Dedicated to JÜRGEN FISCHER, Holzmaden,
on his 50th birthday

Fossil-Lagerstätten Nr. 53[*]:

Ammonite shells as habitats in the Posidonia Shales of Holzmaden – floats or benthic islands?

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With 10 figures in the text

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Abstract: Orientations and patterns of overgrowth on large ammonite shells disagree with E. KAUFFMAN's benthic island model, but indicate that settlement occurred when the host was still alive, or its dead shell still afloat, in a vertical position. Therefore the stagnant basin model is maintained for the background situation, while current indications and isolated benthic horizons are referred to rare high-energy events.

Key words: Toarcian (Posidonia shale), oil schist, Ammonoidea, shell, epibiotism, Serpulidae, Ostreacea, Bryozoa, Inarticulata, Pteriina *(Gervillia)*, Inocerami, stagnant basin, anaerobic environment; South West German Hills (Holzmaden), Baden-Württemberg.

Zusammenfassung: Aus Orientierung, Verteilung und Selektivität der Epöken ergibt sich, daß große Ammonitengehäuse der oberliassischen Ölschiefer vor ihrem Absinken auf den Meeresgrund besiedelt wurden. Damit entfällt ein gewichtiger Einwand gegen das Schwarzmeer-Modell. Fossil-Einsteuerung und gelegentliche Benthos-Horizonte weisen jedoch auf gelegentliche Unterbrechung der Stillwasser-Bedingungen durch Sturmereignisse hin.

This paper was triggered by ERLE KAUFFMAN's (1978 and 1981) painstaking studies on the paleoecology of the Posidonia Shales of Holzmaden and other localities near Tübingen. His picture of dead shells forming "benthic islands" on gyttja-type mud bottoms is very suggestive and may well be valid for the less bituminous upper part of the Upper Liassic Posidonia Shales (Upper Epsilon). But it can not be indiscriminately applied to the more bituminous Middle Epsilon shales (Untere

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Schiefer, lower *falciferum* zone), on which the present observations are mainly based. It is this zone, in which the well preserved vertebrate skeletons are being found and to which previous environmental reconstructions have mainly referred, because it represents the extreme of whatever factors were responsible for the uniqueness of this remarkable "Fossil-Bonanza".

I owe most of the relevant material to the attention of JÜRGEN FISCHER, owner of a Holzmaden quarrying operation, who selected for us all the more heavily overgrown specimens from the large ammonites salvaged during the years in his quarries. This means that the vastly predominant cases, namely small ammonites and non-incrusted large ammonites, are not represented in the sample. For our present study this bias is irrelevant, since there was no discrimination against particular types of overgrowth and since the largest shells would, by their large surface and their higher elevation above a near-bottom oxygen boundary, represent the most attractive benthic islands in KAUFFMAN's model. On the other hand, large shells allow the attachment of so many individuals that their statistical evaluation becomes meaningful. Also irrelevant is the fact that the bottom/top orientations are not recorded in our specimens, because no significant differences have been found with respect to kinds, numbers and distributions of incrusters on the two flanks of the flat lying ammonites anyway.

Also included are overgrown ammonites from a similar, but much thinner and only locally developed oil shale of the Lower Lias (L. Sinemurian) near Balingen, because they show a more specialized relationship between host and encruster.

The poor preservation of the ammonites in this bituminous facies (SEILACHER et al. 1976) was a great help in our studies. Because all preserved incrusters have calcitic or (in the case of *Orbiculoidea*) phosphatic skeletons, they became "pounced" into their host's periostracum foil when it collapsed after diagenetic solution of the shell aragonite (Fig. 1). As a result, the overgrowth of both flanks can be studied in the flattened specimens without preparation. As a phylogenetic by-product, this material also provides evidence about the adaptational history of the exogyrid oysters, which in the Toarcian had their miniaturized stepping-stone stage before they evolved larger free-lying forms in the Upper Jurassic.

A. Cemented epizoans

1. "Symbiotic" serpulids (Fig. 2)

In the Lower Liassic (L. Sinemurian) Oil Shales, which are only a few decimeters thick and developed only locally, ammonites are so poorly preserved that they easily escape the attention of the collectors. The "ammonite phantoms" become more visible, if their spiral outline is accentuated by the calcitic tube of a serpulid worm (Fig. 2). Previous studies of non-compacted specimens (SCHINDEWOLF 1934, MERKT 1966) have shown that these serpulids interacted with the living am-

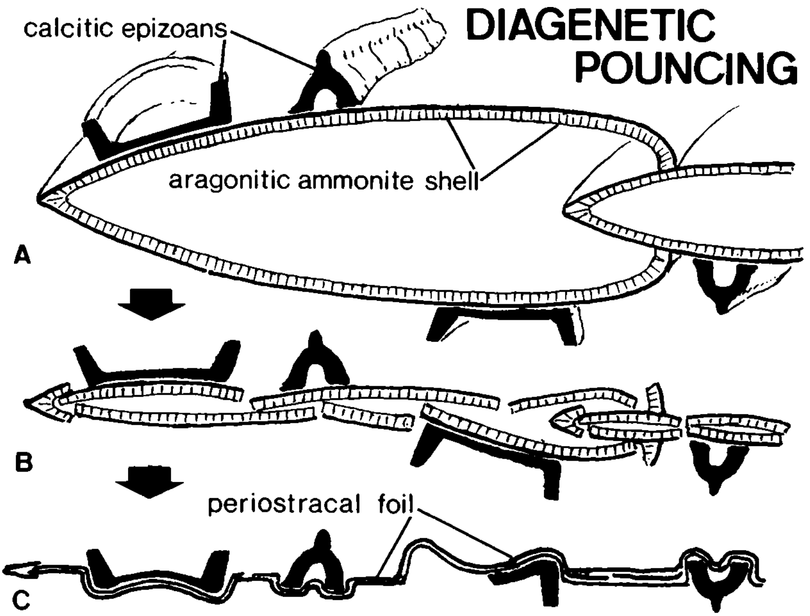
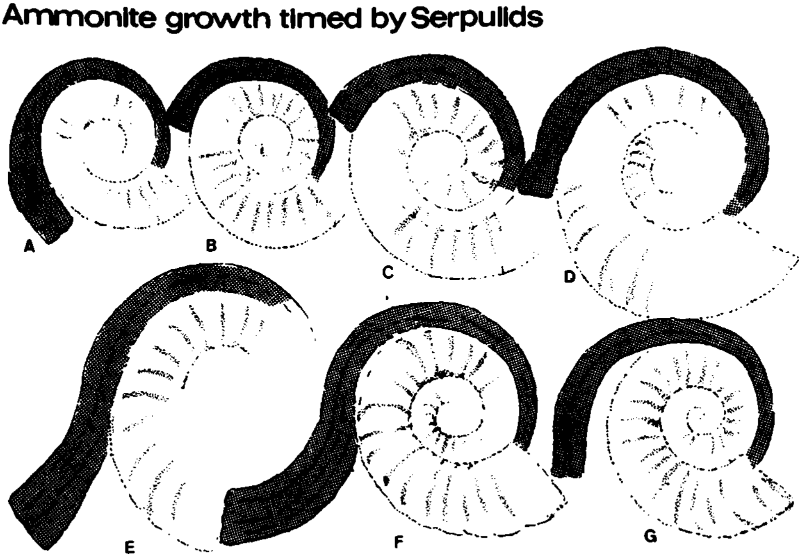


