

Calcitic Nacreous Ultrastructures in Bryozoans: Implications for Comparative Biomineralization of Lophophorates and Molluscs

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Abstract. The occurrence of nacreous-type fabrics in bryozoans has broad implications for our understanding of similarities between lophophorate and molluscan biomineralization. Calcitic semi-nacreous ultrastructures in the skeletons of several species of cyclostome bryozoans belonging to the suborders Tubuliporina and Articulata are described. In these taxa semi-nacre is the dominant ultrastructure of the walls, and often succeeds a precursory fabric of tiny wedge-shaped crystallites. The semi-nacre comprises laminar sheets of irregularly stacked, typically six-sided tablets with frequent screw dislocations. Tablets usually have inclined edges and an upper surface with a central depression. The surfaces of etched six-sided tablets have six subtriangular sectors: three soluble sectors alternating with three less-soluble sectors. The less-soluble sectors have outward-sloping edges and sometimes have slightly longer sides than the more soluble sectors, which have inward-sloping edges. Newly seeded crystallites comprise only the three less-soluble sectors separated by a 'trilete' suture. They are not nucleated on a particular sector type. Similar fabrics have previously been recorded in the cyclostome suborder Cancellata. The substructure of the calcitic semi-nacreous tablets of cyclostomes resembles molluscan aragonitic nacre, particularly that of bivalves, but differs in the precise arrangement of the sectors. Morphologically, the bryozoan semi-nacre is at least as similar to bivalve nacre as bivalve nacre is to gastropod and cephalopod nacre. The existence of a distinct substructure in the component tablets of molluscan nacre has been used as evidence that a greater evolutionary potential characterizes molluscan rather than lophophorate (bryozoans and brachiopods) biomineralization. This

claim is contradicted by the recognition of substructured semi-nacre in cyclostome bryozoans.

Introduction

Processes involved in the secretion of mineralized hard parts in the shells and skeletons of invertebrates are poorly understood. This is true even in phyla such as molluscs for which there is a large literature on biomineralization. We are still documenting basic ultrastructural patterns for bryozoans and some other groups. Bryozoans are a diverse biomineralizing phylum. The great majority of the estimated 5,000–10,000 species of living bryozoans (Horowitz and Pachut, 1992) secrete calcareous skeletons. The ability to do so probably evolved at least twice from soft-bodied ancestors (Taylor and Larwood, 1990), first in the Ordovician (c. 500 million years ago) and subsequently in the Jurassic (c. 150 million years ago). The earlier of these events marked the origin of the class Stenolaemata, of which the Cyclostomata are the only extant order; the later event marked the origin of the order Cheilostomata (of the class Gymnolaemata).

Recent research on the skeletal ultrastructure of cyclostome bryozoans has revealed an unanticipated diversity of calcitic fabrics (e.g., Boardman *et al.*, 1992; Taylor and Jones, 1993; Taylor *et al.*, 1995). Earlier studies of cyclostomes largely employed fractured and polished or etched sections and provided only limited information. However, by examining the surfaces of skeletal walls upon which crystallites are directly secreted and grow, the range of fabrics, as well as the pattern of their growth, can be appreciated more fully. The emergence of a new database of bryozoan skeletal ultrastructures enables broader questions of biomineralization to be addressed. In particular, comparisons of the patterns and processes of biomineralization of bryozoans and molluscs can be reassessed.

Models of skeletal growth developed from brachiopods (the other lophophorate phylum with biomineralized skeletons) are commonly applied to bryozoans (*e.g.*, see Williams, 1990a, b). However, the intricate nature of the bryozoan skeleton entails a more complex pattern of skeletal development than the essentially linear, two-dimensional growth of brachiopod shells. A diversity of fabrics distinct from those of brachiopods is beginning to be recognized in bryozoans. The combination of brachiopods and bryozoans within a single unified secretory model and the relative dearth (in comparison with molluscs) of studies of bryozoan ultrastructures have contributed to the theory that lophophorates are incapable of producing the range and diversity of skeletal ultrastructures found in molluscs (Carter, 1979; Carter and Clark, 1985).

Indeed it has been argued that all skeletal ultrastructural types that occur in lophophorates are also present in molluscs, whereas molluscs have evolved a number of ultrastructures that do not occur in lophophorates (Carter, 1979; Carter and Clark, 1985). This phenomenon has been termed the "L-M discontinuity" (*i.e.*, lophophorate-molluscan discontinuity; Carter and Clark, 1985). It has been particularly stressed that, unlike molluscs, lophophorates generally lack the capacity to form organizationally complex ultrastructural units oriented in all three dimensions of the shell layer (Carter, 1979; Carter and Clark, 1985).

One ultrastructure commonly regarded as being unique to molluscs is nacre, or "mother-of-pearl." Nacre is the best known and most thoroughly studied calcareous fabric in mollusc shells (Taylor *et al.*, 1969; Wise, 1970a). True nacre is, by definition, always an aragonitic structure consisting of thin, flat-lying, platey laminae built up from polygonal to rounded tabular crystals. The tablets and laminae are separated from each other by thin layers of organic matrix. Different structural patterns of this organic matrix are found in nacles from the molluscan classes Bivalvia, Gastropoda, and Cephalopoda (*e.g.*, Grégoire *et al.*, 1949, 1950, 1955; Grégoire, 1957, 1959), and the arrangement of the aragonitic tablets also varies considerably between and within these classes (Wise, 1970a, b; Carter, 1990). Columnar nacre, where the tablets are arranged in vertical stacks, is the most common nacreous fabric among gastropods and cephalopods. Sheet nacre, with tablets in vertical sections in a stair-step or brick-wall pattern, is the common fabric of bivalves and monoplacophorans and occurs less commonly in cephalopods and only rarely in gastropods (Wise, 1970a, b; Carter and Clark, 1985). Hybrid structures—row stack nacre—may also occur in some bivalves, as may columnar nacre (Carter and Clark, 1985; Carter, 1990).

Differences can also be found between the molluscan classes in the internal substructure of the nacreous tablets. These are revealed by differential chemical etching of the tablet surfaces (Mutvei, 1977, 1978, 1980, 1983a, b).

Mutvei suggested that rather than being single crystals of aragonite, the tablets are compound structures composed of "crystal individuals" of different orientation, possibly twinned. The arrangement of the crystal individuals is related to the distribution of new seeds and therefore to the structure of the underlying layer of nacre. Aragonitic nacre is apparently restricted to the Mollusca. However, semi-nacre, which may be calcitic or aragonitic, is found in some other taxonomic groups. Semi-nacre is characterized by sheets of horizontal tablets with higher frequencies of screw dislocations and perhaps less structural continuity of the laminae than in nacre *sensu stricto*. The structure has been recorded in the calcitic craniacean brachiopods (Williams, 1970; Williams and Wright, 1970, pl. 6, figs. 3, 4) and in the Carboniferous archaeogastropods *Platyceras* (*Orthonychia*) *spinigerum* and *Cyclonema* (Batten, 1984; Carter and Hall, 1990). Many laminar fabrics described in bryozoans (*e.g.*, Sandberg, 1971, 1977, 1983; Tavener-Smith and Williams, 1972; Ristedt, 1977; Ross, 1977) were reinterpreted as semi-nacre by Carter and Clark (1985), but none have been fully described nor properly compared with molluscan nacles.

