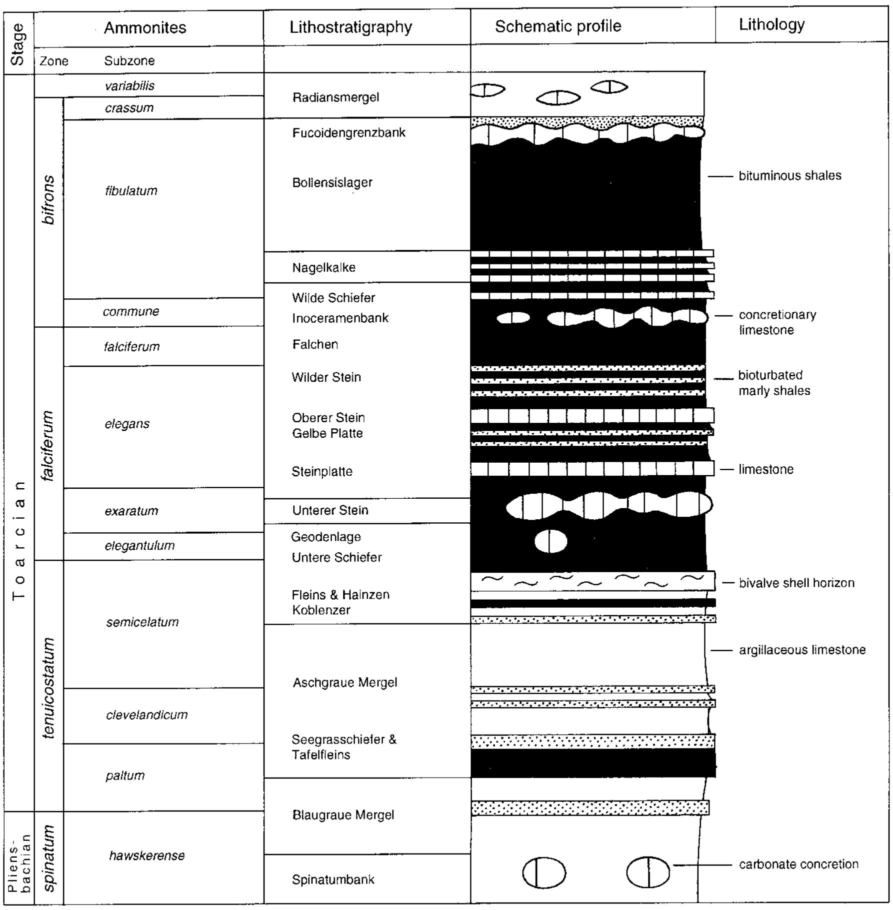

Fig. 193. Biostratigraphy, lithostratigraphy and idealized profile of the Lower Toarcian in southwestern Germany. (After Riegraf 1985.)

a 13-m-long piece of driftwood completely covered with bivalves (*Pseudomytiloides dubius*) and a giant group of about 280 large and small individuals of *Seirocrinus subangularis* with bundles of stems partly wound around the log (Fig. 196).This slab was discovered in 1908 in the *Fleins* at Holzmaden. Its preparation required 18 years of work and was not completed until 1970 for the opening of the museum. An even larger slab with a log close to 20 m in length and an area of about 500 m^2 covered with sea lilies has been discovered at Holzmaden and awaits preparation in the Stuttgart Museum. The largest slab exhibited in this museum measures 6 by 9 m. It was discovered in 1977 in the *Koblenzer* of Ohmden and contains 141 individuals on a partly exposed log. The stems are several metres long, and the crowns reach a diameter of 60 cm. The main point of interest in this colony is a number of crowns in oral view with their tegmen exposed. The sheer size of these logs with their attached crinoids and bivalves is overwhelming, and they are the largest and most spectacular invertebrate fossil remains of all time. Unfortunately, because of their enormous size it is impossible to reproduce them adequately in any book illustration (see Fig. 196).

DENSE CROWNS ON STRONG AND FLEXIBLE STEMS

Small individuals of *Seirocrinus* are superficially similar to *Pentacrinites dichotomus* (discussed in the next section), with a stem length of only a few centimetres. The columnals of large specimens are rounded subpentagonal to circular in cross section (hence the species name, *subangularis*) and typically vary in height (Fig. 197). The articular facets have large, strongly granulated radial areas, separating the crenulate, narrow pyriform petals. This structure gives the impression of considerable flex-

