FUNCTIONAL MICROSTRUCTURE AND MINERALOGY OF THE BYSSAL COMPLEX OF *ANOMIA SIMPLEX* ORBIGNY (BIVALVIA: ANOMIIDAE)

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ABSTRACT

The calcified byssus of *Anomia simplex* Orbigny is produced by a modified byssal gland composed of a series of thin tissue folds. The biogenically produced calcitic byssus is composed of tightly packed lamellae that in turn make up a central, cylindrical core. This core, aligned dorso-ventrally, has a flared byssal attachment surface directed toward the hinge. The calcified lamellae are deposited upon organic threads or sheets. The attachment plaque is also deposited upon an organic layer that may act as a nucleation site and adhesive zone for attachment of the bivalve to the substratum. Small aragonitic spindles typically cover portions of the calcitic byssus. These spindles are likely inorganic in origin and may be a typical mineralogical precipitation upon molluscan calcified structures.

Many bivalve molluscs possess structurally and physiologically complex byssal glands that produce proteinaceous attachment threads. Best known of these bivalves are the epifaunal Mytilacea (Waite and Tanzer, 1981), but byssate molluscs include members from a wide range of higher taxa (egs. Arcacea, Pectinacea, Pandoracea). Yonge (1962) surveyed byssal glands in bivalves and concluded that the presence of an operative byssal gland in adults might be paedomorphic. Most adult anomiacean bivalves also retain a well developed byssus with which they permanently attach to hard substrata. The anomiid byssus, however, is not proteinaceous but instead is composed principally of calcium carbonate. This stout, columnar attachment structure passes from a modified byssal gland through a dorsal byssal notch in the right valve to the substratum. Morton (1979) suggested that the byssal threads of *Anomia* have coalesced "into a calcified cable. . . ." This is difficult to distinguish at the light microscopical level, and although shell microstructure of various members of the Anomiidae has been examined (Wada, 1963; Taylor et al., 1969), no comparable study of the calcified byssus has been published.

In conjunction with their microstructural studies, Taylor et al. (1969) examined shell, but not byssal, mineralogies. With the exception of aragonitic myostracum and ligamental needles, the entire shell of all species of *Anomia* examined by the latter authors was reported as calcitic. Carter (personal communication, 1983) notes that *A. simplex* has a well developed aragonitic crossed-lamellar structure as a very thin interior layer. Mineralogy of the calcified byssus had been left undetermined.

In the Bivalvia the two most common calcium carbonate allomorphs are calcite and aragonite. If we limit our discussion to these two morphs, it might be hypothesized that anomiid byssi are composed of aragonite, the "stronger" and more common of the two morphs (Milliman, 1974). In support of this hypothesis is the fact that aragonite is more typical of molluscan attachment layers [egs. ligostracum of Ostreidae (Carriker and Palmer, 1979), myostracum (Taylor et al., 1969)]. The inner surface of the byssus of Anomia is not only the face for addition of new calcareous material, but also the internal region for byssal anchorage or attachment. In fact, the byssus of *A. simplex* is principally composed of calcite.

This research was undertaken to explore the functional microstructure and mineralogy of the byssus of *Amonia simplex* Orbigny.

METHODOLOGY

Specimens of *Anomia simplex* were collected in December 1980 from along Bowmans Beach, Sanibel Island, Florida. These specimens, having a mean length of 25 mm, were found attached to single valves of *Argopecten gibbus* (Linné) or *Chione cancellata* (Linné). Typically, live anomiids were attached to the internal surface of a single valve substratum and often conformed to the shape of the "host" valve. All specimens were immediately preserved in 70% ethanol.

Anomiids were carefully separated from their substratum; displacement of their valves usually resulted in retention of calcified byssi on "host" shells. This allowed easy

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mounting of byssal specimens on aluminum scanning electron microscopy stubs. Byssi and supportive fragments of attached substrata were placed in a 30% solution of commercial Clorox (sodium hypochlorite) for three hours to dissolve primary organic deposits. Specimens were then washed in distilled water and dehydrated in a graded series of ethanols through absolute ethanol. Several changes of absolute ethanol over several days, followed by an eight-day stay in a 60°C drying oven insured dry specimens. Some byssi, as well as pedal and byssal gland soft tissues, were critical point dried after ethanol dehydration using carbon dioxide as a direct transfer agent in a Denton DCP-1 critical point drier.