Fig. 1. During diagenetic solution and compaction of the empty aragonitic shells, the calcitic incrusters of Posidonia Shale ammonites become pounced into the periostracal impression. This effect allows us, without preparation, to recognize and distinguish individuals that grew on the right and left flank of the host.



monite by growing along the venter of its spiral shell and becoming progessively overgrown from their rear end by the progressing ammonite whorl. For this "chase-growth" to function, growth rates of the two organisms obviously had to be fairly synchronized, since a premature slowdown or stop of growth would have become fatal for the serpulid. On the other hand our oil shale material shows that serpulid growth could go on after the host had stopped to grow. In this case the serpulid (or the pair of serpulids that commonly grows side by side flanking the ammonite keel) lifts free from the substrate to turn its aperture into the swimming direction of the host.

This example is relevant to the Posidonia Shale story, because it most clearly shows incrustation of a living host and because no other incrustations have been observed in this bed that could be referred to post-mortem overgrowth of benthic island shells.

2. **Commensal serpulids** (Fig. 3)

Switching to the Posidonia Shale example, we first discuss the serpulids. Their taxonomic distinction is rather difficult because of the crushed preservation. Nor do they show significant responses to the growth of their host shell, for instance clockwise turning on the left and counterclockwise on the right flank of the ammonite. But statistical analysis shows that their apertures point significantly upwards (slope orientation), relative to the swimming position of the ammonite. Since this position remained the same in a nekroplanktonically floating shell, it is difficult to decide whether the serpulids grew on a live ammonite or on a drifting shell, but likely not on a shell that lay horizontally on the sea floor.

This interpretation is corroborated by an uneven dorsoventral distribution with significantly more serpulids on the upper halves of the ammonite shells. On the other hand left and right flanks differ neither in the numbers, nor the orientations, nor the distribution of serpulids as should be expected in benthic islands. It is also noteworthy that at least two of the three *Harpoceras* shells in Fig. 3 preserve the aptychus in place, indicating that it was still held in this position by ammonite soft parts.

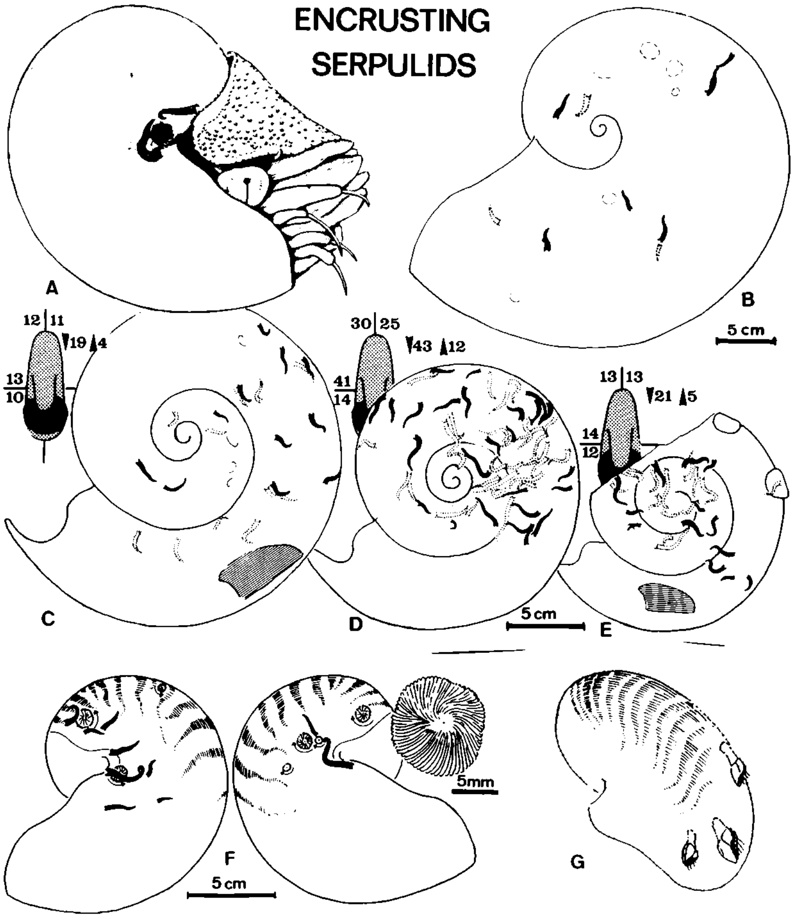
Another significant feature is the substrate selectivity of the serpulids: In the Holzmaden material they were found only on *Nautilus* shells and in one *Lytoceras*

Fig. 2. In the Sinemurian (Lias alpha 3) Oil Shales of Ofterdingen and Engstlatt, small ammonites are preserved only as flattened phantoms. In contrast, commensal serpulids are well preserved. They grew along the ammonite keel synchronously with their host, which overgrew the earlier parts of the serpulid tubes. After ammonite growth had stopped, the serpulid commonly grew on free from the substrate (E, F) in order to maintain the right orientation to the host's swimming. – GPIT Kat. Nr. 1572/13–19. (GPIT = Collections of the Geol. Paläont. Institut d. Universität Tübingen; SMNS = Collections of Staatl. Museum f. Naturkunde, Stuttgart.)

specimen (not figured), in Dotternhausen only on Harpoceratoid ammonites.