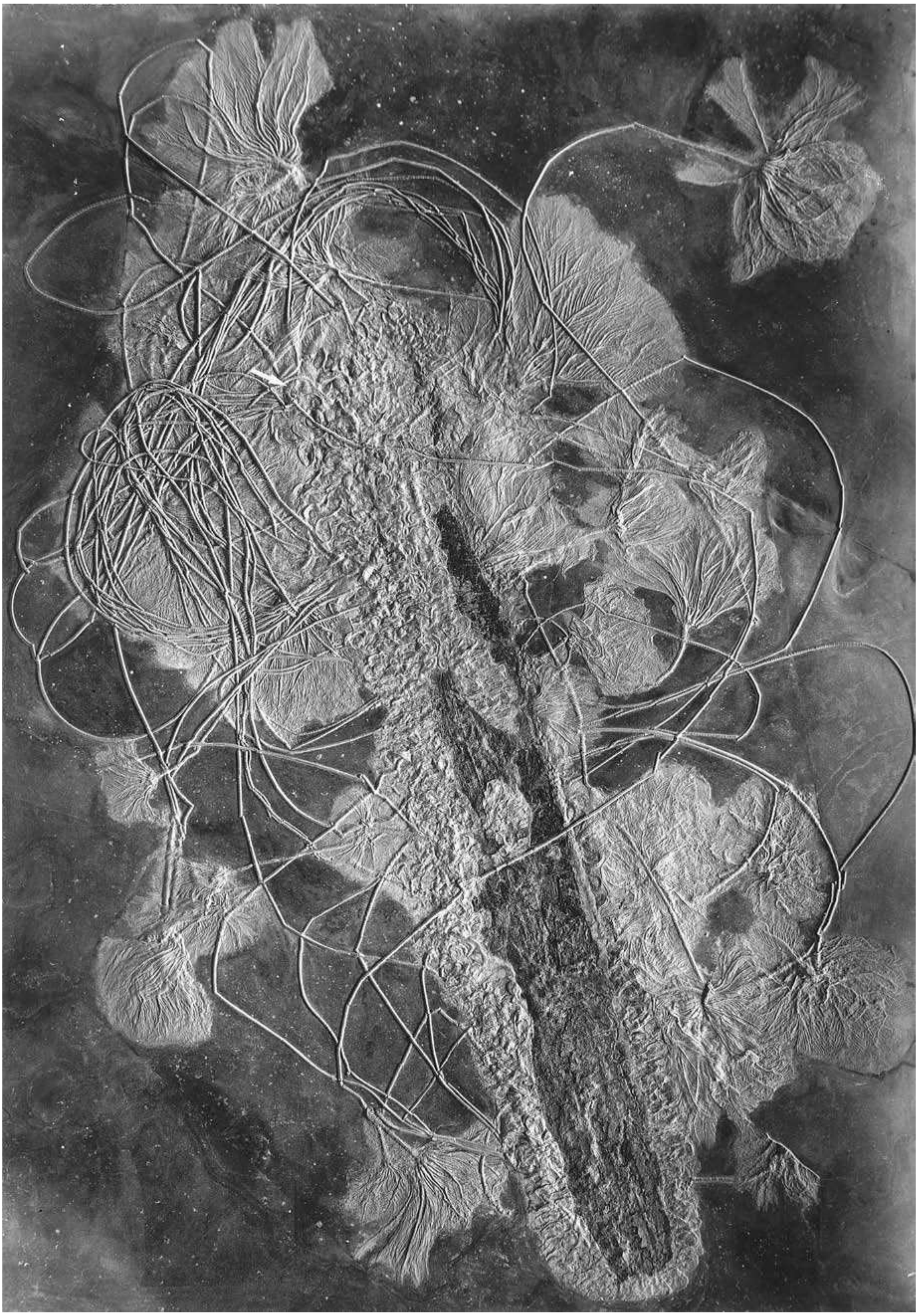

Fig. 195. *Seirocrinus subangularis*. Group with juvenile specimens attached to stem of adult individual; also contains *Pseudomytiloides dubius*. Posidonienschiefer, Ohmden. (Stuttgart Museum; photograph R. Harling; courtesy G. Dietl.) ×0.4.

Fig. 194. (*On facing page*) *Seirocrinus subangularis*. Colony with entangled stems on driftwood. Posidonienschiefer, Holzmaden. The slab was prepared from the lower side; one specimen, whose attachment is close to the upper end of the log (arrow), has a stem that crosses the log twice, proving that the log settled on the bottom on top of the crinoid. Size of slab 2.5 by 3.5 m. (Staatliches Museum für Naturkunde, Stuttgart; photograph R. Harling; courtesy G. Dietl.)

