SHELL STRUCTURE AND INFERRED GROWTH, FUNCTIONS AND AFFINITIES OF THE SCLERITES OF THE PROBLEMATIC *MICRINA*

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ABSTRACT. The stratiform laminae of *Micrina* sclerites originally consisted of rheomorphic successions of monolayers of micrometric-sized, apatitic tablets, presumably interleaved with chitin and glycosaminoglycans (GAGs). Paired laminae enclose slot-like chambers swelling into lobes distally that originally contained GAGs and deposits of spherulitic and prismatic apatite. The laminae are pervaded by apatitic tubes, apparently secreted by microvillous setoblasts and containing, at the surface, chitinous setae. Internal markings suggest that the triangular (sellate) sclerite supported a pair of muscles and the planospiral (mitral) sclerite, a medial muscle and gonadal sacs flanked by a pair of crescentic muscle bases. Both sclerites were secreted by a mantle with a circumferential fold. The sellate and mitral sclerites are homologized with the anterior and posterior shells of *Halkieria* and could have become the dorsal and ventral valves of the ancestral brachiopod by a sequence of transformations. These include: the folding of the halkieriid body axis; accelerated mixoperipheral growth of the anterior (dorsal) shell to enclose, with the posterior (ventral) shell, a mantle cavity lined with modified ciliated epithelium of the foot; reduction of sclerite-secreting epithelium to the locus of the brachiopod pedicle epithelium; and the anterior (dorsal) spread of gonadal lamellae.

KEY WORDS: halkieriid-*Micrina* relationship, halkieriid-brachiopod affinities, organophosphatic lamination, setigerous sclerites.

MICROFOSSILS with bizarre morphologies have long been known from lower Cambrian sediments in many parts of the world. The nature of these assemblages, however, was not fully recognized until the re-awakening of interest in early Phanerozoic phylogenies in the 1960s (Fonin and Smirnov 1967). In a series of studies, largely instigated by S. Bengtson and S. Conway Morris, many assemblages were feasibly shown to be pieces (sclerites) of skeletal mosaics (scleritomes) that once covered metazoans of uncertain affinities although there were tantalizing similarities with well-known phyla, for example, between brachiopod valves and the sclerites of the tannuolinids *Micrina* (Laurie 1986) and *Tannuolina* (Fonin and Smirnova 1967; Qian and Bengtson 1989; Conway Morris and Chen 1990). The potential significance of these morphological similarities came to a head with the discovery of wholly articulated *Halkieria* in the Lower Cambrian of North Greenland. The definitive study of the *Halkieria* scleritome by Conway Morris and Peel (1995) revealed that, amid a complex of sclerite plates and rods, there were two shells, placed at either end of the animal, one of which is remarkably like the ventral valves of some early Cambrian brachiopods. This similarity prompted Conway Morris and Peel to postulate (*op. cit.* p. 343) that brachiopods could have evolved from halkieriids with folded body axes, as was later made explicit by Conway Morris (1998, fig. 86).

Our curiosity in the relationship between the valves of brachiopods and the sclerites/shells of *Micrina* and *Halkieria* was aroused as much by similarities in shell structure as by gross morphology (Holmer 2001). Investigations by Laurie (1986) and Conway Morris and Chen (1990), had already revealed that the organophosphatic shells of *Micrina* and *Tannuolina* are stratiform. Our own studies have confirmed not only that this is so but also that the laminar successions are arranged in sets in much the same way as those of early Cambrian lingulides and acrotretides except that spherulitic crystallization of apatitic aggregates pointed to the mediation of a different suite of calcifying proteins.

The turning point came, however, with the discoveries that the sclerites were almost certainly

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setigerous, and that their internal markings suggested their support of a pair of muscles frontally and gonadal sacs posteriorly. Taking into account all such evidence, we conclude that the sclerites of *Micrina* are homologous with the shells of *Halkieria*; and that, by folding along a transverse plane in the mid-region, the worm-like *Halkieria* could have been transformed into a bivalved brachiopod.

MATERIAL AND METHODS

Phosphatized fossils, principally the sclerites of *Micrina etheridgei* (Tate) (see Laurie 1986, pp. 415–417) were dissolved by 10 per cent acetic acid out of samples of the lower Cambrian Wilkawillina Limestone, collected by one of us (LEH) at the Wilkawillina Gorge, Flinders Range, South Australia (see Bengtson *et al*. 1990, pp. 10–14 for precise localities).

Selected specimens were coated with gold for studying under a Cambridge 360 scanning electron microscope (SEM). Those used to illustrate this paper have been deposited in the Hunterian Museum of the University of Glasgow (GLAHM).

TERMINOLOGY

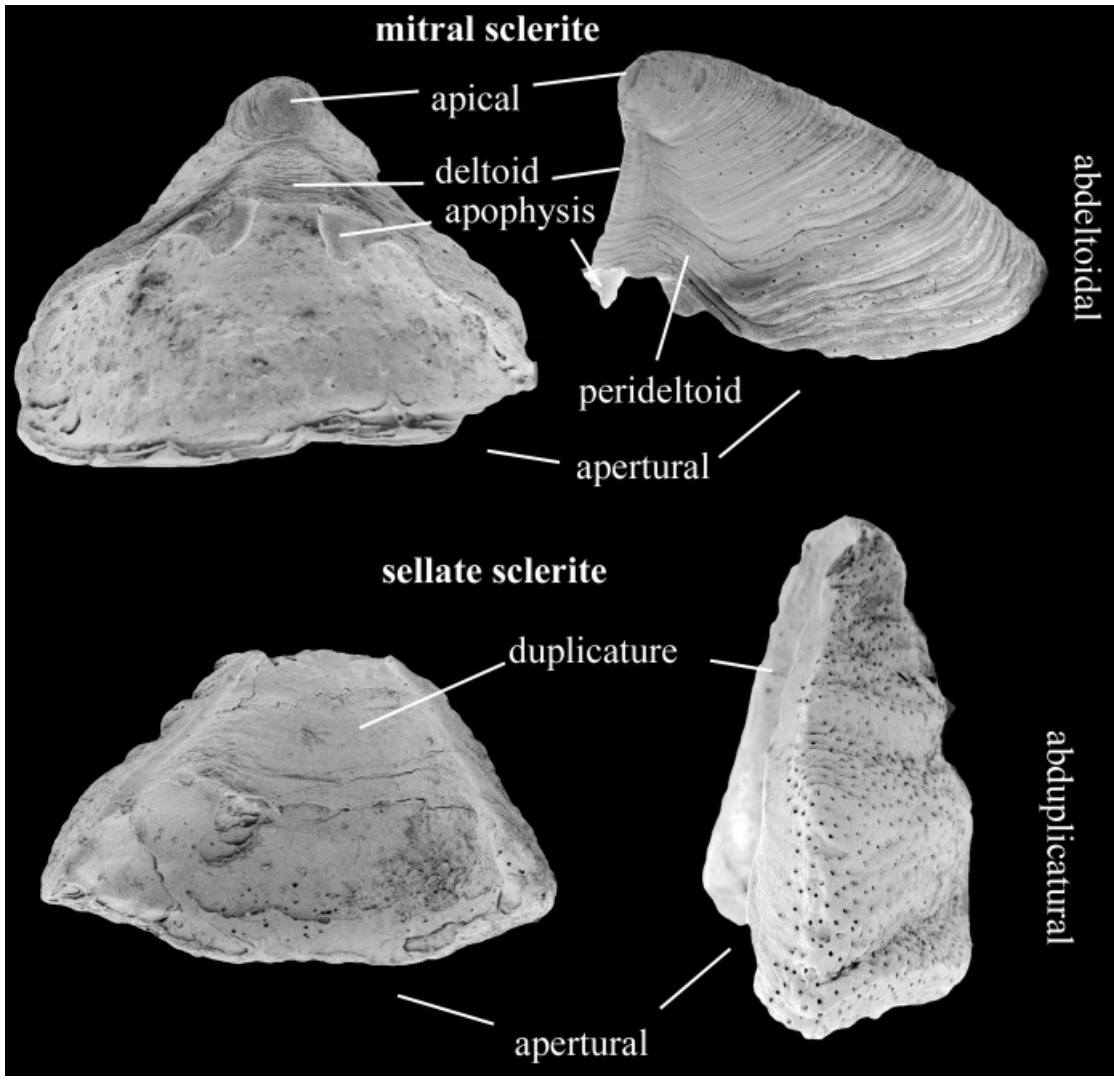
The terms used to identify the various fossilized pieces (sclerites) that make up the biomineralized skeleton (scleritome) of early Cambrian metazoans, have been mainly proposed and standardized by Bengtson (1970), Landing (1984), Laurie (1986) and Conway Morris and Chen (1990). Most terms used by Laurie to describe his genus *Micrina* (*op. cit*. p. 433) have been adopted for this study. The principal change is the discard of 'anterior' and 'posterior', provisionally used by Laurie for orienting the mitral sclerite (Text–fig. 1). There is presently no certainty as to the biological orientation of mitral (and sellate) sclerites and the terms 'deltoid' and 'abdeltoid' (and 'duplicatural' and 'abduplicatural'), are preferred. The bilateral symmetry of *Micrina* sclerites (*s.s.*) also allows for the use of 'medial' and 'lateral' when, for example, identifying a sector of the aperture. The rod-like protrusions, emerging from beneath the deltoid, simulate the teeth of articulated brachiopods in shape and disposition. There is, however, no structural evidence that the protrusions served as articulatory devices; and the non-committal term 'apophyses' is used to identify them (Text-fig. 1).

RESULTS

The mitral and sellate sclerites, on which Laurie (1986, p. 435) founded the genus *Micrina*, do not have the complementarity of a typical metazoan bivalved shell (Text-fig. 1). They are, however, bilaterally symmetrical, signifying that in life they lay astride the medial axis of the animal bearing them. They also have the same ornamentation, apatitic shell structure and relict 'canal' systems. These features will be described before those distinguishing the two kinds of sclerites at juvenile and adult stages of growth.

Ornamentation

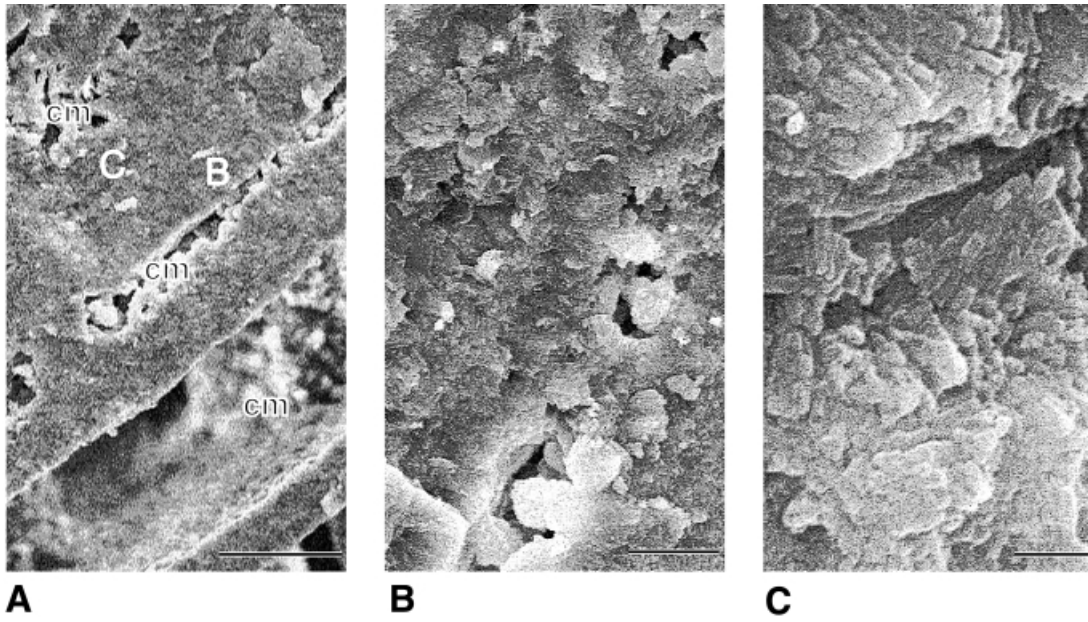
Surface ornamentation consists of folds of varying wavelengths forming rings eccentric to sclerite apices. The folds are gently rounded with steep limbs and anastomosing, arcuate axial planes, up to several hundred micrometres long. There are three orders of folding. The regular pattern (Pl. 1, figs 1–2) is of laterally impersistent folds between 6 and 10 μm wide and up to 3 μm high, culminating at intervals of *c*. 600 μm in second order groups of folds *c*. 60 μm wide (growth bands). At abrupt changes in slope, as at deltoid boundaries and loci of differential growth ('nickpoints' of Williams and Holmer 1992, p. 662), a third order of obliquely trending folds (Pl. 1, fig. 2) may be superimposed on the eccentrically disposed sets. Sharply edged lamellae periodically interrupt folds, usually in overlaps translating one set of folds across another (Pl. 1, fig. 3). Furrows, up to several hundred micrometres deep and usually concentric with first- and second-order folding, occur sporadically. Fracture and degraded surfaces of sclerites show that the folds are composed of flat-lying laminae (Pl. 1, fig. 8).



TEXT-FIG. 1. Views of the mitral and sellate sclerites of *Micrina etheridgei* showing the terms used in describing their morphology and orientation.

