

FUNCTIONAL SIGNIFICANCE OF THE SPINES OF THE ORDOVICIAN LINGULATE BRACHIOPOD *ACANTHAMBONIA*

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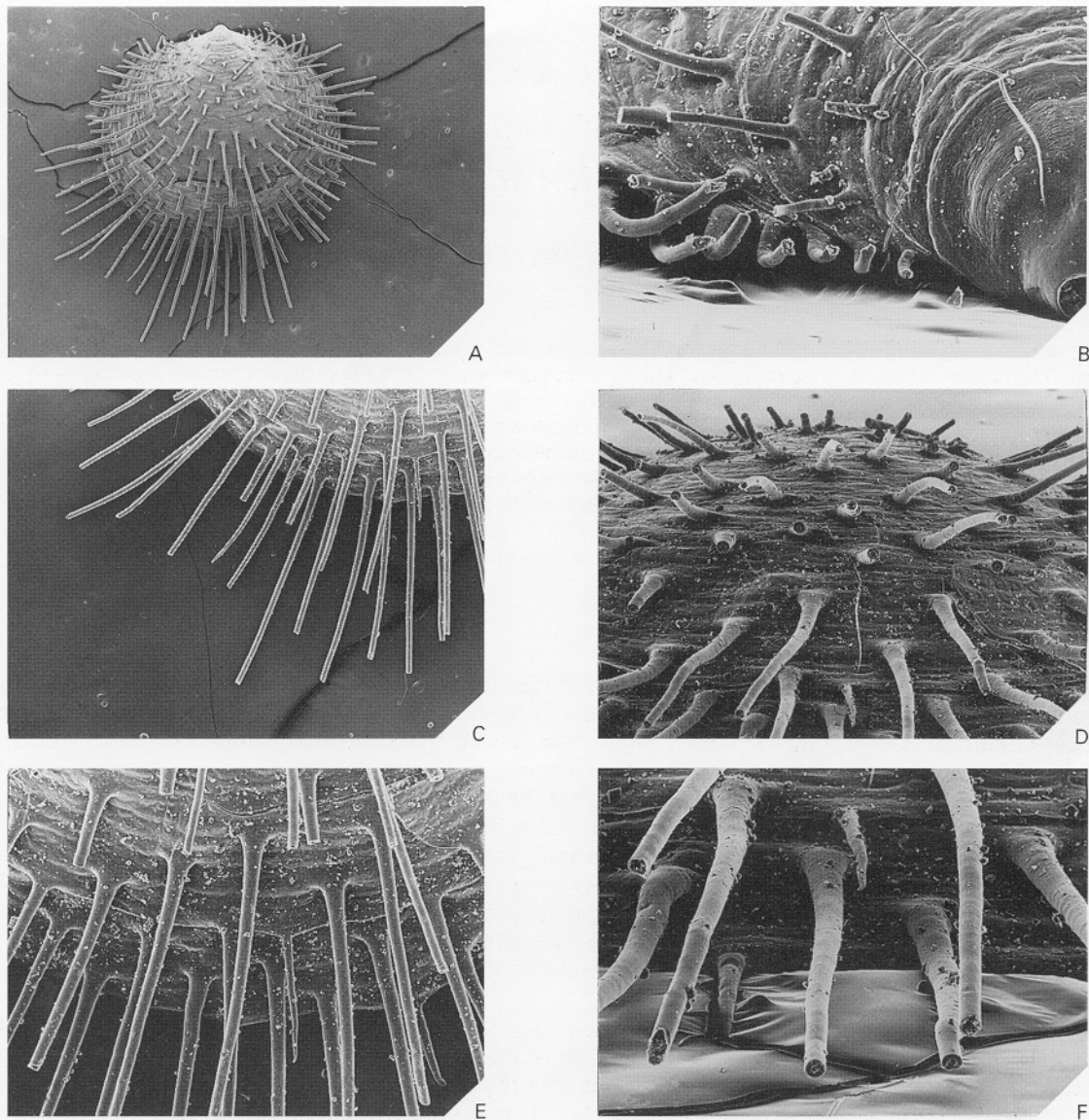
ABSTRACT. The hollow spines of an unusually well preserved specimen of the minute lingulate *Acanthambonia* are interpreted as having three functions. The short curved spines along the posterior margin are envisaged as attachment spines, supplementing a pedicle which is functional throughout ontogeny and regarded as anchoring the animal possibly to algal strands above the sea floor. Apart from rare undersized spines with tapering apices, the bulk of the spines on the shell surface are open-ended, with a length attaining half that of the shell itself. The open distal ends of these thin-walled spines would have housed mantle tissue during life, interpreted as being sensory and substituting for setae in the post larval stages. The alternation of spines along successive laminae indicates their interfingering disposition along the anterior and antero-lateral valve margins, where an additional function would have been to screen out coarse particles from the mantle cavity.