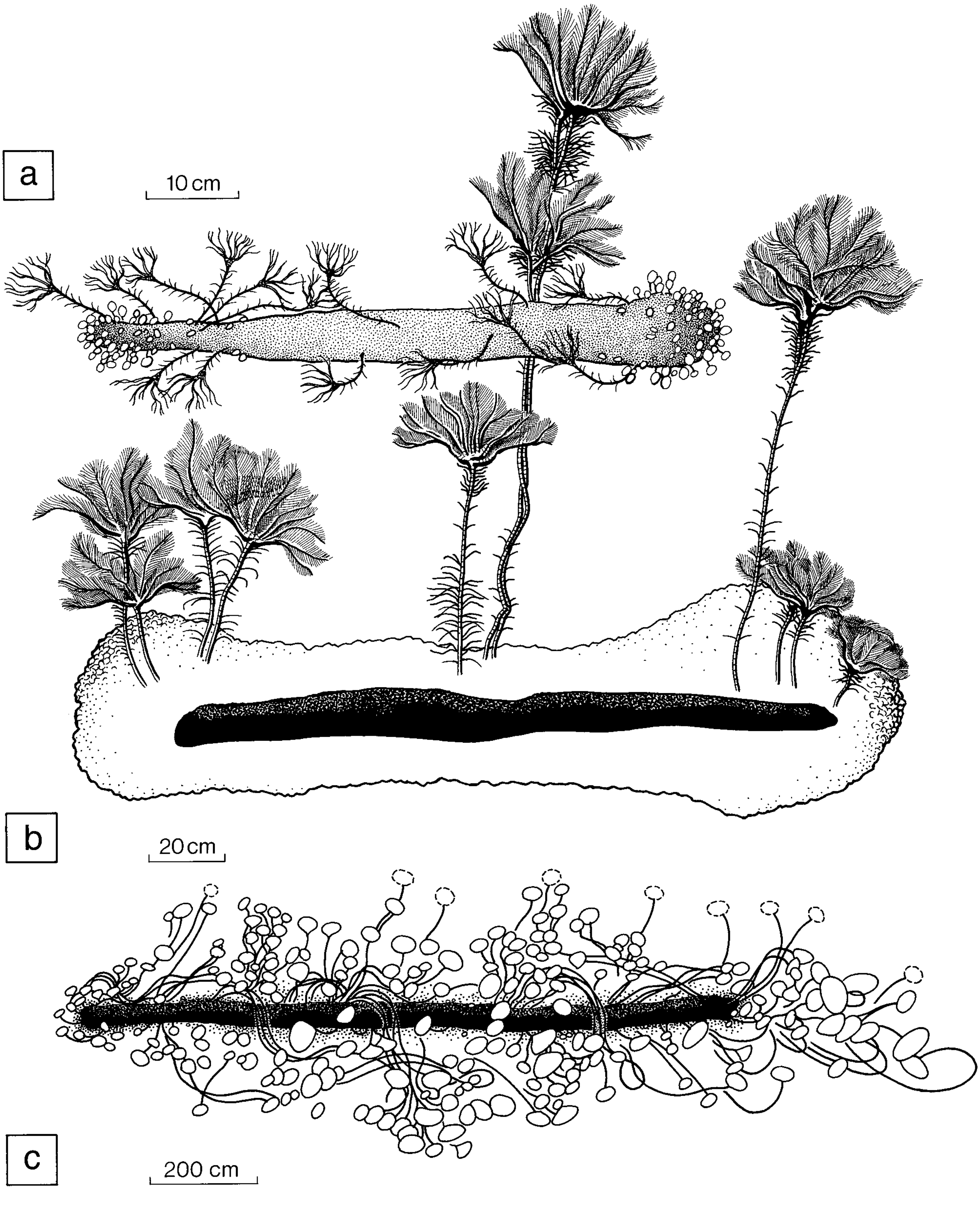

Fig. 196. Completely preserved colonies of *Seirocrinus subangularis* on logs of different size. (a) Colony of juvenile individuals (Göttingen Museum); (b) colony of subadult individuals (Senckenberg Museum; see also Fig. 199); (c) the giant colony of the Hauff Museum in Holzmaden. (Redrawn from Haude 1980.)

Fig. 197. Stem fragments, disarticulated cirrals and brachials of *Seirocrinus subangularis* on upper bedding plane of *Fleins*. Posidonienschiefer, Dotternhausen. (Courtesy Werkforum Dotternhausen.) ×1.

ibility combined with great strength. With increasing distance from the cup, the diameter of the stem 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 stem (Seilacher *et al.* 1968); the total length of the largest stem is more than 26 m (Simms 1989)! Stems of such extreme length suggest plankton-rich zones, and therefore a greater opportunity for food gathering, well below the surface (see also Chapter 11 for the similar case of the scyphocrinitids). In contrast to that in the isocrinids, the articulation between nodals and infranodals in *Seirocrinus* is symplectial. Synostosial autotomy planes appear to have evolved only among the isocrinids and, anyway, would be of no advantage to a pseudoplanktonic crinoid. The cirri are closely spaced in both the most proximal region and distal stem regions, with a dense tuft of cirri acting as a holdfast to the driftwood. The cirri vary from small to large individuals and from the proximal to the distal part of the stem. In small individuals, they are rhomboidal in outline and resemble those of *Pentacrinites*, whereas in large individuals the ossicles are rounded, short and slender. Divisions of the highly branched arms at primibrachials and secundibrachials are isotomous, but succeeding divisions are all endotomous (Fig. 198). Arm length may attain 50 cm in the largest individuals. Heterotomous arm branching provides a very dense filtration fan that would also be needed for rapid growth, as postulated for the pentacrinitids. Most brachial articulations are muscular. Syzygies are absent, allowing complete pinnulation of the arms. This improved the food-gathering process even more.

It is now widely accepted that *Seirocrinus* lived attached to floating logs. Such a pseudoplanktonic mode of life 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 stalks 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. (This genus derives its name from the long, rope-like stems.) As already noted by B. Hauff (Hauff & Hauff 1981), the size of the crinoids is proportional to that of the driftwood on which they are anchored (Fig. 196). The loading capacity of floating trunks has been discussed by Haude (1980). He calculated for the log in the Senckenberg Museum, measuring 190 cm by 8–12 cm (Fig. 199), a load capacity of about 12 kg. The weight in sea water 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 the roughly 5,000 *Pseudomytiloides dubius* lamellibranchs. These figures are in agreement with a pseudoplanktonic life for *Seirocrinus*. Doubts have been raised as to whether the trunks could have floated long enough to allow *Seirocrinus* individuals to grow to such size. According to Haude, unloaded trunks of conifers (a type of tree common in the Lower Jurassic) remain buoyant for 2 years at the most. He therefore 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 water-filling of the pores. Observations made after the eruption of Mount St Helens (Simms 1986) suggest that the trunks could have remained floating for much longer (see also Chapter 22). M. Jäger (pers. comm., 1993) has drawn attention to the absence of wood-boring lamellibranchs; these would have quickly destroyed the substrate. Whereas the first wood-boring, teredinid bivalves appeared toward the end of the Early Jurassic, these Jurassic forms appear to have colonized only wood lying on the bottom, not driftwood (Wignall & Simms 1990). On the large trunks floating near the surface, the large *Seirocrinus* individuals must have been hanging down (Fig. 199 gives an impression of this). Once the buoyancy fell below a certain point, large logs may have sunk quite rapidly, dragging the crowns along like parachutes. After the trunk settled, the crowns would have tilted over and sunk to the bottom. While

