

Sedimentology, taphonomy, and palaeoecology of a laminated plattenkalk from the Kimmeridgian of the northern Franconian Alb (southern Germany)

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Abstract

At Wattendorf in the northern Franconian Alb, southern Germany, centimetre- to decimetre-thick packages of finely laminated limestones (plattenkalk) occur intercalated between well bedded graded grainstones and rudstones that blanket a relief produced by now dolomitized microbialite-sponge reefs. These beds reach their greatest thickness in depressions between topographic highs and thin towards, and finally disappear on, the crests. The early Late Kimmeridgian graded packstone–bindstone alternations represent the earliest plattenkalk occurrence in southern Germany. The undisturbed lamination of the sediment strongly points to oxygen-free conditions on the seafloor and within the sediment, inimical to higher forms of life. The plattenkalk contains a diverse biota of benthic and nektonic organisms. Excavation of a 13 cm thick plattenkalk unit across an area of 80 m² produced 3500 fossils, which, with the exception of the bivalve *Aulacomyella*, exhibit a random stratigraphic distribution. Two-thirds of the individuals had a benthic mode of life attached to hard substrate. This seems to contradict the evidence of oxygen-free conditions on the sea floor, such as undisturbed lamination, presence of articulated skeletons, and preservation of soft parts. However, palaeoecological and taphonomic analyses indicate that the benthic faunal elements are allochthonous having settled out of suspension and thus must have been derived from hard substrate areas of neighbouring topographic highs. Solely the bivalve *Aulacomyella*, which occurs concentrated on a single bedding plane, may have colonised the plattenkalk depression during brief periods of oxygenation. Alternatively, a pseudoplanktonic mode of life, attached to floating sea weed, is envisaged for the bivalve. The formation of the plattenkalk is related to local and global factors: a drop in relative sea level caused the death of the microbialite-sponge reefs. Restricted circulation in depressions between the crests of the former reefs led to anoxic conditions and the formation of finely laminated sediments stabilised by microbial mats. The small depressions received sediment and skeletal elements of benthic organisms that were swept off neighbouring topographic highs by storms and that entered the depressions partly as turbidity currents, partly as suspension clouds. A rise in the relative sea level finally terminated the restricted circulation in the depressions and closed the taphonomic window that led to the preservation of the plattenkalk biota.

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1. Introduction

Thinly laminated limestones, so-called plattenkalk, are classical fossiliferous sites. Assumed to have formed

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under anoxic conditions in lagoons or small restricted basins (e.g., Barthel et al., 1990; Swinburne and Hemleben, 1994; Viohl, 1998; Dietl and Schweigert, 2004), they preserve articulated skeletons and soft-bodied organisms and thus provide exceptionally rich information on fossil ecosystems. The late Jurassic appears to have been a time particularly prone to the formation of plattenkalk deposits, most of them to be found along the northern margin of the Tethyan Ocean (e.g., Cerin in the French Jura Mountains; Nusplingen on the Swabian Alb, and Solnhofen-Eichstätt on the Franconian Alb; Bernier and Gaillard, 1990; Gaillard et al., 1994; Dietl and Schweigert, 1999, 2004; Barthel et al., 1990; Viohl, 1998; Viohl and Zapp, 2005; Röper, 2005a,b). In the case of the last occurrence, we do not deal with a single lagoon, but rather an extensive lagoonal system consisting of a number of sub-basins which partially also differ in age (Schweigert, 2005; Röper, 2005a). Although apparently only of limited lateral extent and thickness, the Wattendorf plattenkalk adds another facet to the known plattenkalk occurrences, differing from other plattenkalks by its abundant benthic macrofauna.

As early as 1891 Gümbel mentioned white, platy limestones with occasional remains of crustaceans from an area between the villages of Wattendorf, Mährenhüll, and Rothmannsthal in the northern Franconian Alb, and regarded them as equivalents of the Solnhofen lithographic limestones. However, subsequently these occurrences received no further attention and little else is known about plattenkalks in the northernmost part of the Franconian Alb. Following its renewed discovery in a quarry near Wattendorf (Fig. 1) in 2002, where it forms thin intercalations within a package of carbonates that unconformably overlies massive, dolomitized microbialite-sponge reefs, an excavation campaign was undertaken in August 2004. The results from these field investigations not only provides information on the northernmost occurrence of the plattenkalk facies on the Franconian Alb, but ammonites recovered during the field work also show that it is the oldest plattenkalk in southern Germany, representing the early Late Kimmeridgian (Fig. 2; Fürsich et al., *in press*). The aim of the paper is the documentation and analysis of the facies and biota of the Wattendorf plattenkalk. In particular palaeoecological and taphonomic analysis of the fauna based on quantitative data allow

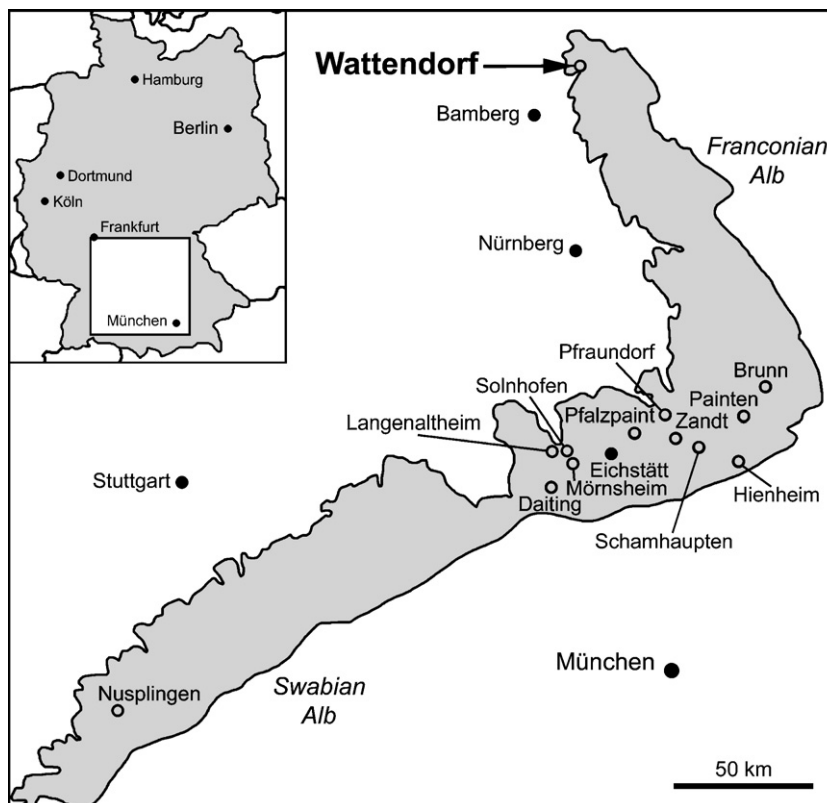


Fig. 1. Upper Jurassic plattenkalk localities of the Franconian and Swabian Alb (shaded) and location of Wattendorf.

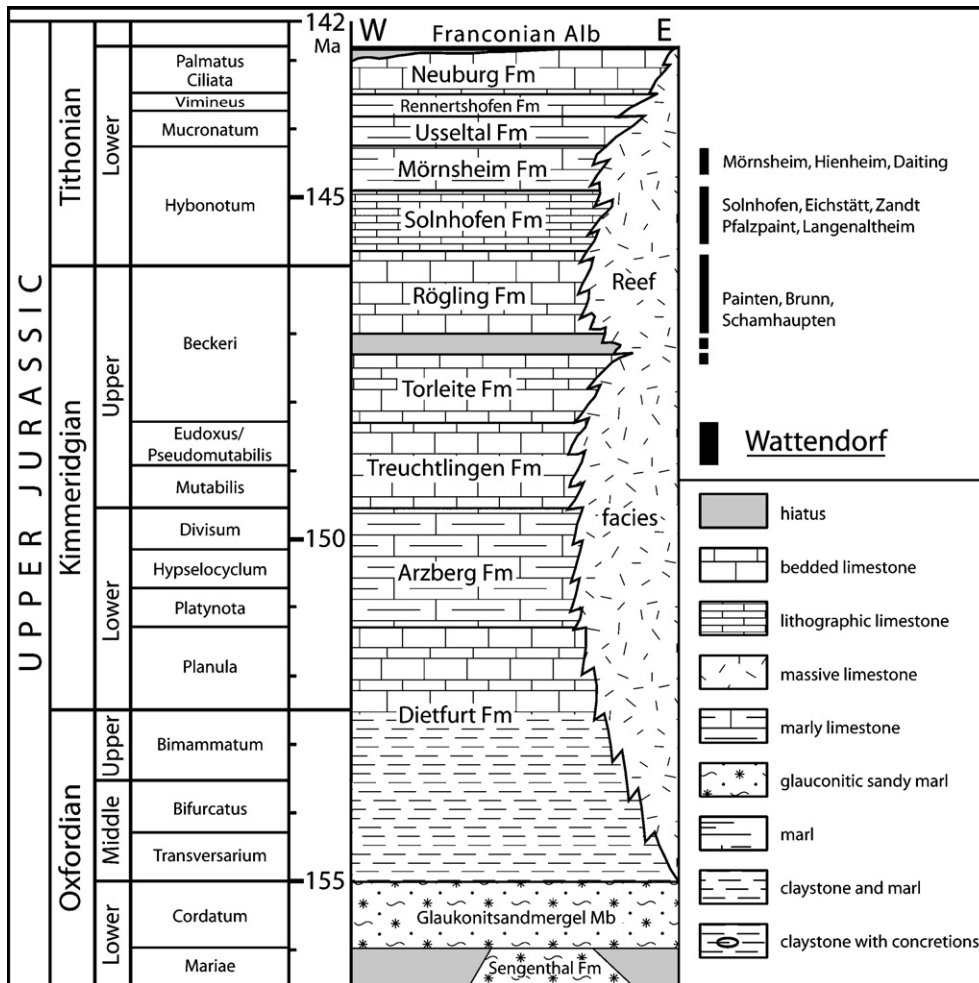


Fig. 2. Stratigraphic table of the Upper Jurassic rocks of the Franconian Alb (modified from Schmid et al., 2005) with position of the Wattendorf plattenkalk. Absolute ages according to Ogg (2004). The lithostratigraphic units have been established for the southern Franconian Alb, the area of most of the other Upper Jurassic plattenkalk deposits. A corresponding scheme for the northern Franconian Alb (Zeiss, 1977; Koch and Weiss, 2005) does not include lithological equivalents of the Wattendorf plattenkalk.

the detailed reconstruction of the depositional environment and of the origin of the biogenic components.

2. Geological framework

The quarry lies in the northern part of the Franconian Alb (Fig. 1) (geological map 1: 25,000 sheet 5932 Ützing) about 800 m NW of Wattendorf, NE of Bamberg. In the northeastern part of the quarry massive dolostones are exposed, whereas in the southwestern part bedded micritic limestones, the so-called Wattendorf Limestone (Wattendorf Member of the Torleite Formation *sensu* Zeiss (1977)) occurs. Thinly bedded to laminated bituminous dolostones onlap the massive dolostones (Fig. 3B), which, by analogy with other occurrences of this type in

the Upper Jurassic of the Franconian–Swabian Alb, are interpreted as dolomitized microbialite-sponge reefs (e.g., Hegenberger and Schirmer, 1967; Flügel and Steiger, 1981; Meyer and Schmidt-Kaler, 1989; Leinfelder et al., 1993, 1996, 2002). Close to the boundary between the two facies the dip of the laminated dolostones reaches 40°, decreasing with increasing distance from the massive reefal dolostones (Fig. 3B). Most likely, this extreme dip has been accentuated due to differential compaction between the presumably early lithified reef limestones, which underwent little or no compaction, and the laminated facies, which appears to have been deposited in depressions between the reefs. As is shown below, in the case of the plattenkalk facies compaction preceded cementation.

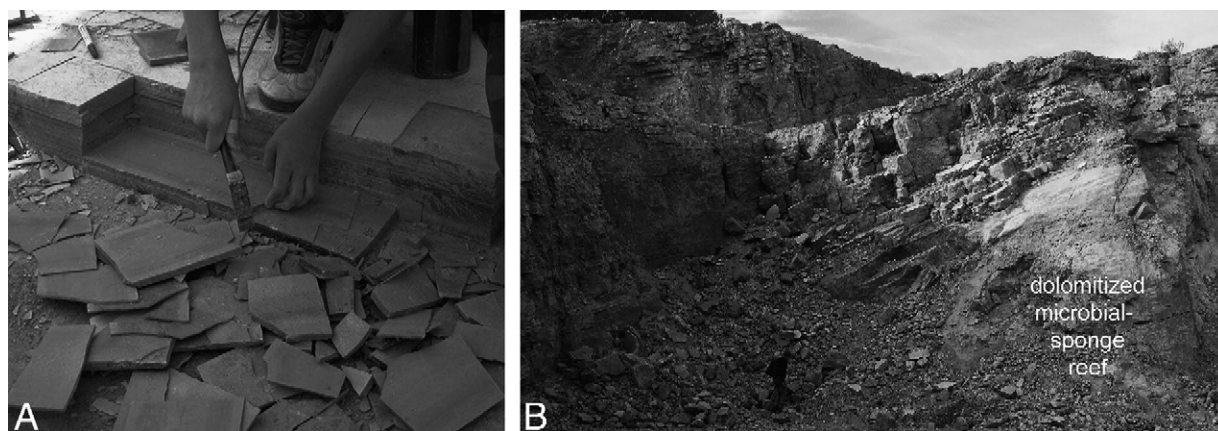


Fig. 3. A The plattenkalk of the excavation level in the southern part of the Wattendorf quarry. B View looking northwest showing thinly bedded dolostones onlap a relief formed by a microbialite-sponge reef (right) now preserved as massive dolostone. The dip of the thin-bedded dolostones corresponds to the slope of the microbialite-sponge reef, but has been accentuated by compaction.