Mounted specimens were coated in an argon environment with a thin layer of gold in a Polaron SEM Coating Unit E5100, and examined at 30kV in an AMR 1000 scanning electron microscope.

Mineralogical analyses were carried out using Feigl solution (Milliman, 1974) and X-ray diffraction. Feigl solution is an easy and fairly accurate method for quickly determining the two primary biological calcium carbonate polymorphs. The stain reacts rapidly with aragonite by dissolution of the mineral followed by precipitation of MnO_2 and Ag°, staining aragonitic deposits black (Carter, 1979). Calcite, on the other hand, is less soluble and resists staining. Mineralogical staining was verified by X-ray diffraction. For the latter, 2–4 byssi were ground to a fine powder in a glass tissue grinder, mounted on double stick tape on a glass slide and analyzed on a General Electric XRD 700 X-ray diffraction unit.

Histological sections of 70% ethanol fixed foot and byssal gland were obtained by embedding specimens in paraffin wax (m.p. 56.7°C) and sectioning at 7 μm. Sections, mounted on albuminized slides, were stained with toluidine blue or a modification of the Pantin trichrome stain (Prezant, 1979). Fractured, non-Cloroxed byssi were also stained with toluidine blue.

All figures are scanning electron micrographs unless otherwise indicated.

RESULTS

Byssus microstructure

The byssus of *Anomia simplex* is a columnar pillar, composed of a series of tightly packed lamellae, that emerges from a modified byssal gland, passes through a byssal shell notch in the right valve and attaches by way of an expanded plaque to a hard substratum (Figs. 1–3).

The byssus emerges anatomically dorsally through the byssus notch of the right (bottom) valve just beneath the hinge. Usually the byssus angles away from the shell ventrum. The column is thus aligned dorso-ventrally and has a flared byssal surface leading toward the hinge. A clam about 25 mm long has a byssus between 5–6 mm long and 1–2.5 mm in diameter. Curvature or angularity of the byssus dictates variations in vertical height. The direct vertical height (i.e. height from substratum to uppermost portion of byssus in a normal plane) rarely exceeds 2.5 mm (Fig. 4).

The upper surface of the byssus, which faces the left upper valve, reveals the lamellar nature of the byssus (Fig. 5). These lamellae remain, at their surfaces, in direct contact with the byssal glandular region of the foot. The lamellar structure of the byssus gradually tapers as the folds approach the basal portion of the byssus [i.e. the region of external attachment to substratum] (Fig. 6). Eventually the byssus flares dorsally into a basal plaque that has a superficially fine granular appearance at low magnifications (Figs. 1, 7). The morphologically ventral portion of the byssus resembles the relatively homogeneous structure of the plaque at low magnifications (Fig. 4).

Closer examination of the plaque reveals a pitted surface with ovoid and "comma" shaped pores (Fig. 8). These may be a natural consequence of incomplete calcification in this basal area and not the result of dissolution or external biogenic forces. The flared dorsal periphery of the plaque molds itself tightly over the substratum surface (Figs. 1, 7–9). This area of merger appears to be one of irregular crystal growth with a heterogeneous leading edge (Fig. 9). Original growth in these areas is of a fine structure that produces irregular growth patterns discerned only at higher magnifications (Fig. 10). Under a dissecting microscope the basal periphery of the byssus appears as a thin brown ring. This is reminiscent of an organic deposit, and the fine, smooth structure of this area under the scanning electron microscope also supports a probable organic nature of this deposit. The brown deposit fills the peripheral gap around the substratum outlining the byssal notch but not covered by the central calcified byssus per se. Calcium carbonate deposits, reminiscent of a leading zone of nacreous growth, appear to be laid down upon an organic sheet (Fig. 9; s). Incipient growth covering this region, however, is substructurally more of a calcified, granular homogeneous type (Fig. 10) rather than a true nacre.

The ventral portion of the byssal column may also show irregularities at higher magnifications. A superficially heterogeneous structure results from numerous small ovoid or spindle-shaped granules (Fig. 11). These granules, which are not always present and sometimes irregularly dispersed, may be secondary, inorganic deposits. The largest spindles seen in this area were less than 5 μm long. Orientation of these spindles was irregular but many were arranged normal to the face of the ventral byssal surface.