New investigations of cyclostome bryozoans have shown that calcitic semi-nacre is widespread, particularly in the fixed-walled suborders Tubuliporina and Articulata. These fabrics are described here for the first time. The organization of cyclostome semi-nacles shows considerable similarity to irregularly stacked aragonitic nacles in some molluscs. Importantly, the tablets are subdivided into sectors or crystal individuals in a very similar way to those of molluscan nacre. The resemblance between the semi-nacre of cyclostome bryozoans and the nacre of molluscs has important implications for the comparative organizational control of skeletal ultrastructures in the two groups. Discovery in bryozoans of more diverse and complex ultrastructures may be indicative of a "greater evolutionary potential" for biomineralization (in the sense of Carter and Clark, 1985) than has been previously acknowledged.

Previous work on bryozoans

Semi-nacreous structures are characterized by growth surfaces with irregularly arranged platey tablets. The tablets are roughly hexagonal, rhombic, or sub-rounded in outline. Screw dislocations are much more frequent than in nacre *sensu stricto*. Using these criteria, Carter and Clark (1985) categorized structures illustrated in various studies of bryozoan ultrastructures as semi-nacreous. These included the cheilostomes *Membranipora* [*Biflustra*] *savartii* (Ristedt, 1977, p. 88; pl. 4, figs. 3, 4, 6; pl. 5, figs. 1–8), *Labioporella calypsonis* (Sandberg, 1977), *Cupuladria biporosa* (Tavener-Smith and Williams, 1972, pl. 13, fig. 45), and *Thalamoporella californica* (Sandberg,

1971, p. 136, pl. 2, fig. 12). In addition, similar fabrics have also been described by Sandberg (1983) in the cheilostomes *Metrarabdotos tenue* (fig. 102, 1, 2), *Tremogasterina robusta* (fig. 102, 3, 4), and *Arachnopusia unicornis* (fig. 102, 5).

Despite Carter and Clark's assignment of the fabrics described in cyclostomes by Ross (1977) to semi-nacre, the first well-supported claim of semi-nacre in cyclostomes was made by Taylor and Jones (1993) for *Hornera robusta* and *H. squamosa* (suborder Cancellata). These free-walled cyclostomes have laminated walls comprising sub-hexagonal tablets, often with characteristic triple spikes located at their centers. The tablets are initially about 0.5 μm in diameter and are best seen near distal wall margins where seeding is concentrated. Small seeds in *H. squamosa* show radial sectoring with three roughly surfaced sectors alternating with three smooth sectors. Only the three rough sectors reach the centers of the tablets where their junction forms a "trilete" structure. Screw dislocations are also common near the distal edges of walls. With increasing maturity the crystallites broaden and may coalesce. A pattern of predominantly proximally imbricated crystallites characterizes older, more proximal walls. Taylor and Jones (1993) suggested that this mature fabric was regularly foliated in the sense of Carter *et al.* (1990).

Other investigations of cyclostome skeletons have failed to reveal unequivocal semi-nacre. In his study of the articulate *Crisia eburnea*, Söderqvist (1968) described an inner fabric of polygonal, tabular crystals, stacked like roofing tiles, and found a similar fabric in the skeletons of *Stomatopora* sp., *Diplosolen intricarius* (Smitt), *Idmonea* [*Idmidronea*] *atlantica* Forbes in Johnston, and *Heteropora pelliculata* Waters. Brood (1976) also described the skeleton of *C. eburnea* as having a laminar secondary (inner) layer, illustrating (figs. 5–6) overlapping, imbricated tablets.

Material and Methods

Eight species of the suborder Tubuliporina were studied for this paper. The following six species were collected from the Marseille region of southern France by J.-G. Harmelin: *Plagioecia patina* (Lamarck) from Rech Lacaze-Duthiers at a depth of 300 m; *P. dorsalis* (Waters) from Morgiou at a depth of 40 m; *Desmeplagioecia amphorae* Harmelin from Moyadon Island at a depth of 27 m; "*Cardioecia*" *watersi* (O'Donoghue and de Watteville) from Jarre Island, cave II, at a depth of 15 m; *Entalophoroecia deflexa* (Couch) from Riou Island at a depth of 30 m; *Platonea stoechas* Harmelin from Canyon Cassidaigne at a depth of 140–170 m. In addition, colonies of *Diplosolen* cf. *obelium* (Johnston) were collected by P. J. Hayward from Emborios Cave on the Greek (Aegean) island of Chios, and *Stomatopora* sp. by PDT from the Otago Shelf (80–100 m), New Zealand.

Four species from the suborder Articulata were also used in the study, three of them collected by J.-G. Harmelin from Riou Island, near Marseille, at a depth of 30 m: *Crisia fistulosa* Heller, *C. sigmoidea* Waters, and *C. oranensis* Waters. Additionally, *Bicrisia* cf. *edwardsiana* MacGillivray was collected by PDT from shoreline drift on the Otago Peninsula, New Zealand.

Colonies were air dried after collection and subsequently soaked in a 20% volume/volume solution of commercial bleach for 48–72 h depending on the thickness of enveloping organic cuticle. The combination of bleaching and periodic ultrasonic cleaning and rinsing in distilled water facilitated the removal of organic material from the calcite skeleton. Air-dried, bleached colonies and broken or sawn parts of colonies were mounted on stubs and sputter-coated with gold-palladium. Stubs were examined with a Hitachi S-800 field emission scanning electron microscope at an accelerating voltage of 8 kV and imaged using secondary electrons. Most detail was derived from observing growth surfaces preserving original crystallite fronts.