Shell structure

The shell structure of *Micrina* is essentially stratiform (rhythmic successions of apatitic and polymeric laminae) and similar enough to that of lingulide brachiopods to warrant the use of the same terminology (Cusack *et al*. 1999, p. 805). Some structures are novel and are best understood by assuming that they were secreted in the same way as any stratiform succession with its innermost surface contiguous with the secreting outer epithelium. This has led to complications in identifying the first-formed or oldest parts of some features. Thus the outer 'strata' of a lamina in the medial part of a mitral sclerite, were secreted before the inner ones. In the retroverted laminar sets at the sclerite margin and in the laminae coating apophyses (see Text-fig. 3 and Pl. 5, figs 7–8), the reverse is true. For purposes of comparison, 'outer' and 'inner' will be used strictly to orient local structures. The secretory chronology of a structure, irrespective



TEXT-FIG. 2. Fracture section of a phosphatized sella of *Micrina* (GLAHM 114739) showing platy apatite (C) that results from the recrystallization of laminar sets because variably developed but recognizable chambers (cm) survive in a stratiform succession (A showing sites of B and C): scale bars represent 25 μm (A), 5 μm (B) and 0·5 μm (C).

of its disposition, will be indicated by the terms 'first-formed' and 'last-formed' as is true for the outermost and innermost laminae of standard stratiform successions.

The biomineralization of early Cambrian fossils has been reviewed by Bengtson and Conway Morris (1992) and there is no doubt that tannuolinid sclerites were originally apatitic. Yet diagenetic phosphatization even of carbonate shells has been noted (Bengtson *et al.* 1990, pp. 171–172) and could have affected *Micrina* sclerites. However, the assumption that the *Micrina* shell structure is stratiform helps to distinguish biogenic apatite from diagenetic phosphatization. The fine structures of the organophosphatic integument of living lingulide brachiopods can be preserved in nanometric detail in the shells of early Palaeozoic species despite several phases of recrystallization (Holmer 1989; Williams *et al*. 1998; Cusack *et al*. 1999). Similar changes affect the fabric of sclerites. Recognizable stratified laminar sets (defined below) can be traced into successions where recrystallization has destroyed the finer structures. More disputable is the occurrence of recrystallized apatite (Text-fig. 2) filling the chambers and/or the distal lobes of laminar sets that normally contain only scatters of micrometric-sized apatitic bodies. Such infills

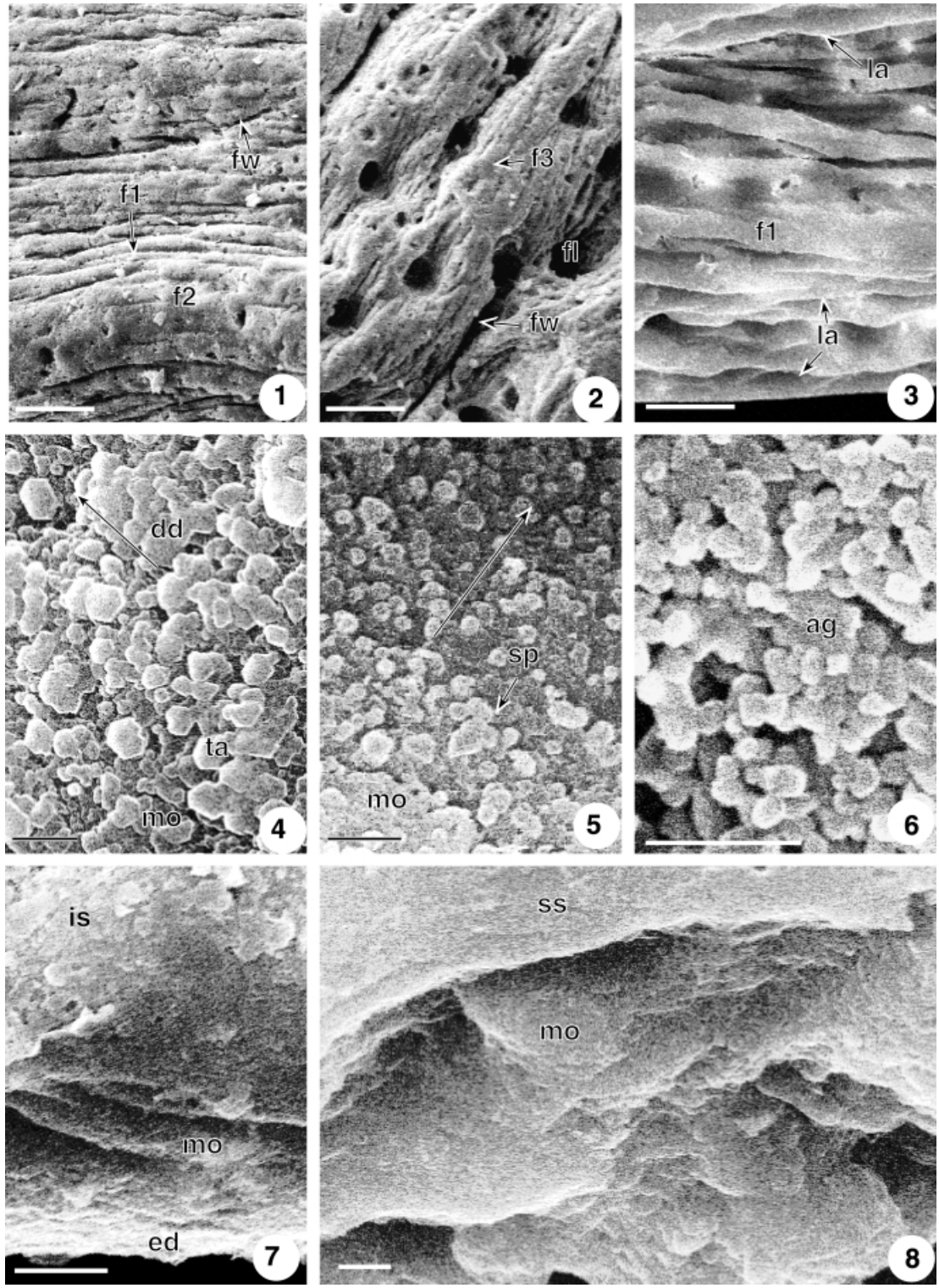
EXPLANATION OF PLATE 1

Scanning electron micrographs of gold-coated surfaces of mitral sclerites of *Micrina etheridgei*: 1–2, GLAHM 114741; 3, 7–8, GLAHM 114742; 4, GLAHM 114743; 5, GLAHM 114738; 6, GLAHM 114744.

Figs 1–3. Surface ornamentation consisting of three orders of folding, f1, f2 (growth band) and f3, with furrows (fw), lamellae (la) and funnels (fl); scale bars represent 50, 100 and 20 μm, respectively.

Figs 4–6. Details of laminar surfaces showing pinacoids and prisms of apatite forming variably aggregated (ag) monolayers (mo) of tablets (ta) and discoids (dd), facing directions of crystallographic steps (sp) indicated by arrows; scale bars represent 2, 1 and 0·5 μm, respectively.

Figs 7–8. Platy monolayers (mo) of the primary layer at the margin (ed) of a young sclerite as seen from the interior (is) and, in an oblique fracture, beneath the external surface (ss); scale bars represent 5 and 1 μm, respectively.



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are unlikely to have been added to sclerites by diagenetic phosphatization as they seldom destroy the fabric of laminae containing them. They are reminiscent of the excessive amounts of apatite obscuring trellises of rods (baculi) in the shells of living *Discina* (Williams *et al*. 1992) and are comparable with infills within laminar sets of Ordovician lingulides identified by Holmer (1989, p. 31) as a collophane-like constituent (CCP). Accordingly, the following description of *Micrina* skeletal structures assumes that compact, recrystallized apatite, filling laminar sets and thickening their distal lobes, is an integral part of the sclerite fabric.

The basic mineralized constituents of both primary and secondary layers of *Micrina* sclerites (Pl. 1, figs 4–6) are pinacoids of apatite, normally 1 μm or more in diameter, forming discoids, or tablets with variably developed prismatic step edges and prismatic laths. They aggregate as poorly ordered mosaics or, more usually, as partly or entirely recrystallized monolayers *c.* 15 nm thick.

Primary layer. In calcitic as well as apatitic shells of all brachiopods, the first-formed, primary layer, which is secreted on the periostracum, is structurally distinguishable from the inner, later-formed, secondary layer. This is not always so in *Micrina* sclerites because of recrystallization. The primary layer, however, typically consists of monolayers of platy apatite that fill the surface folds as successions more or less parallel with the sclerite exterior (Pl. 1, fig. 8). The successions range from 3 to 12 μm thick. The fine structure of the layer is sporadically seen in fracture sections of the sclerite exterior as well as at the margins (Pl. 1, figs 7–8). Its distinction from the stratified laminae of the secondary layer, however, may be obscured by recrystallization and is then little more than a break in slope.

Secondary layer. The basic aggregates of the secondary layer are also monolayers (Pl. 2, fig. 1) which amalgamate into compacted, stratified laminae (Text-fig. 3), averaging 7·2 μm thick (range 4·0–10·3 μm). Variably disposed sheets of stratified laminae are the dominant structures of the sclerite shell. Even in recrystallized, vertically cleaved sections, individual laminae are distinguishable because they form the walls of chambers and, when contiguous, are usually separated by empty slots or sutured interfaces (Pl. 2, fig. 4). The microtopography of laminar surfaces is variable and is commonly given a granular appearance by fine, crystallographic cleavage (Pl. 2, fig. 3). Apart from mosaics (Pl. 2, fig. 2) and recrystallized stepped monolayers, which are virtually planar, surfaces may be hummocky with semi-ellipsoids of two significantly different lengths (Pl. 2, fig. 3). The smaller semi-ellipsoids, up to 4 μm long, occur as crowded arrays without discernible order. The larger, flattened semi-ellipsoids, between 8 μm and 18 μm long, are usually well ordered in open rhombohedral arrays and mainly characterize the last-formed surfaces of laminae (Pl. 2, fig. 3) composing specialized regions of mitral sclerites, like apophyses (Pl. 5, fig. 8) and lateral interiors.

The stratiform shell of the mitral sclerite thickens (Text-fig. 3) from a region more or less coincident with the deepest part of the sclerite and the site of the juvenile shell (the infra-apical zone). This thickening towards the sclerite margin (including the deltoid) is contrary to the variation typical of brachiopods,

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EXPLANATION OF PLATE 2

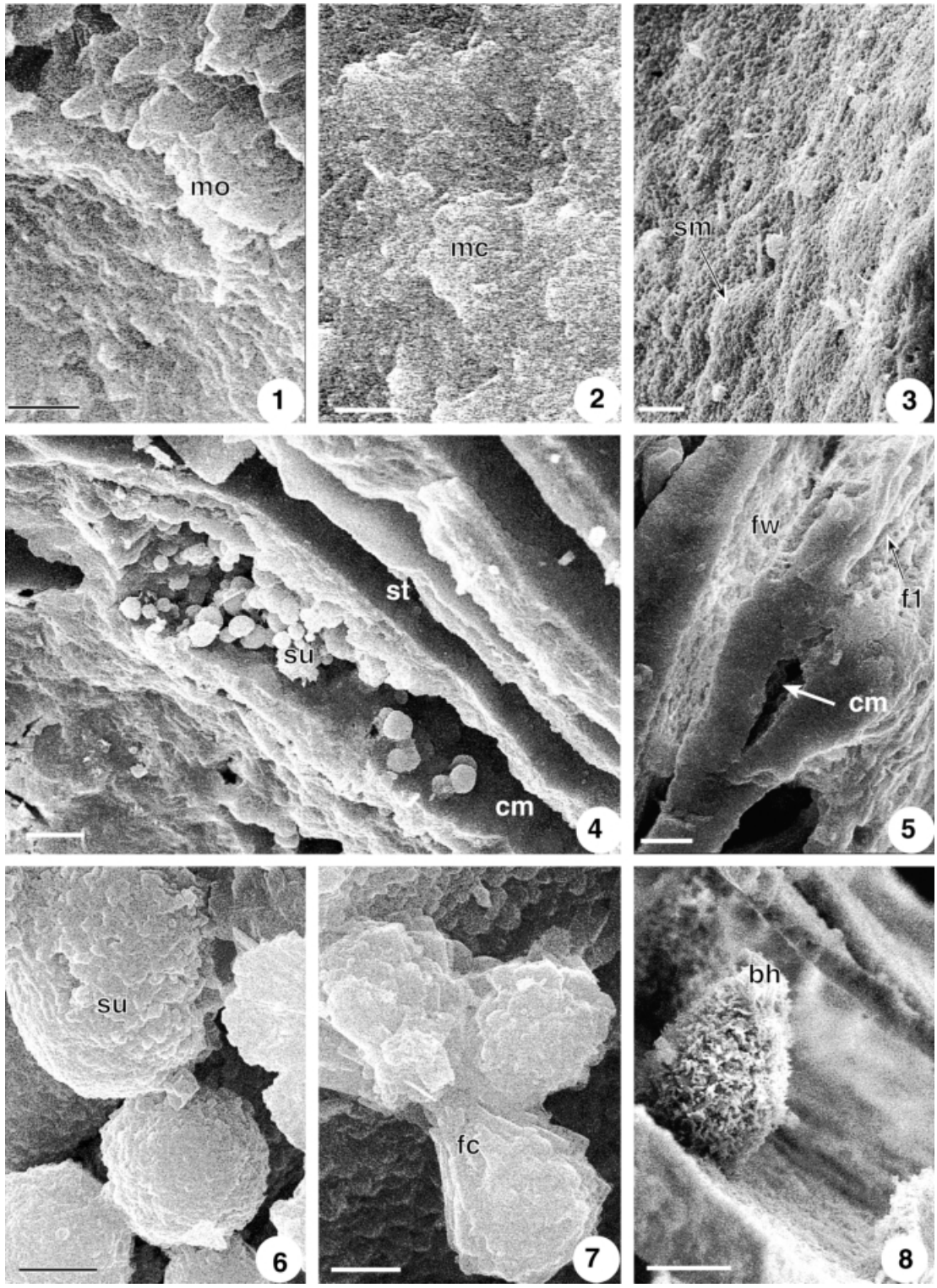
Scanning electron micrographs of gold-coated surfaces and fracture sections of mitral and sellate (fig. 8) sclerites of *Micrina etheridgei*: 1, GLAHM 114745; 2, 5, GLAHM 114742; 3–4, 6, GLAHM 114738; 7, GLAHM 114746; 8, GLAHM 114747.

