

PETER R. CROWTHER

THE NATURE AND MODE OF LIFE OF THE GRAPTOLITE ZOOID
WITH REFERENCE TO SECRETION OF THE CORTEX

Abstract.—Scanning electron microscope studies of well preserved, isolated graptolites have revealed a radically new and unexpected structure to both normal cortex and endocortex, termed here "cortical bandaging". Bandage structure is described and illustrated for several species and the collagenous nature of the component fibrils confirmed. The evidence presented sheds new light on the nature of the graptolite zooid and how it functioned, in particular on the mode of skeletal secretion. A model involving a more pterobranch-like zooid is preferred to the recent idea of Urbanek (1976) and Kirk (1972) for secretion beneath a perithecal membrane.

I am going to restrict this mode of life discussion quite drastically to the freedom of movement of the zooid. Was it really only capable of simple extension and retraction of the lophophore as seems to be generally accepted at the moment? The evidence presented serves to link today's second and third pair of topical lectures as ultrastructural techniques were employed.

No unequivocal observation of the form of the graptolite zooid has even been described. The model utilising a pterobranch zooid, almost universally accepted until recently, resulted from the late Professor Kozłowski's (1949) conclusions regarding graptolite affinity. These were based to a large extent on the homology of the dendroid stolon with the black stolon of *Rhabdopleura*, and the fusellar microstructure of graptolites, *Rhabdopleura* and *Cephalodiscus*, although further supporting evidence was discussed. Professor Kozłowski thought that construction of the fusellar layer was by mortaring of growth increments by a mobile cephalic shield, a method that is widely accepted as applicable to the coenecia of recent pterobranchs.

Secretion of the cortex, thought at that time to have no equivalent in *Rhabdopleura*, presented a problem. Its apparently simply layered ap-

pearance in thin section, coupled with his assertion that graptolite zooids were much more closely connected with their skeleton than *Rhabdopleura*, forced Kozłowski to invoke the use of a rather ill-defined layer of extra-thecal tissue advancing distally along the rhabdosome, some little way behind the growing end and covering the fusellar layer with a secondary thickening. The precise configuration of this tissue, and its relationship to the zooids was never clarified and Urbanek (1976) has recently stressed his difficulty in his reappraisal of graptolite affinities.

Therefore, according to the Kozłowski model, zooids would have little freedom of movement, limited to simple extension and retraction of the food gathering lophophore plus an ability to secrete fusellar half rings at growing margins. The secretory powers of the zooid were restricted to producing fusellar tissue only.

Kirk (1972) and Urbanek (1976) have attempted to solve the problems resulting from the Kozłowski model of periderm secretion by doing away with a pterobranch mortaring method completely, allowing both fusellar and cortical layers to be secreted by an epithelial evagination, Urbanek's "perithecal membrane". The result of Urbanek and Towe's (1974, 1975) excellent TEM investigations of well preserved dendroids and graptoloids were interpreted as confirming this hypothesis. As a result, the skeleton becomes internal and movement of the zooid even more restricted, there being no place for a mobile secretory organ.

The new evidence presented here is the result of extensive electron microscope and light microscope studies of graptolite cortex over the last two years. *Climacograptus typicalis* from the Viola Limestone illustrates the main features (pl. 22: 1, 2). Contrary to previous ideas, the cortex is not a simply layered structure but is composed of an overlapping sequence of rather haphazardly arranged strips of periderm or "bandages". Cortical bandaging has been recognised on at least 30 species from 17 genera spanning much of graptolite evolution and it may well be of universal occurrence. It is best developed on the diplograptids and was first recognised under the SEM on *Climacograptus typicalis*.

A distinct bandaged structure has been found in many other diplograptid species from the genera *Diplograptus*, *Amplexograptus* (pl. 22: 3), *Climacograptus*, *Glyptograptus*, *Orthograptus* (pl. 22: 4), *Paraclimacograptus*, *Pseudoclimacograptus* and in *Dimorphograptus*. Apart from the diplograptids, the Ordovician genera *Dicellograptus* and *Dicranograptus* show similar structures and it has also been recognised, on younger, uniserial Silurian forms such as *Monograptus*, *Pristiograptus* (pl. 23: 1), *Saetograptus* and *Cyrtograptus* (pl. 23: 2).