The degree of dolomitisation of the plattenkalk facies decreases with increasing distance from the reef. At the excavation site, in the southwestern part of the quarry away from the reef body, calcareous preservation is the rule.

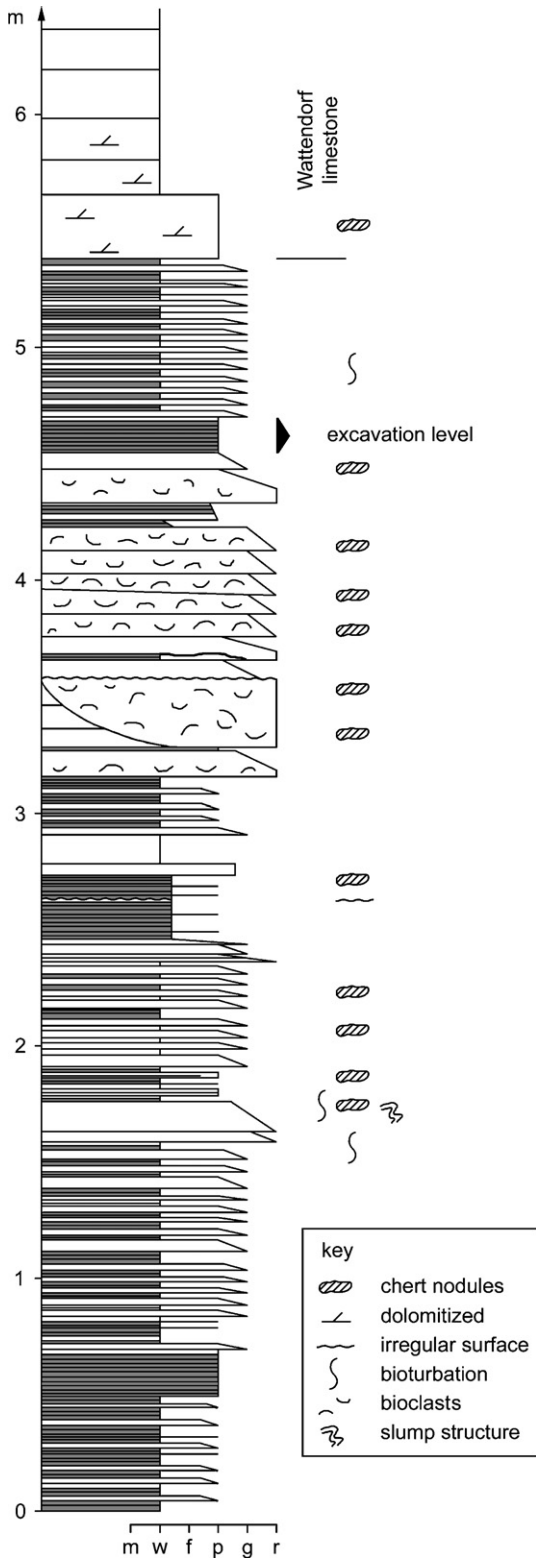
The thickness of the sediment package containing the plattenkalk is around 6–7 m at the margin of the depression but thins to zero on top of the massive dolostones in the northeastern part of the quarry. The overlying Wattendorf Limestone, well-bedded wackestones, is also dolomitized in the immediate vicinity of the reef body, but developed in calcareous facies elsewhere. Gümbel (1891) counted this limestone among his “Krebsscheren (= crustacean claws)” or “Prosoponkalken”, which he regarded as the northern equivalent of the Solnhofen lithographic limestones. Consequently, he assigned it to the Lower Tithonian (Malm zeta). This view was supported by Dorn (1928) and Kuhn (1937, 1983). In contrast, Hegenberger and Schirmer (1967), Meyer (1970), and Schirmer (1985) assigned a Late Kimmeridgian age to the Wattendorf Limestone. The presence of the ammonite *Aulacostephanus eudoxus* (d’Orbigny) in the plattenkalk facies pinpoints its age to the early Late Kimmeridgian. Thus, the Wattendorf plattenkalk is the oldest occurrence of this facies in southern Germany. The age of the base of the overlying Wattendorf Member is, therefore, most likely Late Kimmeridgian (Malm epsilon).

3. Materials and methods

During a three weeks’ period in August–September 2004 about 80 m² of a plattenkalk unit were excavated in the southwestern part of the quarry at Wattendorf.

Excavation of a 6 m deep trench in October 2005 provided information on the facies context of the excavated unit, although the top of the underlying reef body was not reached. The facies consisted of alternations of thick-bedded and finely laminated facies typical of that seen elsewhere in the quarry in the close neighbourhood of the reefal dolostones, but less strongly dolomitized. The detailed excavation was confined to the uppermost, 13 cm thick, plattenkalk intercalation. No large bedding surfaces could be excavated, as the rocks are dissected by numerous small-scale joints and splitting of the laminated facies proved difficult at some levels. Instead, small packages of the plattenkalk were removed at a time and systematically split layer by layer (Fig. 3A). All fossils were recorded, numbered, and their stratigraphic position within the 13 cm thick plattenkalk was noted as accurately as possible. Although excavation was difficult due to small-scale fracturing of the rock, we were able to record the stratigraphic position of fossils with an accuracy of 0.5 cm for the palaeoecological and taphonomic analyses. Altogether approximately 10.5 m³ of plattenkalk facies were searched and about 3500 palaeontological objects recovered. The information was recorded in a field log book and later transferred to excel spread sheets for further analysis. A block of the excavated unit has been fixed in the laboratory with resin and carefully cut so that a complete section of the plattenkalk was available for study.

During a second excavation campaign in September–October 2005, additional material (approximately 800 specimens) was collected from the plattenkalk horizon (although no quantitative analysis was undertaken) in order to obtain a more comprehensive picture of the biota.



So far, only part of the fossil collection has been studied in detail, with most emphasis placed on the shelly benthic macrofauna. Other groups such as fishes and crustaceans, which contain some new taxa, still await study by specialists. For the microfacies analysis thin-sections and polished sections of the complete plattenkalk and of selected horizons above and below were prepared. All fossil material is housed in the Natural History Museum, Bamberg.

4. The section

The thickness of the sediment package between the massive dolostones and the Wattendorf Limestone at the excavation site is at least 6 m (Fig. 4). A more than 5 m thick section measured at a distance of less than 10 m from the excavation site revealed in its lower half millimetre- to centimetre-thick finely laminated plattenkalk facies alternating with equally thin intercalations of graded grainstones and packstones, more rarely of rudstones (Figs. 4 and 5). Some of the graded debris layers have an erosional base. This unit is followed by approximately 1.5 m of graded rudstones and grainstones with oncoids and abundant debris and complete shells of brachiopods, bivalves, echinoids, corals, calcareous algae, chaetetids, *Tubiphytes*, *Lithocodium*, and bryozoans (Table 1). The individual beds are partly amalgamated, partly separated by thin, laminated wackestone intervals. The following units consist of plattenkalk facies, the lowest level of which corresponds to the plattenkalk intercalation studied in detail. Laminated wackestones to packstones with numerous millimetre to centimetre-thick graded grainstone to packstone intercalations follow. The basal bed of the Wattendorf Limestone consists of 30 cm of dolostone. Chert nodules, in some cases forming more or less continuous layers, occur at several levels within the section, usually in association with grainstones and rudstones. The Wattendorf Limestone, exposed for approximately 20 m, is well bedded and locally dolomitized.

The coarse bioclastic debris and other components of the graded beds such as oncoids and coated grains are clearly of shallow-water, possibly reefal origin. Signs of slumping indicate rapid deposition and a certain relief of the sea floor. Thus, these beds are event horizons. Most likely, storms swept the debris from the edge of topographic

Fig. 4. Section through the rock unit intercalated between the massive dolostones (below, not seen) and the well bedded Wattendorf Limestone (above), which consists of thin beds of plattenkalk facies intercalated between graded packstones to rudstones. For a detailed section of the investigated plattenkalk unit see Fig. 5. m: mudstone, w: wackestone, f: floatstone, p: packstone, g: grainstone, r: rudstone.



Fig. 5. Polished section through graded unit within the plattenkalk facies below the excavation level. Rudstone and the following grainstone fabric with microsparitic matrix, top developed as wackestone; the large components of the rudstone are oncoids, coated grains, shell fragments of brachiopods, bivalves, thalli of *Cayeuxia* and *Tubiphytes*; the irregular undulating base of the rudstone is caused by loading effects and show that the underlying finely laminated wackestones and packstones were still soft. N12, at 3.50 m (see Fig. 4).

highs formed by the microbialite-sponge reefs and initiated high density currents, transporting the material into neighbouring depressions. Judging from the composition of the debris, these shallows were no longer populated by microbialite-sponge biota, which form the bulk of the massive dolostones exposed in the quarry. Instead, the microbialite-sponge reefs, probably due to early diagenetic cementation, appear to have provided a hard substrate on which brachiopods, byssate and cementing bivalves, corals, calcareous algae, etc. flourished. We envisage that their debris formed a thin veneer, possibly in the form of small sand waves, on the hard substrate. Based on the common and diverse coral debris, possibly even small coral patch reefs existed on these shallows.

5. Sedimentology and microfacies of the plattenkalk

The following observations refer to the microfacies of the laminated units (Fig. 6), which consist of three facies types; very fine-grained graded beds, microbial laminae, and thin clay laminae.

5.1. Graded beds

The most characteristic feature of the plattenkalk is its fine lamination. The laminae greatly vary in

Table 1

Components of graded grainstones and rudstones which are derived from neighbouring shallow-water areas

Microproblematica

?*Bacinella* sp.
Iberopora bodeuri Granier and Berthou

Cyanobacteria/Algae

Cayeuxia sp.
Solenopora sp.
Solenopora cayeuxiformis Leinfelder
Thaumatoporella sp.

Foraminifera

Troglotella sp.
Ammobaculites sp.
Neotrocholina sp.
Placopsilina sp.
?*Koskinobullina* sp.
Tubiphytes sp.
Lithocodium sp.
Encrusting foram

Porifera

Calcareous sponge
Neuropora sp.

Scleractinia

Microsolena sp.
?*Stylosmilia* sp.
cf. *Thecosmilia* sp.
Ceriod coral (cf. *Actinastrea/Thamnasteria*)

Brachiopoda

Terebratulina substriata (Schlotheim)
Trigonellina pectuncula (Schlotheim)
Ismenia pectunculoides (Schlotheim)

Bryozoa

Bereniceid type

Bivalvia

Ostreid indet.
Bivalvia indet.

Echinodermata

Echinoid spines
Echinoid test

Other components

Oncoids
Coated grains
Intraclasts (lumps)

Some of the components have been observed in thin-sections, others were recovered by mechanically breaking up blocks. Yet others were recovered by sieving weathered de-silicified chert nodules.

