

A NEW TYPE OF DELTHYRIAL COVER IN THE DEVONIAN BRACHIOPOD *MUCROSPIRIFER*

by R. COWEN

ABSTRACT. A new type of delthyrial cover, *stegidial plates*, is described from very well-preserved specimens of *Mucrospirifer mucronatus* (Conrad) from the Traverse Group (Middle Devonian) of Michigan. Stegidial plates are unlike other delthyrial covers, such as deltidial plates and pseudodeltidia, because they are not integral parts of either valve: they are truly independent plates. As such, they can be compared only with the stegidium of some Upper Devonian spiriferides. The stegidium is re-interpreted in the light of its probable homology with stegidial plates: stegidial structures as a whole are regarded as unique within the phylum.

THE genus *Mucrospirifer* Grabau has a wide stratigraphical, geographical, and morphological range in Middle Devonian shelly faunas. This study is based on specimens in the Sedgwick Museum, Cambridge, from the Traverse Group of Michigan, collected and presented by Professor Alwyn Williams. Several authors have studied the Michigan spiriferide faunas; but Tillman (1964) has shown in a semi-quantitative study that too many 'species' have been distinguished among variable populations. On the basis of his work, all the specimens in the sample studied belong to the type species, *M. mucronatus* (Conrad).

Little attention has been paid to delthyrial structures in previous studies. Thus Stumm (1956) did not mention them at all, and Tillman (1964) regarded the deltidium as normal.

There is no normal deltidium, in the sense of a pair of so-called 'plates' continuous with the interarea both in position and mode of growth. Instead there are laminar *stegidial plates*, occupying approximately the same position and probably fulfilling the same function. But these plates are most unusual in structure and mode of growth, being entirely separate from either valve. The closest known equivalent is the stegidium described by Cooper (1954) in *Sphenospira* and *Syringospira*, two Upper Devonian spiriferides. Although the stegidial plates of *Mucrospirifer* show several distinct differences from the stegidium of Cooper, the structures appear to be homologous. Williams (1956, p. 257) mentioned that a stegidium-like structure had been found in *Mucrospirifer*, but this has not yet been described.

The stegidium and stegidial plates are very prone to removal and damage during fossilization, partly because they are not fused to the rest of the shell, and partly because of their laminar shell structure. The Michigan specimens are from a particularly favourable lithology: the shale is very fine and soft, and can be washed off the specimens without any danger of destroying the delicate delthyrial structures. Specimens of *M. mucronatus* from other lithologies in the Traverse Group rarely show any sign of stegidial plates, and it is likely that this is the general case. Even in the shales of the Traverse Group, comparatively few complete delthyrial covers have been found, and breakage and displacement of plates is common.

Terminology. A fairly complex terminology is used to describe the calcareous plate or plates covering the delthyrium or notothyrium of brachiopods (Williams and Rowell [Palaeontology, Vol. 11, Part 2, 1968, pp. 317-327, pls. 63, 64.]

1965, pp. H85–H93). There are cases, however, where it is desirable to refer to these plates as a group, or where it is not possible to determine which interpretative name applies to any given plate. I shall use *delthyrial cover* in these circumstances as a non-interpretative descriptive term.

It is often difficult to describe the direction of growth of structures in the posterior part of the brachiopod shell. Directions are defined with reference to the commissure (*ventral* and *dorsal*) and to the position of the umbos in the plane of symmetry (*anterior*, *posterior*, and *lateral*). But these directions may be confusing when used for the posterior structures. For instance, in orthide brachiopods, an orthocline ventral interarea grows anteriorly, a catacline ventral interarea grows dorsally, and a procline ventral interarea grows posteriorly. To avoid this, I shall describe growth directions in the hinge region with respect to the umbo for any valve, as *apical* or *distal*. Thus a deltidial plate would always grow distally with respect to the ventral umbo.

GENERAL CONSIDERATIONS

Two pairs of laminar plates make up the delthyrial cover. The laminae of each plate overlap like tiles on a roof so that the smallest, central lamina is external; successive laminae underlie this as in a stepped pyramid so that the largest ('basal') lamina forms the internal side of the plate (Pl. 63, fig. 1). Because each plate is made of overlapping laminae, a broken edge has much the same appearance as an original edge which has been slightly damaged, just as a section through a pack of cards looks like the edge of the original pack. In some cases it has proved difficult to interpret fragments of plates, and I have always used the simplest hypothesis, which is to postulate as few plates as are compatible with the evidence.

As in all structures formed by accretion, growth-lines allow the shape at successive growth-stages to be determined. The stegidial plates have been studied as continuously developing parts of the organism, and this has aided their functional interpretation. It is clear from the specimens that there can be only one interpretation of the sequence of growth of the plates. The ontogenetic development from very small plates shows that the first-formed laminae were underlain by subsequently formed, larger laminae (Pl. 64, compare figs. 4, 14); that is, in every plate the youngest lamina was the largest, and was formed underneath previous ones. This interpretation has been used in the descriptions given below.