Fibril "unconformities" on the periderm surface, consistent with a bandaged structure for the cortex, have been observed on dichograptids and dendroids e.g. *Dendrograptus*, *Dictyonema* and *Tetragraptus* (pl. 23: 3). Even the limited development of normal fusellar periderm

at the proximal end of *Orthoretiolites* (pl. 23: 4) is bandaged; fibril patterns along clathrial and reticular lists of other retiolitids may also indicate compatibility with the theory.

Bandages on *Orthograptus gracilis* (recently recognised independently by Andres, 1977, from light microscope studies) are typical of the normal diplograptid types. Their lateral margins are thickened, producing a pair of parallel ridges and giving them a "railway-track" appearance (pl. 24: 1). A study of Holm's beautiful illustrations of *Climacograptus diplacanthus* (in: Bulman 1932: pl. 3: 7, 8) suggests that this form had a similar structure.

Let us take a brief look at the component fibrils within a bandage, the first example again being *Climacograptus typicalis*. A higher magnification micrograph (pl. 24: 2) shows an outer membrane or sheet fabric which has flaked off in places to reveal an orderly array of fibrils beneath, parallel to the bandage margins. Each fibril extends the length of the bandage and, as can be seen from the endocortical fibrils of *Monograptus communis communis*, tapers out at each end (pl. 24: 3). Exceptionally well preserved fibrils from the cortex of *Dictyonemata rarum* show a periodic cross banding along their length with a repeat of just under 700 Å (see Crowther and Rickards 1977: pl. 3: 1). This is consistent with a collagenous composition, as was first suggested by Towe and Urbanek (1974) from TEM evidence. Native collagen commonly exhibits a similar cross-banding with a repeat period of around 670 Å. Fibril size and arrangement, the alignment of cross-banding on adjacent fibrils and the terminal tapering of fibrils confirm this conclusion. Bandage structure is dealt with in greater detail in Crowther and Rickards (*op.cit.*)

So how are these bandages secreted? The important points relevant to this problem can be summarised under 4 headings:

(1) Bandage arrangement, referring particularly to diplograptids. On lateral walls, bandages tend to show a superficially haphazard pattern, criss-crossing at high angles with few bandages parallel to the long axes of the rhabdosome. In contrast, ventral walls are often covered with sub-parallel bandages perpendicular to fusellar growth lines. Bandages sometimes appear to radiate roughly from a thecal aperture.

(2) Locally at any particular point along a rhabdosome, adjacent bandages are of uniform size.

(3) Observations on several species of diplograptids show very clearly that there is a gradual increase in bandage size distally along the rhabdosome accompanying the common increase in thecal size.

(4) Within a bandage, component fibrils are parallel to each other and the lateral bandage margins, however sinuous their course.

In my view, the "painted on" appearance of bandages, their arrangement on the surface of the rhabdosome and particularly the correlation

of bandage size with thecal (and therefore zooid) size, strongly suggests a mode of secretion similar to that used by *Cephalodiscus* to secrete its secondary thickening. Bandages look as if they have been daubed on, one over the other, with a paint brush; if we substitute a pterobranch cephalic shield-like organ for the "paint-brush", I think the analogy is exact. Each bandage would have been produced by dragging or pushing the cephalic shield across the surface of the periderm, secreting as it went. Its size would have been governed by the size and secretory capabilities of the zooid, its course by the direction of motion of the zooid.

If the evidence is accepted then our view of the mode of life of a graptolite zooid is radically altered. In contrast to the very close connection between zooid and theca envisaged by Kozłowski, Kirk and Urbanek, we must now give it the ability to leave its tube to secrete bandages at least in the vicinity of its aperture, and also within the theca itself. Recently, Professor Dilly (1976) has shown that *Rhabdopleura* produces a rudimentary secondary thickening on the outside of its living and creeping tubes so we may safely suggest that members of a colony united by a stolon via contractile stalks are capable of leaving their tubes for a period of time. Pl. 24: 4 is a tentative reconstruction of *Climacograptus typicalis* as it may have appeared during life (from Crowther and Rickards 1977), utilising biramous pterobranch-like zooids capable of leaving their thecae to secrete cortical bandages with a cephalic shield.