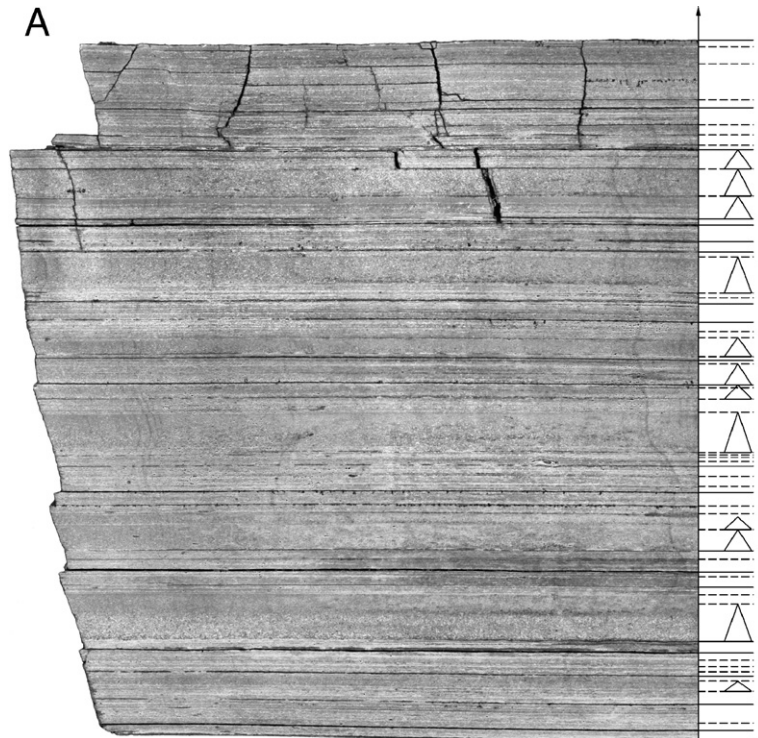


Fig. 6. A, B Polished section through the plattenkalk with the distribution of the fossil groups. Given is the number of specimens recovered during the excavation phase 1 (August–September 2004). The data have been lumped in 0.5 cm intervals. The triangles indicated graded layers, the vertical black bars indicate positions of laminated intervals. Solid horizontal lines refer to major bedding planes, which correspond to thin, clay-rich intercalations (“fäule”). Dashed horizontal lines correspond to less well defined bedding planes.

thickness, ranging from fractions of a millimetre to 10 mm (Fig. 6). The thicker laminae usually represent very finely graded beds with a sharp, planar to undulous base (Fig. 7A). The grain size/microfacies changes from very fine-grained packstone (calcarenite to calcisiltite) at the base to mudstone (calcilitite) at the top. Many of the components are recrystallized and cannot be identified. Larger components are bioclasts, among them fragments of punctate brachiopods and questionable sponge rhaxae. In some cases, two or more graded beds directly overlie each other. In most cases, graded beds are separated by layers that are very finely laminated.

One interpretation for the origin of the graded beds is that they were deposited by high density currents and that the material was derived from shallower areas where, probably caused by storms, sediment was brought in suspension and moved downslope to become deposited in depressions. Such an interpretation is supported by the sharp base exhibited by the beds. An alternative, in our opinion more likely, explanation is that the material was brought into suspension on topographic highs by storms and that this sediment cloud moved away from the shallows to subsequently settle down in the depressions.

The latter interpretation is supported by the small thickness of the graded beds, the fine-grained nature of the sediment, and the fact that the much larger shells of bivalves, gastropods, and brachiopods invariably appear to have been introduced into the plattenkalk depression not by bed load transport but by settling out of suspension (see below).

The apparent contradiction between this interpretation and the sharp base of the graded beds, which suggests erosion by currents preceding deposition of the sediment load of a density current, can be resolved, when this sharp base is interpreted to be the result of biofilms that formed a discrete boundary. Thus, the thin graded beds within the plattenkalk facies are thought to be the result of a sedimentation process different from that depositing the much thicker and coarser graded beds, which occur in between.

5.2. Microbial laminae

Between the graded beds finely laminated layers occur (Fig. 7B), which constitute more than half of the plattenkalk facies. The slightly undulating nature of the laminae, the occasional presence of discontinuous, thin,

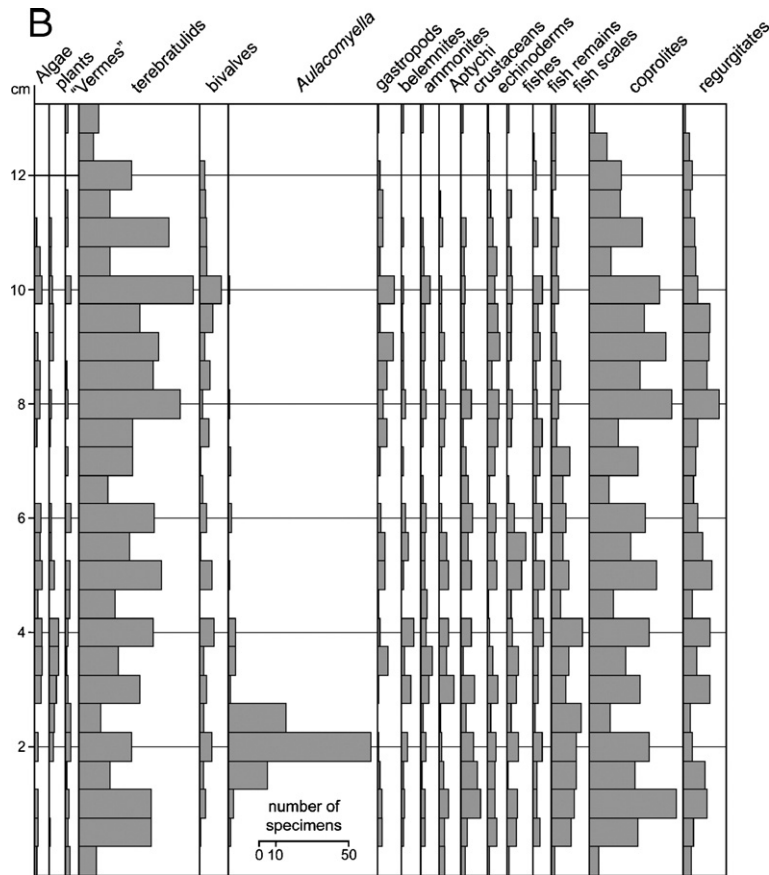


Fig. 6 (continued).

sparitic layers (reminiscent of fenestral fabric) and of small birdseyes strongly suggest that these layers represent microbial biofilms. This assumption is corroborated by the presence of cyanobacterial filaments, which occur in some layers. These bindstones are very fine-grained wackestones to packstones, which became fixed by the biofilms.

5.3. Clay interbeds (“fäule”)

At some levels within the plattenkalk, thin (<0.5 mm) clay layers occur (seen in Fig. 6 as black laminae) along which the rocks split very easily. Altogether around 15–20 of such clearly visible laminae occur (Fig. 6). They are identical in nature to the *fäule* known from other plattenkalk occurrences and represent times of reduced carbonate deposition or, more likely, times of increased influx of fine-grained terrigenous material. Such episodes most probably correspond to times of increased humidity and thus indicate small-scale climatic cycles below the Milankovich band.

5.4. Cyclicality

The distribution of the clay interbeds suggests a cyclic pattern in the deposition of the plattenkalk. Such a pattern is also supported by the distribution of the thicker graded beds (Fig. 6), which alternate with bindstone units and, in most cases, seem to be tied to the clay interbeds. Phases of increased humidity (increased clay input) associated with stronger storm activity (resulting in greater clouds of suspended material and correspondingly thicker graded beds) might reflect small-scale changes in a monsoonal climate. However, the thickness of the plattenkalk is too small to allow a statistical analysis of this pattern and the existence of this small-scale pattern has to remain speculative. The general decrease in thickness of the graded beds and the size decrease of the components (largely bioclasts) in these beds up-section point to a diminished storm intensity affecting the topographic highs, most likely in connection with a gradual rise in sea level.

6. Fossil content

Calculating that a rock volume of approximately 10.5 m³ has been excavated and carefully searched, the

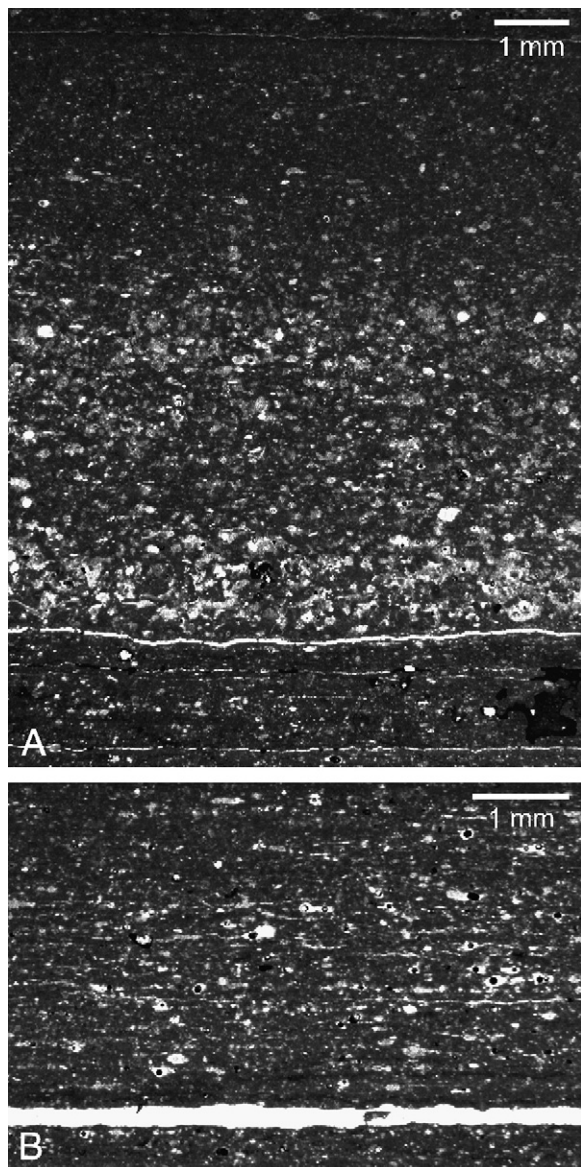


Fig. 7. Characteristic microfacies of the Wattendorf plattenkalk facies. A Thin-section with the two main microfacies types: bindstone (base) with component-poor bioclastic wackestone fabric and well developed lamination accentuated by thin, subhorizontal “fenestral” structures of probably microbial origin, overlain by graded packstone to wackestone. The graded layer is interpreted as having formed by settling of a suspension cloud. The components consist of mostly recrystallized bioclasts. Both microfacies are separated by a thin, slightly undulating layer of clay (“Fäule”) now replaced by resin. FS15-1. B Laminated bindstone with numerous subhorizontal “fenestral” structures interpreted as remains of biofilms. Note: the translucent layer in the lower part of the thin-section corresponds to a former clay-rich intercalation (“Fäule”) replaced now by resin. FS12-1.

3500 fossils recovered show that the Wattendorf plattenkalk is, compared with other deposits of that kind, rich in fossils. The main reason for this is that benthic elements are relatively common. Thus, brachiopods account for half of the specimens and bivalves for another 17% (Fig. 8A). The remaining groups (algae, plants, “worms”, cephalopods, gastropods, echinoids, crustaceans, and fishes) represent less than 10% each, and fragments of higher vertebrates (reptiles) are very rare. When viewing the relative proportion of fragments of organisms or remains of their activities, various kinds of coprolites are most abundant (55%), followed by regurgitates (19%), fish scales, fish remains, and aptychi (Fig. 8B). So far, around 80 taxa have been recorded (Table 2), but this is surely a gross underestimation of the total diversity due to the limited amount of material that has been processed and because for several groups (e.g. fishes) preparation of the material has to precede precise identification. The dominance of brachiopods (50%) contrasts strongly with their low diversity (2 taxa), whereas the bivalves (17%) comprise 18 taxa.

As the benthic shelly macrofauna will be discussed in more detail below, only the remaining groups are briefly introduced in the following. Finds of land plants (2%) indicate that small land areas possibly existed in the neighbourhood of the plattenkalk depression. It is likely that some areas of the microbialite-sponge reef bodies became subaerially exposed and supported some vegetation. Alternatively, the plants were derived from the more distant Bohemian Massif.

Polychaetes (2% of the individuals) are rare elements. Most individuals belong to *Muensteria* (Fig. 9C), which has been interpreted as the agglutinated tube of a fixo-sessile sabellid polychaete (Schweigert et al., 1998). Its attached mode of life is incompatible with the soft substrate of the plattenkalk facies. The crustaceans (6% of the macrofauna; Figs. 9G and 10A), are represented by at least 13 taxa. Some of them, such as *Aeger*, *Bylgia* and *Dusa*, are swimming forms, whereas others (e.g., *Eryma*, *Eryon*, *Palinurina*) had a benthic mode of life. A preliminary investigation of the crustacean fauna revealed that all of them are exuviae (G. Schweigert, pers. comm. 2005). The ichthyofauna (5% of the individuals; Fig. 10B) is dominated by *Tharsis* and *Tharsis*-like teleosteans. Relatively common are isolated placoid fish scales, whereas rhombohedral scales of “holosteans” (in contrast to complete specimens) are conspicuously absent. Reptilian remains are scarce and represented by an isolated crocodilian tooth and a complete skeleton of a turtle.