The uppermost, ventral region of the byssus suggests the lamellar nature that composes the entire anterior surface. At the apical region of the ventral byssus the structure breaks down into a series of apparent ridges (Fig. 12). Examination of the byssus in this region (Fig. 13) reveals that the lamellae are the basic growth structure for the entire complex and in regions where the lamellar structure does not show, it has been obscured by secondary growth, fusion, or dissolution. Just beneath the obvious lamellar pattern of the byssus in this area are hints of slight ridging (Fig. 13). The apical

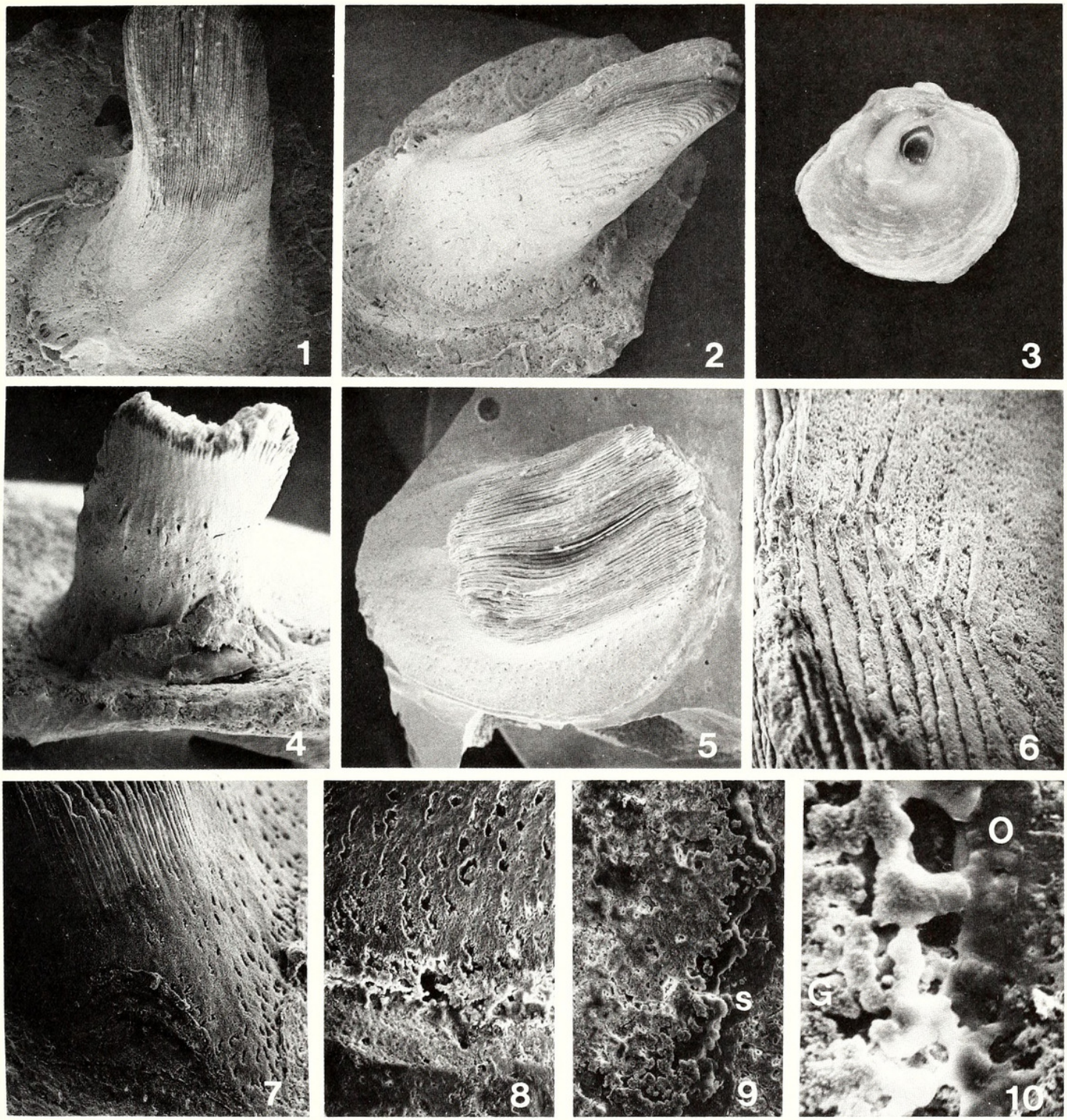

Fig. 1. Byssus of *Anomia simplex*. Uppermost lamellated portion is ventral and basal expanded plaque is dorsal. Horizontal field width = 5.9 mm. **Fig. 2.** Oblique side view of byssus. Lamellae of byssus are readily apparent from this angle. Horizontal field width = 8.5 mm. **Fig. 3.** Light micrograph of byssal notch and right valve. Horizontal field width = 34.0 mm. **Fig. 4.** Ventral view of byssus. Horizontal field width = 2.8 mm. **Fig. 5.** View of dorsally oriented lamellated byssal surface. Horizontal field width = 3.8 mm. **Fig. 6.** Region of byssus showing tapering lamellae as they approach basal plaque. Horizontal field width = 740 μm. **Fig. 7.** Basal plaque at low magnification revealing fine granular surface. This portion of basal plaque in life is covered by flap-like tongue of byssal gland. Horizontal field width = 1.2 mm. **Fig. 8.** Attachment zone of basal plaque and substratum. Basal plaque is pitted with numerous pores in this region. Horizontal field width = 560 μm. **Fig. 9.** Periphery of basal plaque at level of attachment shows irregular outline of active growth zone. Calcareous deposits along the growth zone appear to be laid down on an organic sheet (s). Horizontal field width = 460 μm. **Fig. 10.** Closer view of growth zone on basal plaque reveals an apparently organic substance (0) leading a granular calcified zone (G). Horizontal field width = 135 μm.

