

# Upper Jurassic Solnhofen Plattenkalk of Bavaria, Germany

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## A LIVELY TRADE

The extremely fine grained, even-layered lime mudstones north of Munich have been quarried since ancient times. The discovery of lithography by Alois Senefelder in 1796 has given this stone a worldwide reputation that was increased by the discovery of the remains of the early bird *Archaeopteryx*. Exploitation over many years has produced a plethora of marvellous fossils, even though they are rather rare. The only common fossil is the small crinoid *Saccocoma*, the focal point of this chapter. Quarrying is fortunately still going on because the slabs are valued today for floor and wall tiles. The best-known areas are (from west to east, named after neighbouring communities): Langenthalheim/Mörnsheim/Solnhofen, Eichstätt, Pfalzpaint/Gundolding, Schamhaupten/Zandt, Kelheim and Painten (Fig. 217).

## PLATTENKALK: FLINZ, FÄULE AND KRUMME LAGEN

The Solnhofen Plattenkalk (Plattenkalke) belong to Early Tithonian and are about 150 million years old. The whole time of deposition of the Plattenkalk is within Weissjura or Malm Zeta 2 and belongs to the lower part of the Early Tithonian, which is at most half of the *Hybonotoceras hybonotum* Zone. This means that

the whole series of the Solnhofen limestones represents 500,000 years or less (Barthel 1978). Only a minor part of this platy limestone has been used for lithographic purposes. The regularly bedded Plattenkalk reaches a total thickness of up to 100 m; they are interrupted by *Krumme Lagen*. These are irregularly folded beds, resulting from slumped soft sediment masses that collapsed downslope, possibly triggered by earthquakes. The very fine-grained, micritic limestone slabs of the Plattenkalk are called *Flinz* and occur in packets of sheets with an average thickness of 0.5–1 cm, reaching a maximum thickness of 30 cm in the Solnhofen area. The slabs frequently have some internal lamination but will not split along this due to an absence of clay minerals. They are separated by thinner, fissile shaly layers, called *Fäule*, which contain 10–20% clay. Stacks of *Flinz* can split along bedding planes, and it is along these that the majority of fossils are found. Both *Flinz* and *Fäule* contain the same microfossils (coccoliths together with rare foraminifera). According to most authors (Barthel *et al.* 1990) the Plattenkalk and *Krumme Lagen* were deposited in shallow basins with an average depth of 30–80 m between sponge–algal mounds. In certain outcrops, the transition of Solnhofen Plattenkalk into sponge–algal mound facies can be observed. Such beds are rich in fossils (brachiopods, echinoids, bryozoans, serpulids) and contain abundant shell detritus. The sponge–algal mounds were progressively buried by carbonate sediments. In the eastern part and later also along the south-