Interestingly, serpulid orientation in present-day *Nautilus* is consistently different. In a live *N. macromphalus* observed in New Caledonia (Fig. 3A), *Serpula* grow near the umbilicus with the aperture pointing horizontally in an anterior direction. The same is true in three specimens selected from a commercial sample of *N. pompilius,* probably coming from the Philippines (Fig. 3F).

One specimen in the Philippine sample was also overgrown with some balanid barnacle. Since only the basal plates are preserved in this specimen, their slope orientation can not be determined directly; but as the growth centers are off-centered upwards like in other slope-oriented balanids, we assume that it corresponded to the norm of balanid slope-orientation (SEILACHER 1960, Fig. 1). More surprising is the whirl of the radial lines in the exposed basal plates (Fig. 3F), because it



turns opposite to what should be expected as adjustment to the rotation of the substrate effected by the host's growth. One could assume that the balanid whirl reflects adjustment to a change in attitude during the necroplanktonic phase, since both the decay of the soft parts and the gradual waterlogging of the last air chambers tend to turn the drifting *Nautilus* shell opposite to growth rotation.

While more observations will be necessary to establish the rotation adjustment (which would also apply to the coiling of serpulids), the preference for the upper surfaces is obvious also in these modern examples. In truely necroplanktonic overgrowth, however, the very top of the cephalopod shell should be free from overgrowth above the water line (Fig. 3G).

3. Oysters

These are the most common encrusters, particularly on the large *Lytoceras* shells. Unfortunately the umboes and growth lines can rarely be made out, so that the oysters could not be tested for slope orientation (Seilacher 1960). But with respect to dorsal/ventral and left/right distributions they agree with the serpulids, as can be seen from the countings in Figs. 4, 5, 8 and 10. It should also be noted that they prefer the venter rather than the flanks of the outer whorl, which would have formed the tops of a horizontally lying ammonite. Substrate selectivity is low with reference to cephalopod shells; but the oysters avoid wood, even if they are now found right beside it (Fig. 5C).

Fig. 3. In modern *Nautilus* (A: *N. macromphalus* observed in Noumea, New Caledonia) serpulids use to grow on the umbilical shoulder and face to the front side. In Posidonia Shale *Nautilus* (B) and harpoceratid ammonites (C–E) serpulid overgrowth is less regular. Still, statistical evaluation suggests a distributional perference for the upper half of the host shell and a slope orientation of the serpulid apertures to the upper rather than the lower sector with reference to the host's swimming attitude. In contrast, there is no significant difference in numbers or distribution of incrusters on the right and left flank as should be expected if incrustation had occurred on a dead shell lying horizontally on the mud. The presence of the aptychus in C and E (in D it may be covered by sediment) also speaks for premortal overgrowth.

B: Unt. Schiefer, Holzmaden – GPIT 1572/10.

C: Ohmden – GPIT 1572/11.

D–E: Museum Dotternhausen (counterpart of E: GPIT 1572/12). Scale (5 cm) same for C–E.

F: *Nautilus pompilius.* Overgrowth of 3 specimens, probably from the Philippines, drawn on one specimen. Serpulids, found in all three specimens, show a perferred orientation towards the host's aperture, like in A. The basal plates of balanids, present only in one specimen, suggest the usual slope orientation, but their "whirl" (see enlarged drawing of encircled specimen) is opposite to the one that adjustment to the host's shell growth should produce (GPIT 1572/25–27).

G: Floating shell of *N. pompilius* with broken body chamber, as photographed drifting near Langun, W-coast of Malaysia. Note that the encrusting goose neck barnacles maintain a certain level below the water line.

