EPIFAUNA AS A TOOL IN AUTECOLOGICAL ANALYSIS OF SILURIAN BRACHIOPODS

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ABSTRACT. The epifauna (mostly bryozoans) of some large brachiopod populations from the uppermost Wenlock Mulde Marl (Gotland, Sweden) have been analysed to obtain information on autecology and especially on the life position of the species. After separation of the post-mortem element of the epifauna, an attempt was made to discriminate between forms that settled above or below the water–sediment interface, and between those that settled on the exposed or the shaded side of the brachiopods. The results were tested against observations on a large number of brachiopods found in presumed life position in one bed. The size distribution in the supposed thanatocoenosis was also analysed. In some forms (dalmanellids, *Atrypa*, *Striispirifer*) the life position appears to be the 'normal' one, obliquely, with the beak down in the sediment. Two species gave unexpected results; *Leptaena depressa*, which seems to have lived with the discs in nearly vertical position, and *Meristina obtusa*, which appears to have been freely suspended by the pedicle, like many recent terebratuloids. Size distributions showed that some forms (the dalmanellids, *Atrypa* sp., and *M. obtusa*) had a 'normal' population structure, with many more larval and young valves than adults. Others, such as *Striispirifer* sp. and especially *L. depressa* had an abnormally low number of larval and juvenile valves, indicating special ecological and reproductive conditions.

THE epifaunal growth on brachiopods can give information both on the life position and water-circulation of the hosts, and also on the ecology of the epifauna itself. Such studies have been made on various Palaeozoic brachiopods, i.e. by Richards (1972) and Pope (1976), and in the Silurian growths on faunas of the same age (Wenlock–Ludlow) have been described by Hurst (1974, Eke Beds, Gotland, Sweden) and Watkins (1981, type Ludlow, England). In addition to the classic studies by Yakovlev (1926), Teichert (1945), and Ager (1961), other papers on epifaunas have also been consulted for this review, i.e. Seilacher (1960), Hoare and Steller (1967), Schumann (1967), Holland (1971), Thayer (1974), Pitrat and Rodgers (1978), Kesling *et al.* (1980), and Sparks *et al.* (1980).

The Mulde Marl of Gotland, Sweden, has long been known for its rich and diverse faunas, with excellent preservation of the fossils. Not only are brachiopods numerous, but so too are ostracodes, trilobites, molluscs, and corals. The brachiopod assemblage seems to belong in the *Clorinda* community of Ziegler *et al.* (1968), and in hydrodynamic category III of Faber *et al.* (1977). This community borders on the graptolite facies, and in some localities in the Mulde Marl graptolites (*Pristiograptus dubius* and *Gothograptus nassa*) are quite common. As indicated by Faber *et al.* (1977), the ecological characteristics of this assemblage are not only depth, but more importantly, quiet water, bioturbation, and light penetrating to the bottom.

My studies of the Mulde Marl over a number of years indicate that quiet water conditions may not be due primarily to depth, but more to the baffling effect of macrophytes. This is also suggested by interfingering between the marl and the distinctive shallow water Bara Oolite facies of the Halla beds. The marl appears to have been deposited along the western margin of the Baltic Silurian carbonate platform, along its margin with the deeper water graptolite facies.

MATERIAL AND METHODS

The material used for this study is from two localities in the Mulde Marl of Gotland: (1) Mulde Tegelbruk 1 (see Laufeld 1974, pp. 102–103), where specimens have been collected loose in the old clay pit from 1948 to 1980; some museum specimens from this locality have also been utilized. None of the specimens was collected in life

position. (2) Blåhäll 1 (see Laufeld 1974, p. 23), where a large number of brachiopods were collected in 1973 and 1979 from a *c.* 50 cm thick mudstone bed, with many specimens in life position. Bioturbation has taken place in this bed, but the patterns of disruption (hinge lines may be tilted up to 30°, but still with a marked unimodality on main orientation) indicate that the organisms responsible for bioturbation were too small to reorient the larger brachiopods. The orientation was noted for almost all complete specimens from Blåhäll, but some were also collected loose for the study of the epifauna only.