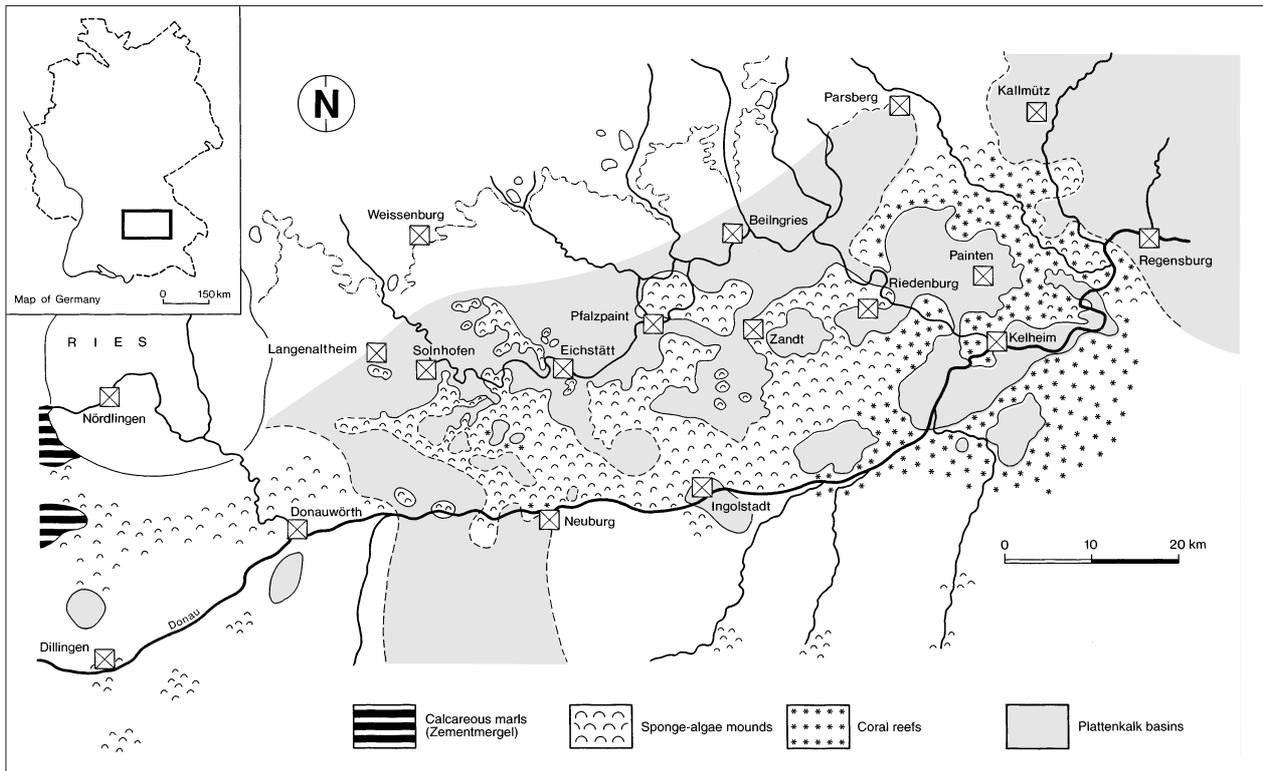


Fig. 217. Map of localities with outcrops and basins of Plattenkalk. (Redrawn from Viohl 1996.)

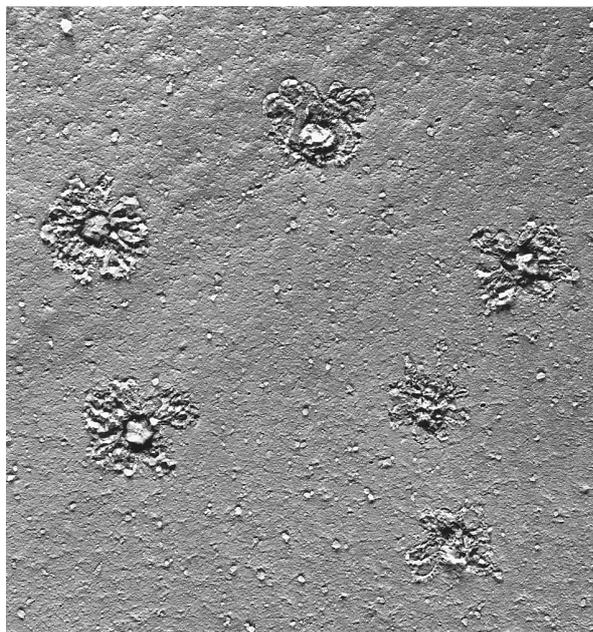
ern margin of the complex, sponges were replaced by corals, which produced more detritus (Fig. 217). There can be no doubt that deposition of the Plattenkalk occurred in relatively shallow water on the landward and most restricted part of a carbonate platform with a very irregular relief. To the north a landmass formed part of the Rhenish–Bohemian Massif. The origin of the Plattenkalk is discussed further in the section titled ‘Plattenkalk Origin: Conflicting Theories and Open Questions’.

## ANIMALS FROM LAND AND SEA

The celebrated Solnhofen Plattenkalk has furnished remains of at least 550 species of animals and plants (Frickhinger 1994), including land animals like insects, crocodiles, lizards, turtles, flying reptiles (pterosaurs) and the early bird *Archaeopteryx*. However, marine organisms, such as cephalopods, fish and crustaceans, are predominant. The largest number of fish are small or juvenile *Leptolepides sprattiformis*, which must have lived in shoals. There are considerable differences in both the content and number of fossils between the localities

(Walther 1904). The Solnhofen area, which has given the formation its name, is rather poor in fossils compared with the Eichstätt area but is renowned for the thick, lithographic limestone beds occurring there. Impressions of jellyfish (*Rhizostomites*) are relatively common in the Pfalzpaint area, and, in contrast to the other fossils, these are preserved within the limestone beds. The famous horseshoe crab *Mesolimulus* has been found at many localities, but most frequently around Pfalzpaint. Mostly juvenile specimens of this animal have left numerous tracks in the Solnhofen–Eichstätt area, in most cases with the animal at the end of its trail (so-called death tracks). This leaves no doubt that these hardy animals remained alive on the bottom, at least for a limited period. Crustaceans, especially decapods (shrimps and the crayfish *Mecochirus*, which also left its tracks), are among the more common Plattenkalk fossils.

By far the most numerous macrofossil is the pelagic *Saccocoma*. The juvenile forms, in particular, are preserved in great numbers on the bedding planes near Solnhofen and especially near Eichstätt (Fig. 218), where *Saccocoma* occurs at seven different horizons. With the possible exception of the Triassic *Encrinurus*



**Fig. 218.** *Saccocoma tenella*. Several curled-up specimens on the lower surface of a slab from Schernfeld near Eichstätt. (Natural History Museum, Basel; photograph S. Dahint.)  $\times 0.7$ .

*liliiformis*, *Saccocoma* appears to have been the most numerous crinoid of all times. The cups of these crinoids split from the rock with the aboral side up, which makes them stand out as knobs. In many cases, the bedding planes split through the fossils, and parts of these adhere to both the underlying and overlying slab. The mode of preservation is discussed in more detail in the next section. Near Zandt a large number of the ophiuroid *Geocomma carinata* occur.<sup>1</sup> The comatulid *Pterocoma pennata* is found mainly near Solnhofen and Zandt, whereas echinoids are uncommon and asteroids (*Lithaster* and *Terminaster*) as well as holothurians are exceedingly rare. Microfossils include a diverse flora of coccoliths (Keupp 1977) and sparse benthic foraminifera.