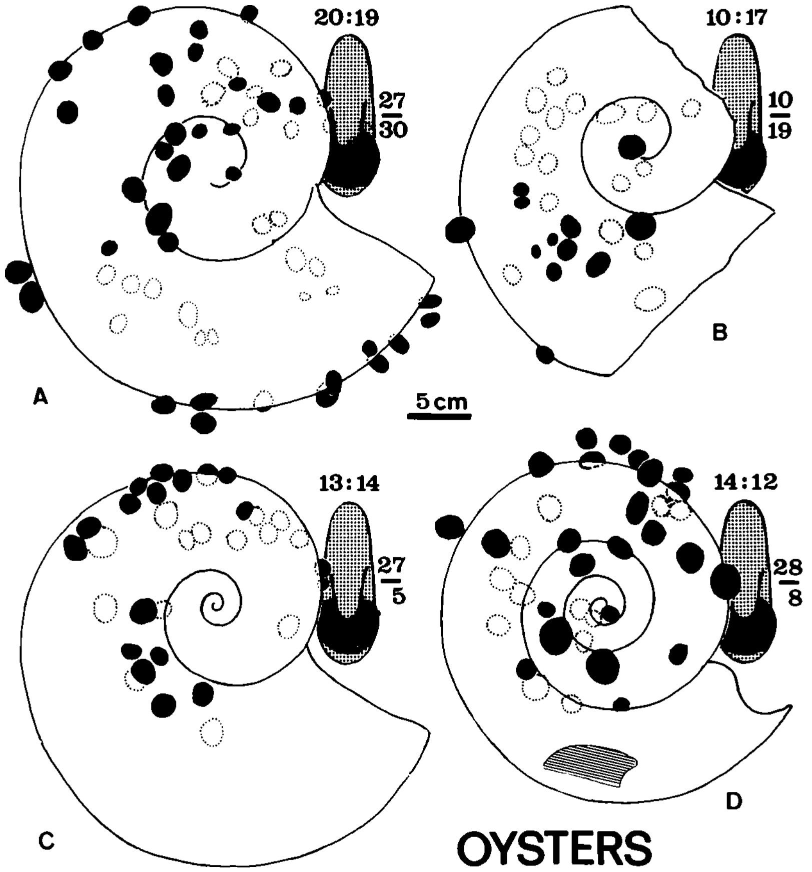


Fig. 4. Almost equal distribution of oysters on right and left flanks, but commonly unbalanced numbers in the lower versus the uppert halves, of these and other ammonite shells (compare Figs. 5, 8 and 10) indicate incrustation when the animal was still alive or the shell drifting in a vertical position. Note that the sums differ, because oysters at or outside the ammonite margin were not used in right/left countings. – A–C: *Lytoceras,* Unt. Schiefer, Holzmaden; A: SMNS 26031, B: SMNS 2603, C: SMNS 16438, D: *Harpoceras* with aptychus, GPIT 1572/13 (= Brenner & Seilacher 1978; Fig. 3c).

4. *Exogyra*

Even though they are only a few mm in length, incrusting *Exogyra* can be easily recognized by the clockwise spiral wall of the attached left valve. Because of their small size, not all *Exogyra* shells may be pounced from the far side to the exposed flank of the ammonite, where they appear as counter-clockwise spirals (dotted in Fig. 5). Nevertheless there is no reason to believe that distributions are different from those observed in oysters and serpulids.

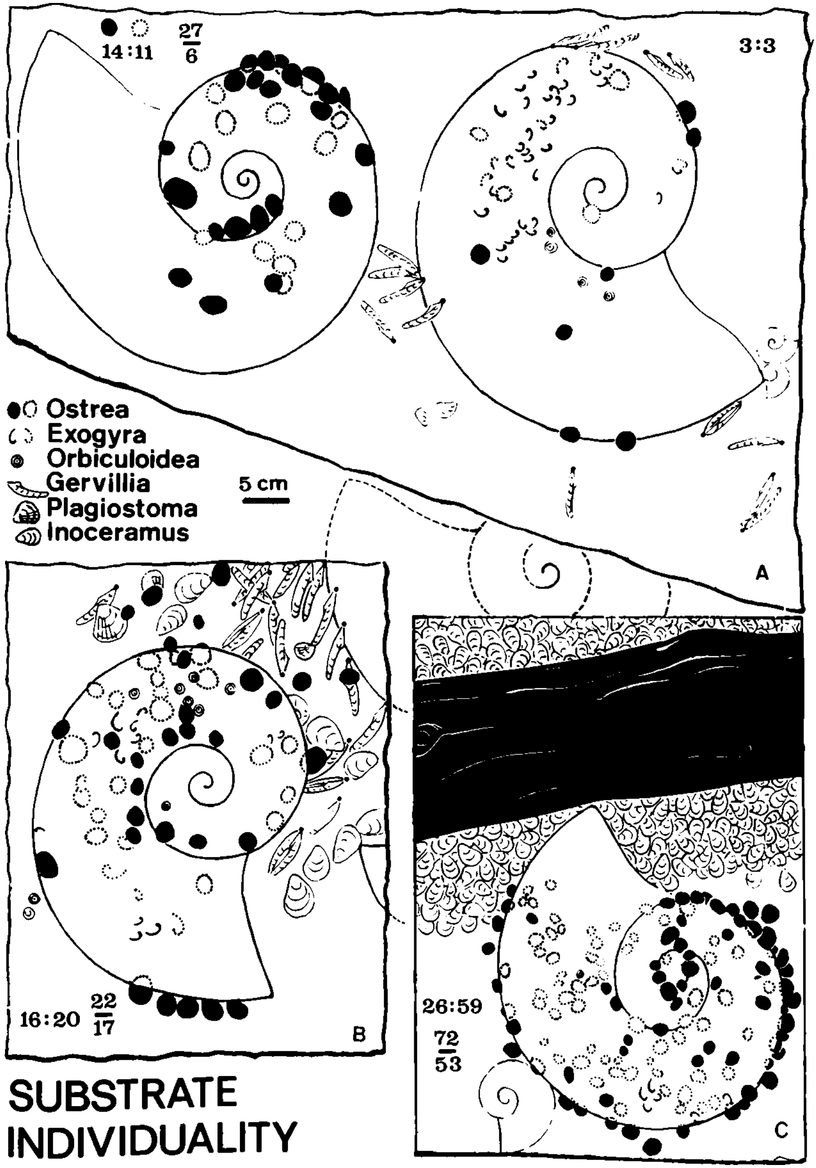


Fig. 5. Conspecific ammonite shells (*Lytoceras*, A–B) lying side by side on the same bedding plane, commonly differ significantly in their kind of overgrowth. This suggests that they did not get incrusted in their place of burial. In C, the difference reflects a general preference of *Inoceramus* for wood as a substrate. Note that in contrast to the oysters the numbers of *Exogyra* are never balanced in numbers, because not all individuals from the far flank may appear pounced through. – All specimens from Unt. Schiefer, Holzmaden (GPIT 1572/14–16).

Since no *Exogyra* had previously been known before the Bajocian (STENZEL 1971), these forms are interesting also in a phylogenetic sense. It is perhaps no coincidence, that, like the oldest *Alectryonia* of the Lower Muschelkalk (SEILACHER 1954), this is a minute epizoan form. Because this mode of life tends to lead to miniaturisation, it seems to have served as the ecoevolutionary stepping stone into the new morphogenetic programs of many secondary soft bottom dwellers (CHINZEI, SAVAZZI & SEILACHER, in pr.) that could later evolve again into larger free-lying forms. It would be interesting to find out, whether by this evolutionary bottleneck the Exogyrids could be linked with the true oyster stock.