The patterns of epifaunal growth observed on the Mulde Tegelbruk specimens, and the life positions that could be inferred from them, were tested against the observed life positions in the same species at Blåhäll. It should be noted that in spite of the resemblance of the brachiopod faunas at the two localities, there are obvious differences in quantitative distribution. *M. obtusa*, which is common at Mulde Tegelbruk, is represented only by a few, small specimens at Blåhäll, whereas *A. 'reticularis'* is more common at Blåhäll. The latter locality seems to represent somewhat deeper water than Mulde Tegelbruk, as indicated by a higher proportion of planktonic and nektonic forms (graptolites and trilobites).

The epifauna was mapped on all brachiopods in which both valves could be observed, and the bryozoans and other epifauna were listed according to a system modified from that used by Kesling *et al.* (1980) and Sparks *et al.* (1980). The epifauna was classified in two main groups: those growing on any hard substrate, regardless of whether the brachiopod was living or not (epifauna typically closing the commisure, very large specimens growing over the brachiopod, and those evenly distributed over the valves); and those that seemed to be related to the life of the brachiopods (symbiotic), by having settled preferentially near the margin of the valves, having grown towards the edge, and those settling in positions supposed to coincide with the inhalant or exhalant currents, or above/below the sediment–water interface. It was also noted whether the epifauna was different on the two valves, and whether some areas were either devoid of or especially rich in epifauna. For ramose (branching) bryozoans, the direction of growth (supposed to be vertical—directed towards the light) was also recorded.

Initial results showed considerable bias in some respects. The degree of infestation by epifauna varied among the different materials. Specimens from the old collections in the State Museum of Natural History in Stockholm have apparently been cleaned artificially to remove epifauna, much in the same way as modern molluscs are often cleaned before they are sold to collectors, or as souvenirs. The rate of infestation was consistently higher for each species in the material that I collected from Mulde Tegelbruk. Specimens from Blåhäll showed higher infestation rates than the material from Mulde Tegelbruk; the latter locality has been exposed to weathering, especially winter frosts, which cause some of the epifauna to spall off. The rate at which the epifauna spalls off is different for different species and depends on the nature of the brachiopod shell, especially the smoothness of the sculpture. There is also a variable degree of post-mortem wear of the sculpture (and the epifauna) on the specimens from Mulde Tegelbruk, and parts of many specimens are obscured by masses of concretionary mud and calcareous encrustations, which are difficult to remove.

Because of all these biases I consider it inappropriate to apply detailed statistical methods to the collections studied, such as those used on better preserved populations by Kesling *et al.* (1980) and Thayer (1981).

The diversity and composition of the epifauna varies considerably, as in Recent materials, and only in a few cases can constant dominances be identified. In the species that are heavily infested, such as *M. obtusa*, all the involved epifaunal organisms are found to dominate in at least one individual. Data on overgrowth relationships between the bryozoan species and their pairwise occurrence or exclusion will be reported in a later paper dealing with the systematic description of the bryozoans.

Special attention was given to bryozoans found in positions related to the inhalant and exhalant water currents of the brachiopods. It has been assumed that such epifaunas gathered around the inhalant current, but the observations by Zumwalt and Delaca (1980), that foraminifera on Recent brachiopods are distributed randomly along the margin, casts some doubt on this. Judging from conditions in Recent forms, it can be assumed that some epifaunal species were coprophagous (and settled preferentially near the exhalant current), some utilized the same food sources as the bryozoans (and settled at the inhalant current), and some did both.

It is rather difficult to discriminate between these groups on fossil brachiopod material, especially as there is some doubt as to where the inhalant and exhalant currents were located. Most authors regard the incoming current to have been lateral, with the outgoing one median. Jones (1982) has argued the opposite for an atrypid, and the whole discussion has been summarized by Vogel (1975). In the material described here *Cornulites* has a weak tendency to concentration along the median

axis of the valves, growing from the umbo towards the margin. Most bryozoans, especially the fistuliporoids, concentrate along the lateral areas of the valves, but many of them grow so large that they eventually cover a great segment of the valve margin. Other forms such as *Allonema*, *Aulopora*, and ceramoporoid bryozoans do not seem to prefer any particular sector of the margin. In one frequently occurring association, between *Atrypa* 'reticularis' and a fistuliporoid, the brachiopod has tried actively to prevent the bryozoans from getting close to the margin in certain areas (Pl. 1, figs. 10, 11). This may be taken to indicate competition for food at the inhalant current, which in this case must be taken to be lateral. This is the only case in my material that may give an indication as to the location of the inhalant current.