The pairs of laminar plates will be referred to as *ventral stegidial plates* and *dorsal stegidial plates*. Implications of affinity with the stegidium will be justified later.

EXPLANATION OF PLATE 63

Mucrospirifer mucronatus (Conrad), Traverse Group, Middle Devonian, Alpena County, Michigan.

All specimens whitened with ammonium chloride.

Figs. 1–5. A series of views of the delthyrium of the best-preserved specimen, SM H9251, from the Ferron Point Shale, abandoned shale pit, Alpena Portland Cement Co.; $\times 20$. This shows the detailed structure of the stegidial plates, with growth-laminae clearly visible. The dorsal plates have been displaced slightly, by slipping distally off the cardinal process into the delthyrial gap (fig. 5).

Figs. 6a, b. Stereo pair, right and left, to show the three-dimensional relationships of the broken stegidial structure of Plate 64, fig. 9.

Figs. 7a, b. Stereo pair, right and left, to show the relationship of the delthyrial cover to the shell as a whole: the pedicle foramen is still relatively large. Same specimen as figs. 1–5.

VENTRAL PLATES

The ventral plates are the larger pair in *Mucrospirifer*, because its ventral interarea is higher than the dorsal. The plates are clearly shown in Tillman's paper (1964, pl. 153, figs. 1-3), where they are interpreted as deltidial plates. But it is evident that the growth-lines on the plates are concentric, and can be traced completely round the edges of the plates (Pl. 63, figs. 1-4). Therefore the ventral plates cannot have been integral parts of the interarea but must have been secreted independently. They must have lain 'free' in the delthyrium, with growth by accretion proceeding on all edges. They could have been held in place only by the mantle secreting them, which must have lain in the delthyrium in a position almost exactly similar to that of the mantle secreting a normal deltidium.

Young specimens, and the growth-lines on older specimens, show that the ventral plates were first formed antero-laterally in the delthyrium (Pl. 64, figs. 4, 14) with their edges defined by the circumference of the pedicle, by the edge of the interarea, and by the functional requirement which causes the distal edge of many delthyrial covers to be curved. (In this case, the curvature is probably a response to the path of the diductors across the delthyrium to the cardinal process, but this interpretation does not affect the main argument.)

In subsequent growth the same factors continued to define the limits of the ventral plates. The growth-lines on the lateral edges are therefore straight and parallel, facing the interarea (Pl. 63, figs. 1-4). The median edge always formed an arc of the circumference of the pedicle, and the distal edge formed an arc comparable with that of a normal deltidial structure.

As the two plates grew, they came into contact in the median line. This implies that the pedicle was not growing at the same rate as the interarea. The plates joined medially, on the distal side of the pedicle, so that they then defined the pedicle foramen. The plates are conjunct, not fused; like conjunct deltidial plates in atrypides and rhychnellides, their line of conjunction is irregular, and there is some overlapping (Pl. 63, figs. 1, 3, 4). After this stage the plates developed as one structural unit.

Laterally, the plates are often set at a high angle to the interarea, and this trend may be continued as far as the pedicle to form a pedicle tube projecting outwards from the delthyrium, very similar to that of *Cyrtia* or *Vellamo* (Pl. 64, figs. 6, 7).

There is some difficulty in interpreting the structures in the apex of the delthyrium. There seems to be no initial deposition on the apical side of the pedicle. In later ontogeny the ventral plates extended completely round the pedicle, so that it was enclosed by a calcite ring. This must have taken place very quickly, as the apical part has only one, or even no growth laminae on it, sometimes giving the impression of a single apical plate (Pl. 64, fig. 8). In very well-preserved specimens, however, this 'plate' can be seen to consist of two outgrowths, one from each side, with a line of conjunction even more irregular and asymmetrical than that distal to the pedicle (Pl. 63, fig. 3).

At this stage the pedicle had been surrounded, and had ceased to grow in absolute size; formerly its decline in growth had been relative to the rest of the interarea. From this stage the pedicle foramen shrank, and shell substance was added to the edges of the ventral plates facing the foramen (Pl. 64, fig. 13). This process is exactly analogous to the sealing off of the foramen in genera like *Cyrtia* and *Warrenella*. During the later stages of the process the remnant of the pedicle sometimes became asymmetrical (Pl. 64,

figs. 3, 6, 7): this also happened in *Cyrtia*. The laminae clearly overlap (Pl. 64, figs. 6, 7) in a way which provides further unambiguous evidence that younger laminae are formed underneath pre-existing ones.