Results

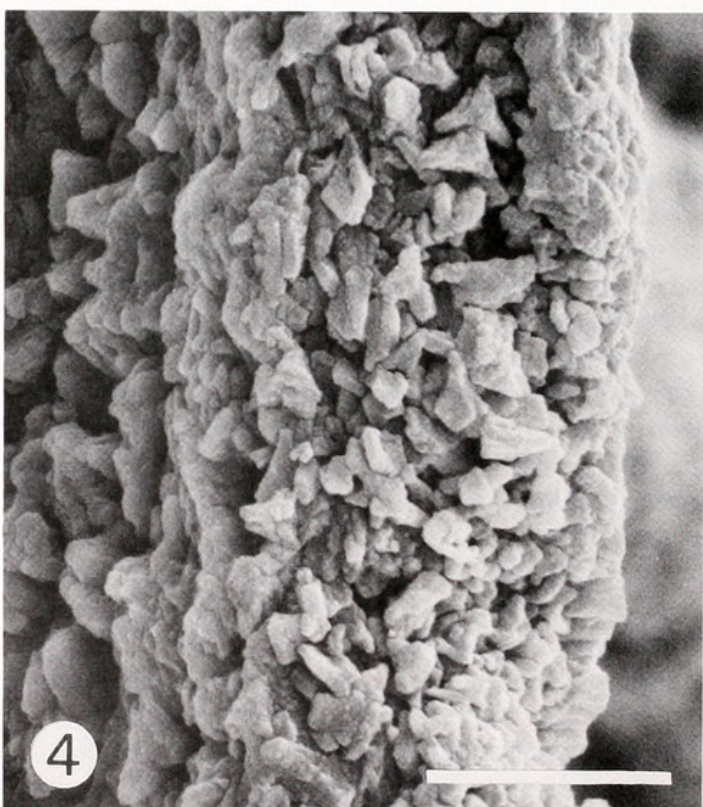
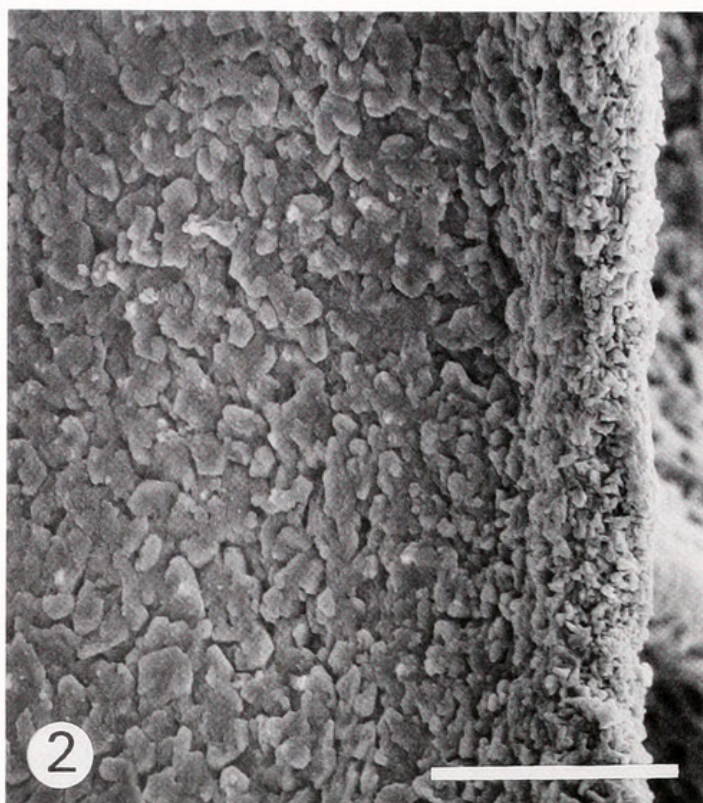
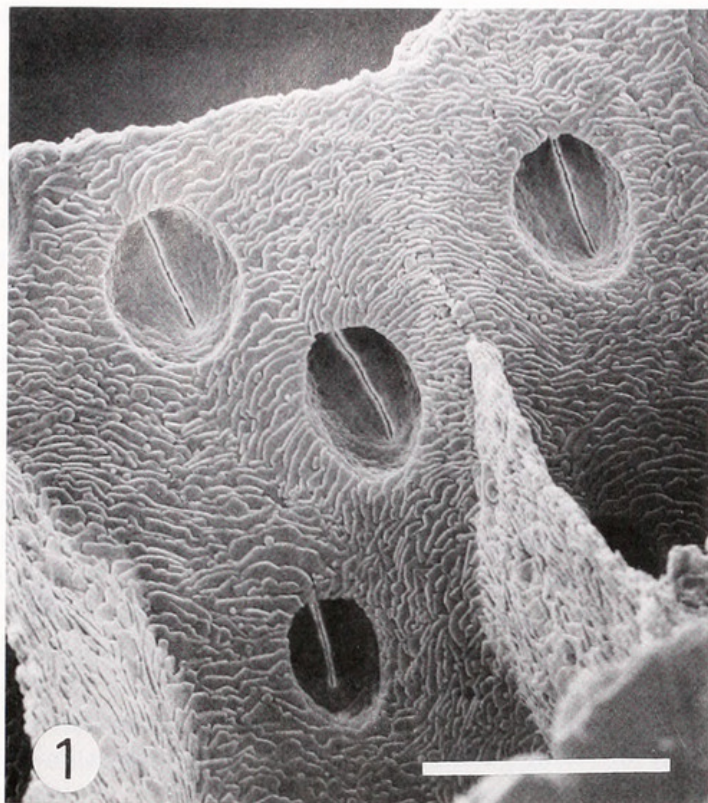
All of the species studied have complex skeletons comprising more than one ultrastructural fabric, but semi-nacre dominates, occurring as the inner fabric of frontal exterior walls (Fig. 1) and peristomes (walls initially secreted directly onto the cuticle). Full details of the ultrastructural compositions of the skeleton in the various species will be given in future papers. This paper focuses on the semi-nacre. However, it is necessary to describe first the precursory fabric of the interior walls laid down prior to the semi-nacre.

Precursory fabric

Interzoooidal walls originate as ridges (septa) on the upper surface of the basal or frontal exterior walls. In the tubuliporines studied, the ridges comprise densely packed, tiny, wedge-shaped crystallites (0.1–0.3 μm in width and up to 0.6 μm in length) with no preferred orientation or alignment (Figs. 2, 4). The wedges are highly variable in size, with the smallest wedges at the distalmost edge of the ridges being secreted on top of progressively larger wedges, suggesting continued growth after initial seeding. Identical crystallites occur along the apertural margins of newly formed zooids, and at the distal edge of the median budding wall in those taxa (*Plagioecia dorsalis* and "*Cardioecia*" *watersi*) where this structure is present. Precursory fabric is absent in newly formed septa of articulates, the leading edges of the walls being formed of semi-nacre.

Semi-nacreous fabric

The bulk of the walls comprise laminar sheets of semi-nacre (Fig. 5). The structure of this semi-nacre is described



Figures 1–4. Scanning electron micrographs of precursory and semi-nacreous fabrics in the articulate *Crisia* cf. *sigmoidea* (Fig. 1) and the tubuliporine *Platonea stoechas*. (Fig. 2–4).

Figure 1. Inside surface of frontal exterior wall with large pseudopores. Note the distally imbricated, “pseudofoliated” semi-nacreous fabric. Tablets curve around and are smoothly continuous between the frontal wall and vertical interior walls. Distal is towards the top. Scale bar = 25 μm .

Figure 2. Distal growing edge of interior wall, showing the precursory fabric of tiny wedge-shaped crystallites, succeeded by a highly irregular semi-nacreous fabric largely comprising more or less anhedral tablets, which increase in size proximally. Distal is to the right. Scale bar = 7.5 μm .

Figure 3. Irregular semi-nacreous fabric. Despite their anhedral outlines, the tablets have internal growth lines delineating euhedral hexagons. Note central depressions in a number of the tablets. Distal is towards the top. Scale bar = 6 μm .