5. Bryozoa (Fig. 6)

That incrusting bryozoa are also represented in this microhabitat is less surprising than their rarity and their seeming substrate specifity. So far they have never been found except in one *Nautilus* specimen, on which they occur in large numbers. Since only the vertical septa between adjacent zoecial tubes are preserved, and exact determination is difficult; but the lyra-like branching of the colonies suggests a cyclostomatous genus similar to *Berenicea*. A non-compacted, immurated version (VOIGT 1966) is preserved on the base of a serpulid tube (Fig. 6D).

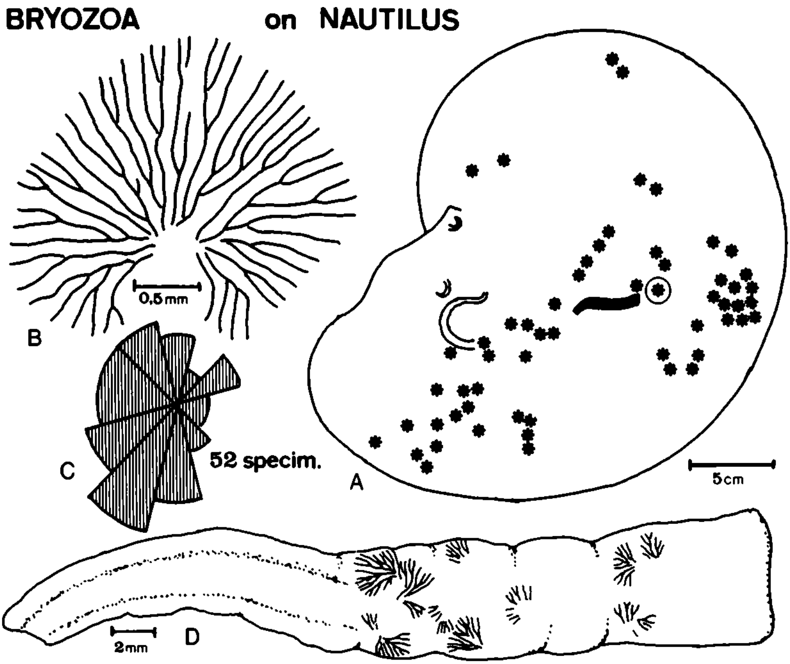


Fig. 6. In the Holzmaden sample, incrusting bryozoa were found only on a single *Nautilus* shell (A; encircled specimen enlarged in B). Statistically they seem to prefer the lower half of the shell and an anterior growth direction (C). A serpulid (D; black in A) preserves overgrown bryozoa on its base, indicating successive generations of overgrowth. – GPIT 1572/17.

B. Flexibly attached epizoans

Byssally or pedically attached organisms fall off the substrate after death, unless they become rapidly buried. In this case, which seems to have been fairly common in the Posidonia Shales, the epizoans may still become secondarily displaced by compaction relative to their substrate. In other instances they fell off before burial; but the fact that they form a halo around their original substrate, and even retain some of their orientations to it, indicates that dismanteling and the subsequent burial happened in completely quiet water.

1. *Orbiculoidea papyracea* (Fig. 7)

This inarticulate brachiopod occurs only sporadically in the Holzmaden sample (Fig. 5). The illustrated specimens (Fig. 7) come from other localities and probably from higher levels within the Posidonia Shales (W. RIEGRAF, pers. comm.). In addition to the cone shaped dorsal valves they show some pedicle valves, which bear a very distinctive pattern of divaricate ridges. These ridges probably served to reinforce the pedicle valve, which is much thinner than the covering brachial valve.

Since *Orbiculoidea* shells are chitinophosphatic, they did not get dissolved, but still were too thin to produce the pouncing effect. Observations are thus restricted to the flank that happens to be exposed in the particular ammonite specimen. In addition, the three *Lytoceras* specimens are incomplete, so that nothing can be said directly about the left/right or dorsal/ventral distribution of the attached brachiopods on the ammonite shell.

However, in the specimen from Reutlingen (Fig. 7B) there is an elongate mosaic of *Orbiculoidea* valves on the bedding surface outside the ammonite impression. In this area, the vast majority of the cone-shaped dorsal valves are seen from the concave side, while they expose the convex side on the ammonite shell. We interpret this in analogy to the well known landing marks in Solnhofen ammonites (ROTHPLETZ 1909): The ammonite shell first landed on the bottom in a vertical position. When, after some time, the residual buoyancy had been lost, and the shell tilted into a horizontal position, the brachiopod pedicles on this side had disintegrated enough to leave the dorsal valves stuck on the mud. This would suggest that *Orbiculoidea* overgrowth was very dense on the lower surface of the floating shell, but leaves open the question, whether the incrustation occured on the living ammonite or on a nekroplanktonically floating dead shell.

This question is answered, however, by the slope orientation of the brachiopods that remained attached to the tilted ammonite. Their orientation can be measured from the excentric position of the apex on the *Orbiculoidea* dorsal valve. The histogram shows a significant preference of the pedicle sides obliquely downwards with reference to the ammonite's aperture in all three specimens. A similarly oblique slope orientation has previously been described in *Discina* attached to