The temporal distribution pattern of the organisms and coprolites within the plattenkalk facies does not reveal

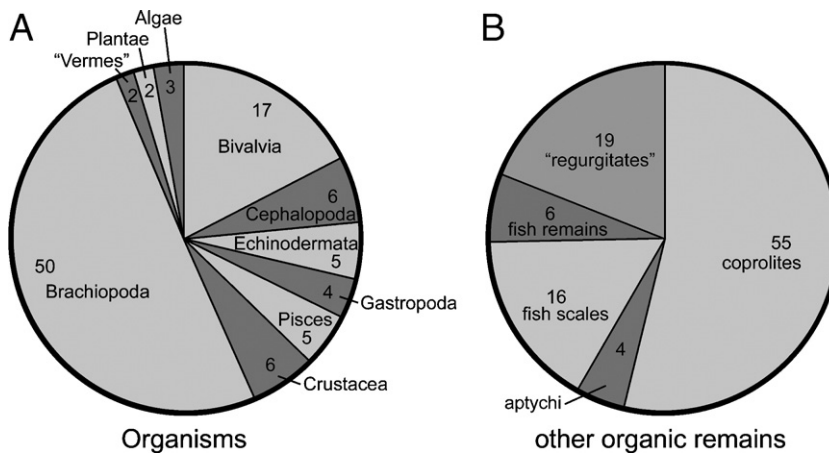


Fig. 8. Relative abundance of fossil groups (A) and of other organic remains (B) given as percentage of specimens recovered in the course of the excavation phase 1. Note that "Pisces" refers to more or less complete specimens, "fish remains" to parts of skeletons, and "fish scales" to isolated scales.

any trends (Fig. 6), except in the case of the coprolite *Lumbricaria* and the bivalve *Aulacomyella*. *Lumbricaria* occurs within the section exclusively at a height of 1.7 cm. *Aulacomyella* (Fig. 9A) occurs in very low abundance throughout the section, but exhibits a distinct peak at 1.7 cm (Fig. 11). As will be argued below, *Aulacomyella* possibly is the only autochthonous benthic faunal element, whereas the others were introduced from neighbouring shallows or reached the sea floor after they had become detached from floating objects. The lack of any trends in the distribution pattern of the organisms shows that throughout deposition of the laminated limestone conditions within the depression and on the surrounding highs remained more or less unchanged.

7. Ecology of the shelly benthic macrofauna

Benthic organisms constitute a large percentage of the taxa and more than 90% of individuals occurring in the plattenkalk. Because identification of taxa belonging to groups such as crustaceans or annelids requires extensive preparation, which has only just started, the ecological analysis of the benthic fauna has been restricted to groups with skeletal elements i.e., bivalves, gastropods, brachiopods, and echinoids. The mode of life and the feeding mode of these taxa is shown in Table 3.

Among the 19 taxa of bivalves, 12 (63%) had an epibyssate mode of life, 2 were endobyssate, 1 cementing, and 4 (21%) were infaunal (Table 3). All were suspension-feeders except the questionable nuculid, which was a deposit-feeder. In terms of relative abundance, the dominance of byssate forms is even more striking: Epibyssate (63.1%; e.g., *Pseudolimea*, Fig. 9B) and endobyssate taxa (24.6%) account for 87.7% of the individuals, cementing

oysters for 5.3%, and burrowing taxa for merely 7%, if *Aulacomyella* is excluded. With the latter taxon, the percentage of byssate individuals rises to 95.7% and the relative abundance of burrowers drops to 2.5% (Table 4).

The posidoniid *Aulacomyella* sp. is the most common bivalve. It occurs predominantly on a single bedding plane 1.7 cm above the base of the plattenkalk facies (Fig. 11). 56.7% of the *Aulacomyella* specimens are articulated, in contrast to the remaining bivalves, most of which (62%) occur as single valves. The individuals range from 16 to 47 mm in length, and a size histogram of 289 specimens shows a unimodal distribution, with a peak at 32–35 mm (Fig. 12). The shell is semi-circular in outline, radially striated, thin, and only slightly inflated (Figs. 9A and 13C). It strongly resembles the shell of Triassic *Daonella* and like that genus (e.g., Schatz, 2005), it is mainly known from very fine-grained sediments, which represent restricted intraplatform or offshore shelf to basinal settings and often oxygen-deficient environments (e.g., Freneix and Quesne, 1985; Schumann, 1988; Kelly and Doyle, 1991). Little is known about the mode of life of *Aulacomyella*. According to its shell characteristics (semi-circular shape, thin and flat valves), it fits the description of a typical flat clam (e.g. Wignall and Simms, 1990), adapted to live on a soft, soupy substrate, often associated with dysoxic conditions. The morphological details known are not sufficient to argue for or against a byssate mode of life, as a weak byssus does not require a pronounced byssal gape. Moreover Kelly and Doyle (1991) recorded an anterior gape in *Aulacomyella* from the Upper Jurassic of Scotland, which they interpreted as a byssal gape. Because of this, some *Aulacomyella* may have had a pseudoplanktonic mode of life, but it is doubtful whether *Aulacomyella* also had this mode of life

Table 2

List of fossils from the Wattendorf plattenkalk

Algae

Algae indet.

Plantae

?Brachyphyllum sp.

Porifera

Porifera indet.

?Codites spp.

Polychaeta

Muensteria vermicularis Sternberg

Crustacea

Aeger elegans Münster

Aeger tipularius (Schlotheim)

Bylgia ruedelli Schweigert and Garassino

Dusa monocera Münster

Hefriga sp.

Koelga curvirostris Münster

Eryma veltheimi (Münster)

Eryma cf. punctatum Oppel

Eryon arctiformis (Schlotheim)

Glyphea sp.

Palaeoastacus cf. fuciformis (Schlotheim)

Palinurina longipes (Münster)

Elder ungulatus Münster

Isopod indet.

Bivalvia

?nuculid

Grammatodon (Grammatodon) sp.

Grammatodon (Cosmetodon) sp.

?pteriid

?Bakevellia sp.

Aulacomyella sp.

Chlamys sp.

?Radulopecten sp.

?Camptonectes sp.

Pectinid indet.

Pseudolimea sp.

Inoceramid

Liostraea sp.

Modiolus sp.

Arcomytilus furcatus (Münster)

Praeonia rhomboidalis (Phillips)

Nicanella sp.

?Tancredia sp.

Burrowing bivalve indet.

Gastropoda

cf. Pileolus sp.

?Bathrotomaria sp.

?pleurotomariid

Neritopsis sp. A

Neritopsis sp. B

Procerithiid indet.

Globularia sp.

Gastropod sp. A (?Globularia sp.)

Table 2 (continued)

Gastropoda

Gastropod sp. B

Gastropod sp. C

Gastropod indet.

Cephalopoda

Aulacostephanus eudoxus (d'Orbigny)

Physodoceras sp.

Streblites sp.

Laevaptychus sp.

Lamellaptychus sp.

Belemnite rostra

Plesiotheuthis sp.

Trachyteuthis sp.

?Acanthoteuthis sp.

Brachiopoda

?Torquirhynchia sp.

?Juralina sp.

Echinodermata

Nucleolites sp.

Pygurus sp.

Irregular echinoid indet.

Rhabdocidaris sp.

?Pseudosalenia sp.

?Pseudodiadema sp.

Ophiuroid indet.

Asteroid indet.

Pisces

Elasmobranchii indet.

Crossopterygii indet.

Tharsis sp. A

Tharsis sp. B

Proscinetes sp.

Allothrissops sp.

Notagogus sp.

Belenostomus sp.

?Callopterus sp.

Actinopterygii indet. (>2 species)

Reptilia

Crocodilia indet. (tooth)

Testudinata indet. (complete skeleton)

Trace fossils

Lumbricaria isp.

Coprolites

Irregular trail

at Wattendorf (see below). Some taphonomic evidence suggests that, at Wattendorf, *Aulacomyella* was an autochthonous element of the plattenkalk depression resting with one valve on the substrate, either free (as assumed for *Daonella* by Schatz, 2005) or weakly attached by its byssus. It appears to have been the only macrobenthic taxon able to live in this environment and, at times, to

establish a thriving population. This population consisted of subadult to adult individuals (Fig. 12). The distinctly unimodal size frequency histogram and the total lack of any juveniles suggest that spatfalls remained single events and that juvenile mortality was very low.

Gastropods (4% of the fossils) are comparatively rare elements and represented by 11 taxa. The most abundant taxon is a pleurotomariid (?*Bathrotomaria*; Fig. 16C), followed by gastropod sp. A, most likely a *Globularia*. In the Jurassic, the latter genus is usually known from soft substrates as is the case of pleurotomariids and both taxa probably were herbivores. Typical hard substrate taxa also occur (cf. *Pileolus* and *Neritopsis*), but in lower numbers.

Brachiopods are the most abundant faunal element of the plattenkalk facies, accounting for 50% of all individuals. Compared with their abundance, their diversity is very low: Except for a few specimens of a rhynchonellid (Fig. 9D), all specimens belong to a single taxon of terebratulid, possibly a species of *Juralina*. The size variation of the terebratulids is considerable, but large shells prevail and most individuals appear to be adults.

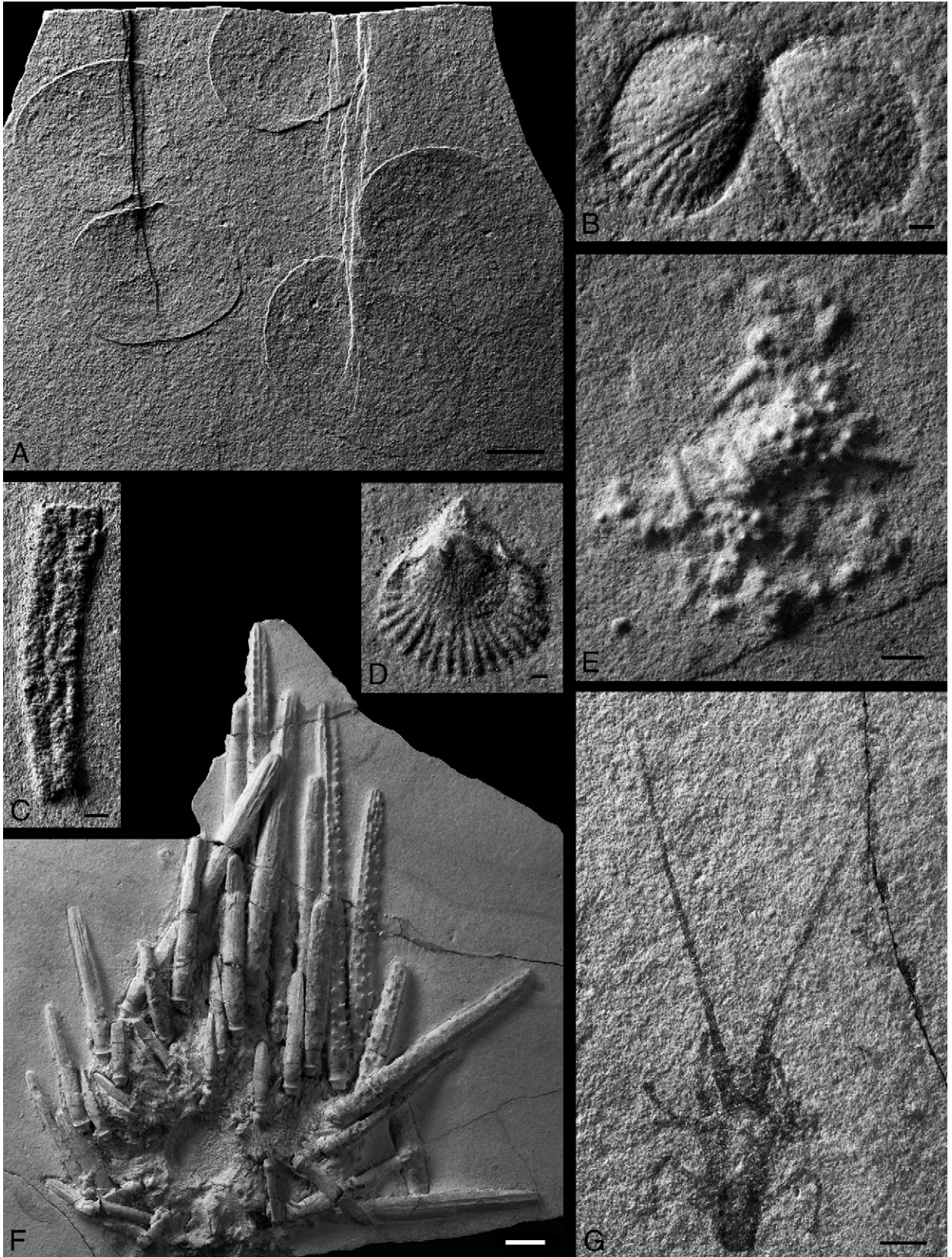
Although most Mesozoic–Cenozoic brachiopods lived attached to hard substrates with their pedicle, in some taxa the pedicle has become byssus-like and enabled the brachiopods to anchor themselves to small objects in the sediment such as bioclasts as in the case of the recent *Terebratulina septentrionalis* (Curry, 1981). The large pedicle opening of the Wattendorf terebratulid points to a stout pedicle and therefore attachment to hard substrates. As such objects were exceedingly rare, it is highly likely that the brachiopods have been swept in from neighbouring shallows with abundant hard substrates.