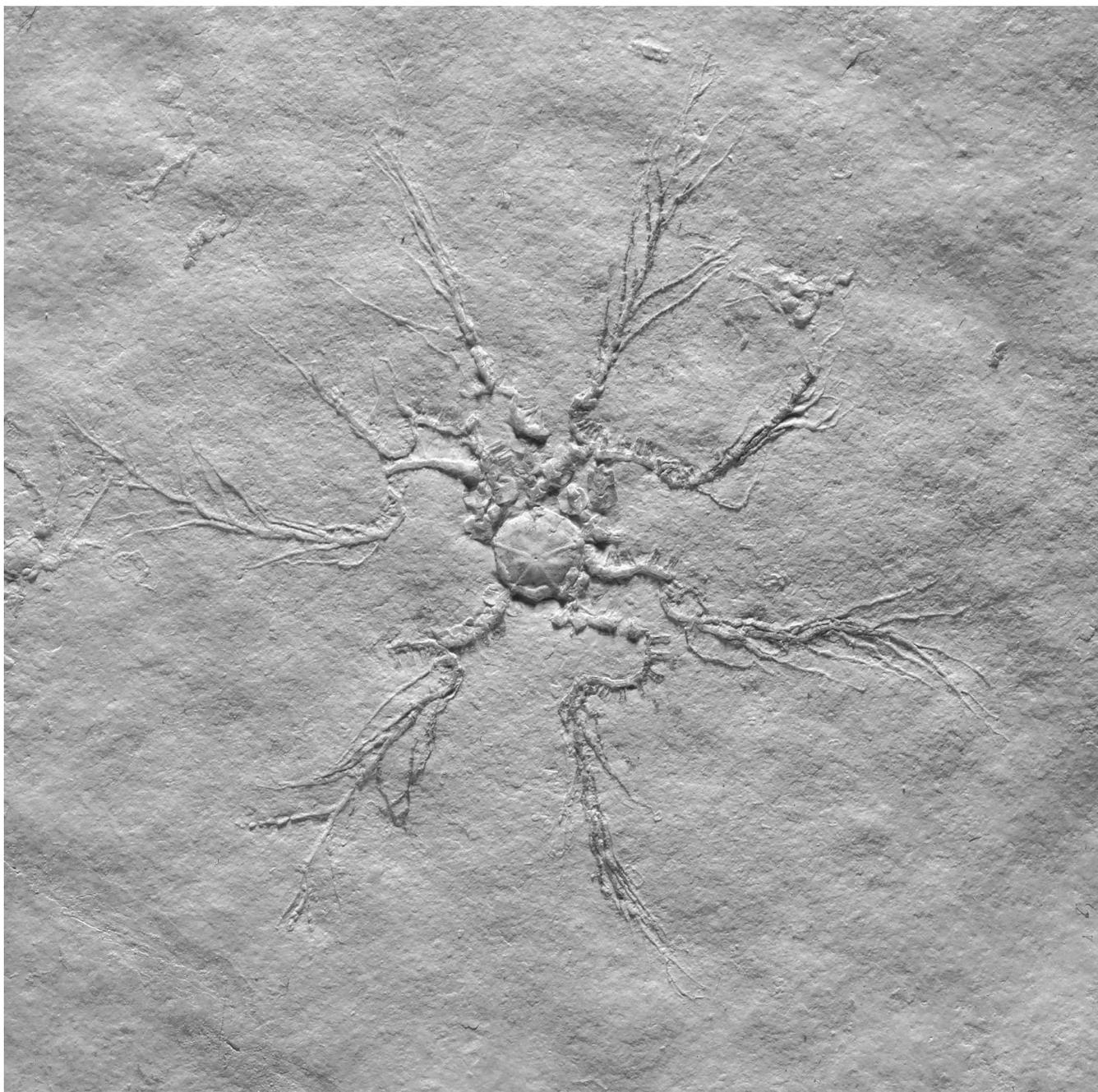
### SMALL CRINOIDS IN ENORMOUS SWARMS

Fixed crinoids are rare; only a few remains of a milleriacrinid have been reported. Conditions at the bottom must have been unsuitable for stalked crinoids. The abundant *Saccocoma* is a small, lightly built crinoid. These delicate crinoids were carefully described by Jaekel (1892) in one of his classic papers. We follow his characterization of the morphology (supplemented by

our own observations on well-preserved specimens and from collecting in the field) to show how well these fascinating small animals adapted to a floating lifestyle. Two species have been mentioned: the smaller *S. tenella*, which differs from *S. pectinata*<sup>2</sup> by the presence of more pronounced lateral flanges or wings on the proximal brachials. In view of the commonly insufficient preservation (Goldfuss, the original author, mentioned that *S. pectinata* was badly preserved), the distinction would appear to need justification. We therefore accept only one species, *S. tenella*, the juvenile specimens being provided with comparatively larger wings. A third species, *S. schwertschlagerei*, is a modification due to preservation (autotomy of arms) (Manni & Nicosia 1986).