Figure 4. Detail of wedge-shaped crystallites of precursory fabric shown in Figure 2. Scale bar = 2 μm .

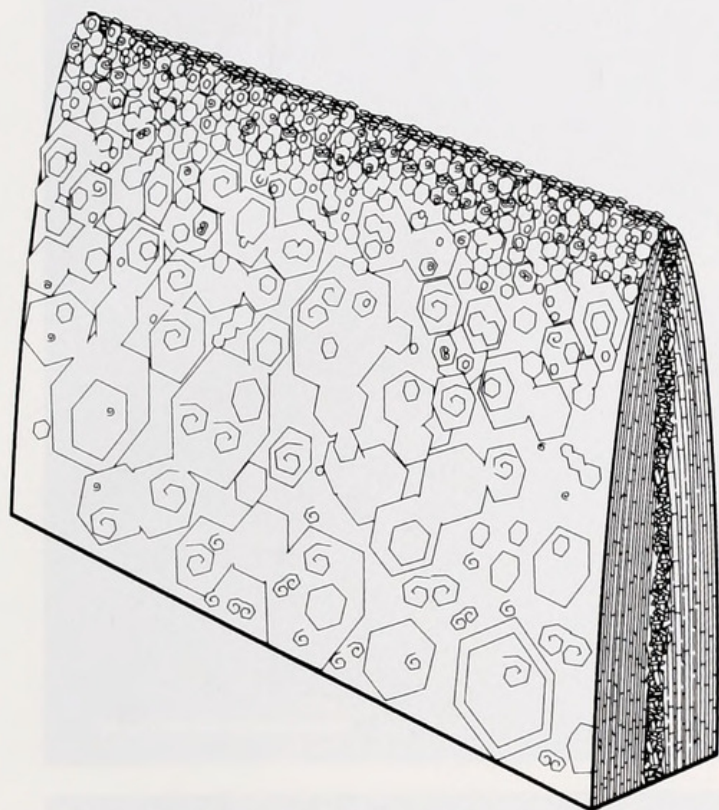


Figure 5. Stylized diagram of the growing edge of an interior wall in a semi-nacre dominated cyclostome. Tiny wedge-shaped crystallites lacking a preferred orientation are seeded at the distalmost edge of the wall. Further seeding of flat hexagonal tablets follows and continues throughout the growth of the wall. Tablets grow by accretion on all sides. Screw dislocations are common and are the dominant mechanism for wall thickening in the older parts of the skeleton.

along a transect running proximally from the distalmost edge of the growing wall.

Immediately proximal to the wedge-shaped crystallites, and overlying them, is a transitional zone of tiny crystallites (up to $2\ \mu\text{m}$ diameter). These flat-lying crystallites are about $0.2\ \mu\text{m}$ thick, have no preferred growth direction, and appear to be randomly distributed (Fig. 2). The boundaries between crystallites are not well-defined: there is considerable overlap or lateral fusion with neighboring crystallites on all sides.

Tablets become better defined further proximally, where they are generally six- or four-sided. On some wall surfaces the tablets are euhedral (Fig. 6, 8): edges are straight and have angular intersections with adjacent edges. On other wall surfaces, however, tablets are anhedral and have subcircular outlines (Fig. 7). The angles between the edges of euhedral hexagonal tablets consistently approximate 120° . In *Platonea stoechas* the mean value was 121.3° (SD = 7.57° ; range = $108\text{--}137^\circ$; $n = 56$). Tablet surfaces often have very fine, concentric growth lines, showing that radial growth rates were equal in all directions (Fig. 3). Surfaces may also have fine striations perpendicular to these growth lines (Fig. 9). Tablets usually

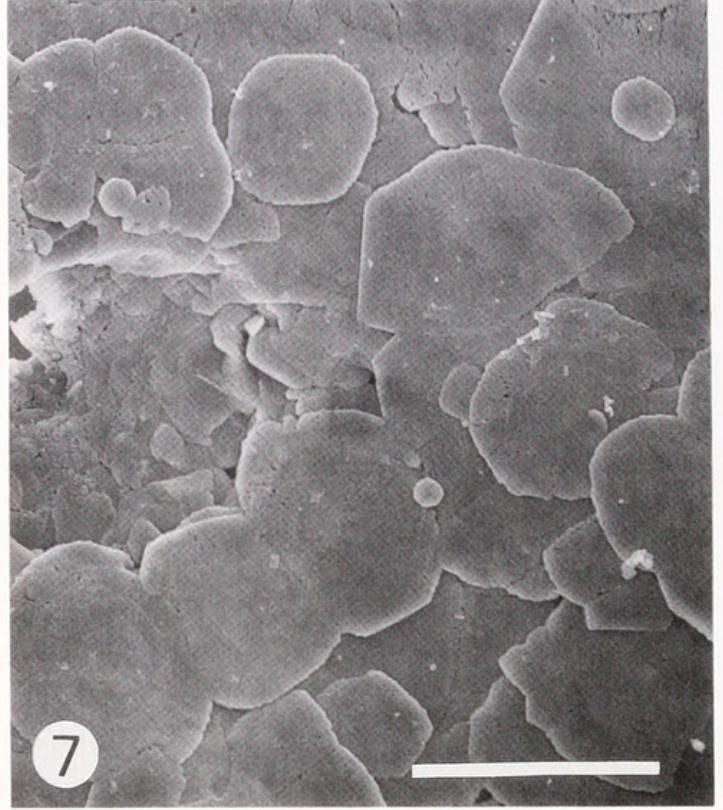
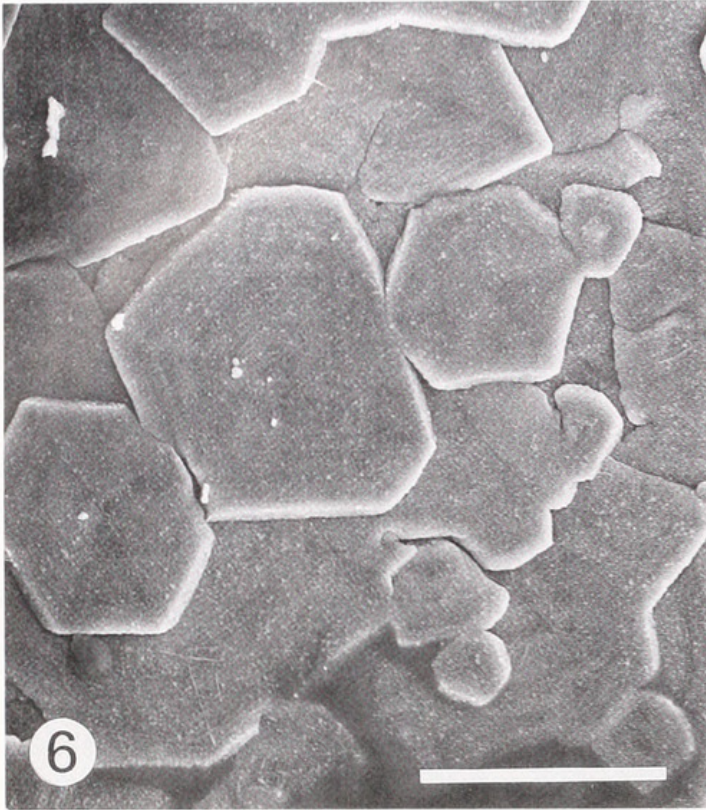
have a gently concave upper surface, with a slight depression at the center. This is particularly apparent on larger crystallites where the central depression may be up to $1\ \mu\text{m}$ in diameter. Newly seeded tablets (less than $0.5\ \mu\text{m}$ in diameter) are distributed without apparent pattern over the surfaces of larger, older tablets. The size of the tablets on any given surface varies considerably. Tablets fuse laterally with neighbors on the same level to form sheets or laminae. The contact suture between fused tablets is visible as a very thin furrow, or as a disruption in the growth lines.