Figs 1–3. The monolayers (mo) of a stratified lamina; and mosaics (mc) and semi-ellipsoidal hummocks (sm) cut obliquely by crystallographic cleavage on the inner and outer surfaces of a lamina within an apophysis; scale bars represent 1, 1 and 10 μm, respectively.

Fig. 4. Transverse fracture section of a laminar succession showing the slots (st) between sets and spherulites (su) adhering to both walls of a chamber (cm); scale bar represents 20 μm.

Fig. 5. Transverse fracture section of terminal arch of a spherulitic laminar set showing a closed chamber (cm) separated from an adjoining laminar set by a furrow (fw) lined with surface folds (f1); scale bar represents 10 μm.

Figs 6–8. Apatitic crystalline bodies, in the chambers of laminar sets, as platy spherulites (su), prismatic fascicles (fc) and bushy clumps of laths and rods (bh); scale bars represent 2, 1 and 20 μm, respectively.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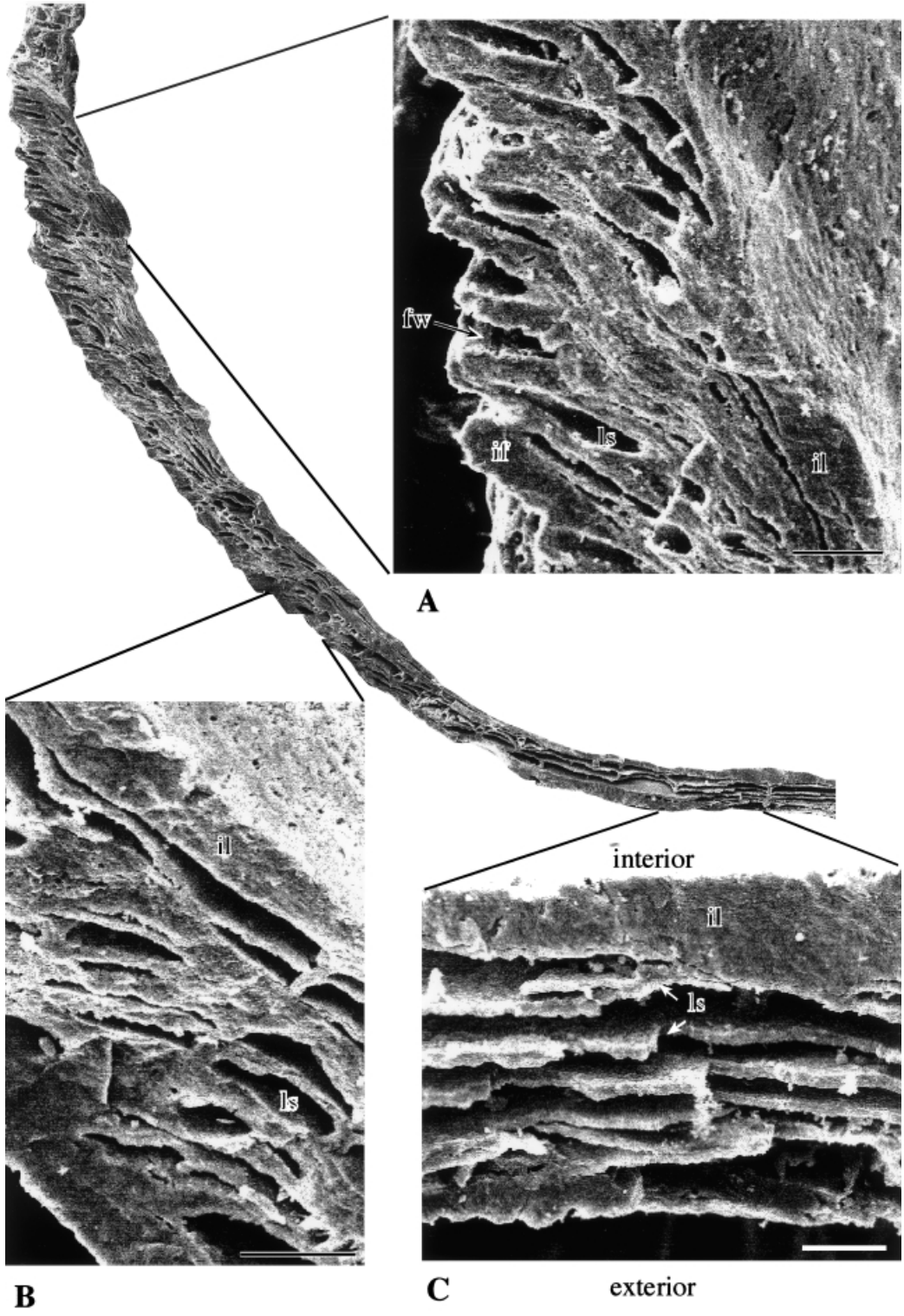
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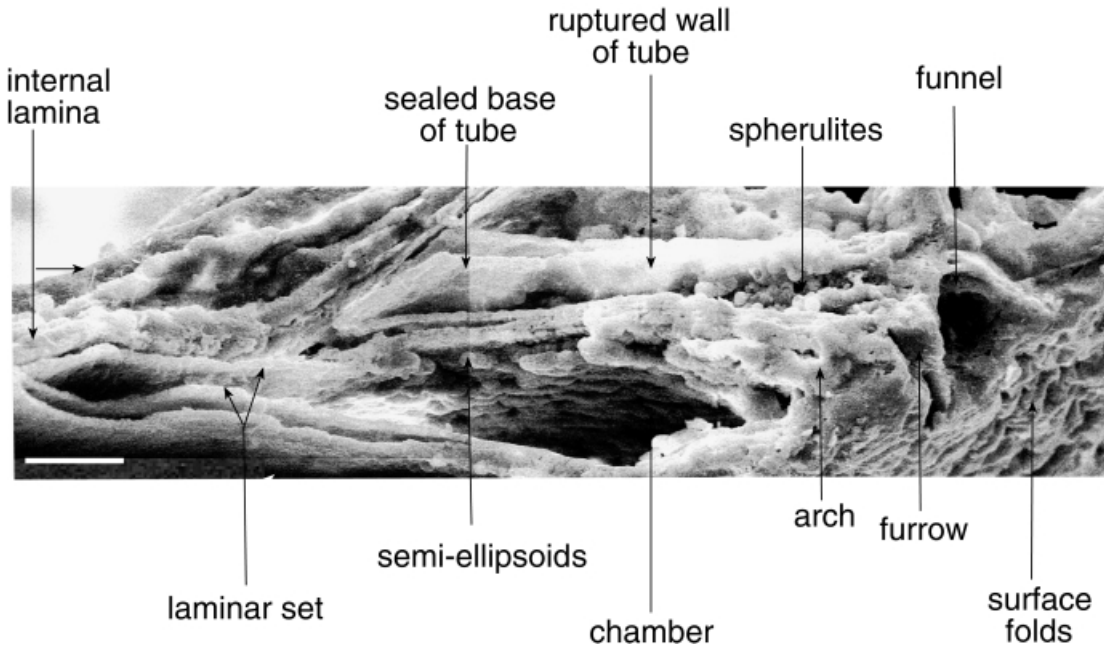

TEXT-FIG. 4. An oblique fracture section of a mitral sclerite of *Micrina* (GLAHM 114740) showing a spherulitic laminar set, separated by a furrow from a setal tube with a ruptured wall and a base sealed by an internal lamina: scale bar represents 50 μm.

where the thickest part is normally in the vicinity of the first-formed shell. The reversed variation in the thickness of the *Micrina* shell reflects progressive changes in the disposition and differential secretion of laminar assemblages (sets).

In the medial-abdeltoid zone where the shell may be less than 100 μm thick, several discrete laminar successions are disposed more or less parallel to the external surface of the sclerite (Text-fig. 3). They interleave laterally to delineate lenticular chambers that can extend for several hundred micrometres in the plane of the shell. Each laminar succession is normally divided medially by impersistent sutures and/or slit-like or narrowly lenticular spaces (Text-fig. 3; Pl. 2, fig. 4). Such breaks are assumed to be the interfaces between contiguous laminae with their last-formed surfaces facing in opposite directions to serve as the bounding walls of adjacent chambers (Text-fig. 4).

The chambers contain sporadically distributed clusters of crystalline bodies, mostly spherulites up to 8 μm or so in diameter but also fascicles and prisms (Pl. 2, fig. 4). The fascicles consist of lath-like prisms of apatite; the spherulites may also consist of radiating laths (Pl. 2, figs 6–7) but tablets, up to 600 nm long, commonly coalesce as surfaces parallel with equatorial planes. These bodies are fused to the last-formed surfaces of the bounding laminae like stalactites and stalagmites along with rarer prisms and hemispheroids, up to 13 μm in diameter. Clusters are especially common around the tubes running through the chambers (Pl. 5, fig. 1). A complete depositional unit, therefore, consists of two stratified laminae with their last-formed surfaces facing inwardly to delineate a chamber containing spherulites and other bodies of apatite (spherulitic set) (Pl. 2, fig. 4; Text-fig. 4).

TEXT-FIG. 3. Half of a transverse fracture section of a mature mitral sclerite of *Micrina* (GLAHM 114738) showing the progressive tilting of spherulitic laminar sets (ls) towards the margin, relative to an internal lamina (il) composed of the bases of sets; furrows (fw); and chambers of sets with apatitic infills (if): scale bars represent 100 μm (A–B) and 50 μm (C).

In the medial zone of a mature, mitral sclerite, the internal last-formed unit (internal set) of the laminar succession is usually up to 100 μm thick (Text-fig. 3). Fracture surfaces of this mainly recrystallized unit are typically cleavage planes. Sporadic, flat-lying slits suggest that the unit was originally a stratified laminar succession.

A three-dimensional model of a spherulitic set can be reconstructed by tracing its laminar walls to the margins of a mature mitral sclerite (Text-fig. 4). At the margin, shell thickness may be four times more than that of the apical zone and usually exceeds 350 μm. The increase is mainly attributable to the progressive tilting of the spherulitic sets, which may become vertical (Text-fig. 3), retroverted or even sigmoidally curved at the lateral and medial margins. The swollen lobes (up to 40 μm thick) that close individual sets also contribute to the increase in thickness. This is especially so where sets are inclined at about 45 degrees to the internal surface of the sclerite so that, for example, a succession of six compressed, spherulitic sets 210 μm thick, increased by one-third as it expanded into stacked lobes.

The lobate ends of spherulitic sets are gently rounded to angular arches of the laminae that bound terminal cylindroid chambers (50 μm or so high) which taper proximally (Text-fig. 4). The crests of the laminar arches may grade into the stratified laminae of the primary layer without a discernible break. The chambers may contain scattered aggregates of spherulites and other crystalline bodies of apatite attached to their bounding laminae (Pl. 2, fig. 4). Spherulitic sets with such lobate ends have been traced, exceptionally for more than 1 mm but usually for 3–400 μm, to vertical or more gently inclined roots, *c*. 100 μm long, that merge into the internal laminae lining the sclerite. Groups or, more rarely, individual spherulitic sets are separated from one another by furrows which may be a few hundred or more micrometres deep. The furrows bear surface folds indicating that they are part of the external microtopography of sclerites (Pl. 2, fig. 5). Lamellae are less commonly seen in sections but are composed of disrupted spherulitic sets or groups of stratified laminae characterized by sharp, asymmetric crests and minor rucking with tilted axial planes.

The structure of both sclerites of *Micrina* is the same. The sellate duplicature, being seldom more than 100 μm thick, is normally recrystallized as a compact shelf (Pl. 3, fig. 1) that subtends an acute angle with the recrystallized internal lamina of the main part of the sclerite. The chambers of the reflexed spherulitic laminar sets of the sellate sclerite also contain apatitic constituents additional to those seen in the mitral sets. They are laths and rods (some apparently with medial canals), up to 3 μm long and *c*. 500 nm thick, that sporadically aggregate in clumps around canals, like twigs in a bird's nest (Pl. 2, fig. 8).