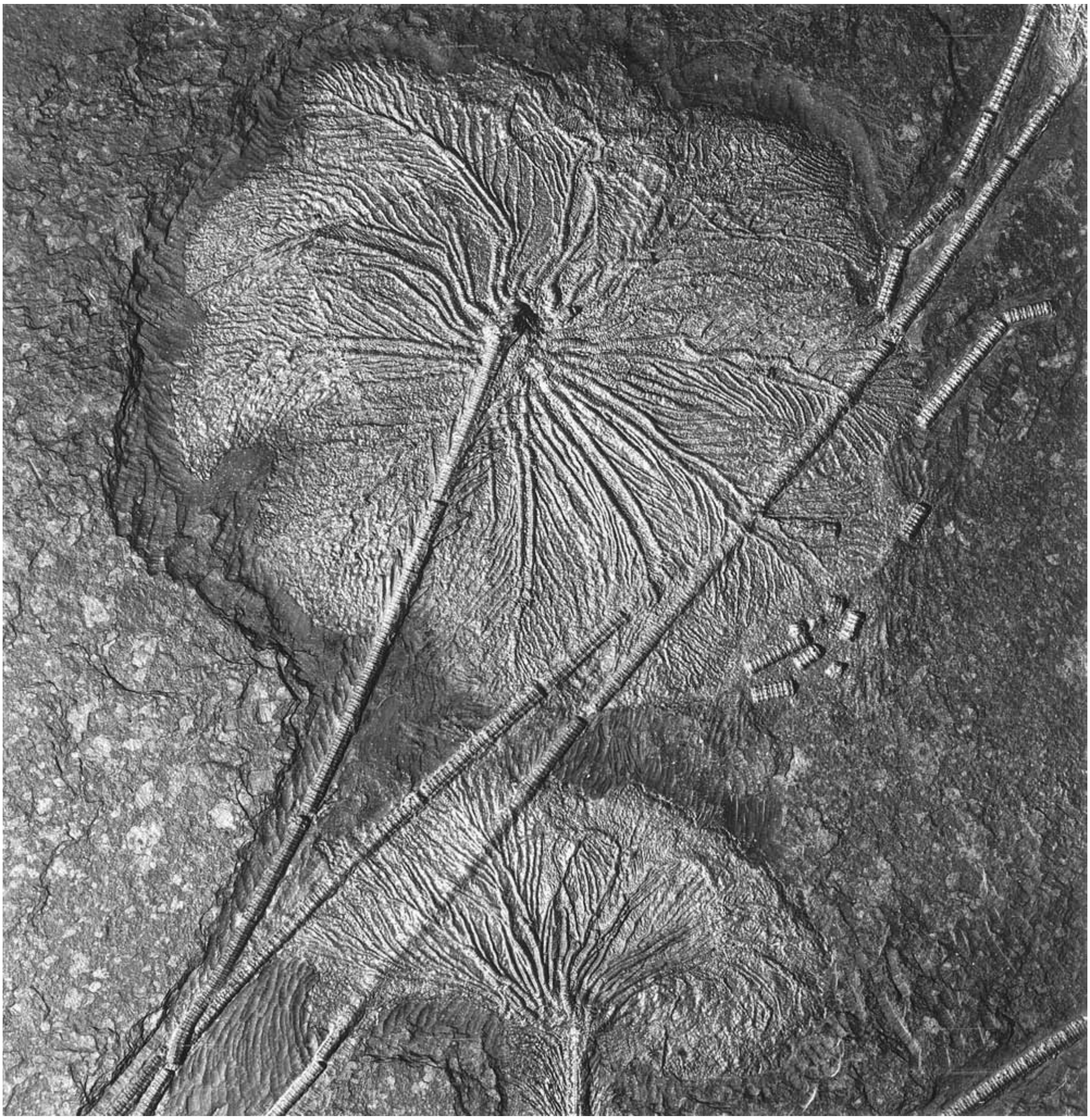

Fig. 198. *Seirocrinus subangularis*. Two crowns belonging to a large group, attached to driftwood on a slab of *Fleins*. Posidonienschiefer, Dotternhausen. Diameter of the larger crown approximately 40 cm. (Werkforum Dotternhausen; courtesy M. Jäger.)

smaller individuals and those with shorter stems came to lie on their sides, large ones with very long stems would have reached the bottom with their oral side downward (Haude 1980). Such a behaviour is shown by a very large group in the Tübingen Museum (Fig. 200) and the large colony exhibited in the Stuttgart Museum. A trunk with a length of about 3 m in the Stuttgart Museum (Fig. 194) has a heavy overgrowth of *Pseudomytiloides dubius* and crinoids with twisted stems that lie partly over the log. Because this slab shows the lower surface, the log must have settled after some of the crinoids touched the bottom.

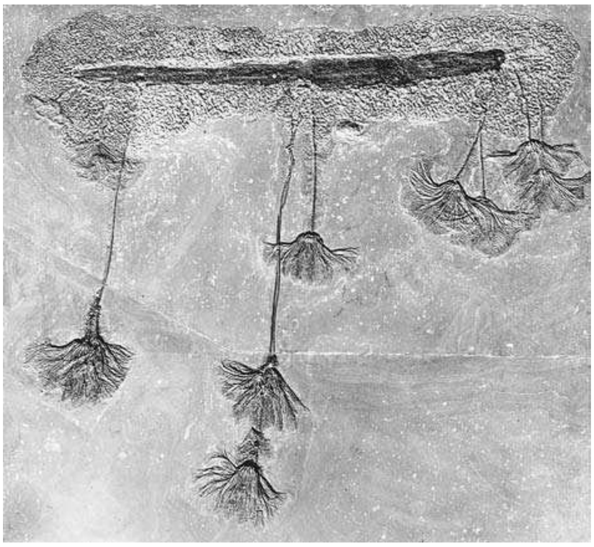

Fig. 199. *Seirocrinus subangularis*. 'Senckenberg log' with crowns hanging down to show presumed life position. This specimen from the Posidonienschiefer of Holzmaden is preserved in the Naturmuseum Senckenberg, Frankfurt, and has been reproduced repeatedly (e.g., by Breimer & Lane 1978), but only once in this position (Seilacher 1990b). Size of slab 250 ×260 cm. (Courtesy R. B. Hauff.)