Following this interpretation, the importance of cortical bandages to our ideas on graptolite affinity is clear. Urbanek (1976) suggested making the skeleton internal and dismissed a pterobranch mode of growth entirely which would necessarily remove graptolites from any very close affinity with the coenecium building hemichordates. However, from the evidence presented it seems likely that not only to the fuselli of both groups show a strong resemblance at the microstructural level, a fact that so impressed Professor Kozłowski, but that cortex too was built from individual growth increments, plastered one over the other in a more haphazard manner. This strongly supports the present classification of graptolites within the subphylum or phylum Hemichordata.

There are several problems resulting from the model; for example, how is the nema secreted and how can they many graptolites with restricted apertures secrete a cortex? On balance it appears that pterobranch-like mode of secretion deals more successfully with the known structure of graptolite periderm than any other current hypothesis. The epithelial evagination or perithecal membrane theories were expounded before the bandaged nature of graptolite cortex was understood or even its very existence appreciated. For that reason alone their applicability to solving the problem of periderm secretion must now be considered doubtful in the light of this important new structure.

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Department of Geology
Sedgwick Museum
Downing street
Cambridge CB2 3EQ
U.K.
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DISCUSSION

A. Urbanek:

While I consider Peter Crowther's observations as very important, I would like only to point out that there is no direct connection between the mobility of zooids

and the mode of secretion of skeleton. We could easily imagine the skeleton as secreted by some sort of perithecal membrane and zooids as being very mobile. What Peter Crowther speaks about is quite a special kind of motions with the secretory behaviour of zooidal body proper.

EXPLANATION OF THE PLATES 22—24

Plate 22

Climacograptus typicalis Hall

Viola Limestone, Ardmore, Oklahoma, USA, Caradoc

1. Lateral aspect of mature distal fragment, $\times 45$.
2. Enlargement of part of 1 showing superposed cortical bandages of regular width, $\times 180$.

SEM micrographs

Amplexograptus cf. maxwelli Decker

Platteville Limestone, Lancaster, Wisconsin, USA, Caradoc

3. Cortical bandages crossing the fuscilli of an immature th 2¹. S.M. A24295. Figured by Walker (1953, figs 7A, B), $\times 110$.

Light micrograph

Orthograptus gracilis (Roemer)

Viola Limestone, Ardmore, Oklahoma, USA, Caradoc

4. Cortical bandages radiating away from the aperture of th 2¹, $\times 110$.

Light micrograph

Plate 23

Pristiograptus dubius (Suess)

Kronvall, Gotland, Sweden, Upper Wenlock

1. Cortical bandages on the lateral prothecal wall of th 3. S.M. A5838. Figured by Cox (1934, text-fig. 13) $\times 110$.

Light micrograph

Cyrtograptus sp.

Cape Phillips Formation, Cornwallis Island, Canada, Upper Wenlock

2. Overlapping arrays of parallel fibrils on the outer periderm surface, $\times 1300$.

SEM micrograph

Tetragraptus cf. pseudobigsbyi Skevington

Ontikan Limestones, Öland, Sweden, Arenig

3. 'Unconformity' between overlapping fibril groups on the outer periderm surface, $\times 1600$.

SEM micrograph

Orthoretiolites hami robustus Skevington

Viola Limestone, Ardmore, Oklahoma, USA, Caradoc

4. Missing prosicula replaced by supporting filaments for regenerated nema. Sub-parallel cortical bandages on metasicula; some converge towards the base of a regenerated filament. S.M. A24581. Figured by Skevington (1960, fig. 10), $\times 110$.

Light micrograph

Plate 24

Orthograptus gracilis (Roemer)

Viola Limestone, Ardmore, Oklahoma, USA, Caradoc

1. 'Railway track' appearance of cortical bandages near the aperture of th 3', $\times 180$.

SEM micrograph

Climacograptus typicalis Hall

Viola Limestone, Ardmore, Oklahoma, USA, Caradoc

2. Fracture in bandage membrane reveals parallel cortical fibrils beneath, $\times 4300$.
4. A tentative reconstruction of a distal portion of a colony. Some zooids are in the feeding position with lophophores extended, others are actively secreting cortical bandages with their cephalic shield-like organ, $\times 20$.

SEM micrograph

Monograptus communis communis Lapworth

Rheidol Gorge, Dyfed, Wales, Llandovery

3. Superposed arrays of endocortical fibrils. The fibrils gradually taper out and lose their parallel alignment at their free extremities, $\times 8600$.

SEM micrograph