These fossils occur on both the lower and upper surfaces of *Flinz*, but only on the lower side of *Fäule* beds (Janicke 1969). However, a number of small individuals have been discovered in a small quarry near Mühlheim on the upper surface of *Fäule* beds, some of them showing the oral side (C. Obrist, pers. comm., 1997). The majority of specimens occur on lower surfaces (Figs. 218, 219), showing the aboral side (the knob of the cup) or a corresponding impression, but never their oral side. In larger specimens the cup is always somewhat crushed, which shows that they were at most only partly infilled with sediment, similar to the preservation of the ammonite shells. Preservation of *Saccocoma* is best in the *Fäule* beds (Fig. 219); in *Flinz* beds, recrystallized calcite may obscure the details. The tips of the arms are usually coiled or lumped together (and then strongly recrystallized), or the animals are curled up as a whole on the bedding planes (Fig. 218).

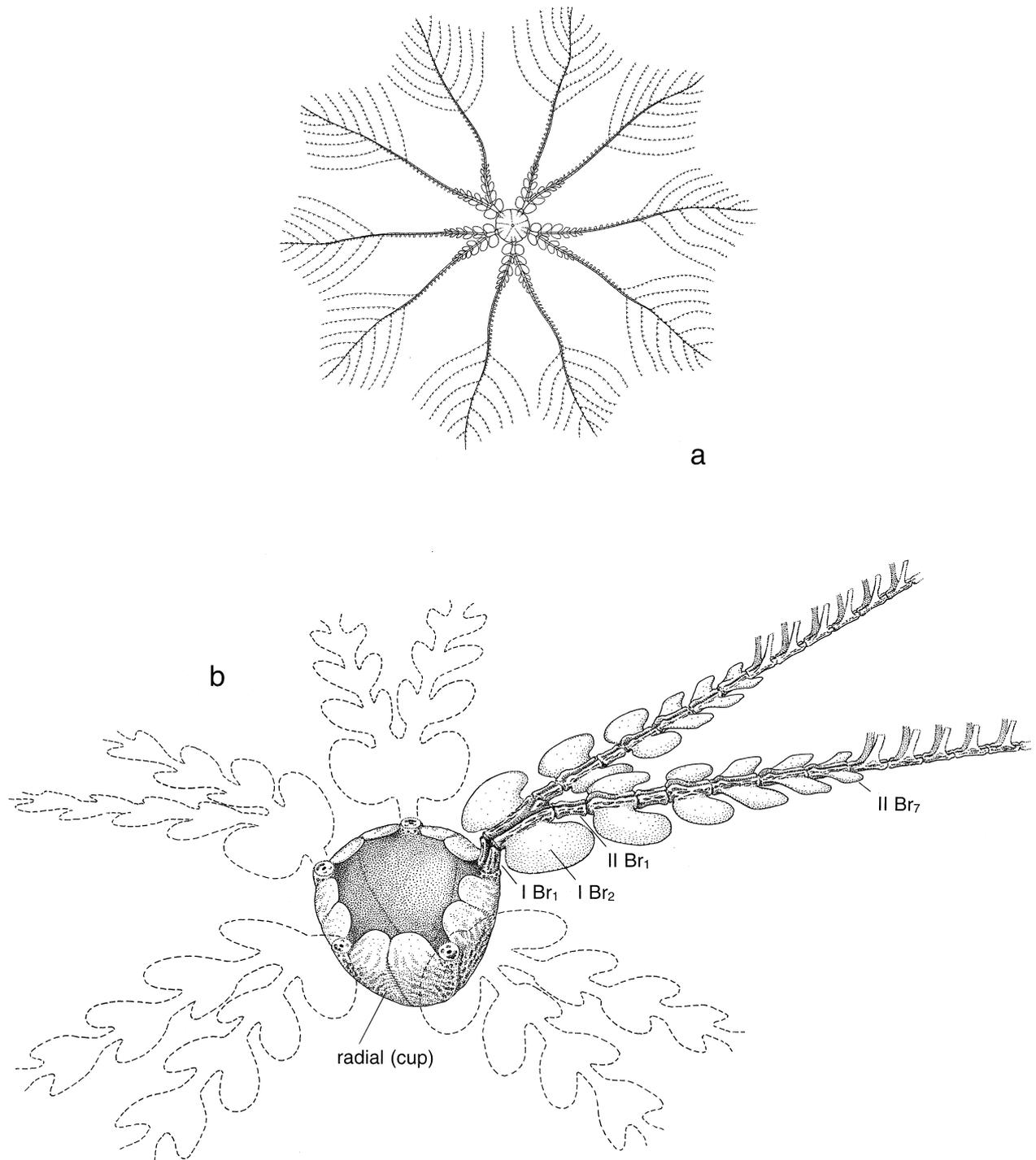
Adult specimens reach an overall arm length of 25 mm (Fig. 219) with a cup height of 4 mm and a cup diameter of 5 mm. Juveniles have arms of 5 mm on a cup less than 1 mm high. The arms of these small specimens are branched only once at the first axillary. The cup, a hemisphere or open bowl without preserved tegmen, is formed by five very thin reticulate radials. They have a median ridge thickened on top with anastomosing ribs to carry a small articular facet for the first primibrachial, which is very short in aboral view (Fig. 220). This articulation is muscular, and the articulation between the first and second primibrachials ( $\text{IBr}_1$ – $\text{IBr}_2$ ) is weakly synarthrial (crypto-synarthrial) and outwardly sloping. The same type of articulation is between the first and second secundibrachials ( $\text{IIBr}_1$ – $\text{IIBr}_2$ ) and between the third and fourth secundibrachials ( $\text{IIBr}_3$  and  $\text{IIBr}_4$ ). Incidentally,  $\text{IBr}_1$ ,  $\text{IIBr}_1$  and  $\text{IIBr}_3$  are wingless (see later in this section). The two distal articular facets