Further proximally still, on more mature wall surfaces, screw dislocations (Fig. 10–13) become very common and are responsible for wall thickening. Seeding is less frequent than in younger walls. The screw dislocations can be either dextral or sinistral spirals. Angles of approximately 120° usually occur between adjacent edges of euhedral spiralled crystallites. Anhedral spirals may also be found. Screw dislocations often occur in congruent groups in which different screws have parallel edges and the same direction of spiralling. Frequently two screw dislocations with opposite coiling directions are linked together to form a double scroll-shape (Fig. 10).

In older walls, well proximal of growing edges, large areas of the wall surface may be covered by crystallites that have undergone multiple divisions by screw dislocation, or by step-like splitting. These surfaces may show regular imbrication in a predominantly distal direction (Fig. 1). Few centers of screw dislocation are evident and the wall surface resembles a foliated fabric (“pseudofoliated”). The semi-nacre may conform to strongly curved surfaces; for example, laminae wrap around the inner surface of pseudopores in exterior walls.

Tablet surfaces are sometimes partially etched (Fig. 14–17), possibly as a result of deterioration after collection or through bleaching during sample preparation. Six-sided tablets are differentially etched in six alternating triangular sectors. In the three more soluble sectors the tablet surface has a pimpled surface, whereas the surface of the less-soluble sectors remains smooth with well-defined growth lines. Persistent bleaching for long periods causes complete removal of the more soluble sectors, leaving the three less-soluble sectors relatively intact. On unetched wall surfaces sectoring may still be detected because the more soluble sectors have a darker shade under SEM, and the less soluble sectors usually appear to be raised and have better defined growth lines and striations.

In many six-sided tablets three of the growing edges are slightly longer than the other three, giving three alternately narrow and broad sectors. The more soluble sectors in these cases are the narrow sectors; the less soluble are the broad sectors. Only the three less-soluble sectors reach the very center of the tablets. Here the three sectors are separated by “sutures” forming a “trilete” pattern.



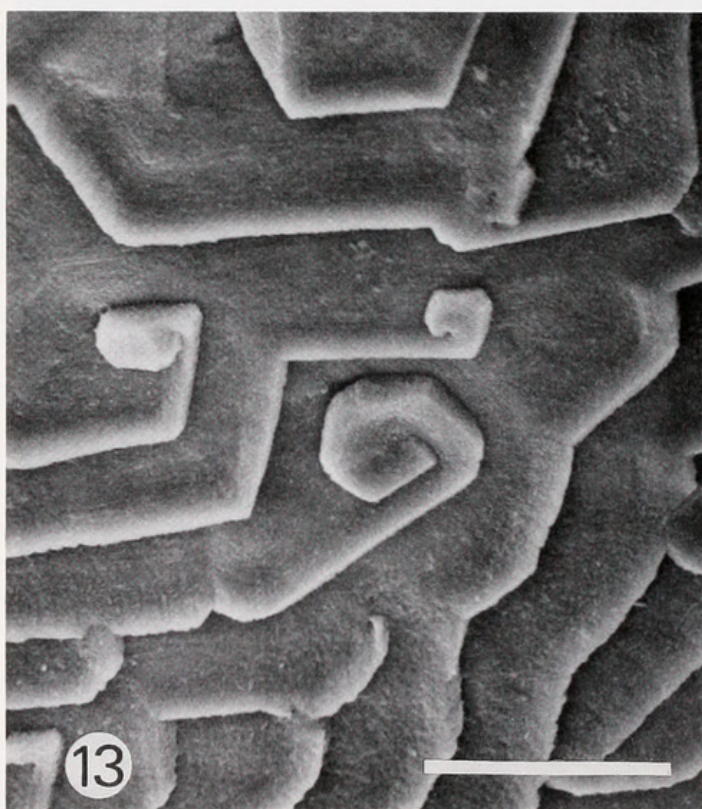
Figures 6–9. Scanning electron micrographs of semi-nacre in the articulates *Bicrisia* cf. *edwardsiana* (Fig. 6, 8) and *Crisia* cf. *sigmoidea* (Fig. 7, 9).

Figure 6. Euhedral hexagonal and sub-hexagonal tablets of semi-nacre. Note differences in the slopes of sector edges and fusion of adjacent tablets to form horizontal sheets. Scale bar = 6 μm .

Figure 7. Laterally fused, anhedral tablets without visible sectoring. Scale bar = 7.5 μm .

Figure 8. Tablets of different ages with sizes ranging from tiny new seeds to broader fused tablets. Note the rhombic form of the central tablet, differences in slope of sector edges and growth lines. Scale bar = 3 μm .

Figure 9. Lightly etched semi-nacre showing well-defined striations perpendicular to tablet edges. Note depressed tablet centers. Scale bar = 3 μm .