THE minute but distinctive Ordovician spiny lingulate brachiopod *Acanthambonia* has been recorded from a dozen or so areas in Europe and North America since it was first established by Cooper (1956). Despite this relatively wide distribution, the individual samples documented are typically of one or two valves or fragments. This paucity of material has impeded any unequivocal assessment regarding the systematic placement of the genus, as noted by Popov and Nölvak (1987). This rarity also characterized most of the East Baltic borehole material examined by them, with the sole exception of the Estonian Viljandi borehole from which over one hundred specimens were obtained from close to the base of the *Dicellograptus complanatus* graptolite Biozone. This material was particularly useful in that, with the high quality preservation, a minute external pedicle foramen and internal pedicle tube were observed on the valve previously regarded as being the dorsal valve. This contributed to the definite placement of the spine-bearing genus with the typically spiny Siphonotretoidea (Popov and Nölvak 1987).

The present paper examines the best preserved specimen from the Viljandi borehole, obtained from a small sample immediately above the base of the Pirgu Stage (sample 14 of Popov *et al.* 1994, text-fig. 2). This specimen is unique for the genus in the outstanding preservation of its spines which are half as long as the valve itself (Text-fig. 1A). This is proportionately similar in length to those described by Grant (1966) for the productoid *Waagenoconcha*, but of a totally different order of magnitude as regards absolute size. This raises the intriguing question of the function of such extraordinarily long spines in such a minute brachiopod.

Figured Specimen. *Acanthambonia portranensis* Wright, 1963. Ventral valve, IGT Br 1313: Viljandi borehole, Pirgu Stage, Sample 14 from depth 311.3 m (see Popov *et al.* 1994, text-fig. 2). Repository – Institute of Geology, Tallinn, Estonia.

Dimensions. Length – 1.19 mm; width – 1.21 mm; height – 392 μm ; diameter of foramen – 32.3 μm ; maximum preserved length of spine – 589 μm .



TEXT-FIG. 1. *Acanthambonia portranensis* Wright, 1963. Viljandi borehole, Estonia; Ordovician (Ashgill), Pirgu Stage (F1c). Ventral valve exterior (IGT Br 1313). A, C, E, direct view of valve, $\times 50$, and enlargements to show spine detail, $\times 100$ and $\times 200$; B, detail of posterior view of valve, $\times 370$; D, F, anterior view of spines, $\times 200$, and detail, $\times 400$.

THE FUNCTIONS OF BRACHIOPOD SPINES

Spines of many forms occur in different groups of animals and have many, indeed often several, functions varying from defence (in porcupines) to attack (in rhinoceroses), and from locomotion (in echinoids) to food trapping surfaces (in planktonic foraminifera).