The brachiopods often show shell damage, in some cases in selective areas, and in a way that may be relevant for determining the life position of the animal. This has been studied, i.e. by Fenton and Fenton (1932), Ivanova and Sarycheva (1963), and Brunton (1966). The relevant information is mentioned below in the discussion of each species.

The population structure of the brachiopods studied here is of two different types. One group has a strongly left-skewed distribution (*Resserella elegantula*, *A*. 'reticularis', *M. obtusa*, and perhaps, to a lesser degree, *S. plicatellus*). The other type has a right-skewed distribution, with very few, if any, preserved larval and juvenile valves (*L. depressa* and *Strophonella euglypha*). The ecological importance of such distributions has been discussed recently by various authors in some detail (e.g. Cadée 1982*a*, *b*).

Richards and Bambach (1975) suggested that the left-skewed populations lived on soft-bottoms, whereas the right-skewed ones were from hard-bottom communities. This cannot be the correct explanation for the material described here, where all the populations lived together. There is no absolute control that all the specimens actually lived on the same bedding plane, and it is known that the sensitivity to the degree of lithification of the bottom sediments shown by epifaunal communities is much higher than the resolution power of sedimentological methods. Even very subtle differences in bottom lithification may influence the animal communities profoundly (Ekman 1927; Spjeldnaes 1978). The present material is so homogenous throughout the whole bed that it is reasonable to conclude that the different populations really lived together on the same substrate. As indicated by Surlyk (1974), much observed material has been strongly affected taphonomically, but in this case, the coexistence of populations with strikingly different structure may indicate that the differences were real and of biological significance.

Noble and Logan (1981) suggested that left-skewed populations had non-planktotrophic larvae, with the right-skewed populations planktotrophic. This may, as indicated by Jablonski and Lutz (1983), have important consequences for the geographical distribution and longevity of the species, but other explanations for a right-skewed distribution have been given by Broadhurst (1964) and Cadée (1982*a*, *b*), such as size-selective destructive predation.

One of the features of the brachiopods of the Mulde fauna at Blåhäll, is that clumping is rare or absent. This is important for the study of life positions, as clumping has a tendency to result in irregular and random orientation (as shown by Stewart 1981 and others).

BRYOZOANS

The Silurian bryozoans of Gotland are in need of a modern taxonomic revision. Only one of the species involved here—*Sagenella consimilis*—has been described recently (Brood 1975), and some of the others have been mentioned by Borg (1965).

The bryozoan epifauna is not very diverse, and informal names are used here for most of them. It includes fistuliporoids, ceramoporoids, trepostomes (several species), and cyclostomes (among them *S. consimilis*). *Allonema* has been described as a ctenostome bryozoan, but Brood (*in* Jaanusson *et al.* 1979) has correctly stated that there is not much positive evidence for this. However, because *Allonema* behaved like the bryozoans as a member of the epifauna, it is included among them for the purpose of this paper. The same applies to the other supposed ctenostome in the fauna, *Vinella*.

An attempt was made to identify shade faunas similar to those found on the underside of corals and

large shells in the Visby Marl (Spjeldnaes 1975), in order to identify upper and lower sides of the brachiopods, but this was not successful. Almost all of the epifauna found in the Mulde Marl seems to have been part of an open, well-lit fauna or to species living below or at the water-sediment interface. Some genera are the same as those of the shade fauna, but the species are different. *Corynotrypa*, which is a genus common in but not restricted to shade faunas, is remarkably rare in the Mulde Marl.