Canals

Micrina sclerites are indented by a variety of tunnels inherent to the shell. Some are randomly distributed, subcircular to elliptical cylindroids formed by constrictions of furrows (Text-fig. 4). Others, apparently also sporadically distributed, extend inwards, exceptionally throughout the shell, from subcircular

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EXPLANATION OF PLATE 3

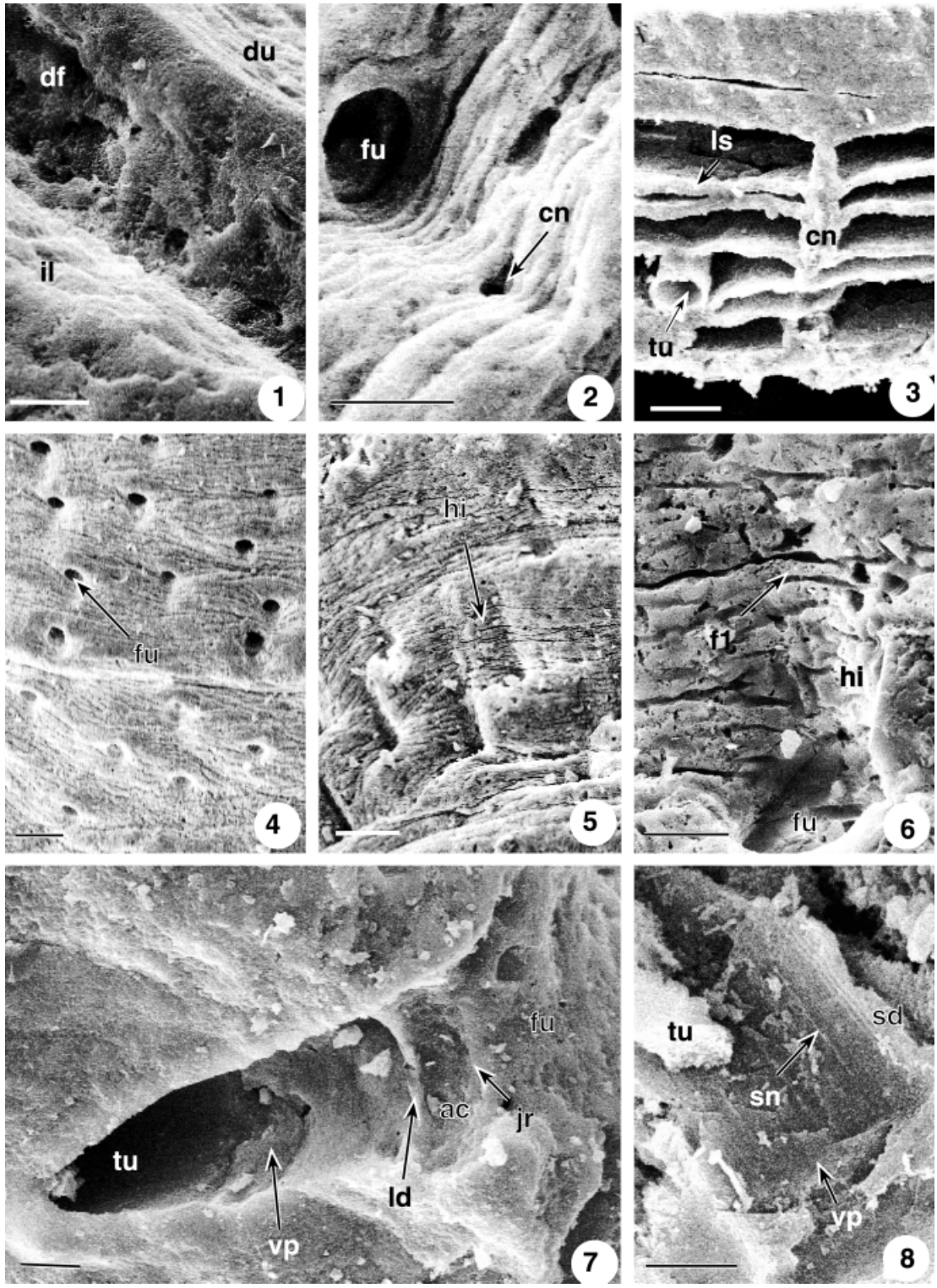
Scanning electron micrographs of gold-coated surfaces and fracture sections of mitral and sellate (fig. 1) sclerites of *Micrina etheridgei*: 1, GLAHM 114748; 2, 5–6, GLAHM 114741; 3, 7–8, GLAHM 114748; 4, GLAHM 114749.

Fig. 1. View of the shelf-like junction (df) of the duplicature (du) with the internal lamina (il) of a sellate sclerite; scale bar represents 20 μm.

Figs 2–3. Surface and fracture section views of canals (cn) orthogonal to laminar successions (ls) relative to an external funnel (fu) and internal tube (tu) of the tubular network; scale bars represent 50 μm.

Figs 4–6. Surface views of the funnels (fu) of the tubular network disposed more or less orthogonally and alternately in 4 and obliquely in 5 and 6 where they are associated with hemicylindroid imprints (hi) indented on rheomorphic folds (f1) of external surfaces; scale bars represent 100, 100 and 20 μm, respectively.

Figs 7–8. Oblique fracture sections showing the main features of a funnel (fu) and a tube (tu); antechamber (ac), jagged rim (jr), ledge (ld), stratified laminar wall (sd), striations (sn) and remains of a concave plate (vp); scale bars represent 20 and 10 μm, respectively.



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openings, up to 10 μm in diameter at the external surface (Pl. 3, fig. 2) where they are usually associated with nickpoints. In section, these canals are defined by conical invaginations of successive laminae and are more or less orthogonal to sclerite surfaces (Pl. 3, fig. 3).

The pre-eminent canal system, however, consists of a regular network of mineralized tubes, almost invariably unbranched (Pl. 5, fig. 1) that open at the external surfaces of both sclerites. On surfaces that grew radially at a steady rate, canal openings are spaced concentrically, *c*. 100 μm apart, in alternating arcs (Pl. 3, fig. 4). In zones where radial growth was slower, as in growth bands or at the sclerite margins, especially towards the perideltoid sectors, openings tend to crowd together in arcs (Pl. 4, fig. 3). Each canal of this system consists of three elements; a superficial, funnel-shaped, opening separated from an internal, hollow, apatitic tube by (an) outwardly concave, perforated plate(s) (Pl. 3, fig. 7). These elements increase in size during growth with the diameters of the funnel aperture and the tube averaging 18·0 and 15·9 μm near the apices and 45·2 and 31·8 μm towards the margins of mature sclerites.

There are also noteworthy variations in their morphology. The external boundary of a funnel is usually a sharp, overhanging lip apically (Pl. 4, fig. 1) but less well-defined marginally where it can extend radially for more than 250 μm as a hemicylindroid imprint depressing the surface folds (Pl. 3, figs 5–6). Such imprints, which are mostly straight with only slight deflection in some, may be deeper along one side and may exceptionally be divided distally by a low medial ridge. A funnel is typically *c*. 10 μm deep with smooth, gently curved surfaces covering horizontally disposed stratified laminae of the primary layer. Its inner boundary is almost invariably a sharply jagged rim (Pl. 3, fig. 7) that separates it from an antechamber, *c*. 10 μm deep, with smooth, bulging walls. The inner boundary of the antechamber is a smooth ledge, *c*. 7–10 μm wide, below which is an outwardly concave apatitic plate. The plate is usually broken (Pl. 3, fig. 7) but complete, well-preserved ones are indented by a pair of divergent, elongately oval imprints, up to 20 μm or so long, with cracked floors perforated by slots (Pl. 4, fig. 1). A third, oval imprint may also lie transversely in the marginal sector of the plate but, like the divergent pair, is normally represented by an enlarged cavity.

The tubes, capped by antechambers and their basal plates, extend throughout most, if not all, of the laminar secondary layer (Text-fig. 4). They are straight to slightly flexed structures, circular to elliptical in cross section and are disposed orthogonal to the external surface in the apical region (Pl. 4, fig. 2). They become increasingly inclined marginally where they may lie virtually subparallel with laminar sets (Pl. 3, fig. 3; Pl. 4, figs 3, 5) and in line with the hemicylindroid imprints extending beyond their funnels. Tube canals are seldom seen on sclerite interiors except marginally. Some may have been obscured by diagenetic recrystallization, but others terminate against internal laminae (Text-fig. 4) or more rarely taper out within laminar sets. The external surface of a tube is typically smooth with accretions of spherulites, laths and prisms sporadically adhering to it (Pl. 4, figs 2, 5), especially at its junction with

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EXPLANATION OF PLATE 4

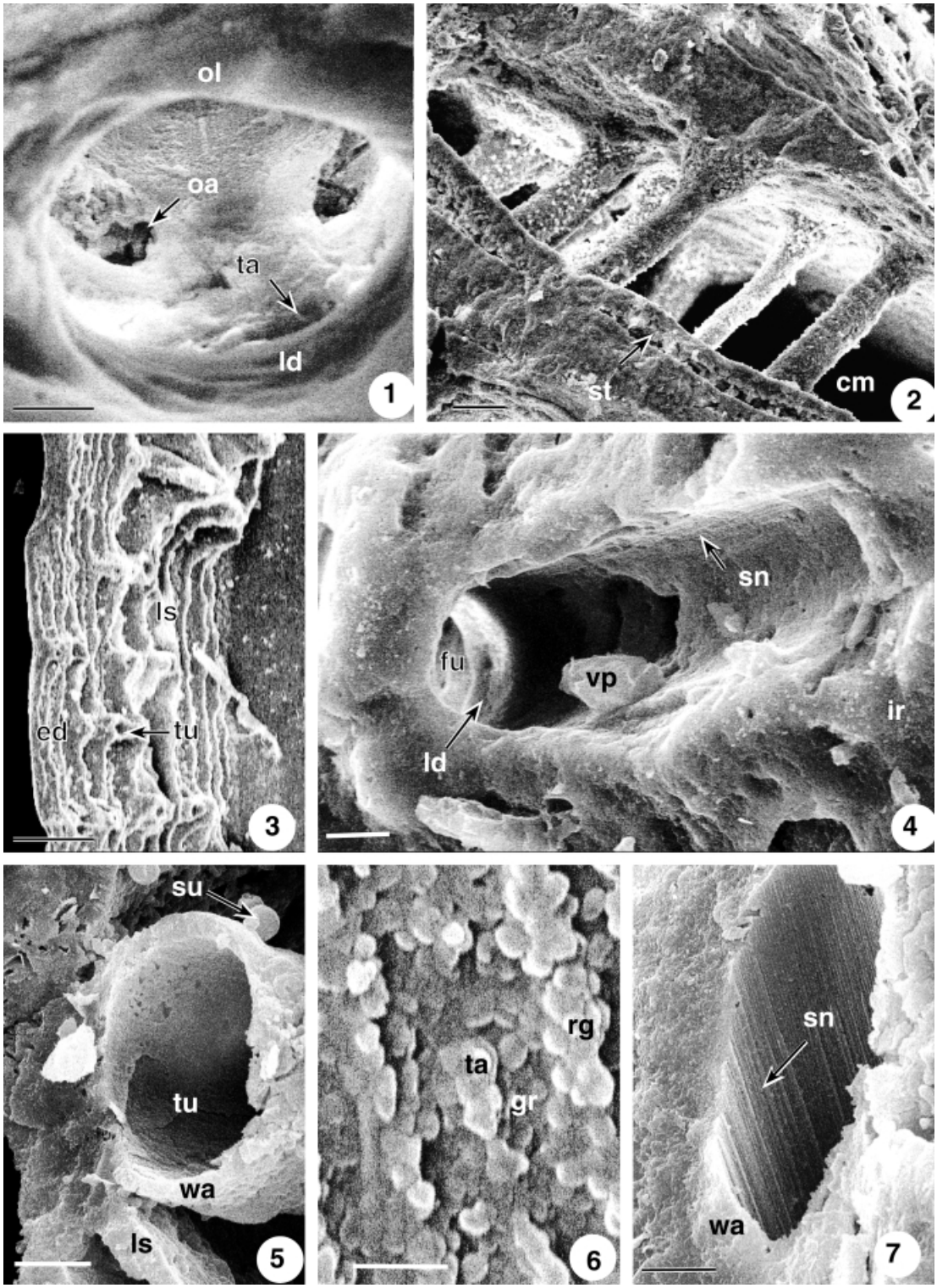
Scanning electron micrographs of gold-coated surfaces and fracture sections of mitral and sellate (figs 2–4) sclerites of *Micrina etheridgei*: 1, GLAHM 114741; 2, GLAHM 114750; 3, GLAHM 114751; 4, GLAHM 114752; 5–7, GLAHM 114738.

Fig. 1. Surface view of an entrance into the tubular network showing a funnel with overhanging lip (ol), ledge (ld) and a concave plate pierced by a pair of oval apertures (oa) and a transverse one (ta); scale bar represents 10 μm.

Fig. 2. Tubes, traversing a chamber (cm) of a laminar set delineated by slots (st), with coatings of spherulitic apatite; scale bar represents 20 μm.

Figs 3–4. Exfoliated laminar sets (ls) at the margin (ed) of a mature sellate sclerite showing the crowding together of near horizontal tubes (tu) with details of a slightly inclined tube (4) opening to the interior (ir) and revealing striations (sn) on the tube wall, remains of the concave plate (vp), the ledge (ld) leading to the antechamber and the funnel (fu); scale bars represent 20 and 10 μm, respectively.

Figs 5–7. Transverse fracture sections showing a tube (tu) with walls (wa) fused with laminae (ls) only by diagenetic recrystallization and bearing spherulites (su); striations (sn), as seen in a rheomorphically deformed tube (7), consist of grooves (gr) and ridges (rg) composed of tablets (ta), running parallel with the tube axis; scale bars represent 5, 5 and 10 μm, respectively.



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laminae. The tube wall is, on average, 4·4 μm thick (range, 2·5–6·0 μm), and is composed of strata *c*. 25 nm thick lying parallel with the surface (Pl. 3, fig. 8). The tube interior is striated by alternating grooves and ridges, parallel with the long axis (Pl. 4, fig. 7). The ridges, up to 800 nm wide, are composed of flat-lying, well-ordered discoidal to subhexagonal tablets, between 120 and 200 nm in diameter (Pl. 4, fig. 6).

Morphology

The morphology of several features unique to *Micrina* merited study because they helped in understanding the way sclerites grew. Moreover, some so closely resemble prime diagnostic features of brachiopods as to invite structural comparisons of potential phylogenetic significance.

Juvenile sclerites. The first-formed sclerites have been identified on the assumption that they are preserved at the apices of mature ones and that, like those of living lingulide brachiopods, are delineated by a conspicuous growth band (cf. lamellar ring; Williams *et al*. 2001). In this context, the juvenile shell of the mitral sclerite is a hemispherical to semi-ellipsoidal structure varying in transverse diameter from 240 to 280 μm (Pl. 5, figs 2–3). One of the five shells studied was virtually featureless. The margins of the others were indented circumferentially by up to eight nickpoints 10 μm wide, while their surfaces were creased by three or four transverse furrows. The shell is composed of granular laminae with rare discoidal pinacoids.

The juvenile shell of the sellate sclerite is a featureless, arched, inwardly concave plate *c*. 270 μm wide and 20 μm thick (Pl. 6, fig. 1).

Deltoid sector. The apical deltoid sector (Text-fig. 1) of the mitral sclerite consists of an acutely (*c*. 30 degrees) triangular, variably arched deltoid with a margin that usually curves outwards, and with lateral boundaries that overlie two narrowly divergent apophyses. The flanking perideltoid sectors (Laurie 1986, p. 433) are set at an angle to the rest of the sclerite. At the apex, the deltoid emerges, not always symmetrically, from beneath the juvenile shell and up to four surrounding growth bands, each *c*. 8 μm thick, as an obtusely triangular flap (Pl. 5, fig. 4). When depressed, the flap is bounded by two short, divergent, ridge-like folds 12 μm or so wide, which transgress obliquely across the deltoid. When arched, the flap is separated from incipient perideltoidal sectors by a pair of furrows. The deltoid is tightly wrinkled into arcuate folds, which are continuous across the boundary ridges or furrows (Pl. 5, fig. 4). Third order, radially disposed folding also affects the perideltoid sectors, which are breaks of slope (Pl. 5, fig. 5) marking the growth track of the underlying apophyses, between which the deltoid is subtended.