In one specimen there is apparently a pair of apical plates separate from, and on the apical side of the ventral plates (Pl. 63, figs. 1–3). Apparent growth-laminae at the distal edge of these 'apical plates' appear to show growth in a distal direction. However, I interpret these edges as broken edges, and the apical structure as a part of the ventral plates, now broken away from the rest. This is the simplest hypothesis to adopt: the specimen is the only one in the sample which shows the 'structure'; other comparable specimens show obvious mechanical breakage (e.g. Pl. 64, fig. 8).

DORSAL PLATES

These are a pair of plates in the base of the delthyrium. They are transversely elongated, together forming a diamond-shaped outline (Pl. 63, figs. 4, 5; Pl. 64, figs. 2, 5; text-fig. 2b). They are medially conjunct above the cardinal process, the line of conjunction being asymmetrical with some overlapping, as in the ventral plates (Pl. 64, figs. 2, 5). The growth-laminae show that accretion proceeded on all edges except the median edge (Pl. 63, figs. 1, 4, 5); this implies that the plates were formed as a median pair, and did not grow inwards from the lateral corners of the delthyrium as the ventral plates did. This is probably because the ventral plates were initially separated by a relatively strong pedicle; no such limitation restricted the development of the dorsal plates. In every other respect the dorsal plates are homologous with the ventral plates, and in particular

EXPLANATION OF PLATE 64

All specimens whitened with ammonium chloride.

Figs. 1–9, 11, 13–14. *Mucrospirifer mucronatus* (Conrad), Traverse Group, Michigan. Specimens 1, 2, 5–7, 9, 14 are from the Upper Bell Shale, Rockport Quarry; specimens 3, 4, 8, 11, 13 are from the Ferron Point Shale, same locality as on Plate 63. Magnification $\times 8$ unless specifically stated.

Fig. 1. Large specimen, to show development of alae. SM H9247, $\times 2$.

Figs. 2, 5. Dorsal and apical views of a specimen to show a residual gap in the centre of the delthyrium, and the dorsal plates held in place over the cardinal process. SM H9249.

Figs. 3, 13. Dorsal views of specimens with pedicle foramina almost closed; that in fig. 3 rather asymmetrical. SM H9255 and H9257 respectively.

Figs. 4, 14. Dorsal views of very young specimens with ventral stegidial plates set in the distal-lateral corner of the delthyrium. SM H9254 and H9258 respectively.

Figs. 6, 7. Dorsal and oblique dorsal views of a specimen with an extremely asymmetrical pedicle foramen in later stages of development. SM H9250.

Fig. 8. Dorsal view of a specimen with stegidial plates largely broken away, leaving an 'apical plate'. SM H9253.

Fig. 9. Dorsal view of specimen with high ventral interarea ('*M. prolificus* Stewart') in which large dorsal stegidial plates have been crushed and broken into the delthyrium. This is an extreme example of the difficulty of interpreting fragments of stegidial plates. SM H9248.

Fig. 11. Oblique dorsal view of specimen showing the 'apical plate' with broken edges simulating growth laminae. SM H9251, $\times 12$.

Figs. 10, 12. *Austrospirifer variabilis* Glenister, Gnendna Fm. (Frasnian), 3½ miles S. of Gnendna Well, Carnarvon Basin, W. Australia. Dorsal view of two specimens, BMNH BB16249–50, $\times 2$, to show the remarkable resemblance to *M. mucronatus* (Conrad), and the imperfectly preserved delthyrial cover which strongly resembles stegidial plates.

they must have been secreted independently from the interarea. The principles, and details, of their interpretation are the same as those for the ventral plates.

The dorsal plates are hardly supported by the sides of the interarea, and are very easily displaced. Sometimes they have been held in position by the cardinal process (Pl. 64, figs. 2, 5), but more often have been crushed down into the delthyrium, with some breakage (Pl. 63, figs. 4, 5). This may create the impression of multiple plates, especially in specimens with a high ventral interarea and correspondingly large delthyrium (Pl. 64, fig. 9), but in no case is it necessary to postulate more than one pair of original dorsal plates.

The lateral edges of the dorsal plates fit the edges of the dorsal interarea, and their distal edges form a curve which extends over the base of the delthyrium (Pl. 63, figs. 4, 5). When all the plates were in their original position, the delthyrium must have been largely closed to the exterior, except for the pedicle foramen (Pl. 63, fig. 4).

Certain exceptions to this are specimens like that shown on Plate 64, figs. 2, 5, in which there must have been an appreciable remaining delthyrial gap. It seems certain that a breakage of the delthyrial cover, as suggested by Tillman (1964, pl. 153, fig. 2, caption) did not take place; there is no sign of a median curved calcite arch over the centre of the delthyrium in any specimen, even the best preserved.