As part of this study the bryozoans encrusting the insides of articulated valves were also examined. They consisted of the ordinary bryozoans that usually settled indiscriminately on available hard surfaces. In some few cases, there was evidence that forms that had settled on selected sites along the shell margin continued to grow after the death of the brachiopod, even to the point where they encrusted the interior of the valve. In two cases, bryozoan epifaunas were observed on the inside of articulated specimens of *Atrypa* 'reticularis' collected *in situ* in life position.

As indicated by Spjeldnaes (1975), the 'cave' fauna was dependent on fairly vigorous water circulation, which probably did not occur on the soft-bottom of the Mulde Marl. In such environments, the availability of oxygen was a major problem, requiring severe physiological modifications in species living below the water-sediment interface of mud substrates, because the pore-water was probably anoxic only a millimetre or so below the surface. Many modern bryozoans can endure temporary drops in oxygen levels, but few, if any, can live under permanently anoxic conditions. The only form which seems to have lived regularly below the water-sediment interface in the Mulde Marl fauna is *Allonema*. It has been found—not only in the Mulde Marl, and not only on brachiopods—in places where position, corrosion of carbonates, and pyrite encrustations indicate anoxic conditions.

The wart-like holdfasts of articulated cryptostome bryozoans (*Ptilodictya*) occur on several of the larger brachiopods. Like the similar holdfasts of crinoids, they probably settled indiscriminately on hard surfaces, but since the articulating joint appears to approach a vertical position it may give an indication of the position of the brachiopods, even if in many cases it may be the position of the valves after the death of the animal.

OTHER EPIFAUNA

In addition to the bryozoans, there are a number of other organisms that occur in the epifauna on the brachiopods in the Mulde Marl fauna.

Cornulites specimens (probably more than one species) grow regularly from the umbo towards the margin of the valves, and there is a weak tendency for concentration in the median sector. This is not significant, as the material is incomplete because of spalling off, especially from the smooth brachiopods which often show 'ghosts' of spalled-off specimens. Schumann (1967) indicates a random distribution along the margin, and Richards (1974), Hoare and Steller (1967), and Sparks *et al.* (1980) had collections in which the *Cornulites* specimens are concentrated in the lateral sectors. Shell damage, supposedly due to absorbtion of brachiopod shell and damage to the mantle edge, is not seen in the Mulde Marl specimens.

Serpulids are common and occur in two associations, the first as 'spat-falls' of numerous, randomly distributed specimens, apparently having simply settled on a hard surface without relation to the living brachiopod. The second association did settle at the margin of the valve (such as shown by Holland 1971), but without any significant concentration in any sector; this settling pattern was probably on living brachiopods. In some mature brachiopod specimens the size of the serpulids increases towards the margin. This, which may appear paradoxical because the inner ones settled first, can be explained by the fact that those which settled on young, fast-growing shells were soon outgrown by the valve margin and therefore their food-source, and thus they died; but those that settled later, when the distal growth of the brachiopod was slower, had a longer effective life-span, and became larger.

A small favositid coral is found preferentially, but not exclusively in the lateral sector, together with many bryozoans, in some cases overhanging the brachiopod valve margin.

In a few cases *Aulopora* occurs along the margin of the valves, but not at all with the regularity demonstrated by Pitrat and Rogers (1978). In most cases it seems to have settled indiscriminately.

Craniid brachiopods are few, and do not appear to have any systematic relationship to the orientation of the host brachiopods.

Crinoid holdfasts, which are not uncommon and are frequently clumped, are mentioned above with the bryozoans.

BRACHIOPODS

The brachiopods involved in this study pose no taxonomic problems at this level. The nomenclature used is that of Bassett and Cocks (1974), and the only species that shows any peculiarity is *L. depressa*, which is distinctively dimorphic (see below).