The fabric of the deltoid is the same as that of the rest of the sclerite and is also perforated by canals with funnels associated with nickpoints. The fine structure of apophyses, however, is different. Apophyses projecting from the first-formed deltoid are divergent rods, *c*. 70–100 μm long. They consist of a fragile

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EXPLANATION OF PLATE 5

Scanning electron micrographs of gold-coated surfaces and fracture sections of mitral sclerites of *Micrina etheridgei*: 1, 8, GLAHM 114738; 2–4, 6, GLAHM 114753; 5, GLAHM 114754; 7, GLAHM 114755.

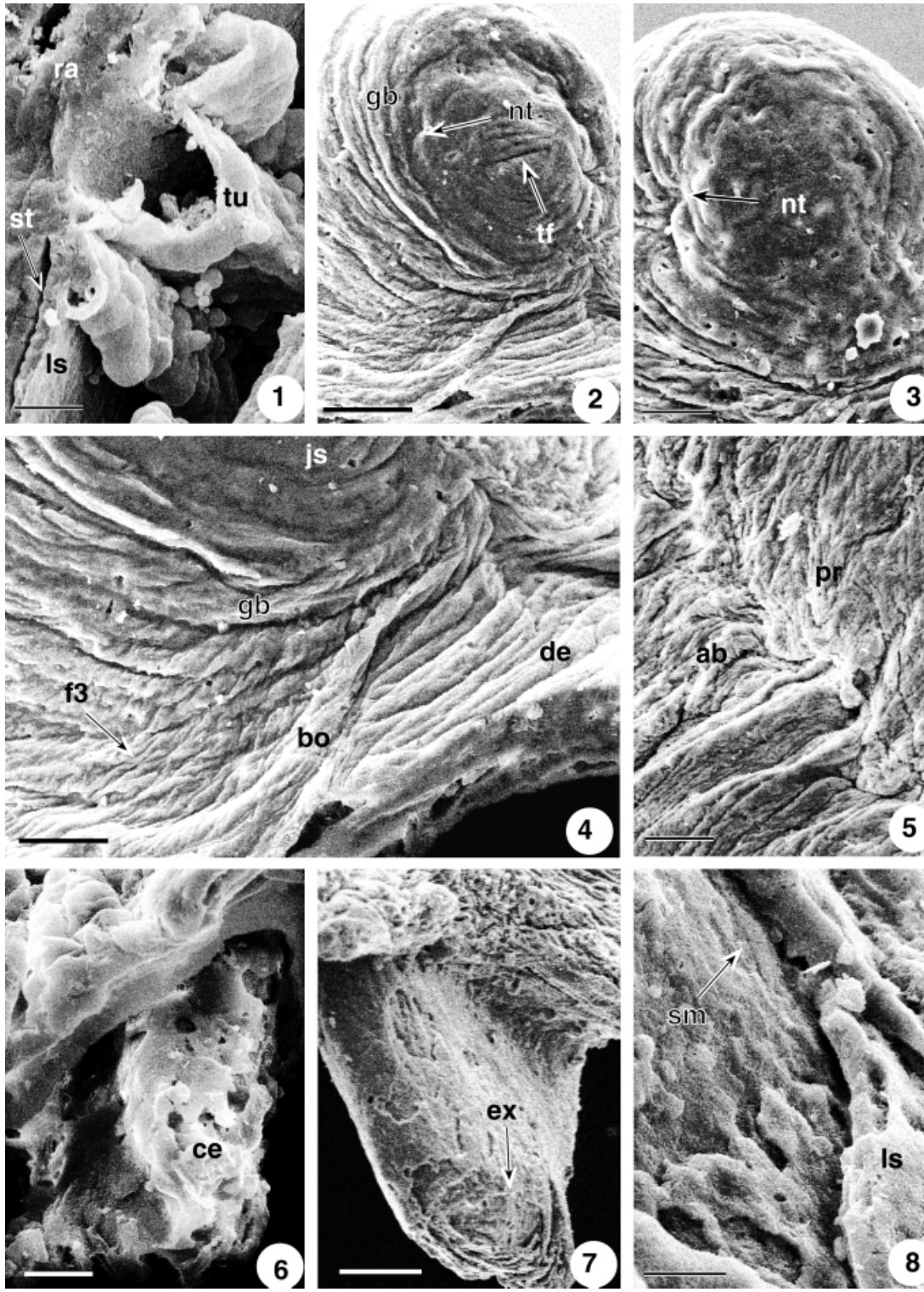
Fig. 1. Transverse fracture section showing a tube (tu) flanked by two branches (?) on a lamina (ls) delineated by a slot (st); the structural relationships are obscured by gross apatitic recrystallization (ra); scale bar represents 20 μm.

Figs 2–3. Juvenile shells at the apices of mitral sclerites with nickpoints (nt), transverse furrows (tf) and growth bands (gb); scale bars represent 100 and 50 μm, respectively.

Fig. 4. The deltoid (de) of a young sclerite with two bounding folds (bo) emerging asymmetrically from beneath growth bands (gb) surrounding a juvenile shell (js); perideltoid region with third order folds (f3); scale bar represents 50 μm.

Fig. 5. Sporadically disrupted junction between the perideltoid (pr) and abdeltoid (ab) regions of a mitral sclerite; scale bar represents 100 μm.

Figs 6–8. Young and mature apophyses with details of exfoliated lamination (ex) in a mature apophysis, showing a loosely aggregated apatitic core perforated by holes (ce) and successive coats of platy laminae (ls) with semi-ellipsoid hummocks (sm) on outer surfaces; scale bars represent 20, 200 and 20 μm, respectively.



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laminar coat and a core of apatitic granules and tablets, loosely aggregated into curved, perforated, laminae (Pl. 5, fig. 6). Mature apophyses are relatively slender (*c*. 100 μm) blades that may project from beneath the deltoid margin for more than 1 mm (Pl. 5, fig. 7). Their surfaces are normally smooth but exfoliation shows that the apophyses (Pl. 5, fig. 8) are composed of a succession of platy laminae, 3·5–10 μm thick, consisting of flat-lying laths and tablets that are commonly compacted and cleaved. The laminae may be separated from one another by lenticular cavities containing crystal growths as do slots within the laminae. The laminae are not arranged in sets but there is a rhythmic pattern to their surface morphology. The outer surface of a lamina is usually ornamented by rhomboidally arranged semi-ellipsoids, up to 16 μm long; the inner, by tabular and pinacoidal mosaics, *c*. 2 μm in size (Pl. 2, figs 2–3).

Duplicature. The duplicature is the triangular plate forming the apical half of the inner surface of the sellate sclerite (Laurie 1986, p. 433). It is an extension of the gently concave limb of the juvenile sellate sclerite and is separated from the rest of the shell by two diverging ridges composed of oblique folds (Pl. 6, fig. 2). The duplicatural surface is ornamented, like the outer sellate and mitral surfaces, by anastomosing folds (with some second order folding), disposed concentrically with the outwardly convex margin of the duplicature. Laterally, these folds curve sigmoidally to traverse the ridges at acute angles and thereby become continuous with the folds of the abduplicatural surface.

As already noted, the structure of the duplicature, complete with canals and their funnels, is essentially that of a laminar plate. Spherulitic laminar sets, however, are not developed, only sporadically occurring narrow slots with compressed crystal growths. The duplicature margin (Pl. 3, fig. 1) varies from a ledge of cleaved laminae to a lamella composed of strata, cumulatively less than 4 μm thick.

Internal markings

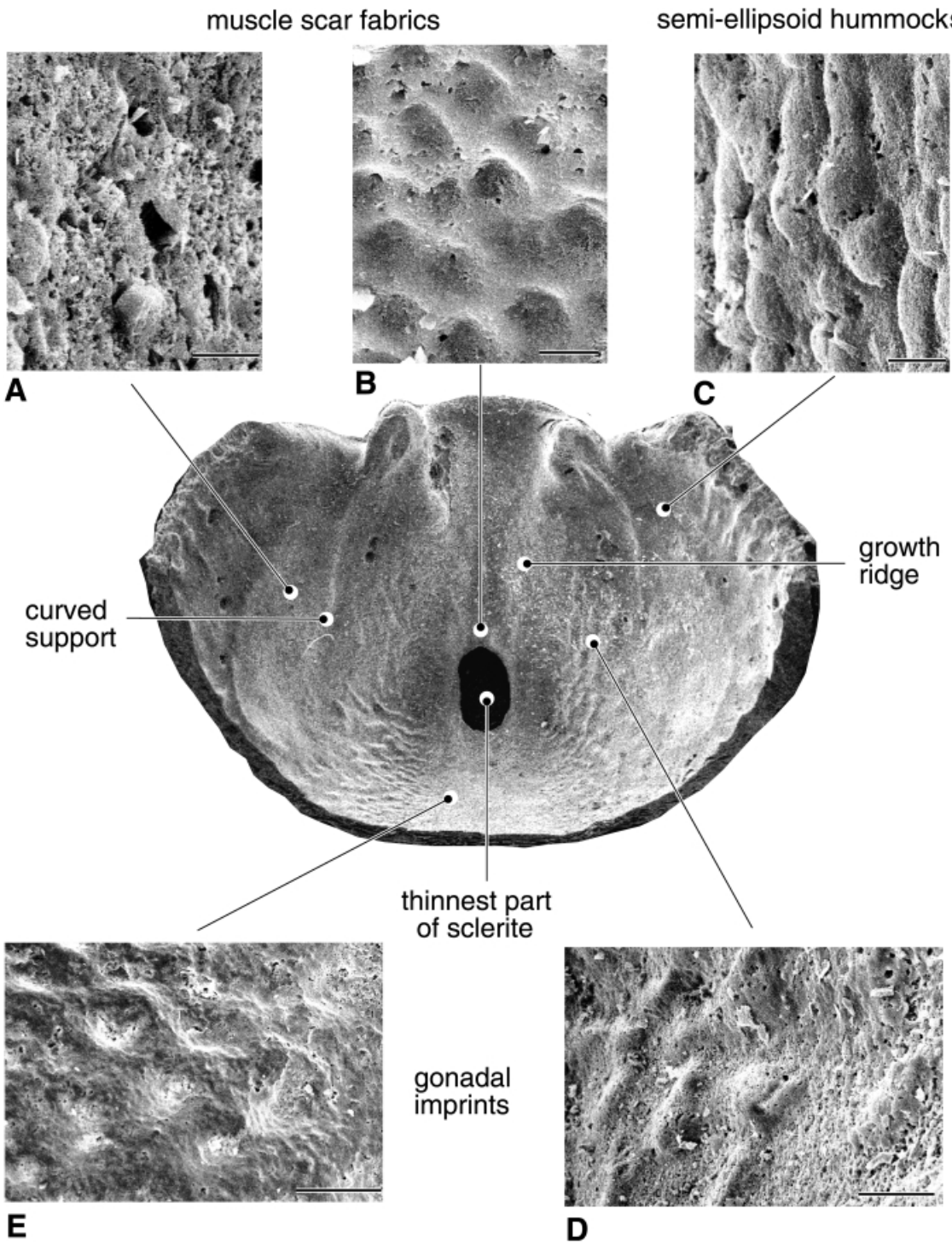
The internal microtopography of the *Micrina* sclerites is usually obscured by recrystallization. In some interiors, however, distinctive markings are preserved and are sufficiently constant in appearance and location to suggest that they are the casts of soft tissues.

Mitral sclerites. The internal morphology (Text-fig. 5) of the mitral sclerite is dominated by the growth ridges of the apophyses beneath the deltoid and their subparallel curved supports (*c*. 100 μm thick), on the floor of the sclerite, which extend from the apical region about halfway submedially towards the abdeltoid margin. A low septum also extends medially from the apical region along the abdeltoidal floor.

In immature sclerites (*c*. 2 mm wide) two kinds of microtopographic markings may be preserved. Most of the floor may be evenly indented by semi-ellipsoidal imprints, *c*. 14 μm long, arranged rhomboidally (Pl. 6, fig. 3). The imprints usually indent several underlying laminae in vertical sequences. The zone just within the abdeltoidal margin may also be crenulated by radially arranged, sporadically paired ridges, *c*. 50 μm thick (Pl. 6, fig. 4). The relationship between these ridges and the margin is not clear. The ridges best develop in mature sclerites where they terminate short of thickened margins with several arrays of canals, with which they have no direct connection. In some mature sclerites, 6 μm or more wide, semi-ellipsoidal imprints or hummocks (Text-fig. 5) are restricted to the medial zone (including the medial septum and the submedial sides of the apophyses) and an intra-marginal zone (including the radial ridges). Lateral to the apophyses and their supports, there occur a pair of crescentic, raised bands, about 1 mm wide and up to about 4 mm long (Text-fig. 5). Their boundaries are sharp and their surfaces, with a lineation parallel to their long axes, degraded with many pits and slots and relict semi-ellipsoidal mounds, up to 20 μm long (Text-fig. 5; Pl. 6, fig. 5).

The most conspicuous change affects the two areas between the apophyses supports and the medial imprint zone. The surfaces of these areas, which are degraded and densely pitted, are raised into sinuous

TEXT-FIG. 5. View of the apical region of a mitral sclerite of *Micrina* (GLAHM114738) showing: imprints made by mantle epithelium (C); degraded surfaces of muscle scars (A–B) and attachment areas of gonadal lamellae (D–E): scale bars represent 25 μm (A), 10 μm (B–C) and 200 μm (D–E).


muscle scar fabrics
semi-ellipsoid hummocks
A
B
C
growth ridge
curved support
thinnest part of sclerite
gonadal imprints
E
D

ridges up to 600 μm long and 60 μm wide, roughly concentric with the supports (Text-fig. 5). In the submedial, marginal lobes of these areas, the ridges give way to hummocks, *c*. 150 μm in diameter, with fine radiating ridges (Text-fig. 5).