RANGE OF VARIATION

There is a wide range of morphological variation in the development of the stegidial plates, but none which implies any basic structural modification. Most of the variation can be ascribed to variation in the absolute size and relative rate of growth and decline of the pedicle (Pl. 64, compare figs. 2, 11) and in the height of the interarea (Pl. 64, compare figs. 9, 13). These contrasted forms are the former *M. alpenensis* (Grabau) and *M. prolificus* (Stewart), which form two end-members of a series showing continuous variation; they were distinguished mainly on the height of the interarea.

STEGIDIAL AND DELTIDIAL PLATES

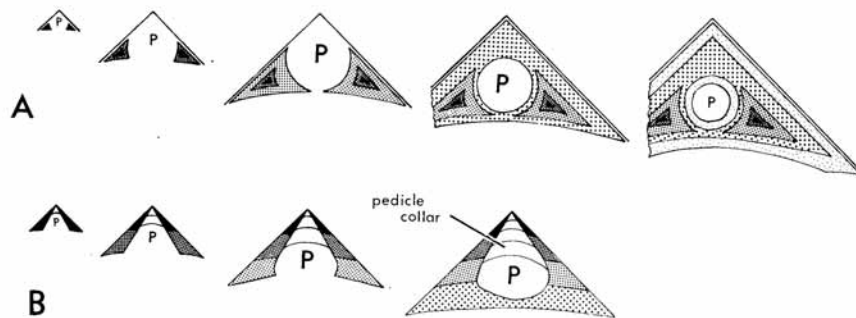
Polished sections of *Mucrospirifer* show primary and secondary layer shell present on both ventral and dorsal valves. But primary layer has not been observed on stegidial plates. If this absence is not a preservational failure, one must assume that stegidial plates were originally composed of secondary layer only. If so, their structure would be radically different from that of deltidial plates, which are homologous with the rest of the shell, and are covered by primary layer.

Text-fig. 1 shows the development of ventral stegidial plates and deltidial plates. As deltidial plates are continuations of the interarea, their growing edges face distally; deltidial plates proper are never secreted by mantle in contact with pedicle epithelium. The pedicle collar, on the other hand, is secreted in contact with pedicle epithelium, and is therefore not a homologous continuation of the deltidial plates. It is the only part of the delthyrial structure in this example which has a growing edge on the apical side of the pedicle.

The ventral stegidial plates were not limited by being integral parts of the ventral interarea; their growing edges were uninterrupted and peripheral. They could, and did,

include a part on the apical side of the pedicle homologous with the rest of the delthyrial cover. This can never occur in brachiopods with normal deltidia; even in amphithyrid brachiopods (e.g. *Megerlia*), the growing edge of the deltidium proper is not found on the apical side of the pedicle in a position corresponding to the apical part of the stegial plates; instead, this position is occupied by the growing edge of the pedicle collar.

The ventral stegial plates lay 'free' in the delthyrium, and accreted on all edges. But this occurred within a triangular gap in the shell, and a continuously expanding



TEXT-FIG. 1A, B. Diagrams to show the development of stegial plates and deltidial plates respectively. P indicates the relative size of the pedicle at various growth stages. In spite of the very different mode of growth of the two contrasted structures, their over-all shape, size, and disposition remains much the same. A is based on *Mucrospirifer mucronatus* (Conrad); B is generalized, based on study of several genera, such as *Hemithiris*, *Cyrtia*, and *Warrenella*. Note the pedicle collar on the apical side of the foramen; this bears strong growth-lines.

plate could not have been accommodated indefinitely in such a gap. It must necessarily have moved distally away from the apex (or umbo); so that any growing stegial plate was mobile with respect to the interarea during ontogeny.

Consequently, if the pedicle was surrounded by stegial plates, it must have moved distally down the delthyrium relative to the interarea. This would have left a gap on the apical side of the pedicle; presumably the apical part of the ventral plates served to close this gap, after an early ontogenetic stage in which an apical part was neither required nor secreted (text-fig. 1A).

These arguments can be extended to include dorsal stegial plates, as contrasted with chlidial plates; the morphology and development of the dorsal plates are simpler because the pedicle does not affect the structures in the notothyrium.

There was a fundamental difference, therefore, between the delthyrial growing edges of epithelia forming stegial plates and those forming deltidial plates. The distribution of epithelial surfaces in the delthyrial region can be reconstructed with some accuracy, because the stegial plates must have lain on the mantle surface which secreted them. Therefore one can infer that the epithelium was distributed much as it is in 'normal' brachiopods with deltidia. But the epithelium differed in the type of shell secreted and in the arrangement of the growing edges.

FUNCTIONAL INTERPRETATION

Probably the primary function of the stegidial plates was protection of the delthyrium. Analogy could be drawn with the opercula of molluscan groups like some cephalopods and gastropods: growth of a calcareous plate takes place peripherally and proceeds in such a way that the plate fills an apertural gap in the rest of the shell at all stages of development. In shape, size, and developmental history the stegidial plates closely mimic the deltidium and chilidium, or pseudodeltidium and chilidium, of other brachiopods. Their mode of secretion removed some of the inherent limitations imposed upon the normal deltidium: for instance, the ventral plates surround the pedicle foramen completely, apically and distally, whilst deltidial plates cannot do this.