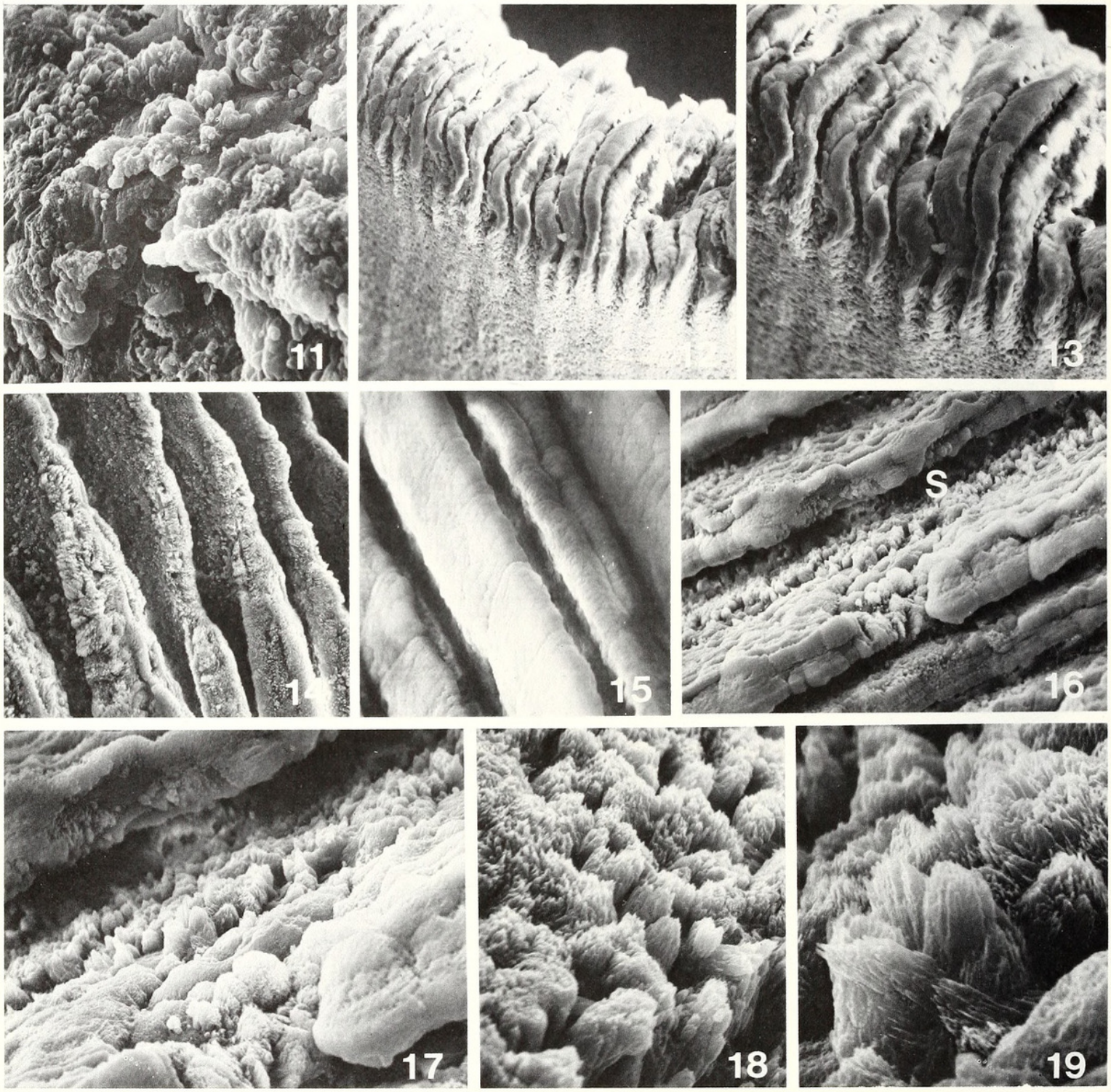

Fig. 11. Ventral surface of byssus reveals irregular surface with numerous spindle shaped granules. Horizontal field width = 40 μm. **Fig. 12.** Outer, ventral tip of byssus occurs as a series of parallel ridges. Beneath these ridges ventrally is a hint of superficial ridges confluent with the lamellae. Horizontal field width = 530 μm. **Fig. 13.** Closer view of ventral tip ridges showing superficially smooth surface of ridges and granular appearance of lower older portions. Horizontal field width = 315 μm. **Fig. 14.** Dorsal lamellae showing highly granular appearance. Horizontal field width = 125 μm. **Fig. 15.** Dorsal lamellae showing very smooth surface. Horizontal field width = 195 μm. **Fig. 16.** Lamellae showing smooth outer surface with spindloid granules (S) in grooves. Horizontal field width = 165 μm. **Fig. 17.** Closer view of spindloid granules in lamellar grooves. Horizontal field width = 85 μm. **Fig. 18.** Spindloid granules occur normal to face of lamellae on dorsal surface. Horizontal field width = 30 μm. **Fig. 19.** Spindloid granules composed of a series of microlathes oriented normal to lamellar surface. Horizontal field width = 12 μm.