It is also noteworthy that the transversely semi-ellipsoidal imprints, situated in the mid-part of the medial septum are asymmetric in profile (Text-fig. 5) with back walls facing the abdeltoid margin and their floors roughened by the exposed edges of platy laminae (Pl. 6, fig. 6).

Sellate sclerites. The main features of the interior of a sellate sclerite are a pair of slightly divergent, rounded depressions extending marginally from the duplicature edge for about 1 mm, on either side of a broad medial elevation. The recrystallized internal surface is smooth except within the depressions (Pl. 6, fig. 7) where it is usually broken by irregularly distributed, subcircular indentations up to 300 μm in diameter. The indentations cut deeply into the shell and frequently expose platy laminae as successions of steps with fretted edges (Pl. 6, fig. 8).

INTERPRETATION

The prime assumption governing the following deductions on the secretion, growth and functions of *Micrina* sclerites arises from their composition and structure. The apatitic laminar shell of *Micrina* is virtually indistinguishable from the organophosphatic stratiform shell of linguliform brachiopods. The latter has been comprehensively studied in the living as well as the fossil state (Iwata 1981; Watabe and Pan 1984; Holmer 1989; Williams *et al*. 1994; Cusack *et al*. 1999). In particular, the way the shells of living lingulides are secreted is well known, as are the effects of recrystallization and degradation on the original skeletal fabric of their early Palaeozoic ancestors. The differentiation and diagenesis of the lingulide integument have, therefore, been used as standards in interpreting the assembled data.

This interpretation is set out in four sections, broadly based on those used in in the previous section. The ornamentation of *Micrina* is really a record of the dynamics of scleritic growth, and is best assessed along with shell structure. The canal system merits separate consideration because it was secreted differently from the shell, while the shape and internal markings of the sclerites reflect the distribution of soft parts. These separate deductions are integrated in a fourth section that also attempts to explain the relationship between the mitral and sellate sclerites.

Ornamentation and shell structure

Micrina sclerites are ornamented by three orders of folds (two eccentric, one oblique), deep eccentric furrows, sharp-edged lamellae and nickpoints. These are similar to strain figures developed in rheomorphic bodies under anisotropic stress. The rheomorphic primary layer would have been secreted by

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EXPLANATION OF PLATE 6

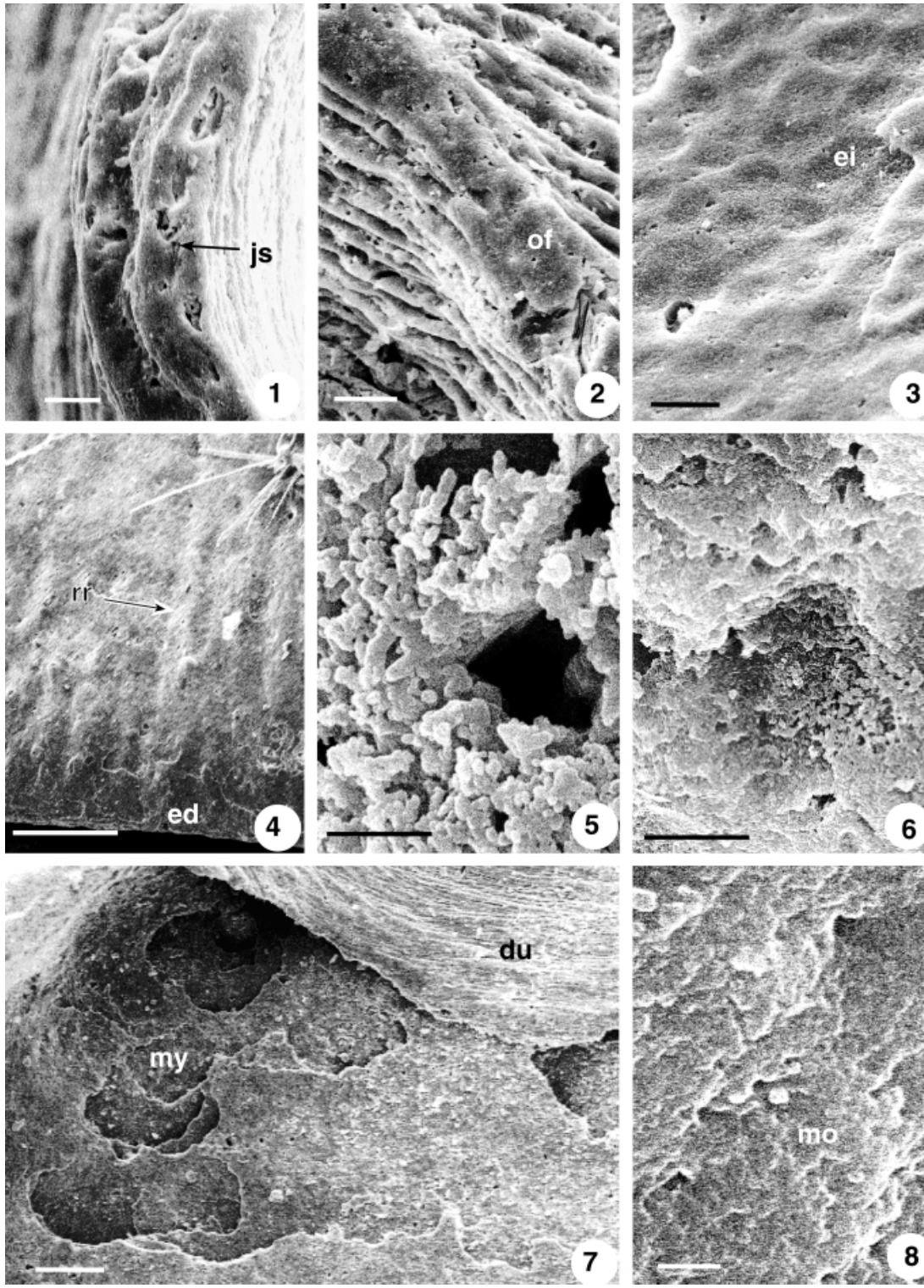
Scanning electron micrographs of gold-coated surfaces of mitral (figs 3–6) and sellate sclerites of *Micrina etheridgei*: 1, GLAHM 114756; 2, 7–8, GLAHM 11457; 3, GLAHM 114742; 4, GLAHM 114758; 5–6, GLAHM 114738.

Figs 1–2. The juvenile shell (js) of the sellate sclerite and details of a ridge bounding the duplicature showing that it is a fold (of) of oblique, anastomosing folds ornamenting the duplicature and the abduplicatural surface; scale bars represent 20 μm.

Figs 3–4. Semi-ellipsoidal imprints (ei) and radially disposed ridges (rr) impressed submedially and marginally (ed) of the interior of mitral sclerites; scale bars represent 20 and 50 μm, respectively.

Figs 5–6. Details of a crescentic and the medial muscle scars of a mature mitral sclerite showing the extent of presumed degradation of muscle insertions: scale bars represent 1 and 5 μm, respectively.

Figs 7–8. General view and detail (apatitic monolayers: mo) of an inferred muscle scar (my) on the internal surface marginal of the duplicature (du) of a sellate sclerite: scale bars represent 200 and 0·5 μm, respectively.



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mantle on an outer organic substrate (compare the chitinous periostracum of lingulides). It would have owed its plasticity to a gel [compare glycosaminoglycans (GAGs) in the lingulide primary layer] with apatitic granules which, during polymerization, aggregated into stratified laminae. The mantle, secreting the primary layer, would have grown outwards eccentrically from the first-formed sclerite shells (secreted by juvenile epithelial collectives as in lingulide discinids). The mantle would have been capable of excessive wrinkling and of abrupt retractions as indicated by the frequent development of lamellae. Such evidence of mobility confirms that the mantles of both sclerites had circumferential flaps (compare the outer mantle lobe of lingulides).

The shell structure of *Micrina* is comparable with that of lingulate brachiopods but with differences in constituent form and skeletal fabric. The pinacoidal form of the basic apatitic constituent is likely to reflect its original state despite recrystallization (as in living *Discinisca*; Williams *et. al*. 1998, fig. 7) because the constituent of linguloid (obolid) valves, from the same fossil assemblage, is granular as in living species. Such pinacoids would have aggregated into platy monolayers interleaved with proteinaceous and especially chitinous substrates to form stratified laminae as in living *Discina* (Williams *et al*. 1992, figs 21–23).

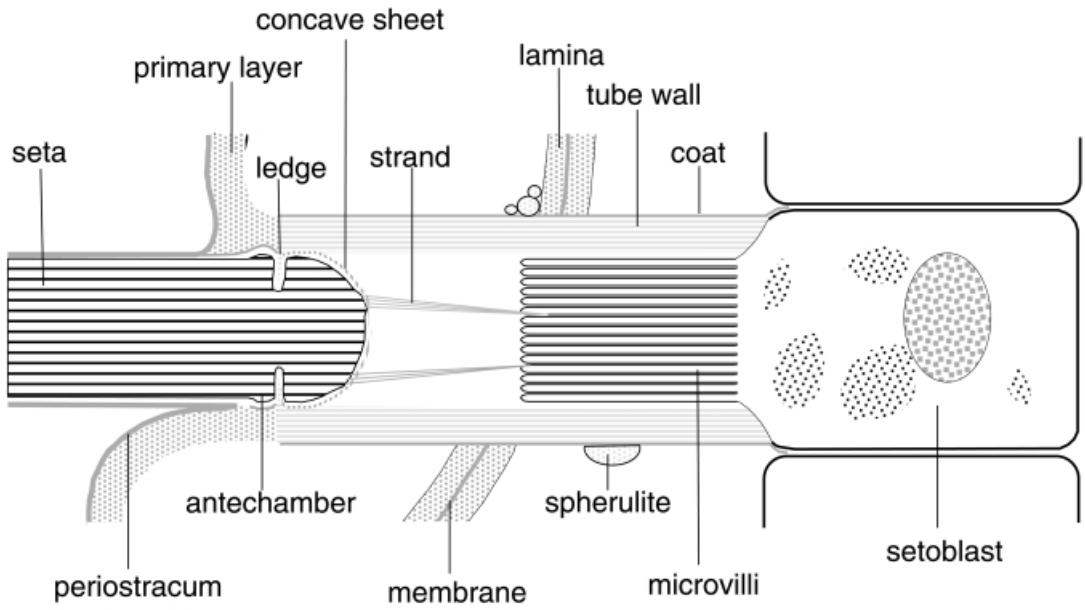
These stratified successions were also segregated by breaks into rhythmic laminar sequences as seen in apophyses. The sequence would have begun with the nucleation of tabular and pinacoidal mosaics on a chitino-proteinaceous substrate with GAGs (represented by breaks in laminar successions) and terminated by a layer of apatite-bearing semi-ellipsoidal casts of the secreting epithelium. The prevalent rhythmic grouping within scleritic successions, however, is the spherulitic laminar set. Their framework is virtually the same as the columnar and camerate sets of acrotretides (Holmer 1989; Williams and Holmer 1992) and the baculate sets of discinoids and linguloids (Williams *et al*. 1998; Cusack *et al*. 1999). It has, therefore, been assumed that secretion of the sclerite shell was the same as that giving rise to lingulide sets.

The secretion of the spherulitic laminar set is likely to have involved a spatially differentiated epithelium. The epithelium in the apical region would have secreted an organic substrate followed by a lamina divided midway into two stratified sequences by a momentary excessive exudation of GAGs. This succession would have constituted that part of a set, which was about to separate outwardly from the internal lamina. Inwardly, beneath the apex, the set could have attenuated to little more than substrates and organic infill.

The epithelium at the abdeltoid margin would have been capable of periodic rapid secretion, especially of GAGs. Here the laminar lobate end of the set could have been thickened fourfold by a sustained exudation of GAGs with varying concentrations of apatitic constituents (as in living discinids; Williams *et al*. 1998, fig. 14). This deposit of GAGs with dispersed apatite would have been in phase with the mid-way interruption within the laminar set in the apical region. Subsequent degradation of GAGs would have created a chamber within the arch of the laminar lobe and would have led to the precipitation of their apatitic contents. Where concentrations had been high, apatite would have formed a meshwork, later recrystallizing into a solid infill. Mostly, however, unevenly dispersed apatitic constituents would have aggregated as spherulites, fascicles and prisms adhering to the inner surface of the laminar wall and the organic coats of permeating tubes.

The retroversion of the lobes of laminar sets in the marginal regions of mature sclerites indicates that they were increasingly constrained from forward expansion relative to those parts of the sets composing the internal lamina. The constraint could have been imposed by a body extraneous to, but intimately associated with, the sclerites.

In general, composites of laminar sets are arranged like a stack of increasingly larger, eccentric bowls with thick rims. Their centres lie just abdeltoid of the juvenile shell and even cumulatively are so thin that the site is frequently a subcircular hole. This disposition is virtually the same as that of columnar and baculate laminar sets in lingulate brachiopods (compare Text-fig. 3 herein with text-fig. 5 of Cusack *et al*. 1999). The main differences are textural. In *Micrina*, laminae are platy (not granular) and the apatitic aggregates in the chamber are spherulitic (not spherular). Such differences suggest that the calcifying proteins responsible for the mineralization of the *Micrina* sclerites were not the same as those controlling the development of the lingulate shell.



TEXT-FIG. 6. Graphical reconstruction of the proximal part of a seta and its associated setoblast that are assumed to have occupied the funnel-like opening leading into an apatitic tube penetrating the stratiform shell of a *Micrina* sclerite.