In the Brachiopoda, Williams and Rowell (1965, p. H84) noted two basic kinds of spine; those formed on a lamellose shell surface by radial ribs projecting away from the shell surface and having

their sides joined beneath (such as in *Spinorthis* and *Tegulorhynchia*), and those which open onto the shell interior and characterize the productidines, chonetidines, occasional rhynchonellides such as *Acanthothiris*, and the siphonotretides. Of these, the largest group is the Productidina, for which the distribution and formation of the spines were discussed in some detail by Muir-Wood and Cooper (1960). The productidine spines were variously employed for direct anchoring in attached forms, for example in reefal environments, or for balancing in the case of forms living free on or partially buried in soft sediment. Other forms were attached by clasping spines in young stages but lay loose on the sea floor as adults. As well as attachment, fine spines, particularly when present on dorsal valves, have been considered to be protective by discouraging epifaunal settlement, the weight of which would have impeded valve opening. Marginal spines (as in *Chonosteges*) would have acted as a strainer for the water entering the mantle cavity.

Whatever the subsequent relationships to the substrate, in the same way that all bivalves have an initial byssal attachment, so all brachiopods attach in the larval stages for stability even if the peduncular structure atrophies before the adult stage is reached. Grant (1963) demonstrated the attachment of a species of *Linoproductus* by spines restricted to the posterior margin of the ventral valve and which grew medianly in an arc to hook round the stem of a crinoid. An entire ring could be formed fortuitously if the epithelia in the apices of two oppositely directed spines happened to meet and fuse, but for the most part the individual spines simply hook around the cylindrical object. The fusion is interesting as it confirms that the distal ends of the spines were of soft tissue during growth so that the characteristically hollow open ends are not necessarily the result of breakage. For *Waagenoconcha*, Grant (1966) showed that the convergent attachment spines of the juvenile stages were replaced in the adult by numerous long, thin spines which served to anchor the animal within the substrate. A third abrupt change in this stock was to smaller spines along the edges of mature ventral valves. These were interpreted as projecting above the substrate, and indicated some function other than that of shell support.

The hollow nature of this type of spine passing through to the interior and lined with epithelium suggested to Williams and Rowell (1965, p. H84) that the apical cells could have served to secrete a chitinous pad for attachment to the substrate, with growth of the spine ceasing should the inner end be sealed over by subsequent shell deposition. Rudwick (1965), with particular reference to *Acanthothiris*, suggested that the tips of the hollow spines could have borne highly sensitive mantle edge tissue which would have functioned in a sensory capacity well in front of the commissure. In this case the apical cells would have had a seta-like sensory function as long as the tips remained open and the internal contact with the mantle was maintained. A half-way stage towards this envisaged spinal function is seen in the numerous orthide stocks which possess adicules along the rib crests. These are interpreted as accommodating setae within the body of the shell (Wright 1981), and which again maintained contact with the mantle before being sealed off internally, sometimes well behind the shell margin (Wright and Rubel 1996, pl. 1). Setae may also have occupied the pits along the posterior margin of the plectambonitoid *Eochonetes* in the living animal (Wright 1996), although the function here is interpreted primarily as one of balancing, as suggested by Brunton (1972, p. 23) for the similarly disposed spines of the chonetidines.

In addition to the sensory function of the spines in *Acanthothiris*, Rudwick (1965, p. 607) also noted that the spines along the commissure projected radially, alternating in position on each valve to provide an additional function as a protective grille for restricting the size of particles entering the mantle cavity as noted above for *Chonosteges* and recorded for a number of other articulate stocks.

In the lingulates, hollow spines are typical of the Siphonotretoidea, the order which now includes *Acanthambonia* as discussed above. The spines may be rather sparsely scattered as in *Helmersenia* (Rowell 1962, pl. 30, fig. 27), but are commonly aligned along growth laminae as in *Nushbiella* Popov. The spine-bearing lamellae are well displayed in *N. lillianae* (Holmer 1989, p. 162). Here the edge of each lamella bears a single row of hollow tapering spines in which larger spines alternate with smaller ones; these again alternate in position in successive rows to produce a fine meshed array. At the front, the rows of spines, extending parallel to the valve surfaces, are depressed across

the commissure. With the convexity of the valves, the spines in this position would have formed an interlocking grill during life as envisaged by Rudwick (1965) for *Acanthothiris*.