**Fig. 219.** *Saccocoma tenella* on a lower bedding plane, Langenaltheim. The specimen has unusually well-preserved *Schwimmplatten*, which also occur on the third secundibrachials; on one of the arms the second primibrachial is not axillary. (Hess Collection; photograph S. Dahint.)  $\times 3$ . To view this figure in colour, see the colour plate section following page xv.

of the second primibrachial or first axillary are muscular. These facets (or at least their visible aboral ligament pits) slope outward at an angle of  $45^\circ$ . Due to the sloping facets of the primibrachials and the first secundibrachial, the arms are more or less horizontal at this point

(Fig. 220b). Such a position is ideal for floating. Each second primibrachial divides in adult individuals into two, giving a total of 10 main arms with a number of side arms. These originate in some sort of pinnule socket, but their elements are essentially comparable to



**Fig. 220.** Reconstruction of *Saccocoma tenella*. (a) Aboral view of a complete animal. (Redrawn from Jaekel 1918.)  $\times 1.6$ . (b) Enlarged oblique oral view of cup and proximal arms, unknown soft parts in cup omitted. Key: IBr, primibrachials; IIBr, secundibrachials.  $\times 6$ .

the elements of the main arms and cannot, therefore, be classified as true pinnules. As judged by the distinct aboral ligament pits, muscular articulations appear to be dominant in *Saccocoma*, and syzgies seem to be lacking altogether.

The axillary plate (primaxillary, IBr<sub>2</sub>), as well as some of the following brachials (IIBr<sub>2</sub>, IIBr<sub>4-7</sub>), bears conspicuous, symmetric, dish-like lateral wings or flanges (Jaekel's *Schwimmplatten*) and weak oral processes (Figs. 219, 220). Interleaved between the winged brachials are the wingless IBr<sub>1</sub> and IIBr<sub>3</sub>, obviously to avoid interference of the winged brachials during movement of the arms. These wings are also on adult specimens (corresponding to *pectinata*). However, it appears that the wings are not any larger on adults than on smaller specimens (corresponding to *tenella*). Therefore, the lateral wings may not be so obvious in the adult individuals whose ability to float was supported by the finely branched arms. The dish-like lateral wings with their dense, porcelain-like, non-reticular structure certainly would have helped to keep the animal floating; such wings occur also in other Roveacrinida. A comparatively larger wing size in juveniles (whose arms were short and less branched) makes perfect sense for a pelagic lifestyle. Away from the cup, the lateral wings are progressively reduced and, in contrast, a pair of vertical projections or baffles is present on each brachial. The length of the vertical baffles (or, more accurately, their height) exceeds that of the corresponding arm ossicle. The baffles usually lie sideways on the bedding planes and were directed orally during life so that the food grooves were lying in a deep trough (Fig. 220b). On proximal elements the baffles are extensions of the arm ossicle with the same reticular structure, and their sides are stiffened by rather strong rods. The baffles occur to the very tips of the arms, where the brachials are reduced to needles and the lateral extensions are lacking altogether. In notes to her unpublished manuscripts, the late H. Sieverts-Doreck described the vertical projections as muscle fields, but such an interpretation is rejected here in favour of a baffle function.

By virtue of the porous nature of the plates as well as of the basal wings, *Saccocoma* must have been well adapted to a pelagic way of life. The branched arms provided a filtration network in which the captured plankton was passed along the food grooves towards the mouth, assisted in its progress presumably by ciliary action. The paired baffles would have improved the food-gathering process as well as protecting the soft parts in the furrow. The dominance of muscular articulations

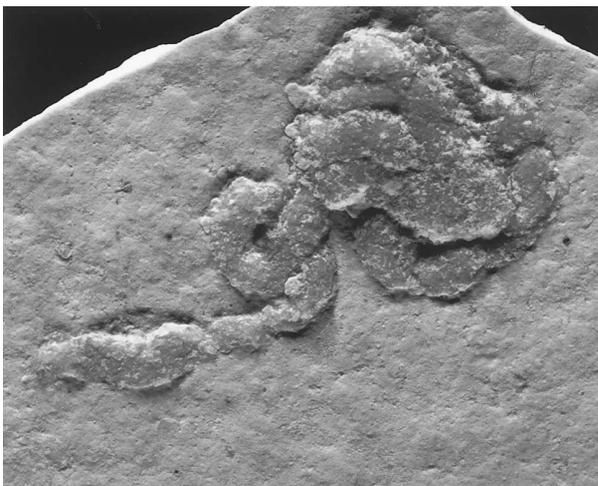
indicates considerable possibilities for displacement, such as moving the arms up and down to adjust the animal to different depths, a process helped by the *Schwimmplatten*, or moving them horizontally with the paired, wing-like baffles standing up, to create a current. A speed difference between the crinoids and the plankton it fed upon was essential; *Saccocoma* thus approached a nektonic lifestyle.