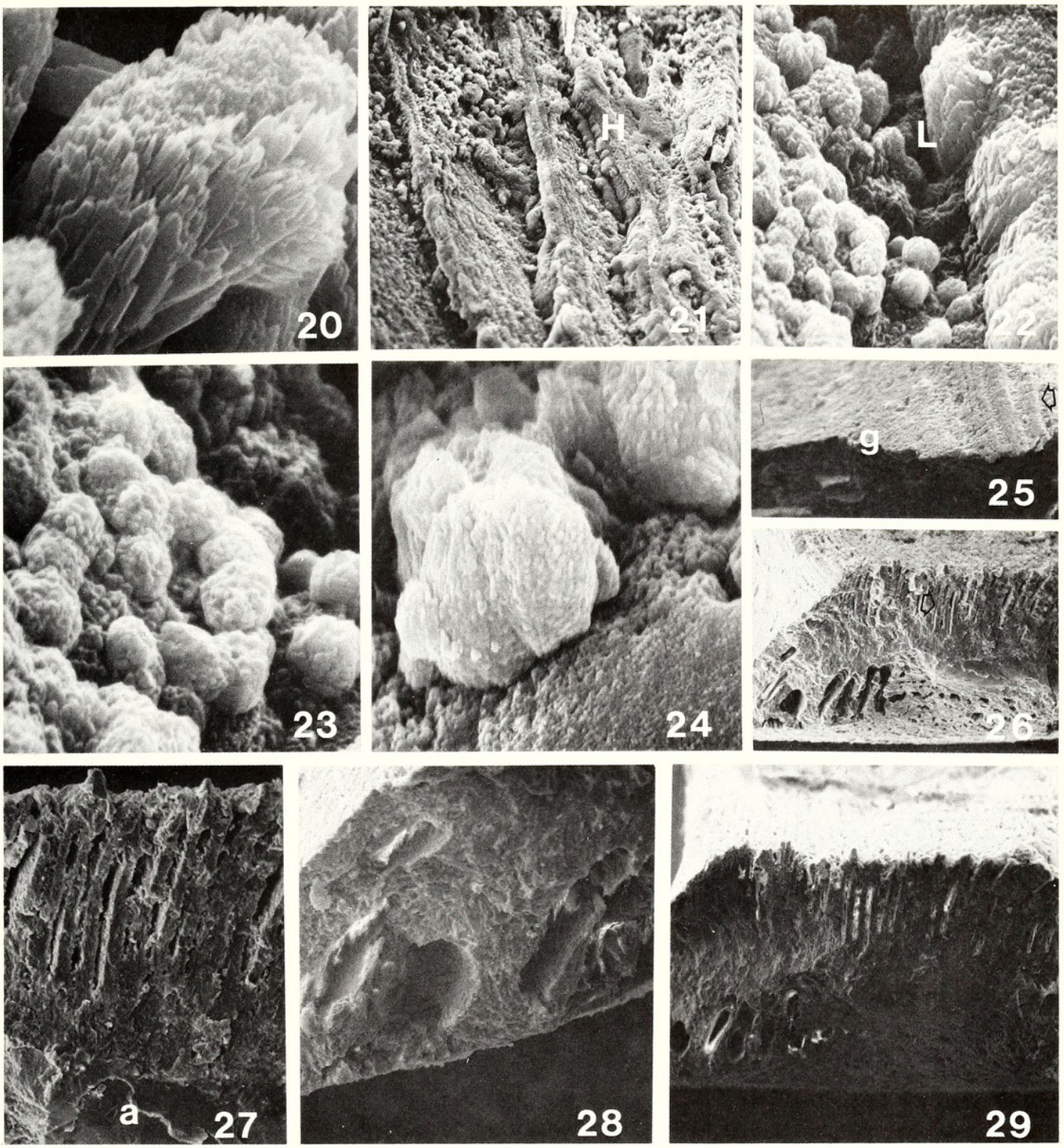

Fig. 20. Closer view of spindloid granule lathes. Horizontal field width = 7.5 μm. **Fig. 21.** Lamellae near point of fusion with basal plaque. Both spindle shaped granules and small hillocks (H) occur here. Horizontal field width = 175 μm. **Fig. 22.** Closer view of hillocks in lamellar grooves. Note lathe-like consistency of portions of lamellar wall (L). Horizontal field width = 8.5 μm. **Fig. 23.** Detailed view of hillocks revealing polygonal subunits. Horizontal field width = 4.5 μm. **Fig. 24.** At higher magnification the compact substructure of the lamellar hillocks is evident. Horizontal field width = 7.0 μm. **Fig. 25.** Cross-sectional fracture of byssus revealing outer fine granular layering (g) with indications of substructural microlathes (open arrow). Horizontal field width = 530 μm. **Fig. 26.** Cross-section through byssus showing submergence of lamellae (arrow) and irregular structural design of internal byssus. Horizontal field width = 1.5 μm. **Fig. 27.** Closer view of submerged lamellar structure and smooth internal region (a). Horizontal field width = 365 μm. **Fig. 28.** Oblique view of fracture zone in byssus showing some relatively large pores and canals. Horizontal field width = 440 μm. **Fig. 29.** Irregular internal structure of byssus revealed in cross sectional fracture. Horizontal field width = 1.1 mm.

lamellae continue around to the dorsum as a system of closely packed folds that show a superficially granular structure in some (Fig. 14), while in others gives an extremely smooth appearance (Fig. 15). In the former, the granular appearance may be spread over the entire structure (Fig. 14) or may be confined to grooves (Fig. 16). In either case a closer look at the granulation reveals that it is caused by spindle-shaped crystals similar to those found on the ventral byssal surface (Figs. 17, 18). The spindles in this case are aligned perpendicular to the lamellar face and average just under 6 μm in length. At higher magnifications the substructure of the spindles is revealed as a series of small lath-like subunits aligned in the direction of the long axis of the spindle (Figs. 19, 20).

As lamellae are followed basally they shorten and there is a distinct change in structure. Near the zone of merger between lamellae and the basal plaque region, lamellar grooves are covered not only by spindle-shaped structures, but often by small hillocks (Figs. 21, 22, 23) composed of irregular polygonal subunits (Figs. 23, 24). Often one side of the groove is dominated by spindle-like substructures and the other by small hillocks (Fig. 21). The underlying surface of lamellae often shows through as being relatively smooth and composed of a very fine grained structure (Fig. 24) or microlaths (Fig. 22).