If these forms with hollow spines around the commissure contained sensory epithelium in their apices, as appears likely, and if the spines were thus deployed as a sensory array well in front of the shell, there would be little point and indeed little space for the simultaneous development of marginal setae. It therefore seems reasonable to suggest that these forms would not have possessed setae in the adult shells. Although setae are almost ubiquitous in Recent brachiopods, modern adult *Neocrania* lacks setae; presumably the extinct spinose *Acanthocrania* also lacked them. *Lacazella* is another living stock which is also known to lack setae in the adult, so although the presence of setae is well known from Cambrian lingulates, especially from the Burgess Shale, it is also reasonable to accept that the shedding of post larval setae may well have taken place in those late Cambrian and Ordovician forms with commissural spinal arrays.

THE SPINES IN *ACANTHAMBONIA*

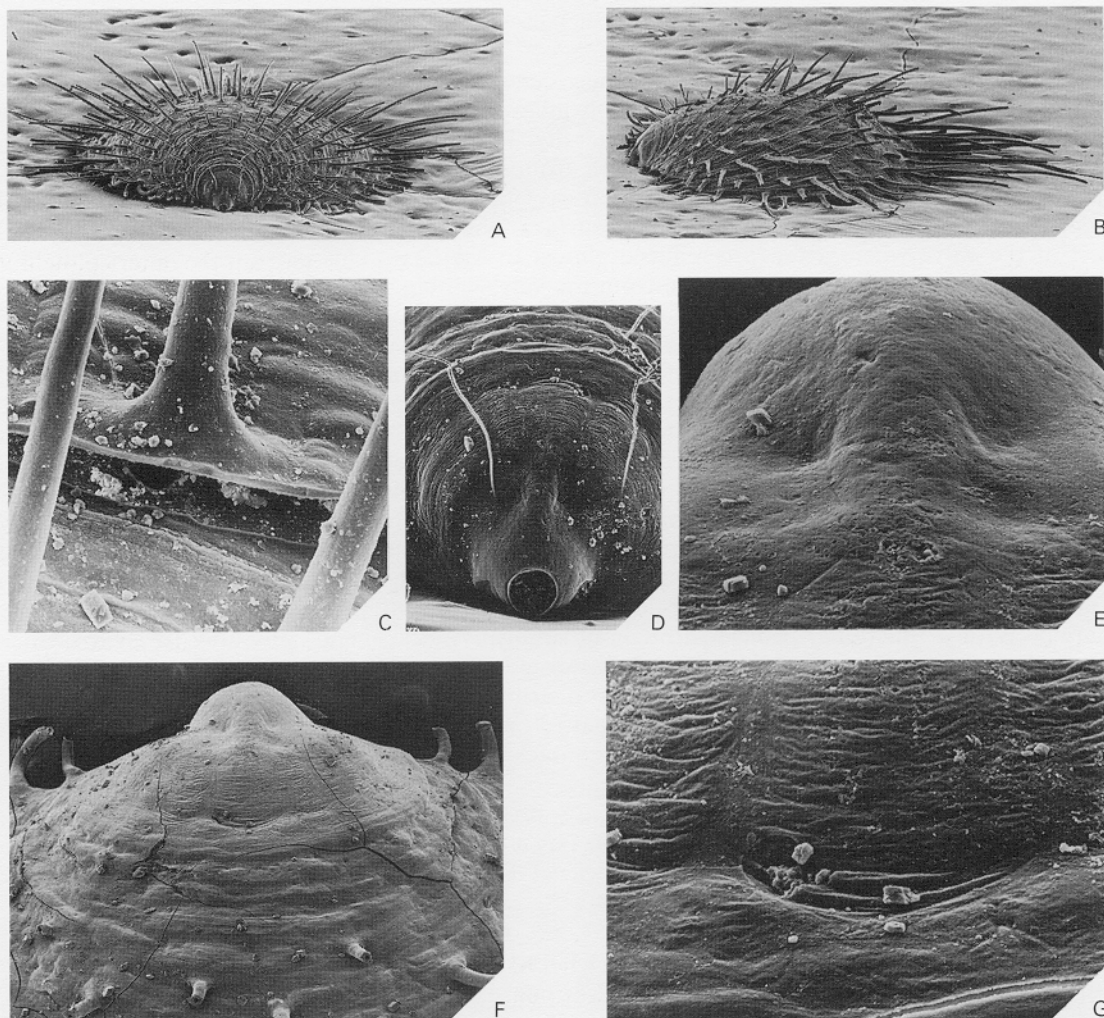
The spines of *Acanthambonia* are typical of the hollow spines in several brachiopod groups which open on the shell interior, and would have developed in the manner indicated by Williams and Rowell (1965, p. H84). Thus the spines would have been lined with outer epithelium proliferated by the apical cells of generative tips secreting the usual sequence of organic and inorganic layers as the spines continued to grow. In *Acanthambonia* there are fairly persistent pits on the inner surface which correspond to the spines on the exterior, as seen in Popov and Nölvak (1987, pl. 2, fig. 1a); these indicate that contact continued to be maintained during growth between the outer epithelium lining the spine and that lining the shell interior.