In two papers, a benthic lifestyle was proposed for *Saccocoma* (Milsom 1994; Milsom & Sharpe 1995), based on the specific gravity of the skeleton and the absence of a plausible buoyancy or swimming mechanism. However, none of the evidence from sedimentology, taphonomy and morphology supports this assumption.

At times *Saccocoma* flourished in the favourable conditions of the upper water layers. During such periods it must have been a key element in the food chain, converting and concentrating plankton (coccolithophorids and possibly other groups that were not fossilized) into food for larger animals such as small fish and small squid. The large number of *Saccocoma* feeding on coccolithophorids would have produced a huge amount of disaggregated coccoliths, contributing to the build-up of the limestone beds. The importance of *Saccocoma* in the food chain is proved by the common occurrence of coprolites (fossilized faeces), which are composed of their remains (Fig. 221). Müller (1969) thought that they originated from fishes, whereas Janicke (1970) claimed that they were excreted by teuthoid cephalopods. A specimen of the aspidoceratid *Physodoceras* from Nusplingen with remains of *Saccocoma* in the living chamber proves that certain ammonites fed on this crinoid (Lehmann & Weitschat 1973). Smaller, heap-like coprolites (Fig. 221) were thus probably excreted by cephalopods. The conspicuous, worm-shaped cylinders, named *Lumbricaria intestinum* and reaching a length of 170 cm (Barthel *et al.* 1990), may have been produced by a fish with a peristaltic gut. This is assumed from the constrictions of *Lumbricaria intestinum*. The coiled nature of *Lumbricaria intestinum* leaves little doubt that these coprolites descended directly to the sea floor from an animal living and feeding in the water above.

## REEFS AS HABITAT OF BENTHIC CRINOIDS?

The comatulid *Pterocoma pennata* is fairly common in the Zandt quarries. It has also been found in the Solnhofen area (Fig. 222) but is rare around Eichstätt. This slender species has 10 long arms (up to 130 mm) with



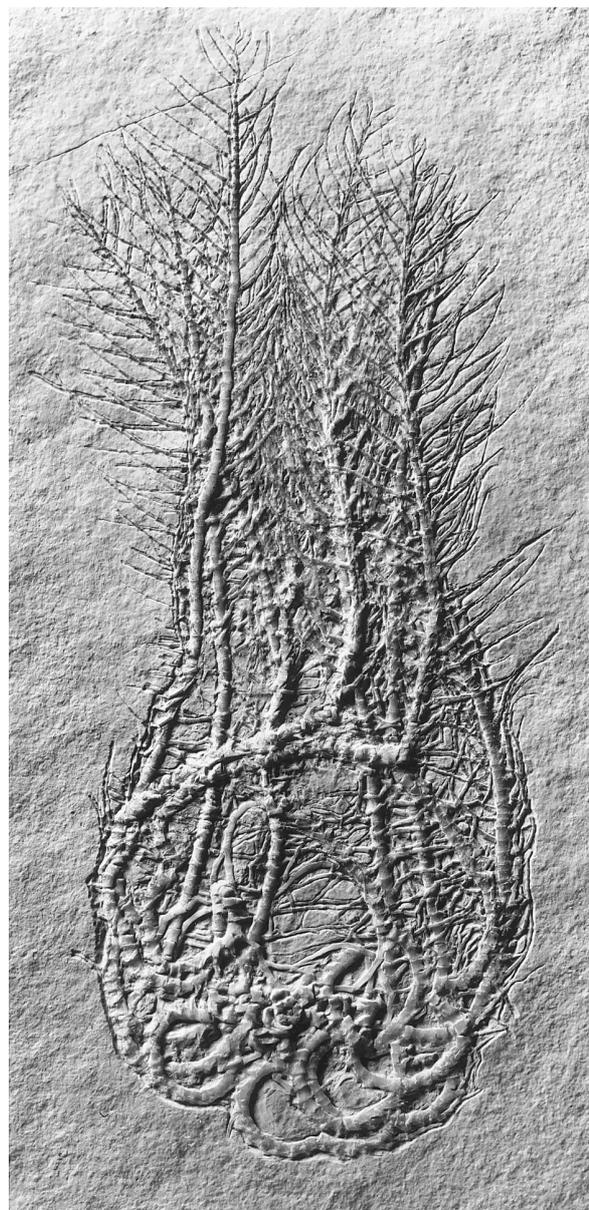
**Fig. 221.** Coprolite, composed of *Saccocoma* remains. Plattenkalk of Schernfeld near Eichstätt, lower surface. (Natural History Museum, Basel; photograph S. Dahint.)  $\times 3$ .

very long pinnules (up to 15 mm). The slender cirri are composed of very long cirrals and lack terminal hooks. Ligamentary articulations (syzygies) occur at intervals of four to five secundibrachials in the proximal part, where many fossils have arm breaks. The arms are typically coiled aborally and tangled in the proximal part, and the tips are straight with pinnules widely extended. This preservation is probably due to the more rapid decomposition of the oral (ventral) muscles than the aborally (dorsally) situated ligament, thus exerting a pull. Such arching is also present in many fish skeletons, and this may also be due to the shrinkage of ligaments after death.