The six taxa of echinoids account for 5% of the plattenkalk fossils. Only 66% of the occurrences are complete tests, the rest fragments of tests and isolated spines, equally divided between irregular and regular forms, but in terms of individuals regular forms strongly dominate (92%; mainly ?*Pseudosalenia* and ?*Pseudodiadema*). Apart from *Rhabdocidaris* (Fig. 9F), the regular echinoids are quite small; most individuals have a diameter of 3–17 mm, and only two individuals are larger (22 and 24 mm). Regular echinoids require a firm or hard substrate, which excluded them from living in the plattenkalk depression. This is also supported by the lack of sediment disturbance by the infaunal and epifaunal taxa, which are either mobile detritus-feeders or herbivores. Most probably they were, like most other faunal elements, swept into the depression from neighbouring hard substrate areas. Interestingly, no remains of *Saccocoma*, the commonest element of the biota in the Solnhofen lagoonal system, were found among the macrofauna.

The predominant mode of life of the bivalve and brachiopod fauna is incompatible with the soft, fine-grained sediment of the plattenkalk facies. The epibyssate taxa required a firm or hard substrate, or at least some coarser grains for byssal attachment. The latter is also true of endobyssate forms, whereas the cementing oysters required a hard substrate. This strongly suggests that the bivalves and brachiopods, with the possible exception of *Aulacomyella*, are allochthonous and were introduced into the depression from shallower hard substrate areas. This appears to apply also to the few burrowing bivalves, because they occur as single valves on bedding planes. Moreover the fine lamination of the sediment, together with the lack of any bioturbation, clearly indicate that the infaunal niche was not occupied. Consequently, the small infaunal echinoids were most likely also swept into the depression as dead individuals, because they generally occur without spines in contrast to many echinoids in other plattenkalk occurrences such as the Solnhofen Limestone (e.g., Bantz, 1969).

The ecosystem of the plattenkalk depression clearly represented unsuitable conditions for macrobenthic organisms for most of the time. Sedimentary and taphonomic features indicate that lowered oxygen conditions most likely were the main limiting factor. Occasionally, however, conditions on the sea floor might have improved to such an extent that larvae of the bivalve *Aulacomyella* established small populations and, at the stratigraphic level of 1.7 cm, also a relatively large population. Even then, high stress conditions persisted as is shown by the monospecific nature of the benthic assemblage. Surprisingly, no bedding planes with juvenile *Aulacomyella* were observed. This one would expect under fluctuating oxygen levels, which occasionally lead to mass killing of newly established populations. Schatz (2001, 2005) noticed the same feature, i.e. the lack or great scarcity of juveniles in populations of Triassic *Daonella* from oxygen-poor environments (e.g. Monte San Giorgio, Switzerland, and Lombardy), although bedding planes rich in larval shells and juveniles do occasionally occur. No satisfying explanation for the lack of juveniles at Wattendorf can be offered so far, except the interpretation of the bivalve as pseudoplanktonic.

Schatz (2005) rightly stressed the importance of other environmental parameters than the degree of oxygenation in limiting the benthic fauna. Under dysoxic conditions, a number of other invertebrates apart from *Aulacomyella* should have been able to colonise the sea floor, in particular soft-bodied organisms such as nematodes, oligochaetes, and polychaetes, among which quite a few taxa are known to tolerate dysoxic conditions (e.g., Bryant, 1990; Schöttler and Bennet, 1990; Soetaert et al., 2002; Levin et al., 2003;



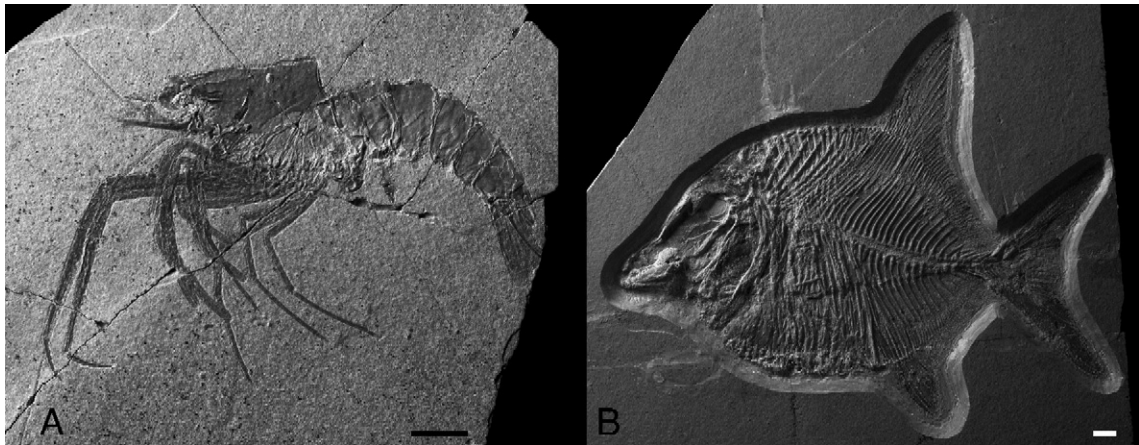


Fig. 10. A *Aeger* sp., B162, lower surface view, scale bar: 1 cm. B *Proscinetes* sp., H04, scale bar: 1 cm.

Hell and Levin, 2004; Bailly and Vinogradov, 2005). Their absence prompted Schatz to invoke a soft and soupy substrate as an additional limiting factor. Similarly to *Daonella*, the large flat valves of *Aulacomyella* could have acted as snowshoes, preventing the bivalves from sinking into soft mud. Whilst a soupy substrate may explain the lack of other epifaunal taxa, it is not clear why this should exclude all burrowing organisms. In fact, in some of the thin, laminated plattenkalk intervals below the excavation level, occasional signs of bioturbation can be observed. Most of them consist of circular arrangements of sand-sized sediment particles which form ring-like structures 0.5 mm in diameter. Rarely, vertical meniscate burrows, 6 mm in diameter, can be seen. As they occur in plattenkalk layers that are only a few centimetres thick, bioturbation may have originated from above. The small diameter of the tubular structures and the ability of the producer to burrow in sediments of very low oxygen content suggest that nematode-like organisms were responsible for most of the bioturbation.

8. Taphonomy

Taphonomy is a powerful tool to gain information on various environmental parameters and to establish the autochthony or allochthony of specific faunal elements. In the case of the Wattendorf plattenkalk, the overwhelming percentage of the macrofauna had a benthic mode of life, which contrasts strongly with the undisturbed, laminated nature of the sediment. In the following, taphonomic

features of the various groups of organisms are briefly described and interpreted in order to understand the depositional environment of the plattenkalk facies and to establish the origin of the faunal elements.

8.1. General features

In contrast to the classical Solnhofen lithographic limestones where larger fossils invariably rest on a pedestal (“Sockelerhaltung”) this phenomenon is not developed at Wattendorf. Seilacher et al. (1976) discussed the origin of this preservational feature but did not reach a final conclusion. It seems highly likely that formation of a pedestal is related to early diagenetic lithification of the sediment below the organisms, facilitated by the decay of soft parts (at Solnhofen such a pedestal is not developed below material lacking soft tissue such as belemnite rostra, aptychi or shell fragments). Subsequent compaction then apparently elevated the fossils above the surrounding bedding surface. Compaction also affected the Wattendorf plattenkalk. This is best shown by the preservation of articulated terebratulid shells which are, with the exception of some very small specimens, strongly flattened and fractured (Fig. 14). However, evidence of soft substrate conditions (such as vertically embedded belemnite rostra) indicate that compaction was not an early diagenetic feature. The reason for the lack of early diagenetic concretion formation at Wattendorf is not quite clear but may be related to higher rates of sedimentation than in the case of the Solnhofen Lithographic Limestone. This way,

Fig. 9. Characteristic faunal elements of the Wattendorf plattenkalk. A Bedding plane with *Aulacomyella* in convex-down butterfly position, upper surface view, scale bar: 1 cm. B *Pseudolimea* sp., in convex-down butterfly position, A905, lower surface view, scale bar: 1 mm. C *Muensteria* sp. (agglutinated polychaete worm tube), P2005-Watt 52, scale bar: 2 mm. D Rhynchonellid brachiopod (?*Torquirhynchia* sp.), B255a, scale bar: 2 mm. E Regurgitate consisting of echinoid with spines, H01, scale bar: 2 mm. F *Rhabdocidaris* sp., B128, upper surface, scale bar: 1 cm. G *Palinura* sp., E110, scale bar: 2 mm.

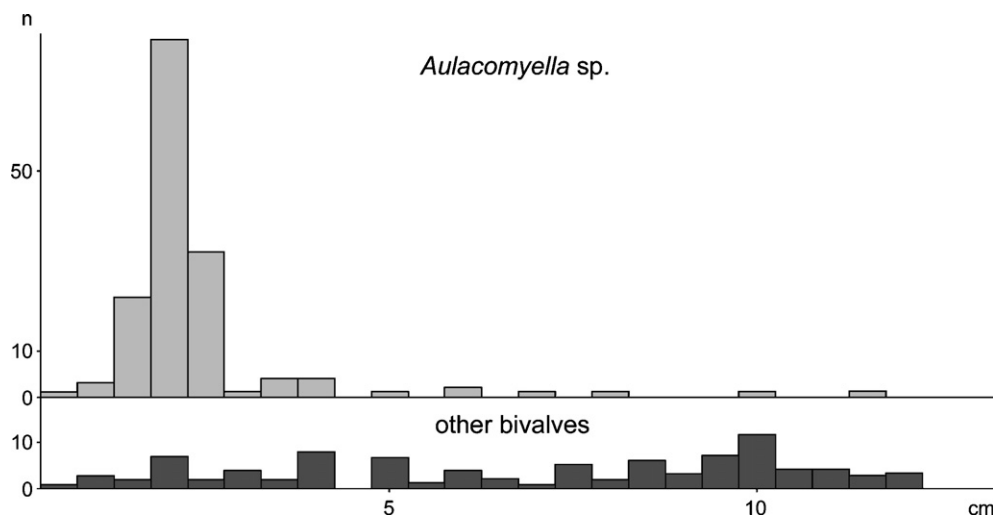


Fig. 11. Distribution of *Aulacomyella* and other bivalves in the plattenkalk section (horizontal axis). Vertical axis: number of specimens. The data have been lumped in 0.5 cm intervals.

larger soft-bodied organisms such as fish were quickly sealed and, together with anoxic conditions both within the sediment and in the lower water column, greatly retarded their decay and with it the release of methane and other decay products. This also helps to explain the common preservation of soft parts in larger vertebrates such as fish.

8.2. Fishes

Most fishes are very well preserved. In many cases preserved soft parts still cover the bones. Preservation of the skeleton without soft parts is the exception. This suggests rapid burial of the carcasses either with sediment or with microbial mats. The majority of the bony fish appear to represent remains of predation: of 38 bony fishes (e.g., *Tharsis*) only 15 are complete. Of the remaining specimens either only the head (10 specimens), the head and a small part of the vertebral column (3), the anterior part of the body (2), the body without the head (1), the posterior part of the body (1), or the tail fin (6) are preserved. Some of these fragments may also be the result of gradual desintegration of floating carcasses. Evidence of fish predation is also afforded by coprolites that contain fish fragments. Unambiguous signs of predation (e.g., head or tails of fishes with parts of the vertebral column still attached and coprolites) demonstrate that the upper part of the water column was well oxygenated and supported a rich nektonic fauna.

8.3. Belemnites

The rare belemnite rostra are predominantly embedded vertically to subvertically with respect to bedding. Rostra,

which became detached and sank to the sea floor with progressive decay of floating carcasses of belemnite animals, penetrated the sediment surface down to a depth of several centimetres. This strongly suggests soft substrate conditions and lack of early diagenetic compaction. The algal films that covered the sea floor during some intervals of the formation of the plattenkalk (see above) obviously were very thin and did not significantly increase the firmness of the substrate.

8.4. Echinoderms

Three out of eight specimens of *Rhabdocidaris* are preserved with spines (Fig. 9F), the remaining occurrences consist of isolated spines, some of them broken. In the case of the small regular echinoids *?Pseudosalenia* and *?Pseudodiadema*, 10 out of 74 specimens (13.5%) are coronae with spines still attached and 52.7% are complete coronae, but without spines. The rest are fragments of the corona or isolated spines or fragments thereof. Only a few specimens, broken coronae with spines, can be interpreted, with some confidence, as a consequence of predation. The specimen figured in Fig. 9E clearly represents a regurgitate. All echinoids must have been derived from topographic highs in the vicinity of the plattenkalk depression. This is also true of the few irregular forms which all are preserved without spines. As autochthonous elements of the plattenkalk depression they would have disturbed the laminated sediment. As the specific weight of echinoderm skeletons is fairly low, coronae can be expected to have been moved very easily during storms and to have been carried away, as suspension load, from the topographic highs into adjacent low-lying areas.