PSEUDOPLANKTONIC *PENTACRINITES*

The short-stemmed *Pentacrinites dichotomus* McCoy (*Pentacrinites briareus württembergicus* Quenstedt and *Pentacrinites quenstedti* Oppel are synonyms; see Simms 1989) occurs in younger beds (*falciferum* and *bifrons* Zones) and, thus, was not contemporary with *Seirocrinus* (this species is restricted to the uppermost *tenuicostatum* Zone). *Pentacrinites dichotomus* is also much rarer. In contrast to the British occurrences of *Pentacrinites fossilis* in the Sinemurian, the species from the Posidonienschiefer is invariably very short-stemmed and, therefore, is comparable to *Pentacrinites dargniesi* described in Chapter 25. The largest specimens known, preserved in the Stuttgart collection, have stems about 20 cm long and an arm length of about 15 cm. Only the nodals are seen from the outside, being mostly covered by the closely spaced, compressed cirri with a length comparable to that of the arms (Fig. 201).

A superb slab with 153 individuals of *P. dichotomus*, with a diameter of 1.15 m, can be admired in the Stuttgart Museum (Urlichs *et al*, 1994). The slab was first figured by Beringer (1926), who gave detailed descriptions of the complete *Seirocrinus* and *Pentacrinites* specimens from the Posidonienschiefer known at the time. Most of the crinoids on this slab are of a similar size, but some small (i.e., juvenile ones) also occur. The crinoids appear to have grown radially from a central area, where the thickness suggests two layers of crinoids. Individuals on this slab are mostly presented on their side, but about a dozen specimens present their oral side. Another slab from Ohmden, preserved in the Stuttgart collection, contains a group measuring 55 by 40 cm with about a dozen individuals as well as two *Pseudomytiloides* (Fig. 202). Its preservation is quite similar to that of the large Stuttgart slab. These *Pentacrinites* were not found together with wood or with other remains of plants, and this is also true of some other groups. They seem to have been floating as a more or less spherical body with their long cirri intertwined for mutual support and grouped around some unfossilized material. It is questionable whether a material comparable to today's seaweeds (such as bladder-wrack) would be buoyant enough to support such a large group. It may well be that the crinoids were separated from their buoyant support before burial. In any case, a group of *P. dichotomus* about 3 m long, preserved in the Dotternhausen Werkforum, is attached to a log of similar length, proving a pseudoplanktonic lifestyle also for this species. The Dotternhausen slab was discovered in the Wilder Schiefer (*bifrons* Zone). It was badly damaged by blasting and had to be reassembled from about 300 fragments. According to F. Lörcher (pers. comm., 1996), who took 2 years to assemble and prepare this important show-piece, the group contains about 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, and their size is comparable to the specimens of the large slab at the Stuttgart Museum. The Dotternhausen collection also includes another group of *P. dichotomus* attached to wood.

Therefore, the Dotternhausen specimens are similar to the Dorset crinoids, which are regularly preserved underneath the lignitized driftwood to which they were attached (see Chapter 22). However, the Dorset *Pentacrinites fossilis* developed longer stems, similar to *Seirocrinus*. It has even been postulated by Hauff (1984) that the long and strongly flattened cirri (Fig. 201) of the *Pentacrinites* species could have been used for swimming, but the lack of muscle fibres between the segments contradicts this hypothesis. The stratigraphically younger *P.*