Cross-sectional fractures through the byssus reveals the sometimes superficial nature of the outer calcareous granular coat (Fig. 25). The thin, outer irregular layer covers a more homogeneous internal structure (Fig. 27). Remnants of lamellae, not yet totally fused into the internal structure, are often evident (Figs. 26, 27). In heavily etched specimens (i.e. prolonged treatment with sodium hypochlorite), deep interlamellar grooves are usually apparent, revealing the organic nature of the interlamellar regions once occupied by byssal gland tissue and byssal gland organic secretions.

In some fractured byssi large pores are obvious, especially along the posterior long axis (Figs. 26, 28). These might be of an extraneous biogenic nature but this is uncertain at this time. Between these pores and buried lamellae, the internal structure of the byssus is finely granular, irregulary lathed and sometimes extremely smooth (Fig. 29).

Under the dissecting microscope fractures also reveal the lamellar nature of the byssus. When stained with toluidine blue, fractured specimens reveal a linear network of parallel lines that stain beta metachromatically indicating an organic substance between calcified lamellae.

Byssus mineralogy

The Feigl stain gave variable surficial results with different byssi. In some it showed a totally blackened outer structure that may indicate all aragonite. In others only the dorsal outer surface stained (Fig. 30), while in still others an irregular superficial mosaic stain was achieved. Fracture cross-sections of the byssus showed only superficial positive Feigl staining and not in all byssi tested. The internal byssal core never gave a positive (black) aragonite stain reaction. Because of the fine, irregular surface of the spindles, which may cause false staining, the Feigl test was backed up by X-ray diffraction. X-ray diffraction left no doubt that both aragonite and calcite were often present in the byssus. Small size demanded the use of several byssi in a single diffraction analysis, so a mixture of 2–4 specimens were tested at any one time. Each case resulted in readings that indicated the presence of both mineral types. Diffraction analysis of even mixed byssi samples always showed a qualitatively greater proportion of calcite than aragonitic.

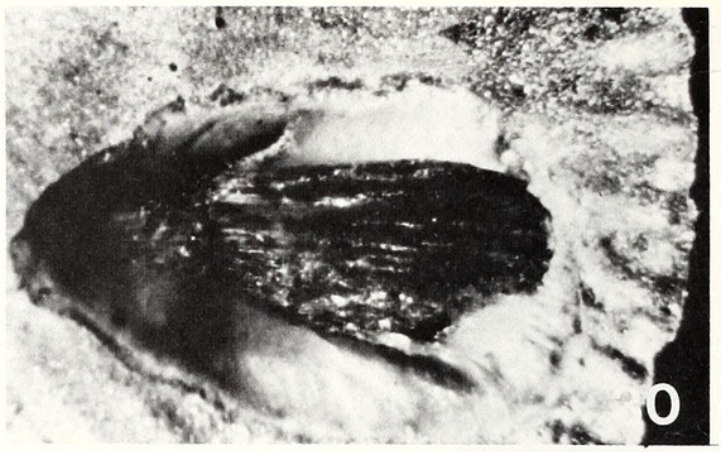

Fig. 30. Light micrograph of byssus stained with Feigle solution. Horizontal field width = 6.5 mm.

Fig. 31. Critical point dried foot and byssal complex. Spatulate foot occurs on the left of the cup-shaped, lamellate byssal gland. Horizontal field width = 8.2 mm.

Byssal gland and foot structure

The foot of *Anomia simplex* is reduced to a small vermiform structure with an enlarged flexible, bulbous to flat tip (Fig. 31). The tip of the foot can inflate and contract into a variety of shapes and sizes. This pedal region is dense with mucocytes and likely functions to keep the byssal notch area free of debris. The tip of the foot when relaxed, very closely approximates the diameter of the byssal shell notch. Although with the byssus present the foot cannot penetrate the notch, the foot is able to flatten out into a spatulate form

and possibly clean the peripheral crevices around the aperture.