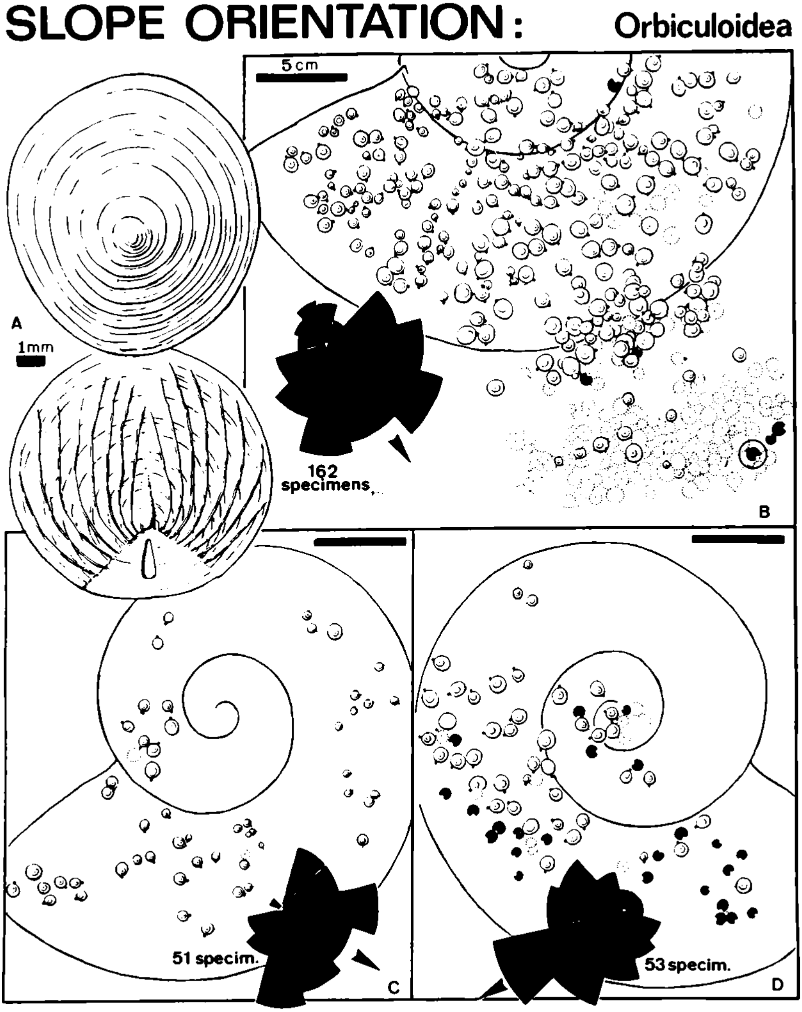


Fig. 7. The inarticulate brachiopod *Orbiculoidea papyracea* (A) has a conical dorsal valve, in which the apex is slightly displaced towards the side of the pedicle. The thinner pedicle valve (black in B and D) is reinforced by divaricate ridges. Although the valves may be secondarily displaced by compaction, they statistically reflect a slope orientation with the pedicle side pointing away from the ammonite's aperture in all three specimens (valves outside ammonite not counted). In B, an elongate group of upside-down (dotted outlines) dorsal valves marks the area with which the vertically landing ammonite shell touched the mud before it fell over. B. Reutlingen SMNS 4603; C. Ofterdingen SMNS 26448; D. Dewangen GPIT 1572/18 (leg. G. Werner, Dewangen).

Gervillia (Seilacher 1954: Fig. 6). The new material, however, suggests a slightly different explanation.

Comparing the incrustation on left (Fig. 7B, C) and right (Fig. 7D) flanks, we see that the obliquity of the orientation can not be slope-induced, because the pedicle ends point to the lower right on the left flank, but to the lower left on the right flank. The obliquity is thus a reaction either to the swimming movement of the host or to the food particles coming from its mouth. In any case, it indicates association with the live ammonite.

2. *Gervillia*

The byssaly attached bivalves are mainly found along the outer spiral, or keel, of the ammonite shells and are therefore unsuited to measure left/right ratios. But they clearly show a preference for the lower side of the swimming or floating shell from which they could freely hang down in a pendant position. One could argue that this area was preferred because it would likely be on the lee side of a current-oriented ammonite shell lying horizontally on the bottom (Brenner 1976). But in this case the venter of the previous whorl just above the aperture would have been even more protected, while it is actually free from byssate bivalves.

In this ecologic group the bakevelliid *Gervillia lanceolata* is the most common species on the large ammonites from the "Untere Schiefer" in Holzmaden, although it has been found mainly on *Lytoceras* (Figs. 8–11). The extreme posterior elongation of this bivalve allows the displacement of the byssus almost to the anterior tip, but also crowded attachment on a limited substrate. That this pelecypod grew on the ammonite shell while it was still alive, or at least floated in a vertical position, is indicated

1. by the preference for the ventral rather than the upper side of the shell,
2. by the avoidance of the aperture,
3. by the parting of ventral *Gervillia* shells during the landing and tilting of the ammonite shell (Fig. 9),
4. by the parallel combing and detachment in Fig. 8D and G, suggesting some drift of the ammonite shell before it tilted.

3. *Inoceramus dubius* (Fig. 10C)

This bivalve is most commonly found throughout the Posidonia shales, but mostly without obvious relationship to any shell or object. Because of its ubiquity, the occasional association with ammonite shells may well be accidental. In our sample, the *Harpoceras* specimen Fig. 10C is the only exception. Here the *Inoceramus* shells form a cluster along the lower surface of the ammonite, i.e. the area which is preferred also by other byssate pelecypods. They are all double valved and, in spite of being detached, maintain a preferred position with the umbo to-