Canals

The small canals, perforating laminae orthogonally, may not be a regular feature of sclerites. They are nonetheless noteworthy because they would have been formed by persistent organic strands secreted by the mantle in much the same way as the canal system of the lingulide shell (Williams *et al*. 1998, fig. 12).

The components of the large, well-ordered canals pervading both sclerites are likely to have been casts of a setigerous tissue (Text-fig. 6). The structures and impressions associated with funnels are consistent with their having contained rods, at least 250 μm long and subcircular to oval in cross section, that were disposed at high angles in the medial regions but tangentially towards the margins of mature sclerites. The cuticle of such a rod could have been continuous with the periostracum covering the sclerite along the jagged inner edge of the funnel. The base of the rod would have consisted of a disk, occupying the antechamber, connected below the inner ledge with a hemisphere with three bosses that fitted into oval depressions or perforations in the outwardly concave plate which could have been little more than a phosphatized membrane. (It is noteworthy that funnels, canals and tubes of *Micrina* had been identified in *Tannuolina* by Fonin and Smirnova 1967, but as unconnected features: pseudopores, pore canals and columnellas, respectively.)

The tubes carrying the canals were secreted independently of laminar sets, which are breached and bent by them without signs of *in vivo* intergrowth. The apatitic walls of each tube would have been deposited within a cylindroid organic coat that determined the diameter of the tube *ab initio*. The grooves striating the inner surface of the wall, which also characterize the tubes of *Tannuolina* (Conway Morris and Chen 1990, p. 178), are consistent in size and disposition with their being the casts of microvilli. This ensemble of inferred setae occupying funnels and postulated microvillous cells secreting the walls of their internal canals suggests that the cells were setoblasts (Schroeder 1984). That being so, the setae and their bases would have been chitinous and presumably mobile, possibly with fibrillar strands connecting the setal bosses to setoblasts which, however, would usually have been sealed off from the mantle during later sclerite growth.

Internal markings

Internal markings are assumed to have been made by soft tissues, notably the mantle and those that are dependent on skeletal systems for leverage and support. Support imprints are common on the interiors of fossil brachiopods (e.g. the Cambrian lingulide *Oepikites*; Holmer and Popov 2000, p. 50) and their interpretation can be confirmed in living species.

The well-ordered, semi-ellipsoidal imprints that can occur on almost any part of a sclerite interior would have been made by mantle epithelium. Their occurrence on the internal surfaces of successive laminae would have been impressed during periodic pauses in apatitic secretion. Peripheral radial ridges could indicate the presence of a canal 'system' within a mantle that consisted of a folded epithelium containing connective tissue; but the system would not have had connection with setoblasts as in living brachiopods.

The pair of crescentic bands with degraded surfaces in the interior of mitral sclerites simulate the *vascula lateralia* of the brachiopod mantle. Their sharp boundaries without impressions of distributaries into contiguous regions of the mantle, preclude such an interpretation. They are more likely to have been the sites of muscle bases with deeply inserted tendons. A muscle base was also probably implanted, albeit more superficially, on the semi-ellipsoidal imprints in the mid-part of the medial septum.

The pair of medio-lateral areas with densely pitted surfaces and raised ridges and hummocks could have been the sites of gonads with their lamellae attached to the raised features. Too few specimens were available to determine whether the apparent segregation of ridges and hummocks was persistent enough to have had hermaphroditic implications.

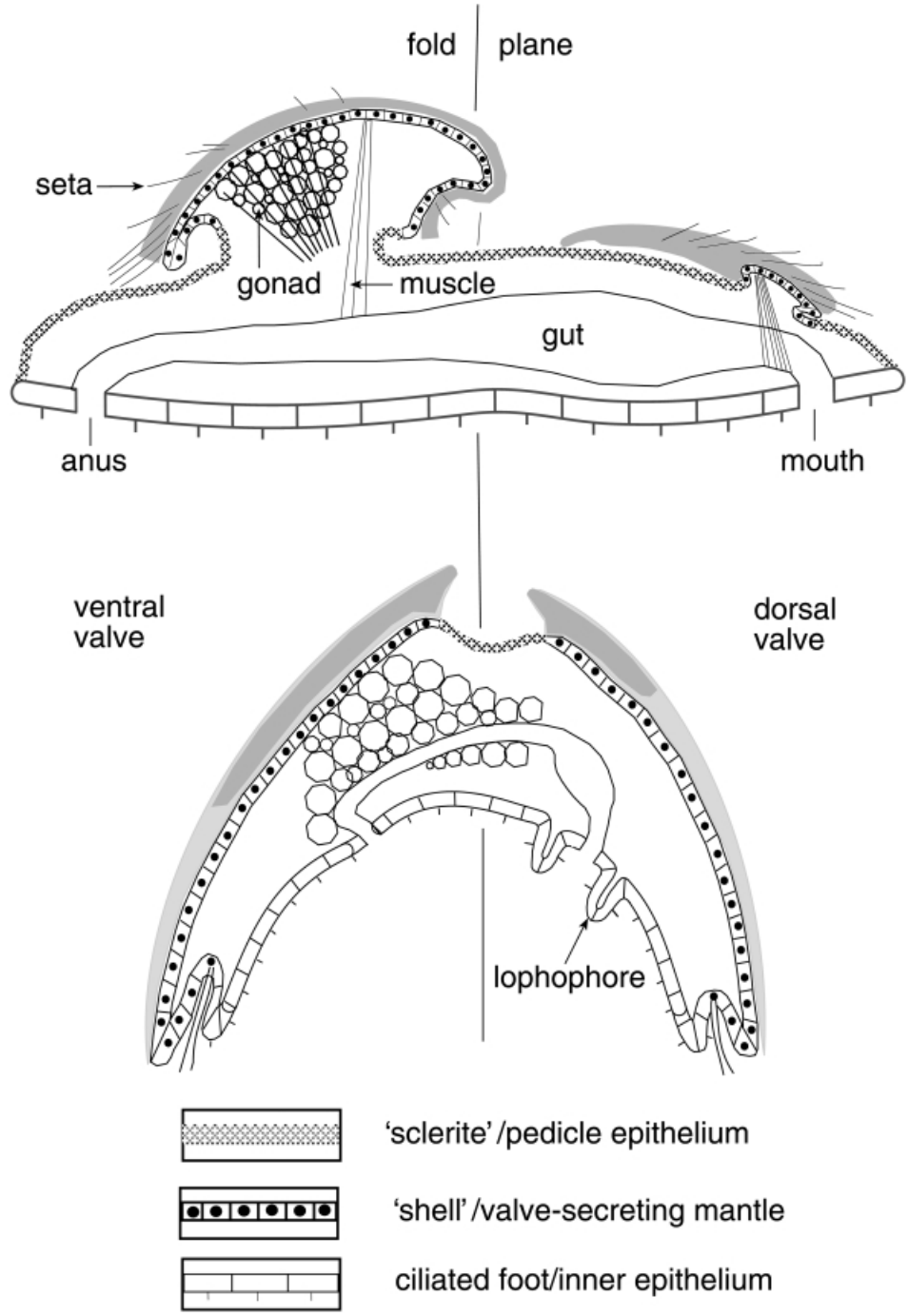
The tendency of the divergent depressions in sellate sclerites to be frayed by indentations suggests that they could have been the sites of paired muscle bases.

Sclerite shape and relationship

Micrina sclerites, especially the mitral component, are very close in morphology and structure to the brachiopod shell. Such features include: the structure of the shell and its secretion by a mantle fold; the mixoperipheral growth of the planospiral mitral sclerite with its deltoid and apophyses simulating the pseudodeltidium and teeth of strophomenate brachiopods; and the internal markings of the mitral sclerite, arranged like a pair of elongate diductor scars, a composite medial adductor scar and a pair of 'saccate' gonadal imprints, as in a typical early rhynchonelliform ventral valve (although the sites of gonadal attachments lie between, not lateral of, the crescentic muscle scars). This assemblage of features, however, does not occur naturally in any one group of brachiopods, as they are typical of different classes within the phylum. Indeed, there are two features that refute any close relationship with the Brachiopoda.

First, the canal system, herein interpreted as the casts of setal tissue, perforates the post-juvenile shells of both *Micrina* sclerites. Its presumed homologue in brachiopods is a band of setae with follicles (not apatitic tubes) that has always been restricted to a groove between the outer and inner lobes at the edge of the mantle lining each valve, and seems never to have been incorporated into the shell, not even of the earliest Cambrian species

Secondly, the mitral and sellate sclerites are not complementary bivalves, only parts of the same scleritome, secreted independently of each other even in the earliest stages of growth. However, their *in vivo* deformation (including retroversion of laminar sets) and their bilateral symmetry, indicate that they bore the same relationship to the body axis of the scleritome but in different sites and, presumably, with different functions (Text-fig. 7). The mitral sclerite could have straddled the dorsal side of an animal and acted as a mineralized container of the gonads, resting with outspread setae on the animal's dorsal surface and attached to the interior by medial and paired lateral muscles. The deltoid would then also have rested on the dorsal surface with the apophyses, ensheathed in secreting epithelium, intruding into the soft parts. The apophyses bear no signs of *in vivo* abrasion and differential resorption that characterize articulating teeth of brachiopods. More likely functions could have been: support of those parts of the mesentery that were connected with gonadal lamellae, and stabilizing the sclerite during muscle contraction. The precise function of the muscles inserted into the mitral sclerite is unknown. The medial muscle could have supported the gonads. The symmetrically placed crescentic pair, however, could have been strong enough to effect the opening and closing of the sclerite relative to the body.



TEXT-FIG. 7. Graphical representation of the evolution of an ancestral brachiopod from a 'halkieriid' *Micrina* by, among other transformations, the folding of the body about a transverse mid-plane and epithelial differentiation. The more lightly shaded brachiopod valves show the assumed acceleration of mixoperipheral growth that would have brought together the valve margins to create a food-gathering mantle cavity and a tentacular lophophore out of the ventral, ciliated 'foot' of *Micrina*.

As for the plate-like sellate sclerite, only a small area marginal of the duplicature would have been in contact with soft tissue. The two depressions in that area, however, could be the scars of a pair of muscles that had supported such an organ as a feeding apparatus.

AFFINITIES

It is taxonomically hazardous to attempt establish the affinities of *Micrina*. The sclerites, on which the genus is based, may have been just two pieces of a complex scleritome. That is not the prevailing view although it has been suggested that sellate sclerites could have formed an imbricate row (Qian and Bengtson 1989, p. 88). Yet the possibility remains because *Micrina* sclerites are part of a vast, early Cambrian assemblage which has yet to be classified satisfactorily let alone grouped into feasible skeletal systems, like those suggested by Evans and Rowell (1990) for *Dailyatia*. Thus, the Tannuolinidae, consisting of *Micrina* and *Tannuolina*, was grouped with three other families under the informal designation 'tommotiids' by Bengtson *et al*. (1990); but two of these families were not so assigned by Laurie (1984) and no suprageneric rankings were used by Qian and Bengtson (1989, p. 74) in their study of 'tommotiids' from South China. Indeed, the following comments on the affinities of *Micrina* may not be apposite even for *Tannuolina* as presently understood.

The fine structure of the *Tannuolina* scleritome (Conway Morris and Chen 1990) including setigerous tubes, is the same as that of *Micrina*. Moreover, sellate and mitral sclerites are also the only constituents recognized as composing the *Tannuolina* scleritome (Fonin and Smirnova 1967). Yet mitral sclerites occur as dextral and sinistral forms (Fonin and Smirnova 1967; Qian and Bengtson 1989; Conway Morris and Chen 1990); and, although the sellate sclerites are bilaterally symmetrical, Qian and Bengtson (1989, fig. 55) show a composite of two sclerites that had grown together in alignment suggestive of imbrication. The larger sclerite is about three times as big as the smaller, an allometric relationship that is more likely to be an abnormality than a fusion of two consecutive sclerites in an imbricate set. We concede, however, that such an interpretation does not preclude an *in vivo* imbrication of sellate sclerites.

In respect of the bilateral symmetry of both sellate and mitral sclerites, the scleritome of *Micrina*, therefore, may reflect a significantly different body plan from that of *Tannuolina*. Yet the prospect that the mitral sclerites of *Micrina* may have been gonadal receptacles (see below) prompts the idea that the dextral and sinistral mitral sclerites of *Tannuolina* may express sexual dimorphism. The validity of this interpretation can be tested by the nature of the first-formed shells of both mitral sclerites of *Tannuolina*. They should be like that of *Micrina* (Pl. 5, figs 2–3) with features suggesting a planktonic juvenile with a fringe of setae. Either way *Micrina* arose from a remarkably variable stock.

Our conclusion is that *Micrina* is a halkieriid with the sellate and mitral sclerites homologous with the anterior and posterior shell of *Halkieria* as described by Conway Morris and Peel (1995). The sclerites and shells are similar in shape, bilateral symmetry and rheomorphically deformed exteriors. The shells of *Halkieria* also appear to bear traces of short, dart-like, radiating to oblique ridges less than 50 μm thick, in mid-regions of anterior (*op. cit*., their fig. 16d) and posterior (*op. cit*., their fig. 27j) 'shells' that could be casts of the setae envisaged as covering *Micrina* sclerites. Furthermore, the anterior shell is described (*op. cit*. p. 313) as having an overhanging posterior margin, which could be a duplicature. The posterior shell may be less convex than the mitral sclerite but it has been noted (*op. cit.* p. 314) as having its anterior edge raised in a 'low arch' which could be a deltoid. The increasing retroversion of laminar sets during maturation of both sclerites of *Micrina* may also support the homology as it could have resulted from resistance of the dorsal surface to the marginal expansion of the attached sclerities (shells). On morphological grounds, therefore, *Micrina* (and possibly *Tannuolina*) seems to be better placed within the Halkierida *sensu* Conway Morris and Peel (1995, p. 310).