Table 3
Trophic groups and life habits of the shelly macrobenthos

	Mode of life	Trophic group
<i>Bivalves</i>		
?nuculid	IM	D
<i>Grammatodon</i> (<i>Grammatodon</i>) sp.	EB	S
<i>Grammatodon</i> (<i>Cosmetodon</i>) sp.	SIB	S
?pteriid	EB	S
? <i>Bakevellia</i> sp.	EB	S
<i>Aulacomyella</i> sp.	?EB	S
<i>Chlamys</i> sp.	EB	S
? <i>Radulopecten</i> sp.	EB	S
? <i>Camptonectes</i> sp.	EB	S
Pectinid indet.	EB	S
Inoceramid indet.	EB	S
<i>Pseudolimea</i> sp.	EB	S
<i>Liostrea</i> sp.	EC	S
<i>Modiolus</i> sp.	SIB	S
<i>Arcomytilus furcatus</i>	EB	S
<i>Praeconia rhomboidalis</i>	EB	S
<i>Nicaniella</i> sp.	IS	S
? <i>Tancredia</i> sp.	ID	S
Burrowing bivalve indet.	I	S
<i>Gastropods</i>		
cf. <i>Pileolus</i> sp.	EM	H
? <i>Bathrotomaria</i> sp.	EM	H
?pleurotomariid	EM	H
<i>Neritopsis</i> sp. A	EM	H
<i>Neritopsis</i> sp. B	EM	H
Procerithiid indet.	EM	H
<i>Globularia</i> sp.	EM	H
Gastropod sp. A (? <i>Globularia</i>)	EM	H
Gastropod sp.B	EM	H
Gastropod sp.C	EM	H
Gastropod indet.	EM	H
<i>Brachiopods</i>		
? <i>Torquirhynchia</i> sp.	EP	S
? <i>Juralina</i> sp.	EP	S
<i>Echinoderms</i>		
<i>Nucleolites</i> sp.	IM	D
<i>Pygurus</i> sp.	IM	D
Irregular echinoid indet.	IM	D
<i>Rhabdocidaris</i> sp.	EM	D/H
? <i>Pseudosalenia</i> sp.	EM	D/H
? <i>Pseudodiadema</i> sp.	EM	D/H
Ophiuroid indet.	EM	S
Asteroid indet.	EM	C

EB:epibyssate; EC: epifaunal, cemented; EM: epifaunal, mobile; EP: epifaunal, pedicle-attached; ID:infaunal, deep; IM: infaunal, mobile; IS: infaunal, shallow; SIB: endobyssate; C: carnivore; D: deposit-feeder; H: herbivore; S: suspension-feeder.

8.5. Brachiopods

Nearly all brachiopods are articulated and exhibit a random orientation: out of 205 specimens 102 are preserved with the pedicle valve down and 103 with the

brachial valve down. Their distribution within the plattenkalk section is relatively uniform (Figs. 6 and 15) and their size-frequency histograms, admittedly based on a limited number of specimens ($n=238$) do not show any signs of sorting. Except for some very small specimens, all terebratulid brachiopods (?*Juralina* sp.) are preserved as compressed shells exhibiting signs of compactional breakage (Fig. 14; terebratulids from the Late Kimmeridgian Nusplingen plattenkalk show identical preservation; Dietl and Schweigert, 2000). This implies that, at the time compaction took place, the shells were not filled with lithified sediment nor had growth of carbonate crystals completely filled the space inside the shell. Therefore, the shells were transported devoid of sediment but some of them probably still with their soft parts (the latter would have promoted early diagenetic precipitation of carbonate) into the plattenkalk depression. The presence of soft parts can be deduced from the peculiar compaction pattern of many brachiopods, in which the area immediately below the umbo of the brachial valve is the only part of the valve that escaped compaction. This suggests that in that area, in which the soft parts are concentrated, early diagenetic growth of calcite crystals was triggered by the decaying soft parts (Fig. 14B,C). In the rudstone layers below the excavated plattenkalk level articulated brachiopods, although devoid of internal sediment, lack signs of compactional distortion.

The fact that nearly all shells are still articulated does not contradict an allochthonous origin of the brachiopods, because the hinge of terebratulids usually forms a tightly interlocked system (e.g., Carlson, 1989) and, even during transport, valves do not become separated without breakage: Breakage is even less likely when transport takes place in suspension.

8.6. Gastropods

The gastropods *Bathrotomaria* sp. A and ?pleurotomariid indet. exhibit an unusual orientation pattern: of 58 specimens 55 (94.8%) are embedded with their apex pointing downwards into the sediment (Fig. 16). This clearly demonstrates that the shells sank to the sea floor from the water column with their apex pointing downwards the sea floor and remained undisturbed in this position. In settling experiments with similar-shaped empty modern gastropod shells (*Gibbula magus*, *G. pennanti*, and *Monodonta atrata*) water-filled shells invariably came to rest in a position with the apex pointing downwards and thus support our interpretation that the pleurotomariids settled out of suspension.

Three of four specimens of the patelliform cf. *Pileolus* are embedded with their apex pointing

Table 4

Relative abundances (%) of life habit groups among the bivalves

	Epibyssate	Endobyssate	Cementing	Burrowing	<i>n</i>
Without <i>Aulacomyella</i>	63.1	24.6	5.3	5.0	57
With <i>Aulacomyella</i>	87.0	8.7	1.8	2.5	162

Aulacomyella is counted here as an epibyssate taxon.

downward, the typical position of bowl-shaped objects when settling out of suspension. In the case of the low-spined *Neritopsis*, orientation of the body axis is oblique to vertical with respect to the bedding plane.

The second most abundant gastropod group, *Globularia* and related forms, exhibits a different orientation pattern. Some of the individuals are oriented with their body axis vertical and the apex pointing downwards or upwards, but most specimens are embedded sidewise, with the aperture either facing upward or downward. The three turritiform gastropods are arranged with their long axis paralleling the bedding plane.

Like all other aragonitic faunal elements of the plattenkalk facies the gastropods are preserved as strongly compressed composite moulds, the shell having been dissolved before compaction took place.

The peculiar orientation pattern of the pleurotomariid gastropods is evidence of their allochthonous nature and also evidence of a fairly soupy substrate; any shell touching the sea floor with its apex had to sink into the substrate to some extent, otherwise the shell would have

tilted over and come to rest on its side. The fact that this mode of orientation is far less common in ampullinid gastropods and does not occur in the few turritiform gastropods is probably due to their more high-spined nature.

8.7. Bivalves

Bivalves carry a range of taphonomic signatures. The following discussion does not include the most abundant bivalve of the plattenkalk facies, *Aulacomyella*, which is discussed separately below. Apart from *Pseudolimea*, most taxa are preserved as bivalved specimens, whereby the so-called butterfly position (i.e., the valves are gaping and lie in the same plane) is the most common attitude. In 62% of these cases, the valves are convex-up oriented. In the case of disarticulated specimens, in particular *Pseudolimea*, 91% are convex-down oriented. The high abundance of convex-down oriented valves points to lack of currents, which would otherwise overturn shells. Moreover isolated, convex-down oriented shells most likely settled out of suspension and are thus clearly allochthonous.

Noteworthy is a cluster of three individuals of *?Bakewellia*, all preserved in convex-up butterfly position. The specimens must have settled out of the water column together. As byssate taxa, their byssal threads might have been intertwined so that they stayed together when swept off the shallows. Alternatively, they might have been attached to some floating object such as seaweed and sank when that object started to decay.

More than half (56.7%) of *Aulacomyella* valves are articulated ($n=176$) (Fig. 17). If one takes into account that each articulated bivalve produces two single valves, this figure rises to more than 70%. Of these nearly all are preserved in butterfly position and 92% of these specimens are convex-down oriented. This very uniform orientation pattern, which in addition differs from that of the remaining bivalves (see above), requires a different explanation. While the other bivalves are clearly allochthonous elements of the plattenkalk facies, autochthony cannot be excluded in the case of *Aulacomyella*. This is corroborated by the fact that *Aulacomyella* is the only faunal element that exhibits a very distinct stratigraphic distribution in so far as it is largely concentrated on a

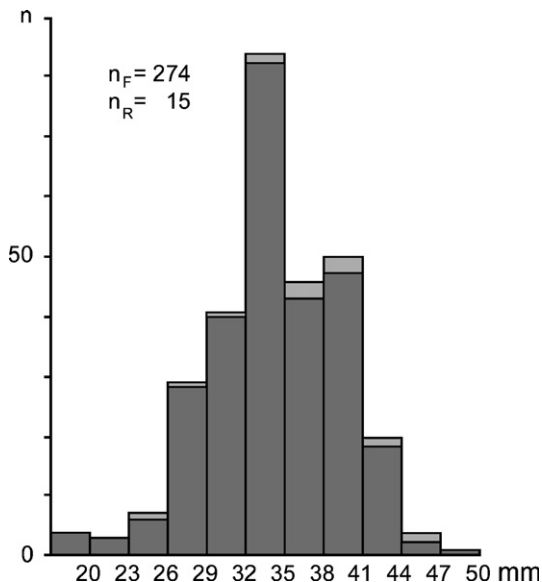


Fig. 12. Size-frequency histogram of *Aulacomyella*. n_F : number of individuals on the bedding plane at 1.7 cm (Fig. 13); n_R : number of *Aulacomyella* from other levels in the plattenkalk section (their distribution in the histogram is indicated by lighter shading).

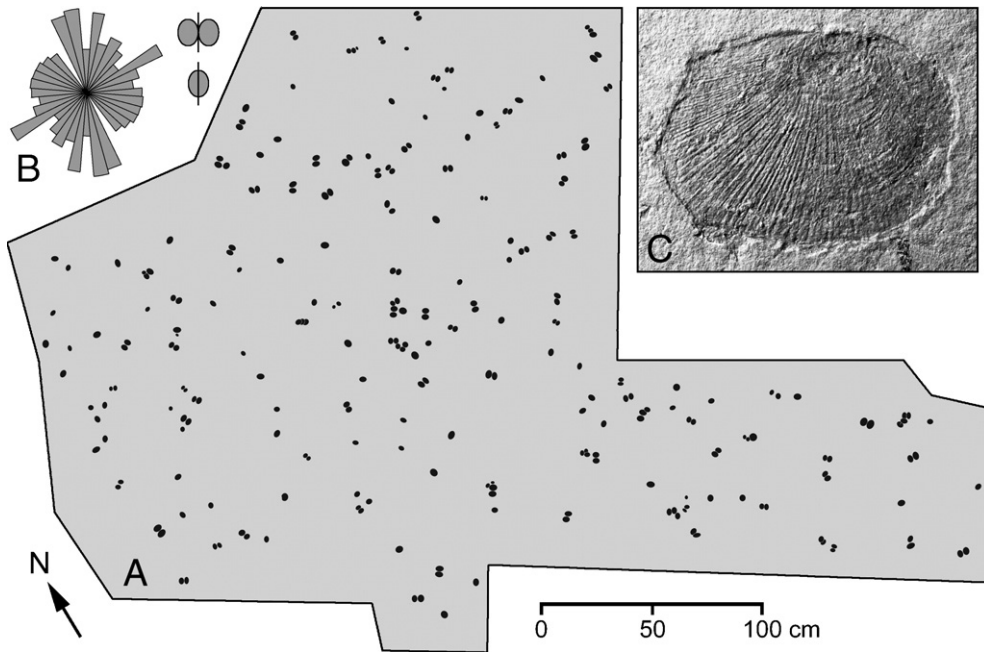


Fig. 13. A Spatial distribution of articulated and disarticulated valves of *Aulacomyella* on bedding plane 1.7 cm above base of investigated plattenkalk section. B Rose diagrams of plan view orientation of *Aulacomyella*, given for articulated and single valves combined. Note that the elongated *Aulacomyella* valves do not show a statistically significant orientation pattern. C *Aulacomyella* sp., P2005-Watt 647.

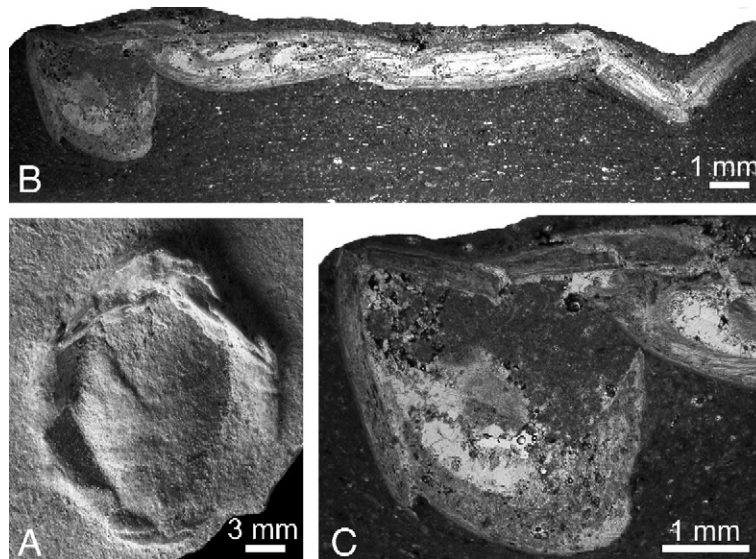


Fig. 14. A Strongly compacted articulated valves of the terebratulid *Juralina*, D 248. B Thin-sections through articulated valves of *Juralina*. Note that the shell cavity contains only little sediment and has therefore been strongly compacted. Two cement generations can be distinguished: a thin, early diagenetic rim cement and a late diagenetic blocky calcite. The lack of extensive early diagenetic growth of calcite crystals within the cavity is evidence that compaction predated such growth. This hints at high rates of sedimentation within the plattenkalk and suggests that the formation of the plattenkalk/rudstone–grainstone alternations (Fig. 4) presumably did not take more than a few thousand years. C The peloidal micrite in the umbonal area is interpreted as automicrite which, being part of an inverse geopetal fill, formed in the original habitat of the brachiopod, prior to its transport. Enlargement of B.