Atrypa 'reticularis' (Pl. 1, figs. 10, 11)

According to Professor V. Jaanusson (written comm.) there is still some doubt as to the provenance of Linnaeus's original specimens, and the Mulde Marl material may not be typical. This species, which is the most common used in this study, has a low average rate of infestation, but this is due to the difference between the small and large specimens. Small, thin specimens have a low rate ($< 5\%$), and the larger, globose ones have an infestation rate of more than 90% in the Blåhäll material. Of the small specimens, about 35% are oriented with the plane of commisure horizontal, parallel to bedding, with the dorsal valve down, and the remainder are randomly oriented. Those that have the plane of commisure vertical, or steeply inclined, have about as many with the umbos up as down. The large specimens are (75%) oriented with the plane of commisure steeply inclined, and umbos down as illustrated by Fenton and Fenton (1932).

About 20–30 % of the large specimens are associated with a fistuliporoid as described above. As shown in Pl. 1, fig. 11, the brachiopod tried to prevent the bryozoan from reaching the valve margin by extending frills, which the bryozoans crept over. This association is seen in all material from the Mulde Marl, and also appears to be present on the supposed lectotype (Alexander 1948, pl. 9, figs. 1*a*–*d*).

The umbos of old specimens often show strong corrosion, even to the point where all traces of sculpture are lost. In two specimens there are colonies of *Allonema*, and one of a trepostome, which are perfectly preserved, and which had evidently settled on the already corroded surface. This indicates that the umbos suffered periodical corrosion because of low pH in the anoxic sediment, and that bryozoans could settle in the intervals when the conditions were less severe. This feature is also seen in some other brachiopods, but it is most spectacular in this species because of its marked sculpture.

From 10 to 15 % of the specimens show marked shell damage, in some cases reaching grotesque proportions so that only the hinge and gradual transitions to more normal individuals serve to identify them. Many specimens are markedly asymmetrical, and studies of disarticulated valves show that many of these are stunted because of internal damage, resembling *Diorygma atrypophilia* (Biernat 1961; Mackinnon and Biernat 1970).

Both the epifauna and its orientation support the life orientation suggested already by Fenton and Fenton (1932), with small specimens attached by the pedicle and old individuals living in a vertical or almost vertical position, with the umbos down in the sediment.

Resserella elegantula (Pl. 1, figs. 1–4)

In this species the infestation rate in the Blåhäll material is about 50%. As in *A. 'reticularis'*, the rate is lower in the younger specimens, but is almost universal in the old ones. The average area covered with epifauna is low, and there is great variation in the density and diversity.

The dominating form is *Allonema*, which forms about 50% of the encrusting colonies, and represent about 80% of the area covered. It regularly grows from the umbo towards the margin of the valves, and in some cases it can be shown to have continued growth after the death of the brachiopod.

It does not show any preferential orientation relative to the assumed water currents. The other bryozoans are mostly small colonies, placed along the margin of the valves, mostly in the median sector.

Of the specimens (adults only) of *R. elegantula* 48% are found with the umbo down, and the plane of commissure vertical or nearly so. There are few cases of shell damage, and most are limited. The growth-lines are often strong, with many on each valve. If they are taken to be annual growth-lines, they will indicate that the species had a very slow growth-rate and reached a surprisingly high age for such a small invertebrate (five to nine years). The irregular interval between the increments and the lack of such marked lines on other species from the same bed may suggest ecological stress (perhaps in connection with lack of oxygen) rather than annual growth cycles as a cause of their formation.

This evidence, especially the heavy infestation with *Allonema* at the umbos, indicates that this species lived burrowed rather deeply in sediments for most of its life.

Striispirifer plicatellus

The material studied of this species is rather limited, but many of the specimens are completely free and well preserved. The rate of infestation is high, but the area covered with epifauna was generally small. *Allonema* is rare, but *Vinella* is common. The other bryozoans, and *Cornulites*, are mostly distributed evenly along the margin from the angles of the hinge-line to the median axis.

Seventy-five per cent of the specimens were found with the umbos down, and the hinge-line less than 30° from the horizontal. This supports the generally held view (cf. Schumann 1967) that spiriferids were free on the surface, attached by the pedicle. Only a few, minimal cases of shell damage were found.