Another comatulid, the sturdier '*Pachyantodon*' *gracilis*, is exceedingly rare (Walther 1886; later referred to *Solanocrinites*). It has been found near Kelheim and must have come from neighbouring sponge–algal mounds or from patch reefs. The same is true of an almost complete specimen of *Millericrinus* (now *Pomatocrinus*) *nobilis* described by Walther (1886) and other millericrinid remains (incorrectly named *Millericrinus mespiliformis* by Frickhinger 1994). *Pterocoma pennata*, on the other hand, with its slender build and its elongated cirri without a terminal hook, seems well adapted to life on a muddy bottom. The extremely long pinnules may have been an adaptation to an environment where currents were weak and, therefore, the supply of food was rather limited. The absence of autochthonous benthic forms associated with *Pterocoma* seems to exclude *in situ* burial at the place of living, possibly higher, sufficiently oxygenated soft grounds (Fig. 223).

## PLATTENKALK ORIGIN: CONFLICTING THEORIES AND OPEN QUESTIONS

The formation of this sediment has long been and still is a puzzle, because no exact Recent analogue is available for comparison. Barthel, who devoted much of his all-too-short life to these sediments, as well as other scientists thought that the Solnhofen Limestone was deposited in partly closed basins (*Wannen*) with re-



**Fig. 222.** *Pterocoma pennata*, on lower bedding plane, Plattenkalk, Solnhofen. (Jura Museum, Eichstätt; photograph left by H. Doreck.)  $\times 1.6$ .

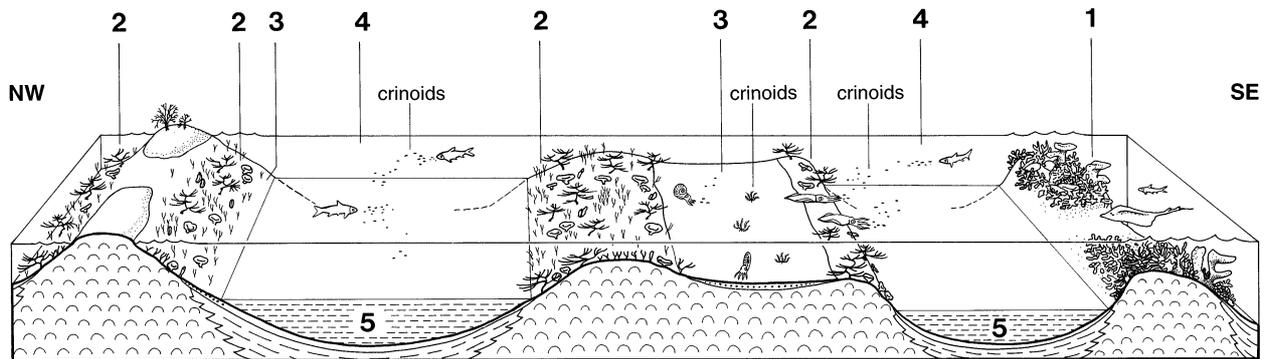


Fig. 223. Deposition areas of Plattenkalke. (1) Coral patch reef; (2) hardgrounds on top of ancient sponge mounds, penetrating into surface waters with normal salinity and colonized by seaweeds, sponges and octocorals; (3) soft bottoms with various invertebrates, including *Pterocoma pennata*; (4) surface waters with plankton (including *Saccocoma*) and nekton; (5) hypersaline, stagnant bottom waters. (Redrawn from Viohl 1996.)

stricted water flow. A tropical climate could have caused rapid evaporation. The bottom environment was very calm, as demonstrated by settling marks next to fossils and scratch marks of decaying fish (Viohl 1994). Many animals, such as the shoals of young fish and also large fish with prey still in their mouth, must have been rapidly killed, presumably due to a lack of oxygen rather than by an increase in salinity, which would not have killed them so quickly. The scarcity of burrows in the sediment together with the lack of pyrite and normal concentrations of iron and manganese (high concentrations would indicate anoxic conditions as in the Posidonia Shale) appears paradoxical. According to Barthel *et al.* (1990), the salinity of the lower water layers must have been sufficiently high (at least 4–5%) that burrowing animals could not exist in the basins.