The stegidial plates and deltidium are interesting demonstrations of the performance of the same inferred function in two different ways; this is not because of any known difference in the physical requirements of the environment, but because of a difference in the soft-part anatomy which changed the intrinsic possibilities of shell development. In this way an important change in the inner organization of an animal is reflected in the hard-part morphology, even though the external environment of the animal may have been unchanged.

The development of the structures of the delthyrium and those of the hinge-line is closely correlated. It is apparent from the growth-lines of the shell that young individuals of *Mucrospirifer* were not alate like the adults (Pl. 63, fig. 7; Pl. 64, figs. 1, 5, 8, 11); at a certain growth-stage the hinge-line suddenly elongated by increased accretion at the cardinal angles, forming alae (Pl. 64, fig. 1). The growth-stage at which this occurred was variable; as described above, the stage at which the pedicle foramen was surrounded by the ventral stegidial plates also varied.

These two significant changes in shell morphology happened at about the same time. Usually the pedicle was surrounded by the ventral plates shortly after the first appreciable alae were formed. This can be reconstructed from the growth-lines on shell and stegidial plates. Thus in one specimen (Pl. 64, figs. 2, 5) the pedicle foramen is quite small, and situated close to the ventral umbo. But it was not surrounded by the ventral plates until fairly late in shell development.

Whatever the main function of the alae may have been, they must to some extent have helped to stabilize the shell on the substratum. It is interesting that the development of a secondary stabilizing structure, the alae, should coincide so well with the decline of the primary stabilizing structure, the pedicle.

THE STEGIDIUM

Cooper (1954) introduced the term *stegidium* for a plate covering part of the delthyrium in *Syringospira* (from the Upper Devonian of New Mexico) and *Sphenospira* (from the Upper Devonian of Ohio). These spiriferide brachiopods have a transverse apical delthyrial plate set in a high delthyrium, the plate occupying about two-thirds of the delthyrial opening. The remainder is closed by the stegidium, which is a plate made up of overlapping laminae with concentric growth-lines, set inside the delthyrium, and closely fitting the sides of the dental plates and the anterior edge of the transverse plate. The anterior edge is concave forwards, perhaps to accommodate the diductors.

Like the plates in *Mucrospirifer*, the stegidium has laminar structure and concentric growth-lines; the larger, basal laminae lie underneath the smaller, exterior laminae. Cooper considered that the stegidium grew inwards from the edges of the delthyrium, closing off the delthyrial gap by encroachment on a diminishing pedicle foramen, the last stage in this process being the formation of a central plug as the pedicle atrophied completely. This interpretation implies that the stegidium did not necessarily lie 'free' in the delthyrium, for if growth was directed inwards, the periphery of the plate could have been fixed to the edges of the delthyrium.

One difficulty in accepting this interpretation lies in the mode of overlapping of the laminae. At the edges of the brachiopod shell, and round the edges of a 'normal' pedicle foramen undergoing diminution (as in *Cyrtia*, *Warrenella*, and *Hemithiris*, for example), new growth layers are secreted to lie *underneath* preceding layers. By analogy with these examples, on Cooper's interpretation of the mode of growth of the stegidium, the overlapping on the stegidium might be expected to be in the opposite direction, with inner laminae underlying outer ones.

Dr. M. J. S. Rudwick, who has examined Cooper's material in the U.S. National Museum, suggested to me that Cooper's interpretation should be reversed, and that the direction of growth of the stegidium was outwards. The largest lamina of the stegidium would then be the last-formed. This suggestion was based on the following reasoning. If the stegidium grew by inward accretion, then one might expect the inner laminae to have deviated during growth from the shape of the original outer circumference; in other words, to have irregularities like those shown in Williams's diagram of the stegidium in the *Treatise* (1965, fig. 91). Furthermore, if the stegidium acted to define a pedicle foramen in the process of decline and atrophy, as Cooper suggested, then the successive stages of decline of the foramen should be preserved in the growth laminae, as they are in the stegidial plates surrounding the foramen of *Mucrospirifer* (text-fig. 1A).