Meristina obtusa (Pl. 1, fig. 5)

In this species, specimens less than 20 mm wide have no real epifauna. The few cases found all appear to be post-mortem infestation. Specimens between 20 and 35 mm wide have a high infestation rate (*c.* 95%), but with only a small area covered. The larger, globose specimens are almost universally covered densely with epifauna; the few specimens without epifauna are all strongly worn. An average of 60% of the area is covered with epifauna, divided equally on both valves. In many cases there is a small area without encrustation, or with only sparse epifauna near one of the beaks, and with about as many epibionts on the dorsal as on the ventral valve. Typically, the bryozoans do not cross the commissure but grow on to it, and may overhang for up to 2–3 mm without interfering with the opening of the valves (Pl. 1, fig. 5). There are only nine specimens from Blåhäll, and they appear to be oriented at random. They are also small, thin specimens, and none of them is globose.


EXPLANATION OF PLATE 1

Figs. 1–4. *Resserella elegantula*. Two specimens in dorsal and ventral views, showing infestations of *Allonema*; Blåhäll 1, Gotland; 1, 3, RM Br115402; 2, 4, RM Br115402; × 1·5.

Fig. 5. *Meristina tumida*. Large globose specimen showing bryozoans growing towards the margin, but not closing it, and two specimens of *Cornulites* growing towards the margin of the valves; Mulde Tegelbruk 1, Gotland; RM Br115404; × 1·4.

Figs. 6–9. *Leptaena depressa*. 6–8 are ventral valves with various epifaunas, 9 is a dorsal valve, with typical growth of *Allonema* from the hinge-line, and a specimen of *Aulopora*. 6, 8 and 9 from Mulde Tegelbruk 1, 7 from Blåhäll. 6, RM Br115405; 7, RM Br11506; 8, RM Br115407; 9, RM Br115408; × 1·6.

Figs. 10–11. *Atrypa 'reticularis'*. 10 is a specimen showing the characteristic association with a fistuliporoid bryozoan, × 1·4. 11 is a thin section of a similar specimen, showing the frills made by the brachiopod to prevent the bryozoan reaching the valve margin, × 12. Both specimens are from an old museum collection labelled only 'Gotland', but the size of the sample (more than 5,000 specimens) and the similarity to the Mulde Tegelbruk material indicates that—like the supposed lectotype (Alexander 1948, pl. 9, fig. 1*a–d*)—it came from that locality. 10, RM Br115409; 11, RM Br115410.

All specimens are in the Department of Paleozoology, Naturhistoriska Riksmuseet, Stockholm (RM).