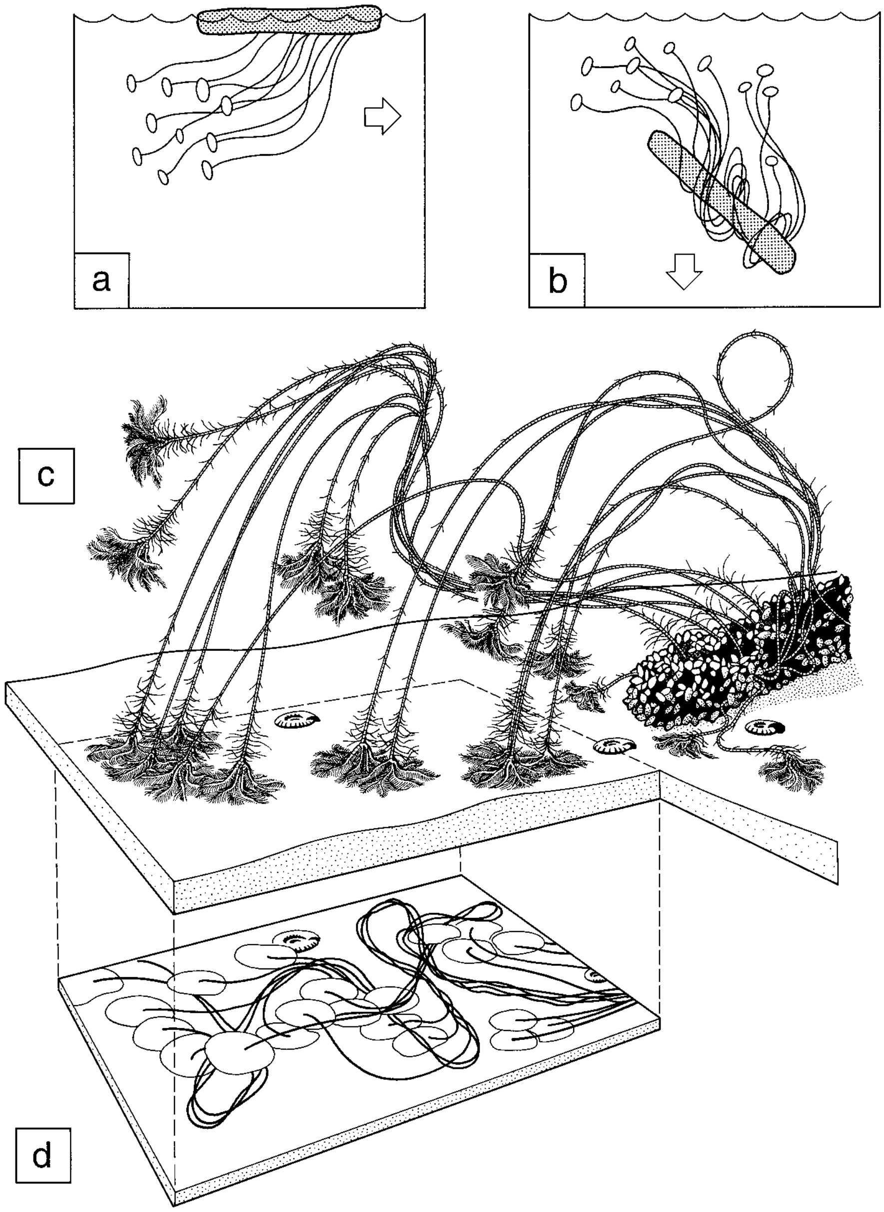

Fig. 200. Reconstruction of the sinking process of a large *Seirocrinus* colony, exhibited in the museum of the University of Tübingen. Length of slab approximately 10 m. (a) Floating log; (b) log at the beginning of the sinking process; (c) log reaching the bottom; (d) slab with the fossils. (The slab was figured by Seilacher *et al.* 1968; redrawn after Haude 1980.)

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 stems. These differences are presumably the result of a somewhat different lifestyle allowing mutual support of the animals.

A RARE COMATULID

A unique intact specimen of the free-moving comatulid *Procomaster pentadactylus* has been described (Simms 1988b). This exotic element in the crinoid fauna of the Posidonienschiefer is one of the oldest comatulids

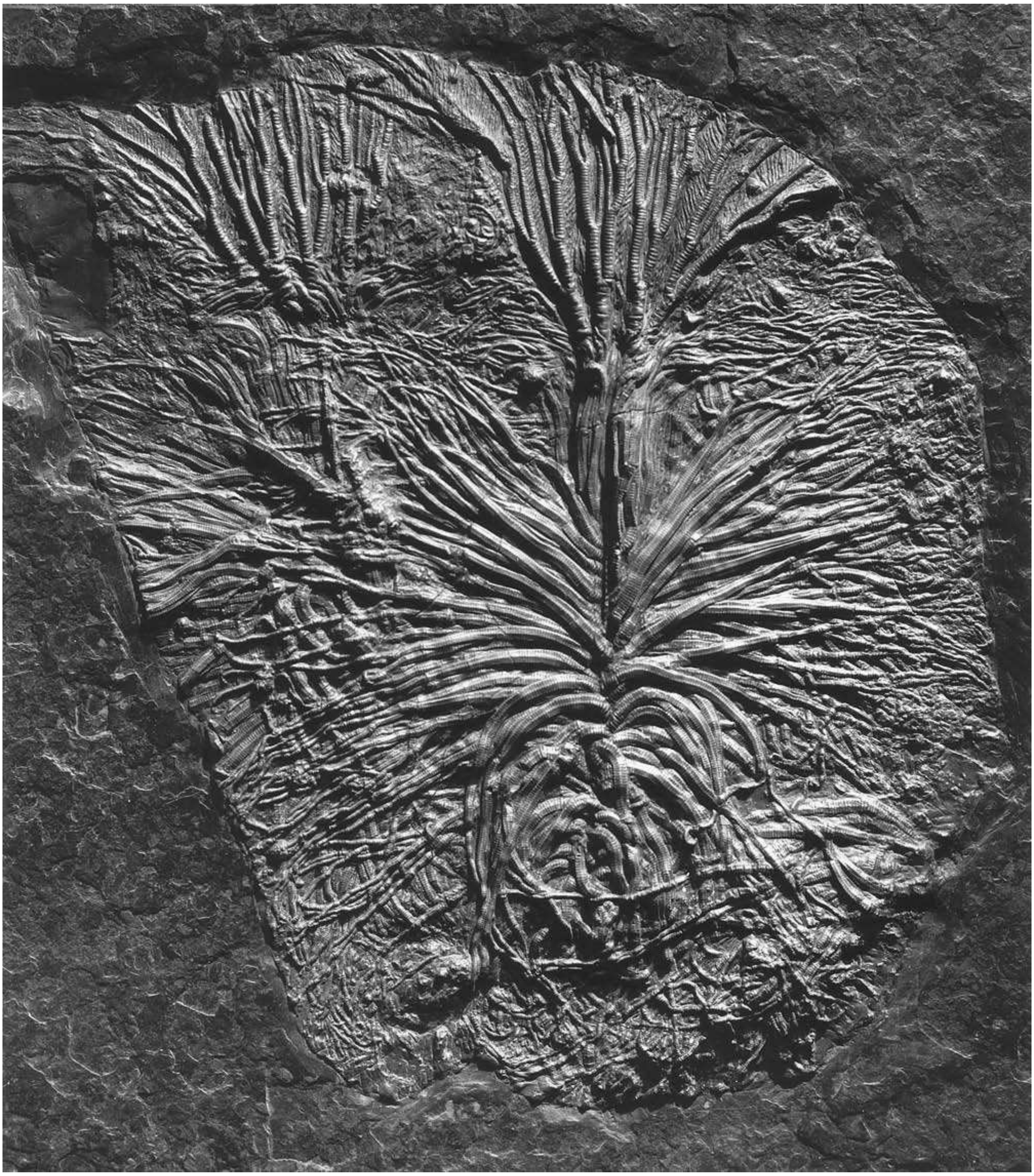

Fig. 201. *Pentacrinites dichotomus*. Two individuals with the base of the crown and well-preserved cirri. Posidonienschiefer, Holzmaden. (Stuttgart Museum; courtesy G. Dietl.) ×0.5.

known. It is the only Lower Jurassic crinoid with only five unbranched arms; the cirri are robust, recurved and without a terminal claw (Fig. 203). The brachials are very low; their articulations are, like those of the other comatulids, either muscular or syzygial. The pinnules are well developed. This individual may have drifted into the basin attached to seaweed or some other floating substrate, which has now disappeared.