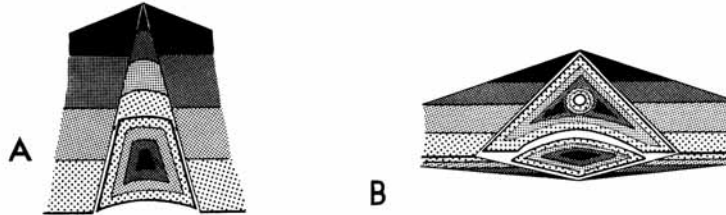
But in fact, as the growth-lines on Cooper's specimens show (see his plates), the lateral sides of the stegidium at every growth-stage were straight and parallel to the sides of the delthyrial gap, with the angle between the lateral sides remaining constant. It is particularly striking that in one specimen (Cooper 1954, pl. 37, fig. 12) an asymmetrical stegidium is lying within an asymmetrical delthyrial gap, and the growth-lines on the specimen show that the stegidium at earlier growth-stages was similarly asymmetrical; yet the growth-lines on the plate are still parallel to one another. There is therefore a rigid conservation of shape during the formation of a stegidium; this evidence strongly suggests that the stegidium was so modified in growth as to fit the delthyrial gap exactly at all times, and this implies that the mode of growth was the reverse of that suggested by Cooper. Rudwick's interpretation is shown diagrammatically in text-fig. 2A.

On Rudwick's suggestion, the growing edge of the stegidium was peripheral, and the plate could have altered in shape and grown in size continuously to fit the delthyrial gap as the latter increased. On all Cooper's figured specimens the stegidia fill the delthyrial gap exactly, even though the specimens are of various sizes; this follows naturally from Rudwick's suggestion, but is difficult to explain on Cooper's hypothesis.

Cooper's hypothesis inevitably implies that the stegidium did not begin to form until the last stage of growth, since only then would the 'first-formed', largest lamina fit the delthyrial gap. The stegidium could not be adapted to any new situation, such as further

growth of the delthyrium, because the growing edge was retreating towards the centre of the delthyrium where it would have secreted the 'pedicle plug'. In summary, on Cooper's hypothesis the stegidium performed its supposed function only at one particular growth-stage; it was not present before that stage, and became inevitably ineffective after it.

All the evidence from the comparable structures in *Mucrospirifer* shows that in this genus there is only one tenable interpretation of the mode of growth of stegial plates;



TEXT-FIG. 2A, B. Diagrams to show the final morphology of stegidium and stegial plates respectively, with interpretation of the sequence of ontogenetic development. A is based on *Sphenospira* and *Syringospira*, discussed by Cooper (1954); B is based on *Mucrospirifer mucronatus*. The shading on the interareas indicates the inferred growth-stages corresponding to stages in growth of the stegidium and stegial plates, and shows the degree of relative migration of the stegial structures down the delthyrium during growth. In 2A, the transverse delthyrial plate is overlapped by the stegidium.

this would confirm Rudwick's suggestion for the stegidium. Reinterpretation of the stegidium, based on the reasoning above, and on analogy (or homology) with *Mucrospirifer*, is now possible.

First of all, the laminar structure and concentric growth-lines of the stegidium, interpreted according to the reasoning above, show that the stegidium, like the stegial plates of *Mucrospirifer*, must have lain 'free' in the delthyrium. This is so unusual in the brachiopods that the two structures are obviously closely allied, which justifies the term 'stegial plates' for the delthyrial cover of *Mucrospirifer*.

The stegidium is not an integral part of the interarea, but was mobile with respect to the delthyrium. It must have migrated from the apex towards the base of the delthyrium during growth, and if it enclosed the pedicle, the latter would have been transported with it. Cooper said that the formation of the stegidium was consequent on, and contemporaneous with, the atrophy of the pedicle, 'an act of the adult animal' (1954, p. 328). This was the only possible interpretation on his hypothesis, but must now be revised.

The change in interpretation alters the *sequence* of events in the delthyrium, but the result is the same. The pedicle must have been in the centre of the stegidium if it was present at all.

This is the 'plug' of Cooper's interpretation, and there is no trace of a foramen in this region, except possibly his plate 37, fig. 14, nor is there any trace of the stegidium ever having been more than a single unit. By analogy with the development leading to the decline of the pedicle in *Mucrospirifer*, it is clear that the pedicle of *Syringospira* and

Sphenospira, if developed at all, must have atrophied extremely early in ontogeny. This inference reinforces the deduction made by Cooper about the mode of life of the two brachiopods. His suggestion that the very high wide interarea was a stable platform on a muddy or fine sandy bottom seems even more likely if the pedicle was never properly functional; and it is consistent with my observations on the alae of *Mucrospirifer*.

STEGIDIUM AND STEGIDIAL PLATES

The stegidium of *Syringospira* is obviously closely related to the stegidial plates of *Mucrospirifer* in origin, mode of formation, and structure. But there are distinct differences (see text-fig. 2):

- (a) the structure of *Mucrospirifer* is multiple; in *Syringospira* it is a single (ventral) plate;
- (b) the stegidium of *Syringospira* is sunk into the delthyrium, but in *Mucrospirifer* the stegidial plates occupy roughly the same positions as a normal deltidium;
- (c) there is no dorsal equivalent of the (ventral) stegidium of *Syringospira*.