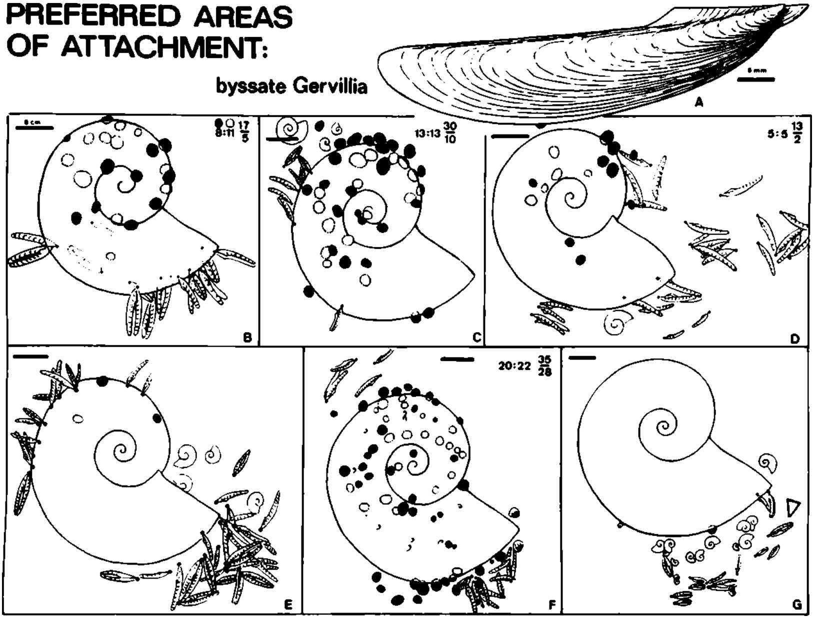


Fig. 8. In contrast to the cemented oysters and serpulids, and in accordance with its bysally attached and pendant mode of life, the elongate *Gervillia lanceolata* (A) prefers the lowermost side in a vertically floating ammonite shell, but avoids the apertural area where it would have interfered with the ammonite's head (compare also Figs. 5, 9 and 10). All specimens are *Lytoceras* from Unt. Schiefer, Holzmaden. – B: coll. Prof. ADAM, Tübingen; C: private collection (inverted); D: SMNS 26027; E: GPIT 1572/19; F: GPIT 1572/20 (BRENNER & SEILACHER, 1978); G: GPIT Ce 1558/2.

wards the ammonite center, indicating that they not merely fell down from the ammonite shell before it tilted. Again, the apertural area is spared.

One might argue that *Inoceramus* had the ability to become actively detached when its float sank down; but this was certainly not the case in drift woods (Fig. 5C), which are commonly densely overgrown by this pelecypod. Therefore we assume a strong selectivity for wood as a substrate and maybe also for *Harpoceras*, but both in a drifting state. The argument, that the number of *Inoceramus* shells is much too high in comparison with the driftwood preserved in the Posidonia Shales, is not necessarily valid. Wood is not only larger than ammonite shells, but may also drift long enough to support many generations of pelecypods. Their shells drop to the ground after death, while the log is more likely to be washed ashore instead of sinking to the bottom. Thus the preserved amount of drift wood may be far from representative.

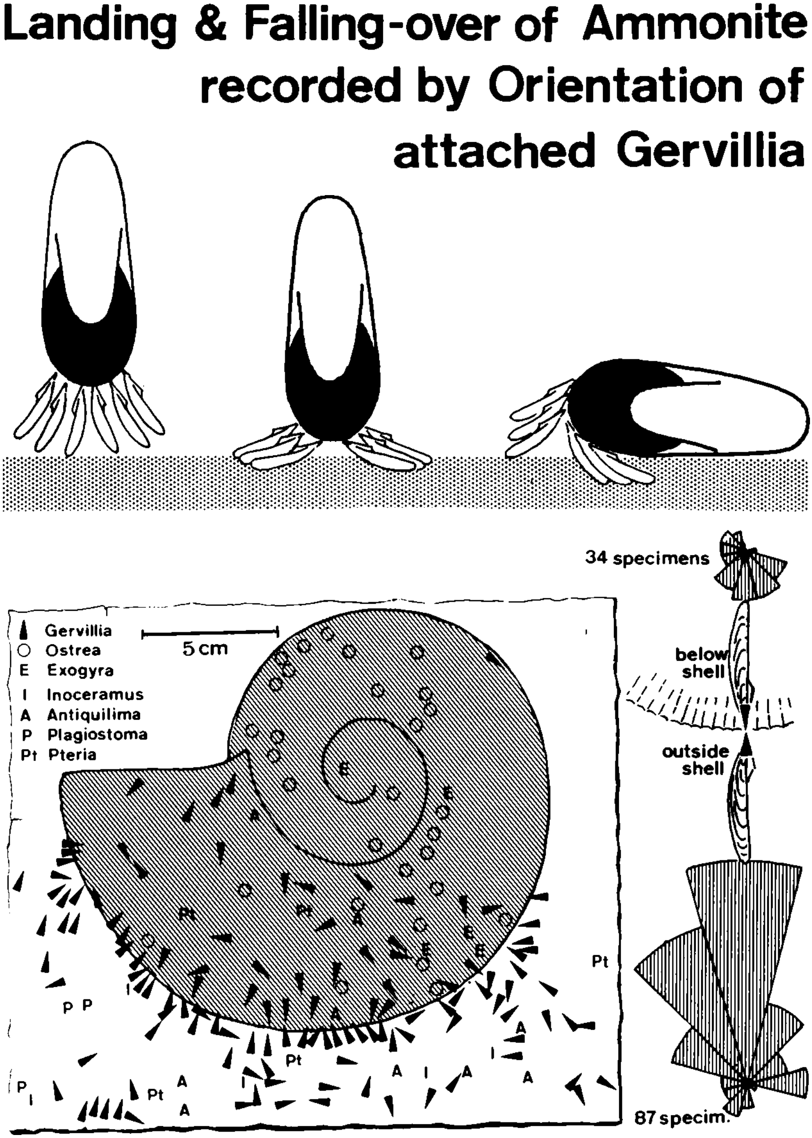


Fig. 9. In this heavily and diversely overgrown *Lytoceras*, the orientation of *Gervillia* (see histograms) records the vertical landing and falling over of the ammonite shell. This may also have bathymetric implications. GPIT 1572/21.