Development and function

At the posterior apex of the larval shell is situated the pedicle foramen (Text-fig. 2D). In this specimen, and in all the specimens studied by Popov and Nölvak (1987), the foramen and internal pedicle tube remained open throughout all stages of ontogeny. Thus the pedicle was functional throughout life even though its size remained constant as the shell grew. The median position of the pedicle tube is reflected on the surface of the smooth larval shell and defined laterally by a pair of depressions (Text-fig. 2E). With growth, fine concentric fila, commonly broken into drapes by nick points (Text-fig. 2G) as described for acrotretoids generally by Williams and Holmer (1992), are succeeded by five or six coarse, irregular but spineless concentric folds (Text-fig. 2F). The first sub-erect and anteriorly directed spine then appears at the front followed by another (Text-fig. 2F) before the first pair of spines developed on the posterior margin. The latter, together with the subsequent spines along the posterior margin, are curved medianly towards the umbo (Text-fig. 1A) in the manner of productidine clasping spines. Even allowing for breakage their shortness and moreover their stronger curvature, in which they hook over antero-medianly (Text-fig. 1B), indicate that they could not have formed encircling spines as noted for *Linoproductus* (Grant 1966), *Plicatifera* and other forms (Brunton 1966). The hook-like appearance does, however, suggest a function of attachment, and it may be that they served to provide ancillary support for the pedicle attachment of the growing shell by hooking over algal strands, to glue on to an attachment surface or into sediment. If the hooks were related to algal strands, their disposition would suggest that the hinge lay parallel to the growth direction of the alga and essentially perpendicular to the sea floor if the algae were benthic. Alternatively, if the tissue-filled distal ends remained sensitive, the curvature of these spines may simply reflect a response away from a surface to which the shell was attached by the pedicle. The possibility of attachment of *Acanthambonia* to algae is supported by the convincing demonstration of Havlíček *et al.* (1993) for such attachment by the larger lingulid *Rafanoglossa* and also small fossil articulates. However, an alternative attachment surface would be that of sponge spines, as demonstrated by the attachment of *Dictyonina* to *Pirania* in the Burgess Shale fauna (Whittington *in* Conway Morris *et al.* 1982, p. 25, pl. R). In the case of

microbrachiopods, the attachment scar of the *Eoconulus* can take the form of smooth groove, suggesting attachment to a very fine cylindrical object (Wright and McClean 1991, p. 125) which could well be a sponge spine. A sponge substrate would certainly have been available for the *Acanthambonia*, as the association of sponge spicules with the lingulates in the Estonian faunas has already been noted by Popov *et al.* (1994, p. 628).