The first difference can be ascribed to the different development of the pedicle in the two genera. The early atrophy of the pedicle in *Syringospira* would leave an 'empty' delthyrium which could be filled by a single plate. In *Mucrospirifer* the pedicle was much stronger and longer-lasting, and the stegidial plates had to be moulded around it. An interesting analogy is *Acrospirifer*: here, early atrophy of the pedicle led to the formation, apparently, of a single structure in the delthyrium. This was in fact mistaken by de Koninck (1846) for a pseudodeltidium, although it is a true deltidium. The deltidium of *Warrenella* or *Vellamo*, on the other hand, is closely analogous to the stegidial plates of *Mucrospirifer*. The Australian Devonian spiriferide *Austrospirifer* (Pl. 64, figs. 10, 12) has a delthyrial cover closely similar to the stegidial plates of *Mucrospirifer*, and in addition, the external morphology of the two genera is strikingly close. I think it most likely that the delthyrial cover of *Austrospirifer* is a stegidium, although material I have examined is not well enough preserved to display the mode of growth of the cover.

The second difference between stegidium and stegidial plates is a reflection of the distribution of mantle epithelium in the delthyrium. In *Mucrospirifer* it must have formed a convex curve projecting above the interarea, but in *Syringospira* it was deeply sunk into the delthyrial cavity. I shall discuss elsewhere the significance of this difference.

The third difference is probably one of preservation. I hope to describe elsewhere occurrences of both ventral and dorsal components of stegidia in cyrtospiriferid brachiopods closely allied to *Syringospira* and *Sphenospira*. I predict, therefore, that a dorsal component of the stegidium exists in these two genera, but has not yet been observed. Williams and Rowell (1965, fig. 91) figure an 'antygidium' in *Syringospira* which may in fact be the dorsal component of the stegidium.

CONCLUSION

The differences between stegidium and stegidial plates cannot be regarded as great in view of the fact that both structures were secreted in the same manner, otherwise

unknown among the brachiopods. Some internal structures may be secreted independent of either valve: calcareous spicules are secreted by the internal mantle of some terebratulides, *Platidia* for example. But the only external structures laid down independent of either valve are stegidial plates and stegidia. They are true plates in the sense that deltidial 'plates', socket 'plates', dental 'plates', and so on, are not. They are a morphological alternative, and a functional equivalent, for deltidium and deltidial plates. It is likely that stegidial structures will be found very sporadically in time and space, because they are fragile and easily detached from the shell, and although they represent important modifications in the soft-part anatomy responsible for their secretion, they will probably be difficult to use in routine classification. However, they are likely to be significant at higher taxonomic levels.

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REFERENCES

- COOPER, G. A. 1954. Unusual Devonian brachiopods. *J. Paleont.* **28**, 325-32.
- DE KONINCK, L. 1846. Notice sur deux espèces de Brachiopodes du terrain paléozoïque de la Chine. *Bull. Acad. r. Belg. Cl. Sci.* **13**, 415-25.
- STUMM, E. C. 1956. A revision of A. W. Grabau's species of *Mucrospirifer* from the Middle Traverse Group of Michigan. *Contr. Mus. Paleont. Univ. Mich.* **13**, 81-94.
- TILLMAN, J. R. 1964. Variation in species of *Mucrospirifer* from Middle Devonian rocks of Michigan, Ontario and Ohio. *J. Paleont.* **38**, 952-64.
- WILLIAMS, A. 1956. The calcareous shell of the Brachiopoda, and its significance to their classification. *Biol. Rev.* **31**, 243-87.
- and ROWELL, A. J. 1965. Morphology. In MOORE, R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part H, Brachiopoda, H57-H138. Univ. Kansas Press and Geol. Soc. Am.