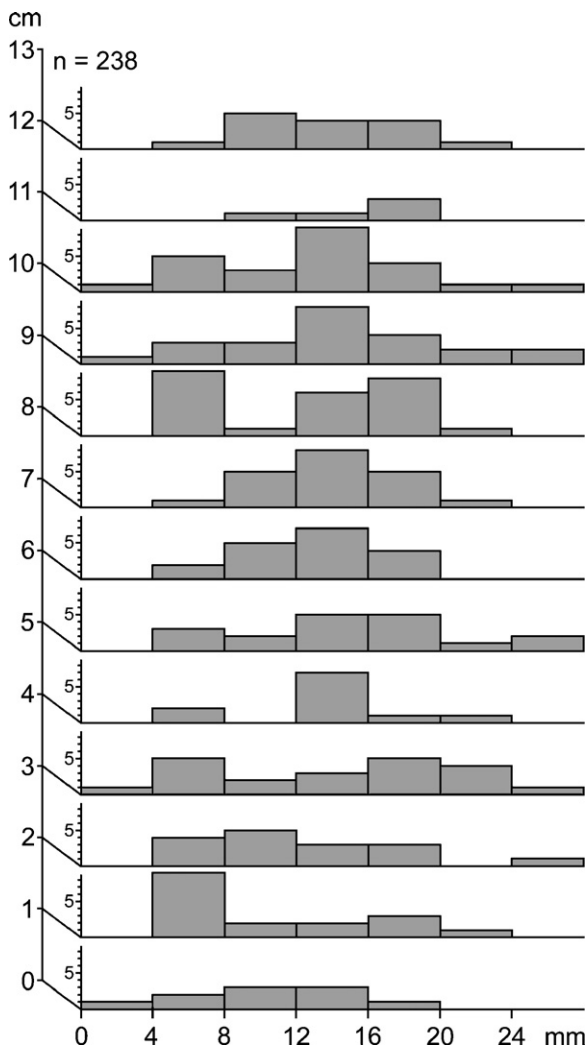


Fig. 15. Size-frequency distribution of the commonest fossil within the plattenkalk, the terebratulid ?*Juralina*. In the histograms the specimens occurring within 1 cm intervals are lumped. Vertical axis: Plattenkalk section, scale in cm. Vertical axes of histograms: numbers of specimens, horizontal axis: size classes.

single bedding plane. In-situ preservation of *Aulacomyella* is suggested by the uniform convex-down orientation of the valves and with the majority of the valves articulated despite lacking hinge teeth. Preliminary settling experiments with poorly inflated articulated bivalve shells of a shape similar to that of *Aulacomyella* revealed that opened articulated valves, when settling out of suspension starting their descent in a convex-up orientation quickly reorient themselves and assume a convex-down orientation. However, it may be speculated that the ligament of *Aulacomyella* was quite flaccid so that during descent the valves might have folded up and come to rest on the sea floor sideways.

The plan-view orientation of 179 specimens of *Aulacomyella* on the bedding plane 1.7 cm above the base of the plattenkalk has been analysed to detect influence of currents. For this purpose, the orientations of the hinge lines were measured on a scale of 180°. To test for non-random distribution of the orientations, the data were converted to a circular scale by mirroring each datum. The Raleigh test evaluates the null hypothesis that the sampled population is uniformly distributed around a circle (i.e. there is no mean direction; Zar, 1996). The Chi-square test evaluates the null hypothesis that the directions are evenly spread. Both tests were computed with the PAST software (Hammer et al., 2001). Both tests show that the data are not unidirectional nor have an uneven spread of directions (Table 5). The Raleigh test is not appropriate for bidirectional data, but such outcome is improbable, because the data are axial (i.e., on a scale of 180°). Nevertheless, the angles were mirrored in order to test for the bidirectionality of the axial data with the Raleigh test (Zar, 1996), but all tests were similarly insignificant.

Certain inconsistencies remain with the interpretation of *Aulacomyella* as an opportunistic benthic recliner (see also under the chapter palaeoecology): How can the rare, scattered occurrences of adult *Aulacomyella* at other levels of the plattenkalk facies be explained? Why does *Aulacomyella* not exhibit a polymodal size-frequency pattern, which one would expect in census populations? Why do we not find bedding planes with spat of *Aulacomyella*, signs of unsuccessful colonisation attempts? As these features, in fact, support a pseudoplanktonic mode of life, a benthic mode of life of *Aulacomyella* still is problematic (Table 6). Regardless of whether one assumes a benthic or a pseudoplanktonic mode of life of the bivalve, the ligament must have, after death, opened the valves more than 90°, otherwise, the preferred convex-down orientation of articulated specimens in butterfly position cannot be explained (Fig. 18).

8.8. Preservation of fossils with respect to bedding

Whereas some faunal elements such as *Aulacomyella* invariably are preserved on the bedding plane, others occur within graded beds (e.g. some of the brachiopods), and yet others occur close to bedding planes but are covered by a thin film of sediment (many of the brachiopods). In the latter case, the fossils were overgrown either by a microbial mat which, in the case of soft-bodied organisms, increased their preservation potential, or else they became covered by a thin veneer of sediment that settled out of suspension in the aftermath of the storm that introduced the shells into

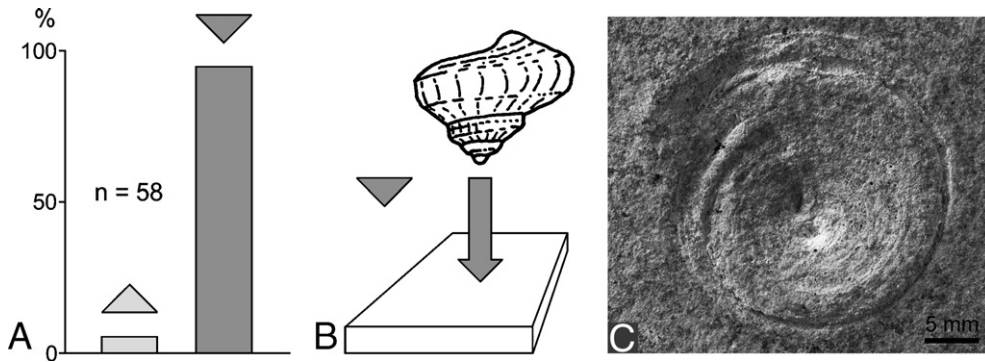


Fig. 16. Low-spined pleurotomariid gastropods overwhelmingly are oriented with their apex pointing downward (A, C). Settling experiments with similar-shaped modern gastropod shells show that this is the characteristic mode of orientation when such empty shells settle out of suspension (B). C ?*Bathrotomaria* sp., E86b, upper surface.

the depression. The occurrence of shells within graded beds thus supports their allochthonous nature.

8.9. Compaction

Most shells exhibit signs of compaction (flattening and fracturing). This is particularly well seen in bi-

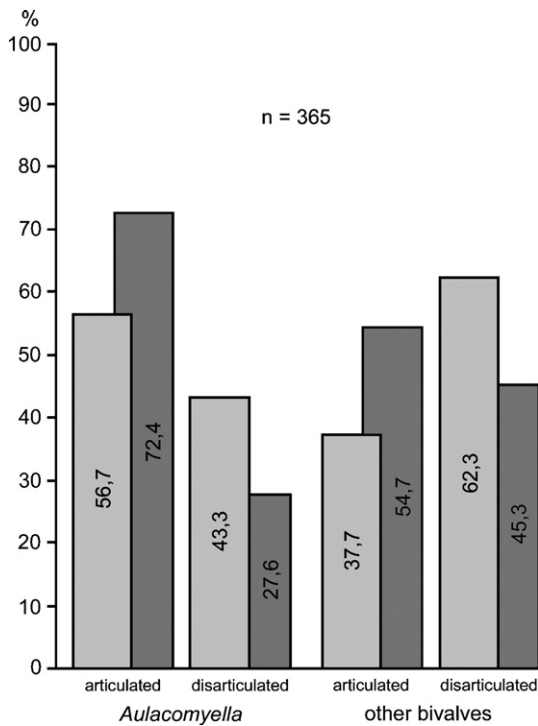


Fig. 17. Percentage of articulated valves of *Aulacomiyella* and of other bivalves. The data are presented in two ways: Relative abundance of articulated versus single valves (light-grey bars) and relative abundance of articulated versus half the number of single valves (dark-grey bars), as each articulated bivalve produces two single valves.

convex shells such as those of terebratulid brachiopods (e.g., Fig. 14). Thus, lithification of the sediment and of any sedimentary infilling, as well as growth of diagenetic calcite clearly post-dated compaction (see above). This might be explained by relatively high rates of sedimentation.

8.10. Differences in diversity of imported faunal elements between the plattenkalk and underlying allodapic biorudstones

The allochthonous faunal elements occurring in the plattenkalk facies differ from those found in the biorudstones, which occur below the plattenkalk and have been interpreted as turbidites derived from shallow-water hard substrates, both in diversity and composition. For example, whereas the terebratulid ?*Juralina* is the commonest taxon in the plattenkalk, where altogether only two species of brachiopods occur, this brachiopod is rare in the rudstones. There, instead, *Terebratulina substriata* and *Trigonellina pectuncula* are common elements, together with rare *Ismenia pectunculoides*. Corals and bryozoans, both components of the rudstones, are absent from the plattenkalk facies. It therefore appears that the skeletal elements introduced into the depressions represent different subenvironments of shallow water hard

Table 5 Results of the statistical tests of the orientation of *Aulacomiyella* specimens on the bedding plane of Fig. 13

	All data (n=179)	Single valves (n=82)	Articulated valves (n=97)
Rayleigh test	R=0.06, p>0.1	R=0.036, p>0.1	R=0.096, p>0.1
Chi-square test	χ²=3.06, p=0.08	χ²=2.39, p=0.12	χ²=1.02, p=0.31

Table 6

Arguments supporting/against a benthic and pseudoplanktonic mode of life, respectively, of *Aulacomyella* at Wattendorf

Arguments in favour of a	
benthic mode of life	Pseudoplanktonic mode of life
<ul style="list-style-type: none"> • flat clams are adapted to live on soft, dysoxic substrates • known to occur in dysoxic environments elsewhere • the high density occurrence at section level 1.7 cm is typical of opportunistic r-strategists able to colonise unfavourable environments • the presence of a flexible ligament would cause articulated valves to fold up when sinking to the sea floor, not producing the characteristic butterfly position 	<ul style="list-style-type: none"> • relatively high proportion of single valves in a low energy setting • occurrence of adult individuals in low numbers on many bedding planes • no bedding planes full of juveniles • undisturbed lamination as evidence of lack of oxygen within the sediment; preservation of soft parts and presence of articulated vertebrate skeletons indicate lack of oxygen also in the lowermost water column • no polymodal size-frequency distribution • biological and taphonomic evidence that all other benthic organisms at Wattendorf are allochthonous

For both modes of life a post-mortem gape of the valves of more than 90° has to be assumed to explain the preferred convex-down orientation of valves in butterfly position. For a detailed discussion see text.

substrate areas. Part of this faunal differentiation may also be due to the different transport mechanisms: The skeletal elements of benthic organisms in the plattenkalk facies such as echinoid tests, articulated bivalves and brachiopods, and gastropods invariably exhibit a high floating capacity and thus support the interpretation that they were introduced into the depression by suspension clouds. In contrast, bryozoan, coral, and shell fragments are more easily transported by density currents.

9. Environmental model

In the following, the various sedimentological, palaeoecological, and taphonomic features are summarized in a model of the depositional environment (Fig. 19).

Geometries of rock units observed in the field indicate a distinct relief of the sea floor prior to deposition of the plattenkalk facies. This relief was formed by microbialite sponge reefs, which are now represented by massive dolostones. At some stage towards the end of the Early Kimmeridgian, reef growth stopped, possibly when shallowing in connection with a fall in sea level closed the ecological window of the microbial-sponge associa-

tion. As this association underwent early diagenetic lithification as elsewhere on the Franconian and Swabian Alb (e.g., Flügel and Steiger, 1981; Koch and Schorr, 1986; Koch and Liedmann, 1996; Reinhold, 1996; Schröder et al., 1996) they provided hard substrate areas on which small patches of corals and calcareous algae developed and a fauna of mobile grazers and byssate, pedicle-attached, and cemented suspension-feeders thrived. The shallowest parts of these hard substrate areas were situated well above storm wave-base. Some probably formed even small islands, which is indicated by the occasional presence of well preserved land plants within the plattenkalk. The deeper parts formed depressions in which, due to their protected nature between shallows, quiet water conditions prevailed and, as a result, low oxygen conditions developed. Very likely, such conditions were facilitated by a density stratification brought about by concentration of higher saline waters in the depressions. Occasionally, storms swept sediment off the topographic highs. It accumulated as aprons around the shallows and in the depressions. Depending on the distance from the shallows and on the severity of the storms, grain size of the transported sediment varied. Some was carried downslope by turbidity currents, other sediment was brought into suspension and carried further away to settle down when calm conditions returned. In both cases graded beds developed. Where the sediment accumulated on slopes small slumpings occasionally developed, probably in connection with rapid sedimentation events.