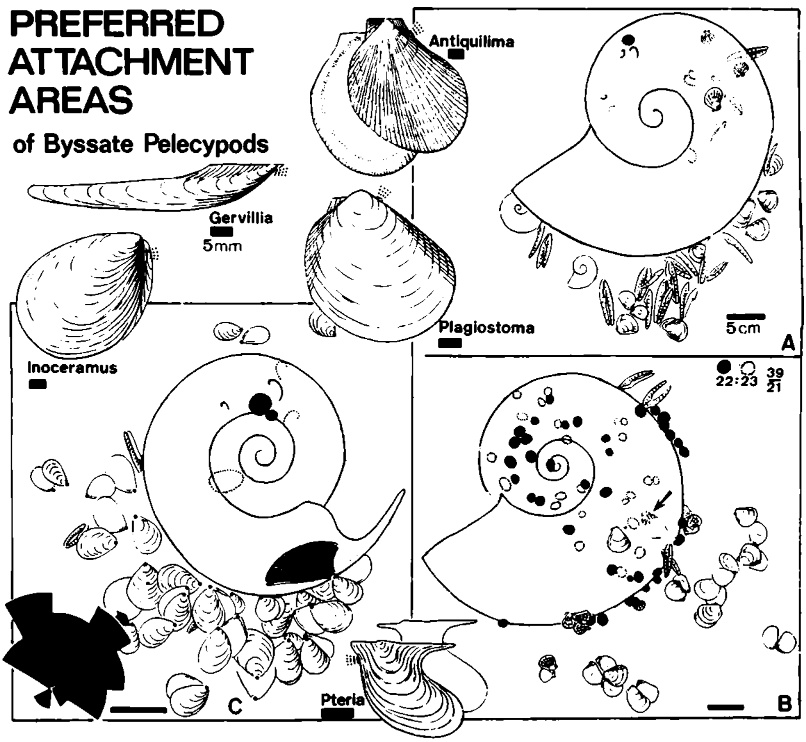


Fig. 10. Preference for the lower side of a vertically swimming ammonite and avoidance of the apertural areas seems to be shared by all byssally attached pelecypods. A pendant mode of life is also indicated by the radial orientation of *Inoceramus* (histogram of 27 double-valved individuals) in the rare case that this pelecypod is demonstrably attached to an ammonite shell. Note in C, that the aptychus is still in place and in B, that a small, short-spined echinoid (arrow) is associated with the epizoic community. – A: GPIT 1572/22; B: SMNS 26028 a; C: GPIT 1572/23. *Antiquilima* and *Plagiostoma* from unfigured *Lytoceras* (GPIT 1572/24).

4. *Pteria, Plagiostoma* and *Antiquilima* (Fig. 10A–B)

We mention these genera only for completeness. They rarely occur in large numbers, but otherwise show a similar preference for the ventral side of a live or drifting ammonite shell as was observed in other byssate pelecypods.

Conclusion

None of the ammonite incrusters in a representative sample show the distributions to be expected from the "benthic island" model. Instead they suggest that the ammonites became overgrown while the host was still alive or at least while the dead shell was still drifting. This interpretation is also supported by the selectivity of many species for certain hosts or substrates, and the faunistic individuality of conspecific shells, even though they came to rest side by side at the sea floor (Fig. 5). All these substrates have in common that they were available within the water column. In contrast, the endoskeletons of vertebrates or belemnite rostra, which are heavily overgrown and bored in other facies, did never become affected in the Posidonia Shales, because they became available only after they had sunk to the sea floor.

As a result, we maintain the stagnant basin model as the prevailing background situation for the Posidonia Shales. Stagnant conditions were only rarely interrupted by turbulence events, probably related to severe storms. These events commonly reached the level necessary to orient dead shells and carcasses lying on the sea floor, but only rarely did their oxygenating effect last long enough to allow ephemeral and lowly diverse communities of small and specialized epi- and infaunal organisms to colonize the nutrient-rich sapropelitic bottoms (BRENNER & SEILACHER 1978).

To what extent the benthic island model can be applied to other, less extreme variants of the bituminous shale facies within the Posidonia Shales, or in other parts of the Jurassic section, remains to be studied by similar methods.

In addition, our observations indicate that ammonites were very slow swimmers, for which neither the hydrodynamic shell shape, nor the friction by heavy overgrowth did become a critical factor.

Acknowledgements

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Literature

BRENNER, K. (1976): Ammoniten-Gehäuse als Anzeiger von Paläo-Strömungen. – N. Jb. Geol. Paläont. Abh., **151**: 101–118.

BRENNER, K. & SEILACHER, A. (1978): New aspects about the origin of the Toarcian Posidonia Shales. – N. Jb. Geol. Paläont. Abh., **157**: 11–18.

CHINZEI, K.; SAVAZZI, E. & SEILACHER, A. (1982): Adaptational strategies of bivalves living as infaunal secondary soft bottom dwellers. – N. Jb. Geol. Paläont. Abh.

KAUFFMAN, E. G. (1978): Benthic environments and paleoecology of the Posidonienschiefer (Toarcian). – N. Jb. Geol. Paläont. Abh., **157**: 18–36.

— (1981): Ecological reappraisal of the German Posidonienschiefer (Toarcian) and the stagnant basin model. – In: GRAY, J.; BOUCOT, A. J. & BERRY, W. B. N. (eds.): Communities of the past., Hutchinson Ross publ. Co.: 311–381.

Merkt, J. (1966): Über Austern und *Serpula* als Epöken auf Ammonitengehäusen. – N. Jb. Geol. Paläont. Abh., **125:** 467–479.

Rothpletz, A. (1909): Über die Einbettung der Ammoniten in die Solnhofener Schichten. – Abh. K.bayer. Akad. Wiss. II. Kl., **24:** 313–337.

Schindewolf, O. H.: Über Epöken auf Cephalopodengehäusen. Paläont. Z., **16:** 15–31.

Seilacher, A. (1954): Ökologie der triassischen Muschel *Lima lineata* (Schloth.) und ihrer Epöken. – N. Jb. Geol. Paläont. Mh., **1954:** 163–183.

— (1960): Epizoans as a key to ammonoid ecology. – J. Paleont., **34:** 186–193.

Seilacher, A.; Andalib, F.; Dietl, G. & Gocht, H. (1976): Preservational history of compressed Jurassic ammonites from Southern Germany. – N. Jb. Geol. Paläont. Abh., **152:** 307–356.

Stenzel, H. B. (1971): Oysters – In: R. C. Moore (ed.): Treatise on Invertebr. Paleont., N, 3.

Voigt, E. (1966): Die Erhaltung vergänglicher Organismen durch Abformung infolge Inkrustation durch fossile Tiere. – N. Jb. Geol. Paläont. Abh., **125:** 401–422.

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