R. COWEN
Department of Geology
University of California
Davis, California 95616

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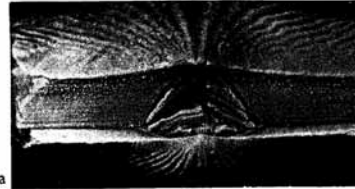
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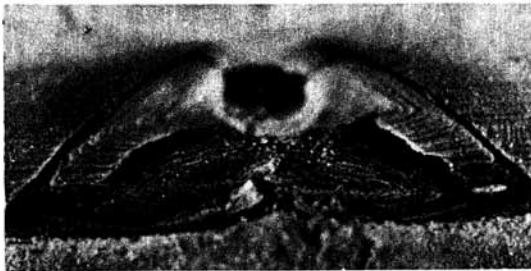
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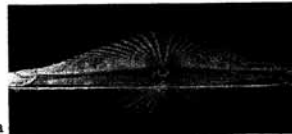
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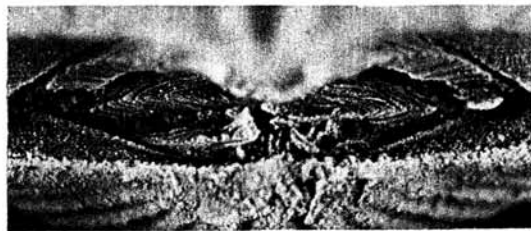
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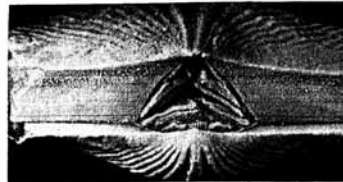
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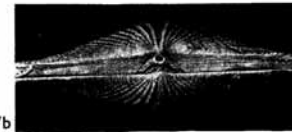
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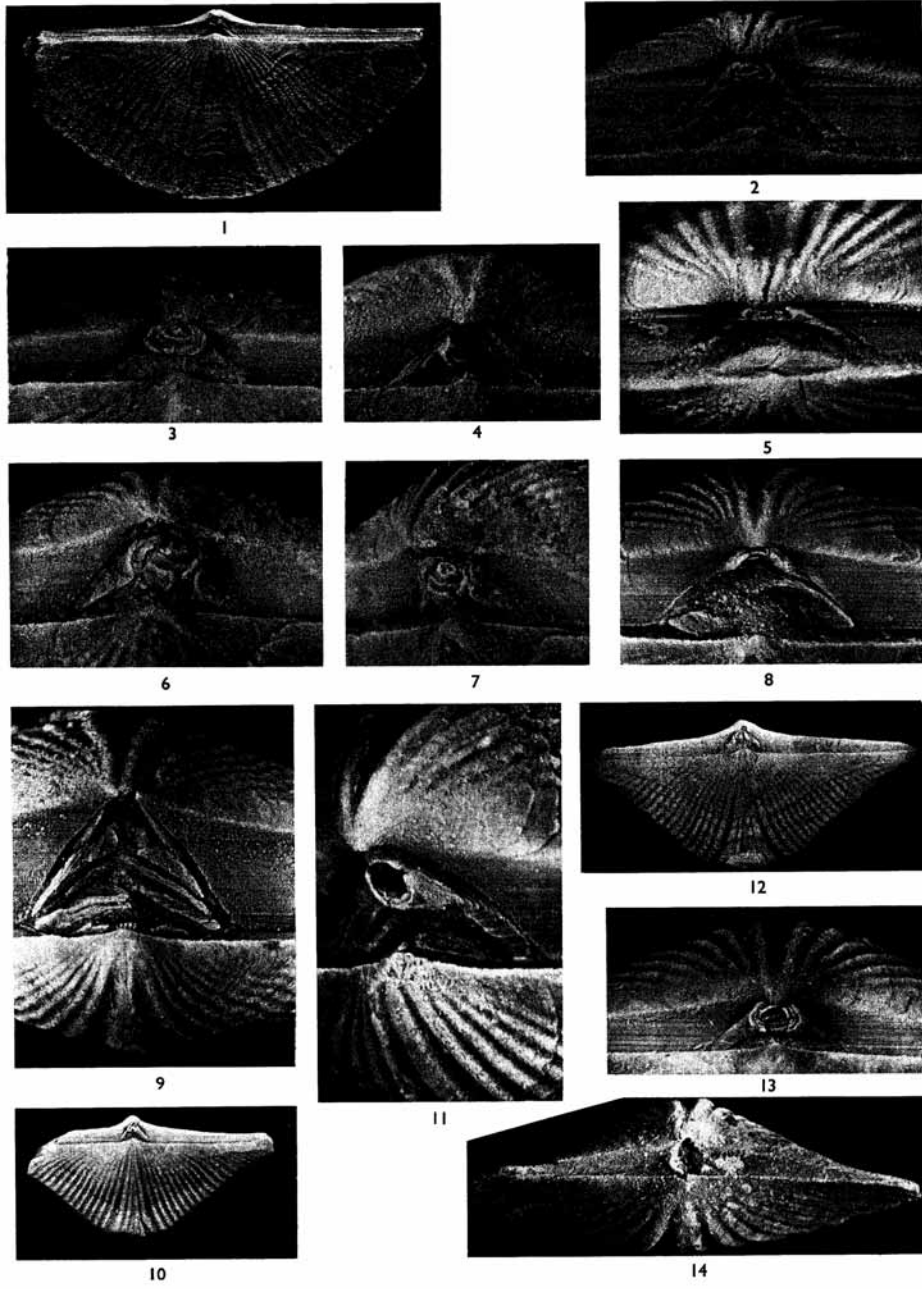


6b



7b

COWEN, Stegidial plates in *Mucrospirifer*



COWEN, Stegidial plates in *Mucrospirifer*