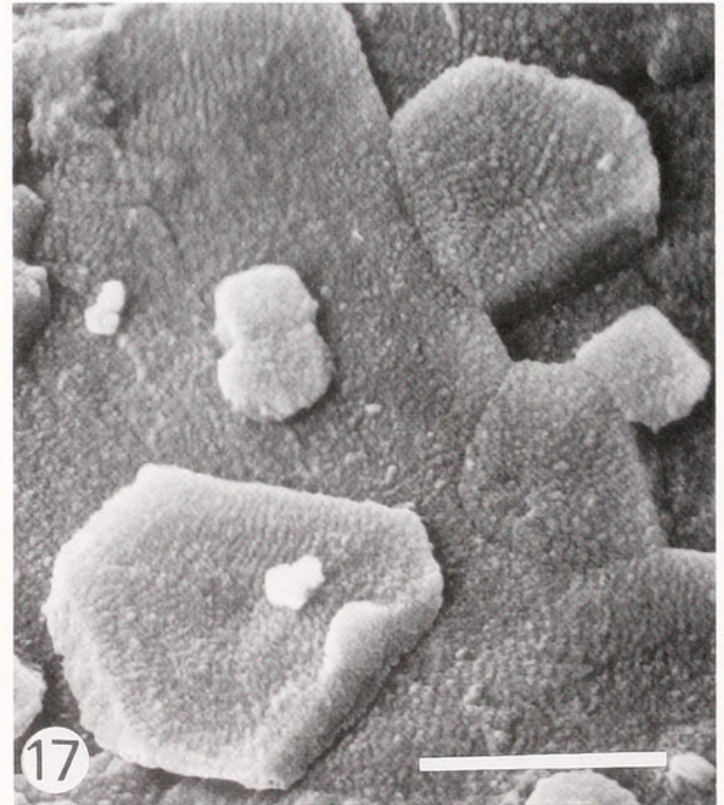
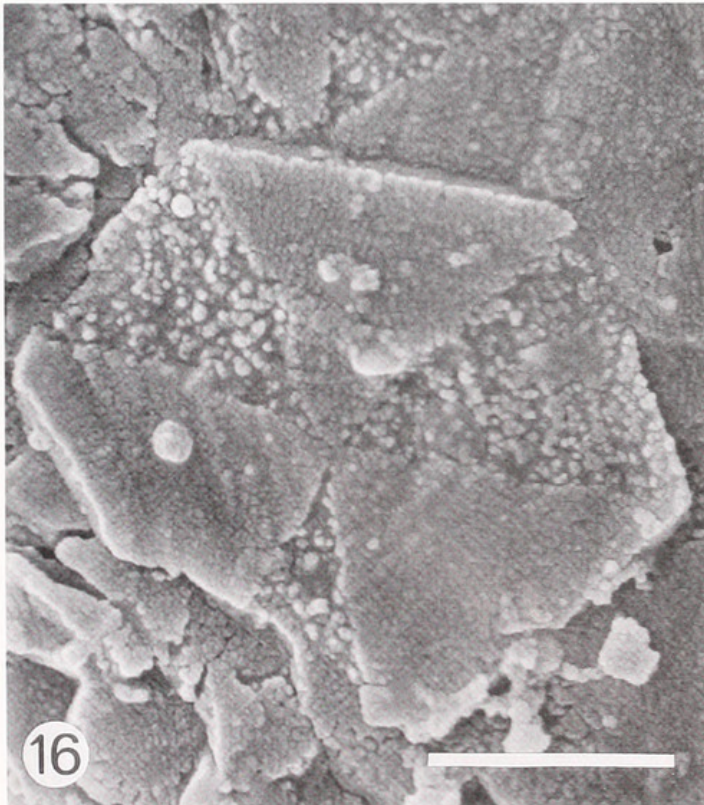
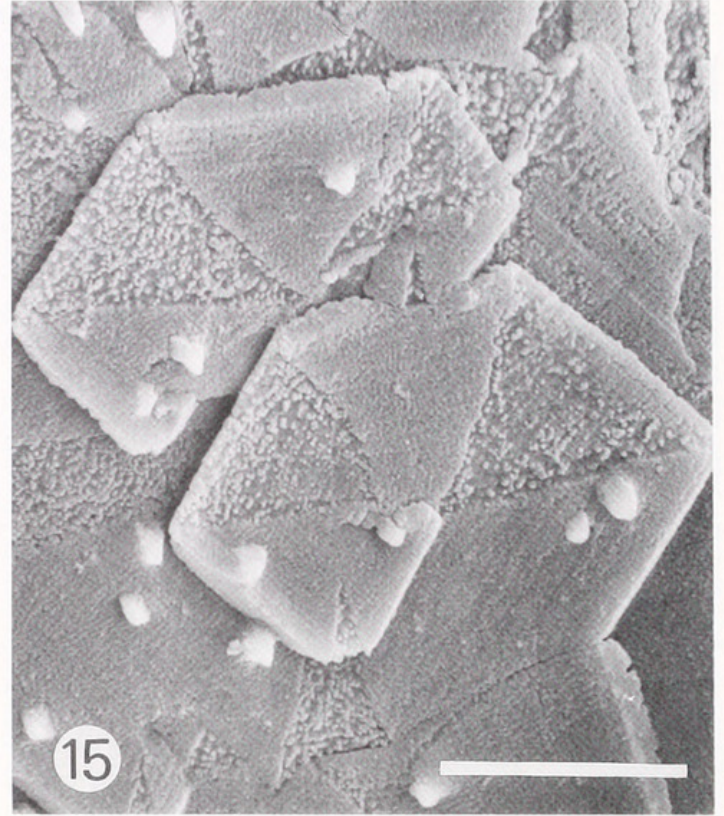
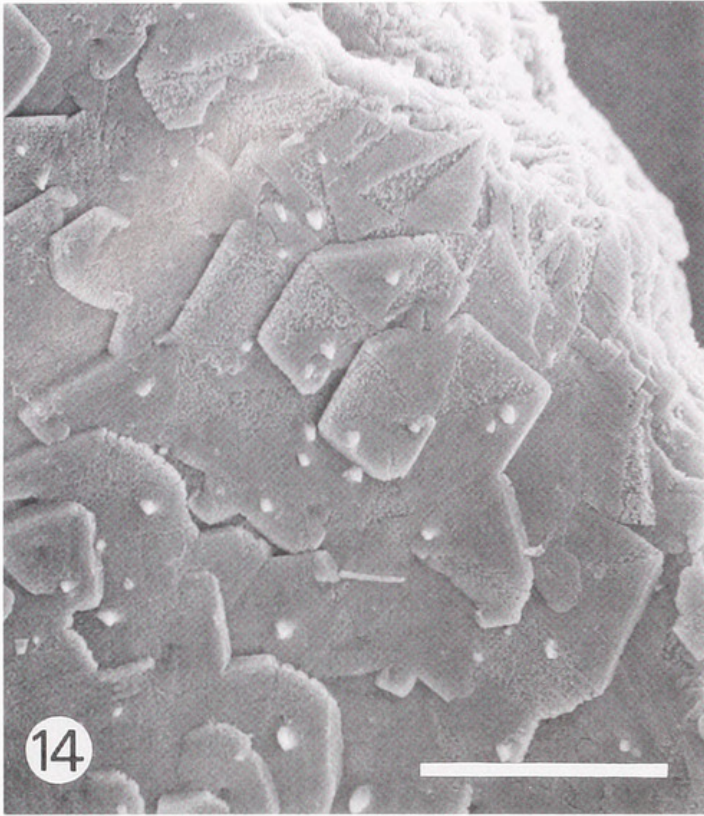
Figures 10–13. Scanning electron micrographs of semi-nacre in *Plagioecia dorsalis*.

Figure 10. Anhedral tablets with abundant screw dislocations, some occurring as pairs with opposite spiral directions. Scale bar = 10 μm .

Figure 11. Detail of screw dislocation from Figure 10. Note the different surface textures of the more-soluble and less-soluble sectors, the former having slightly rougher surfaces with less well-defined growth lines. Scale bar = 2.5 μm .

Figure 12. Euhedral tablets with screw dislocations. Scale bar = 10 μm .