PLATE 1
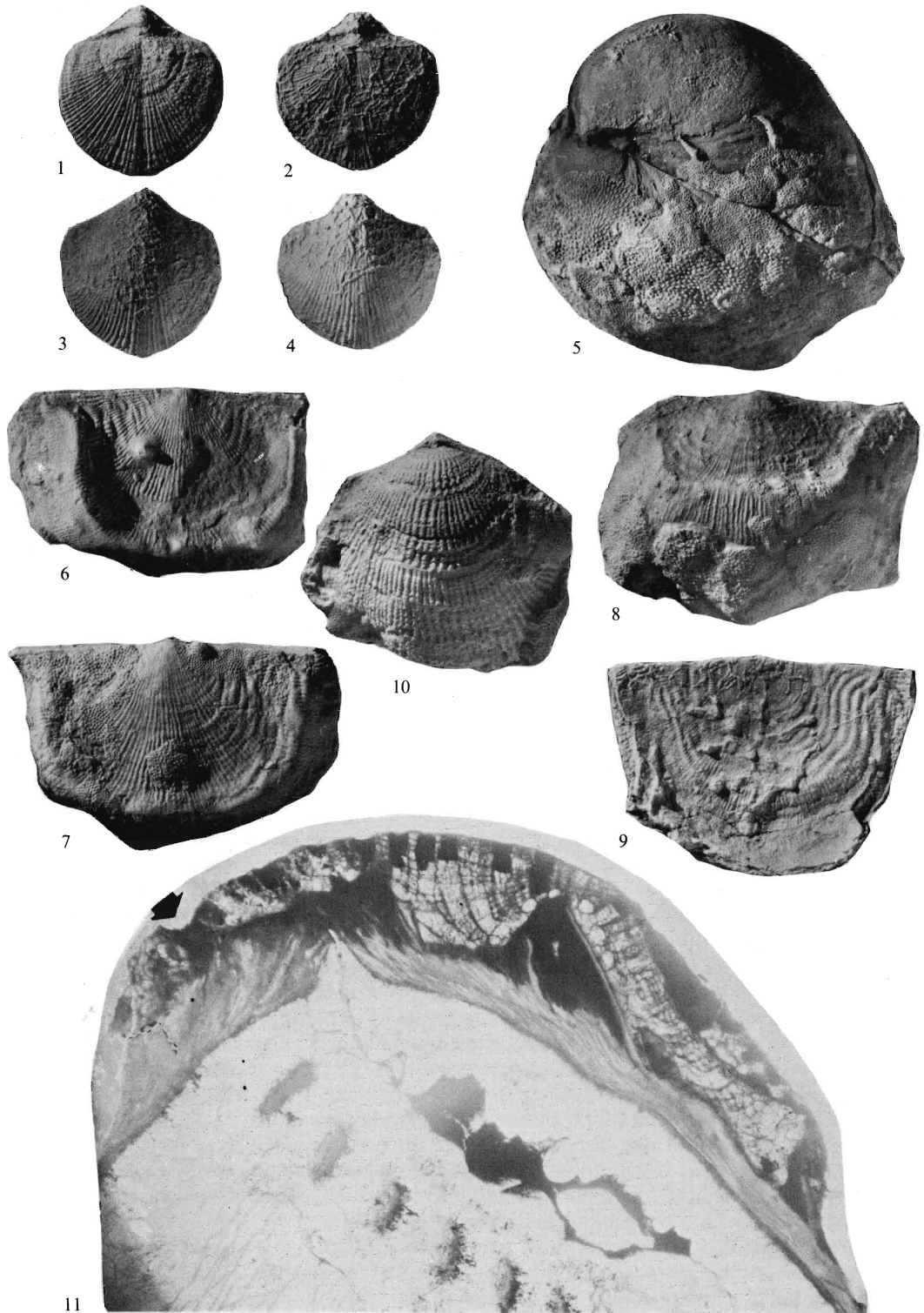
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In the material from Mulde Tegelbruk there are fourteen specimens that have been overgrown post-mortem with large bryozoan or coral colonies. In eleven cases the orientation of the brachiopod was vertical (umbo down) or nearly so. A number of specimens with presumably post-mortem crinoid and bryozoan holdfasts also indicate that the normal position on the bottom was vertical, with the beak down. Such a life position is suggested for many other large brachiopods such as pentamerids (Ziegler *et al.* 1966), and for the related *Cryptothyrella* (Gauri and Boucot 1970).

There is a strong umbonal thickening of the shells, and most specimens have a sizeable pedicle opening. As in some recent terebratulids with umbonally thickened shells, there is a marked furrow in the excess shell substance for the pedicle and its attachment.

There are some contradictions in these observations. The umbonal thickening, and the similarity to other Silurian brachiopods (see above) would indicate that *M. obtusa* was resting by gravity in a vertical position. The partly bare spots on the beaks and the well-developed pedicle would indicate that it was resting on the bottom, with the commisure horizontal and attached by the pedicle. On the other hand, the pattern of epifaunal growth is more strongly suggestive of a similar orientation to that of Recent terebratulids, that hang freely by the pedicle from some protruding object, such as a rock, sponge, or plant. Several of these recent species do have umbonal thickening of the shell.

The model suggested here is that *M. obtusa* was attached by the pedicle to a non-preservable object, perhaps a macrophyte, as there is independent evidence for their existence. When the brachiopods died and fell to bottom, they would normally come to rest with the beaks down due to the massive umbonal thickening.