Away from the posterior margins, the increasing valve size resulted in an increasing number of evenly spaced spines being developed on the growth lamellae. These extended perpendicularly to the margin of the time and built up an array, with the spines of each lamina being offset with regard to those of the preceding and succeeding laminae (Text-fig. 1). When viewed directly (Text-fig. 1E) these spines appear straight, but some irregularity in growth is clear when viewed anteriorly (Text-fig. 1D, F) or laterally (Text-fig. 2B). Two of the spines, the seventh and seventeenth from the



TEXT-FIG. 2. *Acanthambonia portranensis* Wright, 1963. Viljandi borehole, Estonia; Ordovician (Ashgill), Pirgu Stage (F1c). Ventral valve exterior (IGT Br 1313). A–B, posterior and lateral views of valve, $\times 65$; C, broken outer layer showing opening through inner layer below, $\times 810$; D–G, posterior and anterior views of larval shell (D, F), $\times 370$, $\times 400$, and details (E, G), $\times 1600$, $\times 1600$.

left in Text-figure 1C, and also in Text-figure 1D–F, have sealed tips. The latter has a particularly narrow base and suggests that growth was inhibited by its smaller number of secreting cells with consequent narrowing of the diameter and distal closure. A small spine that is distally sealed can also be observed in a specimen of *Cyrbasiotreta* figured by Williams and Curry (1985, fig. 56b), another form in which the edge of each lamella possessed a single row of fine, evenly spaced hollow spines.

These examples raise the question of whether distal tapering and sealing was the norm, and that those with open ends are simply reflecting breakage of the fine points. Certainly the spines must have remained distally open during growth otherwise there would have been no growth. When spines go out of commission through proximal sealing, as in the case also of setae embedded in the shell as well as in productide and *Acanthothiris* spines, the bulk of the envisaged sensory function would have been lost as the isolated tissue within the spine withered. But the *Acanthambonia* ventral interior figured by Popov and Nölvak (1987, pl. 2, fig. 1a–b) suggests that sealing at the inner ends of the spines is less common in this stock. In such cases there seems to be no necessity for a closure at the distal end.

The longest spines occur at the front of the specimen, which would perhaps be expected as the shell increments here are greatest. For the Bohemian species *A. klabavensis*, Havlíček (1982, p. 74) noted that the longest spines were directed laterally. The view of the entire Estonian shell (Text-fig. 1A) suggests that the spines increased in length around the shell margin from posterior to anterior, and also with the increase in shell size. Impressive though the spines are, some are broken and indeed a broken spine is still lying across the surface. The spines are shortest in the postero-central part of the valve where a few are reduced almost to the base. This presumably is a result of a taphonomic effect rather than abrasion from the valve rubbing against a surface during life, as a similar shortening is to be seen on a dorsal exterior (Popov and Nölvak, pl. 1, fig. 1a–b).

It is noticeable in the *Acanthambonia* that the internal diameter of the spine distally is relatively large (Text-fig. 1D, F); there is no evidence of the wall of the spine becoming thicker as in the typical productidine spine. In the latter case, the more robust the spine becomes, the better it is for the supporting function; the thinner, non-thickening wall in *Acanthambonia* allows the maximum amount of tissue internally which would be important to the sensory function, so on this criterion the *Acanthambonia* spines are here interpreted primarily as sensory.

The alternating arrangement of the long spines around the anterior and antero-lateral parts of the shell suggests that these long mature spines also functioned to screen coarser particles from entering the mantle cavity in the manner envisaged for the very much larger articulate *Acanthothiris* by Rudwick (1965). A supportive role appears to have applied only to the spines along the posterior margin. With a functional pedicle throughout ontogeny, attachment, probably to algal strands above the sea floor, is assured; the minute size would have mitigated against a sedentary position directly on a mud surface. Further, the similar distribution of spines on both valve surfaces would be unlikely were one to be continually adjacent to or partially submerged in sediment; this again suggests that both valves were in immediate contact with the water.

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