Figure 13. Screw dislocations in imbricated semi-nacre. Scale bar = 4 μm .



Figures 14–17. Scanning electron micrographs of semi-nacre in the tubuliporine *Platonea stoechas*.

Figure 14. Semi-nacreous fabric near a broken edge of an interior wall. Note screw dislocations, differential etching of tablets, revealing their sectorized substructure and spikes predominantly associated with the less-soluble sectors. Scale bar = 6 μm .

Figure 15. Detail of etched tablets that have undergone screw dislocation. Note the parallel alignment of sectors in different layers of the screw dislocations as well as between adjacent screws, perhaps indicating crystallographic continuity. The more-soluble sectors are narrower than their less-soluble neighbors and have edges with different slope angles. Scale bar = 2.5 μm .

Figure 16. Heavily etched tablet showing differentiation of less-soluble and more-soluble sectors. The broader, less-soluble sectors meet at the center of the tablet with a trilete suture. Growth lines and perpendicular striations are most clearly seen on the less-soluble sectors. Scale bar is 2 μm .

The three more soluble sectors first appear about 0.1–0.3 μm outward from the centers of the tablets.

The bounding edges of the tablets are not perpendicular to the upper surface but are inclined at an angle, producing a “bevelled edge.” The angle of inclination differs in the three less-soluble and the three more-soluble sectors. The edges of the more-soluble sectors slope inwards to form an overhang, whereas those of the less-soluble sectors slope outwards.

In some species (*Platonea stoechas*, *Crisia* spp.), tiny spikes occur on the surfaces of tablets (Fig. 14–16). The spikes are up to 1 μm long (usually $<0.5 \mu\text{m}$). They occur in highest concentrations inside interzoooidal pores and around pustules (short mural spines). The great majority of spikes arise from the less-soluble sectors, and sometimes can be observed to originate along the growing edges of the tablets.

Discussion

Comparison with other cyclostome bryozoan ultrastructures

The wall structure described here comprises thin hexagonal or sub-hexagonal tablets arranged in horizontal sheets, or laminae. The platey tablets are arranged in well-defined laminar sheets but do not form regular columnar stacks, brick-wall, or row stack patterns. The abundance of screw dislocations and steps, the disordered distribution of newly seeded crystallites, the arrangement of the tablets, and the calcitic mineralogy permit the fabric to be characterized as semi-nacre (*sensu* Carter and Clark, 1985; Carter *et al.*, 1990).

The interior walls of tubuliporines with predominantly semi-nacreous skeletons comprise two types of ultrastructural fabric: an initial precursory fabric of wedge-shaped crystallites, which is succeeded by a fabric of flat-lying, hexagonal semi-nacreous tablets. A fabric of wedge-shaped crystallites also occurs as the initial layer in the interior walls of lichenoporids (Taylor *et al.*, 1995). In these free-walled cyclostomes (suborder Rectangulata) there is a gradation between the granular fabric and a succeeding foliated fabric of elongate crystallites that are distally oriented and imbricated. A very similar gradation has been found in the basal wall of tubuliporines (Weedon and Taylor, unpubl.). Crystallite seeding in lichenoporids is almost totally restricted to the initial layer of wedges, with the succeeding platey laminae developing by accretion of

the wedges. In the interior walls of the tubuliporines described here, however, the platey crystallites succeeding the wedges are discrete tablets that accrete radially and initially lack a parallel growth orientation or imbrication. Seeding is of two types: as wedge-like laths in the initial layers of the walls, and as the hexagonal tablets in the succeeding platey layer. Thickening of the walls occurs by continued seeding of new tablets as well as by screw dislocations and divisions of the tabular crystallites. Parallel growth of imbricated crystallites can develop in older walls where screw dislocations are few and a pseudofoliated fabric appears.

The semi-nacreous structure is very similar to that described in *Hornera* (Taylor and Jones, 1993), a free-walled cyclostome belonging to the suborder Cancellata. In *H. robusta* MacGillivray the tablets are characterized by distinctive spikes, usually arranged as triplets at the center of the tablets, and always arising from the less-soluble sectors. These spikes are similar in size and shape to the single spikes found in some tubuliporines and articulates but differ in their location in the middle of the tablets as well as their increased abundance in areas of new seeding. Spikes are largely absent in older, more mature walls.

Seeding of new crystallites in hornerid semi-nacre is concentrated at the distal edges of walls. Subsequently, a pseudofoliated fabric quickly develops, with the imbricated crystallites growing predominantly proximally (Taylor and Jones, 1993). In the tubuliporines and articulates described here, most seeding similarly occurs near the distal edges of walls, but seeding can also be found in more mature areas where screw dislocations provide the dominant means of wall thickening.

Like tubuliporines and articulates, the semi-nacreous tablets of hornerids are subdivided into alternating triangular sectors that are susceptible to different degrees of surface etching. [Note that the more-soluble sectors described in tubuliporines and articulates are the equivalent of the “smooth-surfaced sectors” of hornerids described by Taylor and Jones (1993; p. 136); the relative smoothness of the more-soluble sectors in hornerids is probably a consequence of greater etching of these sectors.] On very small, relatively young tablets, the three less-soluble sectors reach the center of the crystallite where their contact forms a trilete “suture.” The more heavily etched sectors do not reach the center of the tablets but appear slightly later in crystal growth (Taylor and Jones, 1993). Screw dislocations are quite frequent in hornerid semi-nacre. Hence

Figure 17. Lightly etched sub-hexagonal tablets newly seeded upon a sheet of fused tablets. The edges of the less-soluble sectors slope outwards and downwards. The more-soluble sectors are narrower and their edges form overhangs. Note the striations perpendicular to the edges, the development of a spike on the lower right hand edge of tablet at bottom left, and the slight depression in the center of the tablets. Scale bar is 1.5 μm .

the semi-nacre of tubuliporines and articulates is a very similar fabric to that of hornerids. However, tubuliporine and articulate semi-nacre differs in the absence of triple spikes, the more widespread occurrence of seeding and screw dislocation, and in the predominantly distally imbricated pseudofoliated fabric of the mature skeleton.

The close similarity of the semi-nacres of tubuliporines and articulates has potential as a synapomorphic character shared by the two suborders. With further investigation of fossil and Recent cyclostomes it should be possible to evaluate this and other skeletal ultrastructures as phylogenetic characters.