Leptaena depressa (Pl. 1, figs. 6–9)

Specimens from Blåhäll show an infestation rate of about 90%, whereas the material from Mulde Tegelbruk shows only 25%, and the museum collections less than 10%. The difference is explained by both natural and artificial removal in the two latter cases, so that the description here is based only on the Blåhäll material. Infestation is strongest on the geniculated fringe and is distributed unevenly between the valves, as the pedicle valve has about three times more specimens, with even more area covered. *Allonema* is more common on the dorsal than on the ventral valve, and grows (in both valves) mostly from the hinge-line parallel to the median axis (e.g. Pl. 1, fig. 9). There is no significant concentration on any sector of the margin, but there are fewer and smaller specimens close to the hinge-line.

As mentioned above, this species is dimorphic in several morphological features, including curvature of the discs, length of geniculated margin, and sculpture, but particularly in its body volume. Analysis of this dimorphism will be discussed elsewhere, and it does not appear to be relevant for the problem treated here as both dimorphs have the same pattern of epifauna and orientation.

The orientation of *Leptaena* and other geniculated strophomenids is generally assumed to have been resting on the ventral valve, with the geniculated fringe upwards (e.g. Richards 1972; Pope 1976). This is based on a logical analysis of functional morphology, as it would be unreasonable to suppose that the geniculated fringe was pointing down into soft, anoxic sediment.

My material contradicts this logical model in two ways. First, the epifaunal growth is strongest on the ventral valve, which should be down, towards the sediment. The dorsal valve show some, but less growth, which is not consistent with a contact with the sediment, but rather with a position in the shade of the geniculated fringe. Secondly, 80% of the specimens collected from Blåhäll are found resting on the geniculated fringe, with the ventral valve obliquely upwards. These data from Blåhäll indicate that *Leptaena* lived in a vertical position, with both valves free of the sediment, and fell down onto the dorsal valve and the geniculated fringe after death.

The great majority of specimens show considerable shell damage on the geniculated fringe. In many cases the whole edge is ragged and many specimens are strongly asymmetrical. Damage to the discs is less, but is also common. The damage to the fringe may indicate that it was exposed to predators or suffered accidental breakage because of its position, but this could have taken place both in the conventional model and the one suggested here.

OTHER BRACHIOPODS

Besides the species discussed above, there are numerous others in the Mulde Marl, most of which are small species and either they did not have any appreciable or characteristic bryozoan epifauna, or the material available with both valves exposed for analysis was insufficient.

Among the latter is *Strophonella euglypha*, which as indicated by Bassett (1972, *in* Jaanusson 1979) is rather variable in shape. Most valves are found in the rock matrix, with only one valve completely exposed, and this shows an epifaunal pattern similar to that of *L. depressa*, with dominance of epifauna on the dorsal valve (the curvature is opposite in the two species), and no preference for any special areas along the shell margin. The orientation (ten out of fourteen specimens were resting on the ventral valve, with the commissure down in the sediment) was also the same. There was also extensive shell damage, not only on the geniculated fringe but also on the discs of the valves. This may indicate that *S. euglypha* lived vertically in the sediment such as suggested for *Leptaena*.

In the relatively small species *Amphistrophia funiculata*, the epifauna was dominantly on the ventral valve, mostly on the fringe, but also on the disc. The epifauna on the dorsal valve was restricted almost entirely to the geniculated fringe. This may indicate that this species lived in the 'conventional' way, resting on the dorsal valve with the geniculated fringe upwards. Shell damage was concentrated in two lateral sectors 20–45° from the hinge-line, and was found in 80% of the specimens studied. It may be related to attack from predators, or due to parasites interfering with the shell-secreting epithelium in the position of the water current.

Mesopholidostrophia laevigata is different from the other brachiopods, not only because of its unique shell structure (Harper and Towe 1967). Of the species studied it is the one with the lowest rate of epifaunal infestation (< 1%). The few bryozoans found show no preferred orientation, having probably settled randomly on dead shells. The population structure varies strongly from sample to sample, with some of them left-skewed in contrast to other strophomenids. The samples look very much like census samples, and this, together with its occurrence in some beds with dominantly nektonic–planktonic forms, and suspected epiplanktonics like *Orbiculoidea*, may indicate that *A. funiculata* was epiplanktonic or epiphytic, or both.

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