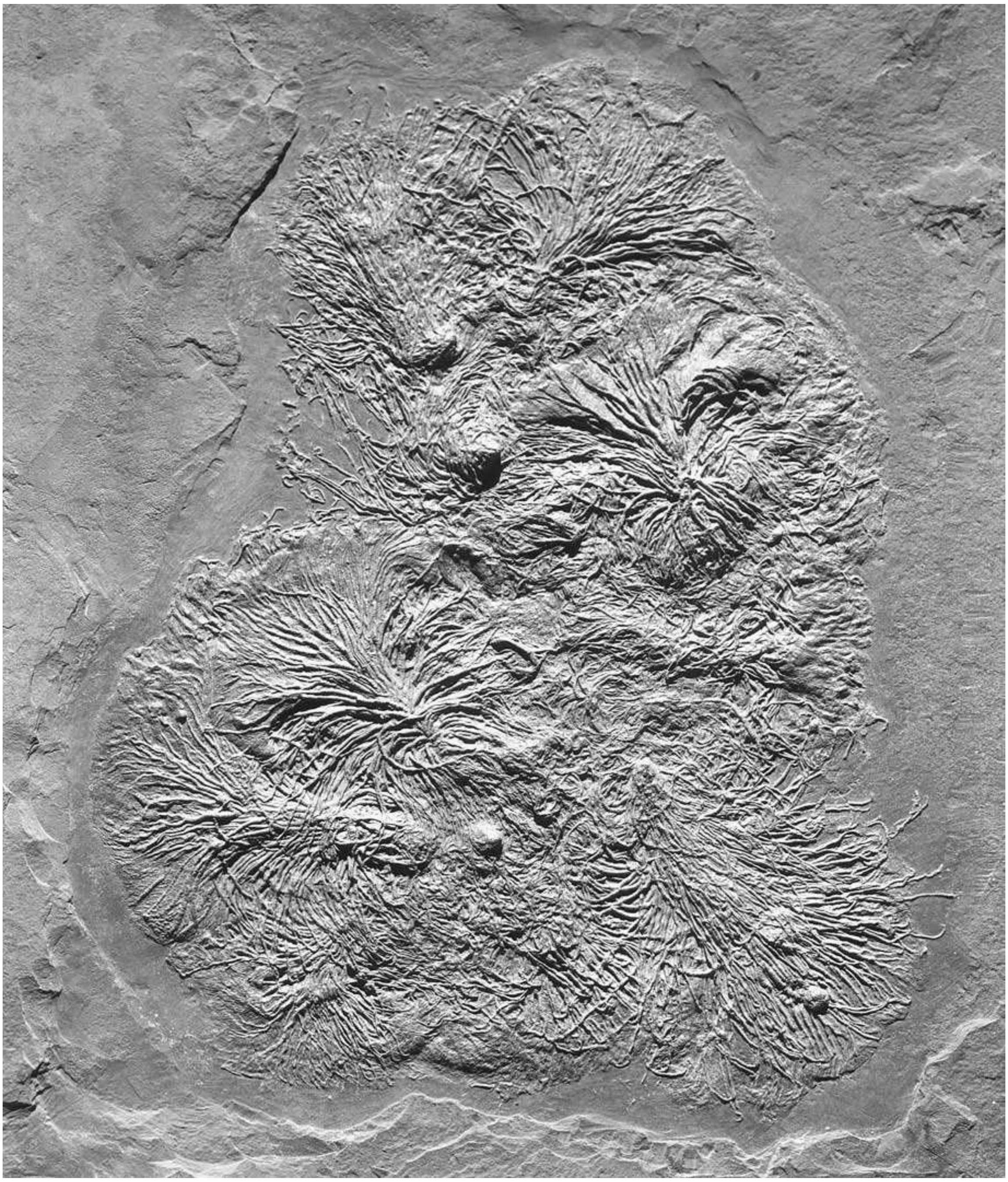

Fig. 202. *Pentacrinites dichotomus*. Posidonienschiefer, Ohmden (J. Fischer Quarry). Size of group 55 ×40 cm. (Stuttgart Museum; photograph R. Harling; courtesy G. Dietl.)

A LIFELESS BURIAL GROUND

The bituminous Posidonienschiefer are characterized by their high content of organic matter (kerogen), undisturbed fine laminations and almost total absence of benthic animals, as well as excellent preservation of many of the fossils. These facts point to stagnant, anoxic bottom water. The rich supply of organic material has been explained by upwelling of phytoplankton, caused by an opening of the Atlantic in the west and the Tethys