Comparison with molluscan nacres

The subdivision of the cyclostome bryozoan tablets into alternating soluble and less-soluble sectors has important bearing on the relationship between cyclostome calcitic semi-nacre and molluscan aragonitic nacres. Mutvei (1977, 1978, 1980, 1983a, b) has described a range of internal sectoring and substructures in molluscan aragonitic nacre, using glutaraldehyde etching to enhance the differences in the radial sectors. Importantly, different tablet substructures occur in different molluscan classes (Fig. 18B, C). In bivalves (specifically *Mytilus*, *Nucula*, and *Unio*), the etched hexagonal tablets are subdivided into four "crystal individuals" or sectors, which Mutvei suggested were probably cyclically twinned (Fig. 18B). The crystals represent two structurally distinct pairs, with the individuals of each pair arranged opposite each other. One of the pairs comprises relatively insoluble triangular sectors with a central angle of about 64° . These crystal individuals are more or less fused at the center of the tablet. The other pair of crystal individuals are rhombic in outline with a central angle of about 116° . They lack the lamellar substructure and are much more soluble. It is possible that the rhombic crystal individuals are really two adjacent triangular sectors (H. Mutvei, *pers. comm.*, 1994). Etching enhances concentric "lamellae" on the tablet surface, just as in bryozoan semi-nacre. Nucleation, or seeding, of new tablets occurs invariably on the relatively insoluble sectors. Hence a more or less regular brick-wall or staircase pattern of arrangement of the tablets is generated. The tablets have inclined edges so that in side view incipient tablets have a sub-pyramidal shape with a broader diameter at the base than at the top. The inclination of the edges may be as great as 40° . In some tablets the direction of inclination is reversed, with the broader diameter being on the top surface. The tablets have a concave upper surface with a central depression.

In gastropods (specifically *Gibbula*, *Calliostoma*, *Trochus*, and *Haliotis*) the tablets comprise radial sectors of polysynthetically twinned individuals (usually 1 to 6 pairs but exceptionally up to 25 pairs), separated by thin vertical

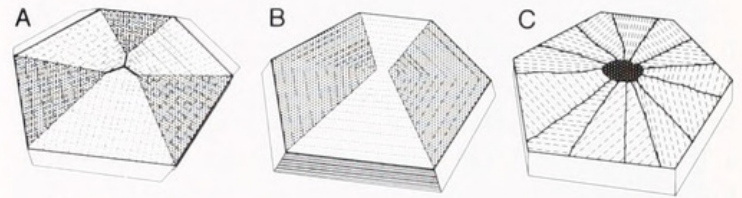


Figure 18. Schematic diagrams of typical nacreous and semi-nacreous tablets in cyclostome bryozoans and molluscs. (A) Cyclostome semi-nacreous tablet. The tablet is divided into six roughly equal sectors or crystal individuals. The more-soluble sectors (shaded darker) do not occur at the center of the tablet where there is a "trilete" suture. Note the sloping outer edges of the less-soluble sectors. (B) A typical bivalve nacreous tablet divided into a pair of sub-triangular, less-soluble sectors that meet at the center and two rhombic (or paired triangular), more-soluble sectors. Note that the less-soluble sectors have a finely laminated appearance and all the outer edges have regularly sloping surfaces (after Mutvei, 1977). (C) A typical gastropod or cephalopod nacreous tablet divided into polysynthetically twinned sectors (crystal individuals). The central hollow represents the site of the central organic accumulation. Note the vertical side faces (after Mutvei, 1978).

organic partitions (Mutvei, 1978; Fig. 18C). The center of the tablets has a partially calcified organic accumulation that serves as a nucleation site for successive layers of newly seeded tablets. Hence vertical columns develop; the greatest concentration of growth occurs at the shell margin. A similar pattern of development occurs in the nautiloids (Cephalopoda; Mutvei, 1980).

The form and complexity of the organization of the calcitic semi-nacre of cyclostome bryozoans resembles that of the aragonitic nacreous tablets in molluscs. The cyclostome fabric is especially similar to bivalve sheet nacre, which also has a regular arrangement of sectors (or crystal individuals) of different solubilities. Both types of tablet also have gently concave surfaces with a slight central depression as well as inclined (not vertical) side faces. The bryozoan semi-nacre differs structurally from the molluscan nacre only in the particular pattern of sectoring and in the more irregular stacking of the tablets. Indeed the structural differences between cyclostome semi-nacres and molluscan nacres are no greater than the differences between the nacres of different classes of molluscs.

Carter and Clark (1985) and Carter *et al.* (1990) devised classifications of invertebrate microstructures that stressed structural and morphological arrangements rather than mineralogy, and could be applied across the different biomineralizing groups. Paradoxically, however, they incorporated into the definition of nacreous fabrics that true nacres must be aragonitic; cf. semi-nacre that could be calcitic or aragonitic. In view of the considerable morphological similarity demonstrated here between the calcitic semi-nacres of bryozoans and the aragonitic nacres of molluscs, it seems reasonable to group these structures together regardless of their different mineralogy.

It has been proposed that the perceived greater diversity of ultrastructural fabrics in molluscs compared to lopho-

phorates is a consequence of the greater evolutionary potential of molluscan biomineralization (Carter, 1979; Carter and Clark, 1985). Comparison of lophophorate and molluscan skeletal fabrics revealed a pattern that Carter and Clark (1985) termed the "lophophorate-molluscan discontinuity" (L-M discontinuity). They claimed that lophophorates are incapable of developing the range of aragonitic and calcitic structures found in molluscs, whereas all of the fabrics found in brachiopods and bryozoans have also evolved in molluscs.

Carter and Clark (1985) used two main arguments to support their hypothesis for greater evolutionary potential of molluscs with respect to lophophorates. Their first argument was that all organizationally complex molluscan fabrics that are uniformly oriented in the plane of shell deposition as well as with respect to the shell margins are absent in lophophorates. They cited as examples of such fabrics radial and concentric crossed lamellar and crossed foliated structures, row stack nacreous structure, and crossed composite prismatic structure.

The second argument cited by Carter and Clark (1985) in support of the L-M discontinuity is the complex substructure of nacreous fabrics in molluscs. They suggested that tablet substructures, which could have a direct bearing on tablet stacking patterns, may be unique to the Mollusca and absent in the semi-nacre of lophophorates. The tablet substructures described here in bryozoan semi-nacre indicate that conclusions about evolutionary potential of biomineralization should not be drawn until the balance of research on molluscs and lophophorates is equalized. The bulk of research on calcareous skeletal biomineralization in invertebrates has been dedicated to molluscs, but current studies of bryozoans are revealing an increasing range and complexity of fabrics.

Convergence of microstructures is common within the Mollusca. It has been argued that, of the common molluscan shell microstructures, only nacre evolved just once within the phylum (see Carter and Clark, 1985). Regular aragonitic nacles occur in the gastropods, cephalopods, and bivalves, all of which may have evolved from nacreous monoplacophoran ancestors. The differences in the substructures of the nacreous tablets in the different classes may, however, indicate convergent evolution of nacreous fabrics. The Ordovician bivalve *Palaeoconcha* has a tablet substructure resembling more closely that of modern and fossil gastropods and cephalopods than modern bivalves (Carter and Clark, 1985). Therefore, the modern four (six?) sectorial bivalve nacre must have evolved separately (Carter and Clark, 1985). The separate evolution in bryozoans of semi-nacre, which is very similar morphologically (if not mineralogically) to molluscan nacre, lends credence to the possibility that nacre evolved more than once within the Mollusca.

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