One feature appears to cast doubt on this postulated homology. The shells of the Greenland *Halkieria* are inferred to have originally been 'calcareous' (*op cit*. p. 309). It is, however, possible that the *Halkieria* scleritome was at least partly apatitic. The shells of the Greenland *Halkieria* were sufficiently rheomorphic in the living state to have been deformed by drapes and nickpoints (*op. cit*., figs 16d, 39c) that so characterize organophosphatic lingulide shells (Williams and Holmer 1992, pl. 2, fig. 5; pl. 7, fig. 5). Deformation of this complexity is indicative of a high organic content (GAGs). It has not been seen on the

surfaces of calcareous brachiopod shells, including those of living laminar-shelled craniids, nor on living serpulid tubes composed of mucin-cemented calcitic laths (unpublished studies; see also Weedon 1994). Accordingly, readily degradable organophosphatic shells as part of the *Halkieria* scleritome cannot be ruled out. Indeed, living halkieriid scleritomes could have been composed of more than one biomineral in line with brachiopod skeletal systems. Apart from the basic distinction throughout the geological record between mature calcitic and apatitic brachiopod shells, there is implicit (Williams in press) and explicit (Williams *et al*. 2001) evidence that early Palaeozoic organophosphatic lingulates had apatitic, calcitic and even siliceous juvenile shells (mosaics). Similarly differentiated skeletal secretion in halkieriids could have given rise to calci-apatitic as well as calcareous or phosphatic scleritomes. In such differentiated secretory regimes the scleritome of *Halkieria* could have been calcareous except for its anterior and posterior shells that deformed like organophosphatic brachiopod valves. *Micrina* could even have been a halkieriid with organophosphatic anterior and posterior shells but with the rest of the body covered with discrete setae instead of other biomineralized or polymeric sclerites.

If the homology proposed herein is valid, views on the body plan and the phylogenetic status of halkieriids may have to be revised. The various functions attributed to the halkieriid shells have been comprehensively assessed by Conway Morris and Peel (*op. cit*. p. 324). There is concurrence in assuming that the anterior shell (sellate sclerite) served as a base for the attachment of muscles. We believe that the paired muscles inserted thereon, supported the mouth and feeding apparatus of the animal. The internal markings of the posterior shell (mitral sclerite) indicate that it served as a gonadal receptacle. Evidence that the posterior shell was capable of swivelling (Conway Morris and Peel 1995, fig. 43) is consistent with the muscle sets identified as having been attached to the three scars within the mitral sclerite. The muscles would have regulated the position of the shell relative to the dorsal surface, especially by opening a gap at the abdeltoid margin. The apophyses would not have impeded such mobility. In any event, they were not essential to the functioning of the sclerite as they were not developed in *Tannuolina* (Conway Morris and Chen 1990, p. 182).

This assumption that the shells of *Halkieria* are homologous with the sclerites of *Micrina* calls for a review of the phylogenetic relationship between brachiopods and halkieriids. Conway Morris and Peel (*op. cit*. pp. 343–344) postulated a foreshadowing of the bivalved condition of the brachiopod by the transverse folding of a halkieriid that would have brought the shells together. Such a folding would accord with Nielsen's deductions (1991, p. 25) on the disposition of the gut in the ancestral brachiopod. Conway Morris and Peel also perceptively noted: 'Presumably, the halkieriids were equipped [with] a mantle, at least one mantle lobe and a shell material capped with an organic periostracum.' (*op. cit*. p. 349). As previously shown, a lobed mantle (of *Micrina*) did, indeed, secrete stratiform shell that was structurally indistinguishable from that of early linguliforms. Taking account also of the setigerous state of sclerites and the location of gonads, we suggest that the following transformations resulted in the emergence of a brachiopod stock from a halkieriid ancestor (Text-fig. 7):

1. Reduction of the skeletonized coat to only the anterior and posterior shells.
2. The transverse folding of the body axis in mid-region and the juxtaposing of the apices of the shells with the duplicature and adnate deltoid (homologous with pseudointerareas) separated by a strip of dorsal integument.
3. Accelerated mixoperipheral growth of the shells (apatitic and/or calcareous), especially of the anterior (dorsal) one, well forward of the mouth and developing lophophore, to fit the margin of the posterior (ventral) one thereby creating a food-gathering chamber (mantle cavity).
4. Conversion of the ventral integument, lining the mantle cavity and coating a developing lophophore, into ciliated (inner) epithelium with a reduced proportion of mucin cells.
5. Restriction of setae to a ring of follicular setoblasts between the outer and inner mantle lobes at the junction of the outer (original dorsal integument) and inner (original ventral integument) epithelia.
6. Development of coelomic sinuses (*vascula media)* within the mantles, especially to connect with the mantle lobes and setae (*vascula terminalia*).
7. Regrouping of muscle systems to co-ordinate valve control of the mantle cavity.
8. Expansion of gonadal lamellae into the dorsal coelom.
9. Tubular extension of the vestigial dorsal integument (posterior body wall) between the pseudointerareas to form an attachment organ (pedicle).

These transformations are not necessarily in chronological order, especially those involving modification of the coelom. On the broad scale, the most important transformation was the postulated folding of the halkieriid body axis, an event explored by Cohen *et al.* (in press). There are, however, 'boundaries' separating specialized parts of the integument, which are also noteworthy because they help us to understand the anatomies of extinct groups. They are the boundaries between the dorsal and ventral integuments of the halkieriid ancestor and those delineating the shell mantles within the dorsal integument. All three tissues would have played a crucial role in the evolution of the derived brachiopod. The dorsoventral boundary is marked by a ring of setoblasts that would have been lost from the rest of the dorsal integument. With the shortening of the ancestral body axis, a strip of dorsal integument would have survived between the juxtaposed apices of the anterior and posterior shells. This strip would have been cytologically different from the mantles underlying the shells as well as the ventral integument although it shares boundaries with both. It is the third kind of integument found in brachiopods (Williams 1997, p. 45) that gave rise to the pedicle. According to standard staining techniques, the pedicle epithelia of linguliform (Williams *et al*. 1997, p. 47) and rhynchonelliform (Williams and Hewitt 1977, p. 109) brachiopods secrete chitin, despite basic differences in development. Chitin is presumed to have been a dominant constituent of the halkieriid dorsum; and the pedicle is the only source of this polysaccharide in the rhynchonelliform integument (confirmed by pyrolysis MS; J. Carter, pers. comm. 2002).

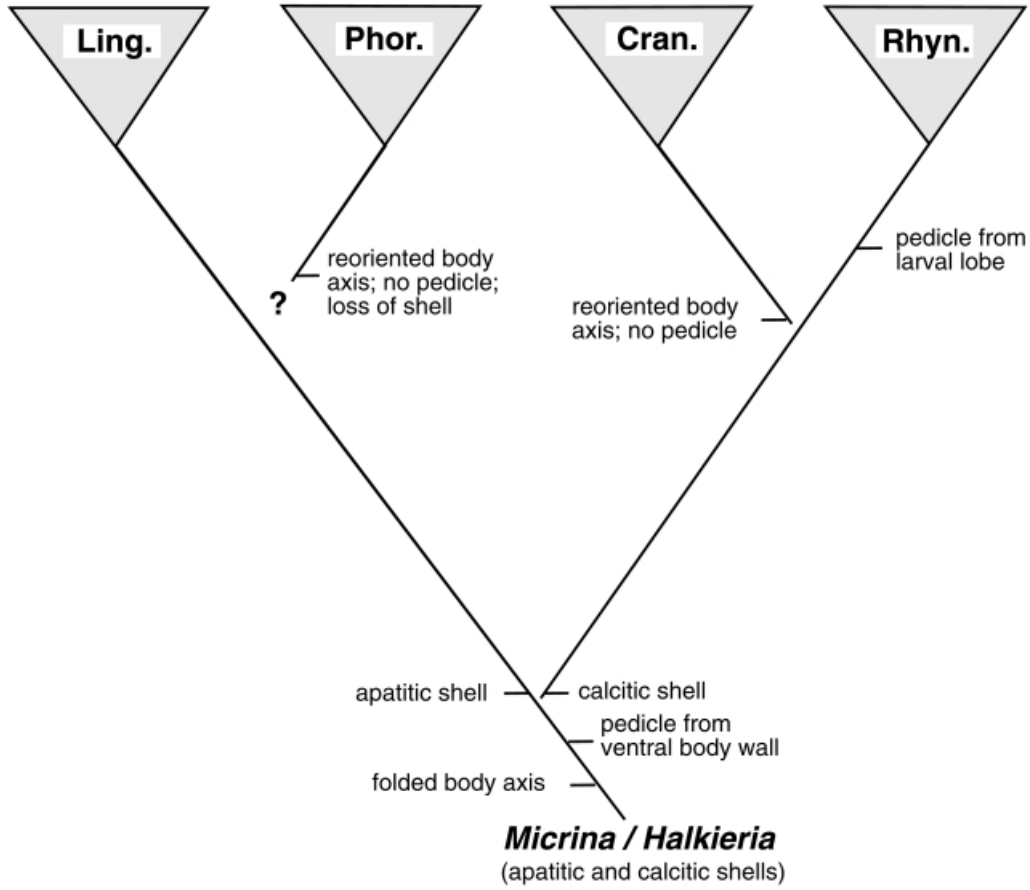
The assumption that halkieriids were the stem group of the Brachiopoda does not help reconcile molecular and cladistic versions of brachiopod phylogeny with the current classification. Three subphyla are presently recognized (Williams *et al*. 1996): laminar organophosphatic-shelled linguliforms attached by a pedicle developing as an extension of the posterior body wall; fibrous organocalcitic-shelled rhynchonelliforms attached by a pedicle developing from a larval lobe; and laminar organocalcitic-shelled craniiforms attached by an adhesive ventral valve in place of a pedicle.

Living species of these three subphyla have differently developed and disposed guts. The linguliform gut is U-shaped with both mouth (originating near the blastopore) and anus opening into the mantle cavity (Freeman 1999, p. 238). The curved rhynchonelliform gut lacks an anus but the mouth, opening into the mantle cavity, also originates near the blastopore (Nielsen 1995, p. 318; Williams *et al*. 1997, p. 163). Morphological evidence (Williams *et al*. 1997, p. 387) suggests that the particular pedicle and gut of living rhynchonelliforms are synapomorphies of all rhynchonellate ordinal taxa originating after the Cambrian. The pedicle of older, extinct rhynchonelliforms, like the protorthides, orthides and pentamerides, which first occur in the Lower Cambrian, must also have been accommodated in the notch (delthyrium) that indented their ventral valves. We assume that their gut was also disposed like that of the crown rhynchonelliforms, but with an anus entering the mantle cavity as in their linguliform sister group.

There are some early rhynchonelliforms (Chileata, Obolellata and Kutorginata), in which the anus may have breached a posterior body wall, as has been inferred for the kutorginate *Nisusia* (Rowell and Caruso, 1985). Such an intestinal disposition would have accorded with that of the craniiform crown group; but this interpretation is not consistent with all morphological evidence. The groups are being further considered, especially in the light of craniiform organization.

The development and organization of living craniiforms are different. No pedicle develops and attachment is effected by epidermal cells migrating ventrally from the dorsal surface to secrete an adhesive ventral valve. The blastopore becomes the site of the future anus on the posterior body wall and the future mouth breaks through anteriorly into the future mantle cavity (Nielsen 1991; Freeman 2000). The absence of possible pedicle openings from the shells of all groups assigned to the Craniiformea, suggests that their body plan has not changed much since the early Cambrian. In effect, the anus could always have breached the posterior body wall and never have opened into the mantle cavity with an attendant U-shaped bend in the gut as in linguliforms.

The difficulties in relating craniiforms to other brachiopod crown groups, had they evolved from a halkieriid stem group, echoes the contradictions posed by molecular, embryological and classical phylogenetic studies. Analyses based on 18S rDNA gene sequences place the craniids firmly with living linguliforms (Cohen 2000). Embryological studies indicate a close relationship with the rhynchonelliforms (Nielsen 1991) while classical interpretations found their affinities so equivocal as to prompt their provisional classification as a separate subphylum (Williams *et al.* 1996). In the proposed



TEXT-FIG. 8. Proposed relationships among the crown groups of the brachiopods Linguliformea (Ling.), Craniiformea (Cran.), Rhynchonelliformea (Rhyn.) and *Phoronis* (Phor.) if they form a monophyly derived from a 'halkieriid' stem group.

halkieriid–brachiopod lineage, the anterior-posterior alignment of the craniiform gut is incompatible with the presumed transverse folding of the body axis in mid-region. Nor can the craniiform body plan, with the anus at virtually the same site as the linguliform pedicle, be interpreted as precursory to folding as inferred in Nielsen's review (1991, p. 25) of brachiopod evolution. Moreover, the evolution of craniiforms directly from a halkieriid ancestor would be inconsistent with the molecular and biological support of brachiopod monophyly. We, therefore, assume that the craniiforms are the most derived brachiopod group. Their laminar shell structure is unique but is, at least, calcitic and, on balance, we conclude that the group diverged from one of the early rhynchonelliform stocks (Text-fig. 8).

The close relationship between phoronids and brachiopods has long been recognized and has continually inspired taxonomic recognition at the intra-phyletic level (Emig 1997). More recently, molecular studies have perpetuated the controversy with some in favour of nesting the phoronids within the brachiopods (Cohen 2000) and others of retaining phoronids as an outgroup (Petersen and Eernlisse 2001). Molecular support for a brachiopod/phoronid monophyly is presently not strong enough to encourage departure from traditional taxonomic practice. Apart from lacking a shell, *Phoronis* has a U-shaped gut, the outer side of which is ventral not dorsal (Nielsen *op. cit.* p. 26). Such an orientation even suggests that *Phoronis* could not have evolved directly from a halkieriid by an orthodox folding of the

body axis. The relationship between phoronids and brachiopods, therefore, remains unresolved; but if they are monophyletic, the presence of sulphated GAGs in the chitinous cuticle of *Phoronis* (Herrmann 1997, p. 215) suggests a link with linguliforms as GAGs are unknown in rhynchonelliform shells (Text-fig. 8).

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