The sudden death of marine vertebrates, so obvious in these sediments, is paralleled by the occurrence of *Saccocoma*, deposited mainly articulated and in life position (i.e., aboral side of cup downward). The reason for the coiling of the arm tips or the complete curling up of the arms so frequently observed is not known, but it seems unlikely that this preservation was due to posthumous changes such as dehydration. The cause of death of huge swarms of *Saccocoma* is unknown. Theories include an influx of fresh water from rain or poisoning by blooms of phytoplankton, a rather unlikely explanation in view of the low organic productivity of the basins (Barthel *et al.* 1990). Reproduction of *Saccocoma* may not have been uniform throughout the basins, but dependent on temporary favourable local conditions of water movement and food supply. Once these conditions failed, the crinoids would have died off quickly.<sup>3</sup>

One of the keys to the reconstruction of the environment is the origin of the extremely fine-grained lime mud. To what extent coccolithophorids (planktonic algae), possibly the main food of *Saccocoma*, contributed to the lime mud making up the beds is uncertain. Coccoliths are found mainly on the bedding planes. Barthel (1978) concluded from the scarcity of fossils in the *Flinz* Beds that these were rapidly deposited, with the bulk of sediments washed in during storms. A possible Recent analogue may be on the Bahama Bank, where during the present highstand of sea level, fine-grained carbonates on the bank tops are stirred up during storms and swept away in suspension (Heath & Mullins 1984). These bank-derived muds then settle in adjacent basins which can be tens of kilometres away. A geochemical analysis of beds from Eichstätt suggests that carbonate and clay particles may have been transported into the area from an outside source as a ready mixture (Bausch *et al.* 1994). The occurrence of *Krumme Lagen* points to some relief in the Plattenkalk area; and as a consequence, some beds may also have been the result of gravity flows or turbidites of uniform, fine-grained lime mud. This carbonate ooze is the fine debris originating from calcareous algae, but may also contain carbonate resulting from the precipitation of tiny aragonite needles in shallow water. (Such whitening of the water occurs regularly in the Bahamas and the Persian Gulf, where precipitation is caused by the removal of CO<sub>2</sub> by assimilating algae.)

On the basis of fish taphonomy, Viohl (1994) inferred very rapid deposition of the *Flinz*, with several laminae representing less than a year. One problem in the *Flinz* layers is that appreciable diagenesis has altered

the original nature of the fine-grained carbonate material to a micrite, the origin of which is now difficult to determine. *Flinz* periods were followed by quiet, marly *Fäule* episodes. During such times cyanobacteria, whose spherical remains occur in some of the *Fäule* beds, could have formed mats on the lime mud, reflecting the presence of some oxygen in the lower water layers. The scarcity of benthic organisms points to rather hostile conditions on the bottom, but rich life must have been possible at times in the upper water layers, as documented by *Saccocoma* and the coprolites containing them (Fig. 223).

### THE WIDE DISTRIBUTION OF SACCOMIDS IN THE MESOZOIC

*Saccocoma tenella* is a wide-ranging Tithonian species that has been reported from Russia to Cuba (Nicosia & Parisi 1979). Remains of saccocoids are frequently encountered in thin sections of pelagic Jurassic and Cretaceous limestones of the Mediterranean zone and the Atlantic area. Elements isolated from marly sediments include an Upper Oxfordian species with lateral wings (*Schwimmlatten*) on brachials and branched, antler-like spines on the cup, called *Saccocoma quenstedti* (Verniory 1961; see also Pisera & Dzik 1979). Secundibrachials, described by Verniory (1962) from the Tithonian of the French Alps, have lateral wings (Verniory's *expansions nataoires*) of amazing size, with a length up to six times that of the corresponding brachials! A number of ossicles assigned to several Upper Jurassic species were recovered during Leg 11 of the Deep Sea Drilling Project off the Florida coast (Hess 1972b).

### IMPORTANT COLLECTIONS IN GERMANY

Many museums all over the world contain fossils from the Solnhofen Plattenkalk. Fine specimens are, for ex-

ample, preserved in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich. We would, however, recommend a visit to the local museums, such as the very interesting Jura Museum in Eichstätt, beautifully set in a castle (Willibaldsburg), and one of the private museums – for example, the Maxberg Museum near Solnhofen, which also has an interesting exhibition of the technique to produce lithographic plates. Such a trip could be combined with a visit to one of the quarries – for example, in the Eichstätt area – which abound with *Saccocoma*.

### NOTES

1. The ophiuroids *Sinosura kelheimensis* and *Ophiopetra lithographica* are from the somewhat younger Mörsheim Beds (Malm Zeta 3) of the Kelheim/Eining/Weltenburg area. They appear to have lived on the bottom at or near the place of burial.
2. The paired vertical, orally directed projections that give the arms their pectinate appearance on the bedding planes are common to both species. The corresponding brachials are usually preserved sideways, in contrast to the proximal brachials with their lateral wings, which present their aboral side in accordance with the cup.
3. Very fine sediment brought in by storms would have impaired the crinoids' feeding abilities, preventing further movement. The immobilized animals then sank to the bottom in a cloud of settling sediment; by virtue of their higher density and their center of gravity near the cup, the crinoids would have reached the bottom in life position before the bulk of the sediment. This new theory, reached by the author only at the page proof stage, gives a plausible explanation for the taphonomy observed. It may also resolve the mystery of the curled-up specimens with their orally enrolled arms (Fig. 218). This unusual behaviour must have resulted from muscular contractions of the brachials, presumably to protect the food grooves against invasion of mud. Posthumous decomposition of the muscles can be ruled out because this would have caused the arms to become aborally flexed, as in the case of *Pterocoma pennata* (Fig. 222).