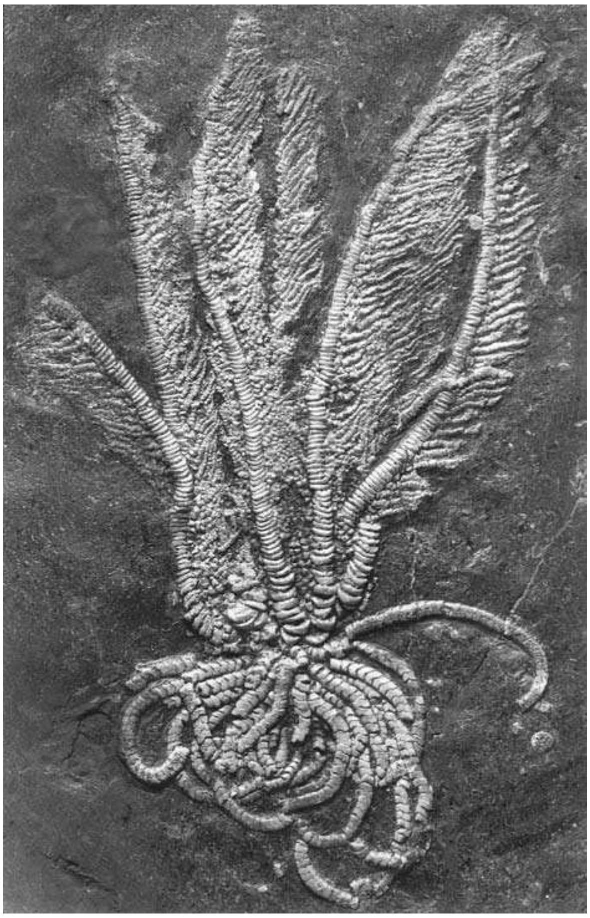

Fig. 203. *Procomaster pentadactylus*, holotype (Simms 1988b). Posidonienschiefer, Zell. (Stuttgart Museum; photograph H. Lumpe; courtesy G. Dietl.) ×1.5.

Ocean to the south (Riegraf 1985). As Littke *et al.* (1991) have pointed out, an inflow of nutrient-rich open waters from the Tethys over and through the entire shallow epicontinental Posidonia Sea during the long duration of Lower Toarcian time is difficult to conceive. Such a mechanism is also in conflict with the lack of evidence from much current activity. Therefore, these authors have proposed that there was a supply of nutrients from the many nearby emergent areas that were also the source of detrital clay (Fig. 192). Bioturbated horizons occur repeatedly, indicating short periods of higher oxygen content at the bottom (perhaps by increased water circulation), making life for benthic animals possible. The so-called Seegrasschiefer (containing the trace fossil *Chondrites*) is one of the earliest and best-known of the bioturbated horizons and appears to be the result of burrowing worms. Such horizons also contain benthic foraminifera, which become impoverished or disappeared under the anoxic conditions of the highly bituminous sediments (Riegraf 1985). Life on the bottom is also documented by the occurrence of the rare burrowing bivalves *Goniomya* and *Solemya* (Seilacher, 1990b). Recent *Solemya* carries chemosynthetic, anaerobic bacteria and may be gutless. The bivalve *Steinmannia radiata* (var. *parva*) is densely packed on certain bedding planes and was considered a hardy bottom dweller; a planktonic lifestyle with some kind of buoyancy device as postulated by Oschmann (1995) is questionable (Etter 1996). Encrusting algae (*Girvanella*) were quite common at times of reduced or interrupted sedimentation (Riegraf 1985) and also point to the presence of some oxygen at the bottom, with anoxic conditions underneath the algal mats. The absence of bioturbation and benthos in horizons with such mats may indicate increased salinity in the bottom layer. The beds with the *Seirocrinus* specimens, which are usually attached to driftwood as already discussed, contain few benthic foraminifera and lack benthic macrofossils. The same appears to be true of the horizons with *Pentacrinites*. It has been pointed out by M. Jäger (pers. comm., 1993) that the crinoids may have attached to bivalves (strongly anchored to the wood by their byssal threads) rather than to the naked wood. This view is supported by the fact that Posidonienschiefer crinoids almost always occur together with bivalves (*Pseudomytiloides dubius*), whereas wood occasionally contains bivalves but no crinoids, but rarely crinoids without bivalves. However, Simms (1986) described a specimen from the Lower Jurassic with larval attachment discs of *Pentacrinites fossilis* on a piece of coalified driftwood, and bivalves are lacking on this specimen (see Chapter 22).

It is now assumed that the Posidonienschiefer was deposited at a rate of about 0.1 mm per year in a shallow but extended marginal sea with a depth of about 20–50 m and warm, intermittently hypersaline water (Riegraf 1985). The accumulation and preservation of the organic matter were favoured by a density stratification of the water column caused by the influx of low-salinity nutrient-rich water from high latitudes (Prauss *et al.* 1991). Under conditions of reduced sedimentation, algal mats (cyanobacteria) produced carbonate crusts that stabilized the sediment. At times, weak water movement and/or bioturbation destroyed the algal mats. However, conditions were never favourable enough for bottom-living crinoids such as *Isocrinus (Chladocrinus)*, a form otherwise common in Liassic strata. The spines of the

tiny echinoid *Diademopsis crinifera* are found in large numbers in the *tenuicostatum* Zone before the appearance of the bituminous facies, indicating strongly increased algal growth on the bottom for a short period.

IMPORTANT COLLECTIONS IN GERMANY

Museum Hauff, Holzmaden. This splendid museum, devoted to the fossils from the Posidonienschiefer, was built near the famous fossil site (where collecting is still possible) and contains, among other specimens, a huge piece of driftwood covered with bivalves and crinoids.

Staatliches Museum für Naturkunde, Stuttgart (Museum am Löwentor). It has, together with the Hauff Museum in Holzmaden, the richest collection of Posidonienschiefer fossils, including a spectacular slab with *Pentacrinites dichotomus*.

University of Tübingen, Geological Institute. Exposed is the large slab described by Seilacher *et al.* (1968).

Werkforum Dotternhausen (Portlandzementwerk Rudolf Rohrbach, D-72359 Dotternhausen). This beautiful museum was opened in 1989 on the site of a Posidonienschiefer quarry and shows the fossils typical of these strata, including a unique slab with numerous individuals of *Pentacrinites dichotomus* attached to a log, as well as a large group of *Seirocrinus subangularis* from the *Fleins*, also attached to a piece of driftwood (Jäger 1993).