In the depressions, at times anoxic conditions prevailed near the bottom and resulted in the formation of fine-grained, finely laminated sediments (plattenkalk facies). Due to the fine-grained nature of the sediment and high rates of sedimentation, the consistency of the sea floor was very soft. These conditions were inimical to higher life and the only benthic organisms were microbes that covered the sea floor with a thin film. In contrast, higher up in the water column a normal biota of nektonic and planktonic organisms flourished. In rare cases, during phases of dysoxic conditions, the flat clam *Aulacomyella*, a bivalve seemingly adapted to cope with soft substrate and low oxygen conditions, might have been able to colonise the sea floor.

?Nektonic organisms such as fishes, some crustaceans, and teuthoids, which died in the water column, sank to the sea floor and were overgrown by a thin bacterial film. They escaped disarticulation and were subject to retarded bacterial decay so that occasionally soft parts became preserved. Additionally, shells of brachiopods and bivalves as well as exuviae of crustaceans, which were swept off the shallows by storms, accumulated in the depression. The faunal spectrum was augmented by some facultatively pseudoplanktonic organisms, in particular some byssate bivalves,

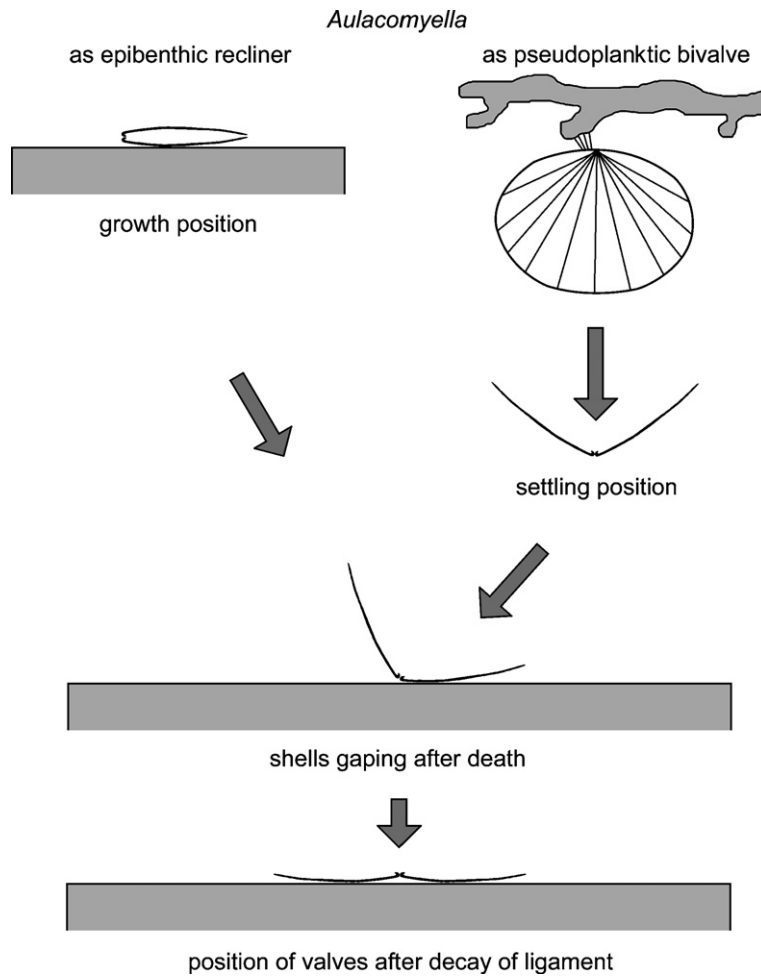


Fig. 18. The preferred convex-down orientation of articulated *Aulacomyella* valves can be explained as resulting from two different modes of life of the bivalve: as epibenthic recliner and as pseudoplanktonic. However, in both cases, the ligament must force open the valves for more than 90° after death.

which lived attached to floating algae and sank to the sea floor after death.

In the depressions, the anoxic conditions existed only for relatively short periods, most likely in the order of a few thousand years. They were replaced by well aerated conditions, probably brought about by generally more turbulent conditions in connection with stronger storm activity. These resulted in deposition, within the depressions, of thicker beds of graded, bioclastic debris derived from the shallows. Several alternations of finely laminated (anoxic conditions) and thicker bioclastic debris beds (well oxygenated conditions) suggest a control of the sedimentation by small-scale climatic cycles. A still smaller-scale cyclicity is seen within the plattenkalk facies, where bundles of graded beds and thin intercalations of sub-millimetric clay layers alternate with more finely laminated microbial layers. They might reflect variations in the strength of a monsoonal-type

climate where drier and calmer conditions alternate with wetter and stormier phases.

Environmental conditions changed again when, due to gradual levelling of the sea floor relief, the isolated depressions ceased to exist and, in combination with a relative rise in sea level, a more uniform depositional environment became established, now represented by the Wattendorf Limestone. Thus, the Wattendorf plattenkalk formed during a transitional phase, when the pronounced relief of the microbialite-sponge reefs, which were killed by a relative sea-level fall, was gradually levelled due to sedimentation during the ensuing sea-level rise. The reason for the stratigraphically discontinuous nature of the plattenkalk facies most likely lies in the bathymetry of the depositional area: The small-scale, shallow water topography of the dead microbialite-sponge reefs was much more easily affected by climatic fluctuations than, for example, the much larger and deeper lagoonal

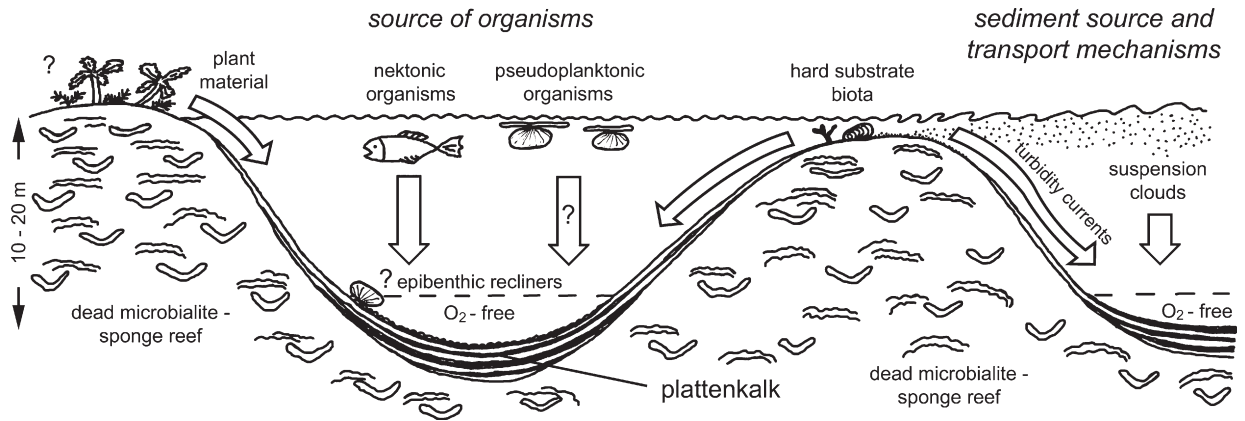


Fig. 19. Environmental model of the Wattendorf plattenkalk. For explanation see text. Note that turbidity currents are thought to have produced the graded packstones to rudstones between the plattenkalk occurrences, but not the graded layers within the plattenkalk, which are thought to result from material settling out from a suspension cloud. The mode of life of *Aulacomyella* could not be clarified with certainty, because some evidence supports that it was an opportunistic epibenthic recliner, other evidence points to a pseudoplanktonic mode of life.

system, in which the Solnhofen lithographic limestones formed.

10. Comparison of the Wattendorf plattenkalk with other Upper Jurassic plattenkalks from the Franconian–Swabian Alb

Laminated limestones with exceptional fossil preservation are not uncommon within the lagoonal systems existing along the northern margin of the Tethys during the Kimmeridgian–Tithonian (Fig. 1). In the following, the Wattendorf plattenkalk and its fossils are briefly compared with these occurrences in order to demonstrate similarities and differences.

10.1. General setting and microfacies

Most of the other plattenkalk occurrences differ from the Wattendorf plattenkalk in that they are of much greater lateral extent and thickness, and thus represent deposits of much larger depressions in which inhospitable conditions at the sea floor, caused mainly by dysoxia or anoxia, persisted for long periods (e.g., Solnhofen, Eichstätt, Nusplingen; Keupp, 1977; Barthel et al., 1990; Viohl, 1996, 1998; Dietl and Schweigert, 1999). The most similar setting is a small occurrence of laminated dolostones at Pfraundorf (Fig. 1; Heim, 1999), which occur in small pockets between massive dolostones (presumably diagenetically altered microbial-sponge reefs). In the classical plattenkalk occurrences of the Solnhofen–Eichstätt area we are, in contrast to Wattendorf, far from the margins of the lagoon and we therefore lack intercalations of coarser-grained turbidites (graded grainstones and rudstones). Nusplingen appears to occupy an intermediate position, as

graded packstones to grainstones are occasional intercalated between the laminated mudstones to wackestones (Dietl et al., 1998). Common intercalations of such turbidites in the plattenkalks of Schamhaupten (Viohl and Zapp, 2005), Painten (Link and Fürsich, 2001), and the Kelheim area (e.g., Schairer, 1968) indicate more marginal settings within the lagoonal system. Similarly, the plattenkalk occurrences at Brunn and Hienheim (Röper et al., 1996; Röper and Rothgaenger, 1998), with their comparatively rich benthic fauna, represent a more marginal lagoonal setting, but appear to lack close-by microbial-sponge reefs with a steep relief and corresponding turbidite intercalations.

SEM investigations have shown that coccoliths and calcispheres are significant constituents of the classical plattenkalks (e.g., Keupp, 1977; Dietl and Schweigert, 1999); both groups of microfossils have not been found at Wattendorf. In contrast, microbial layers similar to those at Wattendorf are widespread also in other plattenkalk occurrences (e.g., Solnhofen; Keupp, 1977; Öchselberg near Schamhaupten; Eichiner, 1999; Painten; Link and Fürsich, 2001).

10.2. The fauna

A comparison between the Wattendorf biota and that of other plattenkalk occurrences may seem premature, considering that some of the classic plattenkalk occurrences have been quarried for centuries, whereas our excavations were restricted to a few weeks and the recovered fossils surely do not represent the complete set of organisms that are preserved in the plattenkalk. In particular, additional taxa of large vertebrates can be expected to turn up in the course of future excavations. Thus, the

present species diversity of around 80 taxa, which is far lower than that at Nusplingen (250 taxa; Dietl and Schweigert, 1999) and Solnhofen—Eichstätt (around 400 taxa; Barthel et al., 1990) most likely is a gross underestimation of the total preserved fauna. However, the strong dominance of benthic organisms at Wattendorf in the present data set clearly singles it out from most other plattenkalk occurrences, where nektonic and planktonic organisms dominate.

The strongest similarities exist with the occurrence at Pfraundorf. There, fish remains, crustaceans, and the bivalve *Aulacomyella* are the most common faunal elements (Heim, 1999) and suggest a very similar environmental setting.

Abundant benthic faunal elements occur also at Hienheim and Brunn (Röper et al., 1996; Röper and Rothgaenger, 1998), in particular ophiuroids, asteroids, bivalves (both infaunal and epifaunal taxa), and gastropods. Commonly, these taxa form loose, mono- to paucispecific pavements at some levels within the plattenkalk. Moreover, the gastropods and bivalves are usually quite small. In their faunal composition, these localities differ greatly from that of the Wattendorf plattenkalk where asteroids and ophiuroids are represented by rare, isolated skeletal elements, and burrowing bivalves are extremely rare.

Another characteristic feature of the Hienheim and Brunn plattenkalk occurrences is the presence of bioturbated horizons, which suggest that episodically favourable conditions enabled a low diversity benthic fauna to colonise the lagoonal floor. Thus, many of these faunal elements appear to be autochthonous. Most likely, these two plattenkalks represent more marginal conditions where anoxic conditions alternated with dysoxic and oxic conditions.

11. Conclusion

Whereas the Wattendorf plattenkalk shows some similarity with other plattenkalk occurrences from the Swabian–Franconian Alb with respect to facies and general setting, the composition of its fauna differs strongly from that of nearly all other occurrences. The present documentation and analysis therefore adds another facet to the spectrum of known plattenkalk lagerstätten, which represent a far greater array of palaeoenvironments and biota than thought for a long time.

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