At the base of the foot is an expanded, cup-like structure that composes the byssal lamellar gland (Figs. 31, 32). This cup-like region is formed of numerous fine tissue folds. Each pair of byssal gland folds border a single calcified byssal lamella. In adult individuals, there are between 30–45 calcified lamellae. The central lamellated or folded region of the gland is surrounded by a thin extension of the periphery of the byssal gland cup. The latter cradles the exterior of the byssus within the bivalve (i.e. interior to the byssal notch). Elongated finger-like projections are present on the fused, ventral side of the byssal gland cup (Fig. 32), and a tongue-like flap is located dorsally and covers the basal flare of the byssus (Fig. 33). The digitate extensions border the apical lamellae near the outermost portion of the byssus ventrum.

Histological sections reveal the very thin structure of individual gland folds (Fig. 34). Folds are extensions of the byssal-pedal musculature and muscle fibers frequently extend into the tissue folds (Fig. 35). This arrangement may account for the firm connection between byssal gland and byssus. Muscle tension may narrow gaps between adjacent gland folds and place pressure on the calcified byssal lamellae.

Periodically in histological section, organic fibers or ribbons occur between the gland folds (Fig. 36; O). These organic secretions produce a beta metachromatic stain with toluidine blue.

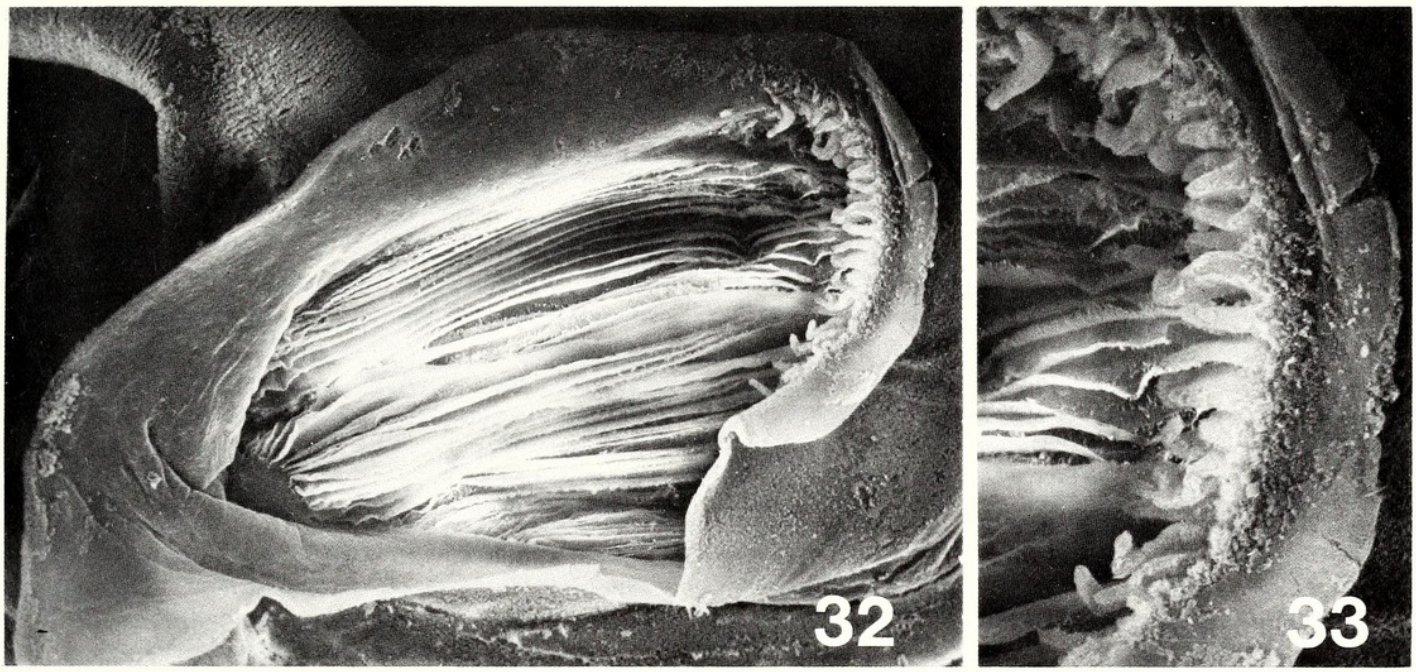

Fig. 32. Closer view of byssal gland showing numerous fine folds composing secretory surface of byssal calcified lamellae. Horizontal field width = 5.4 mm. **Fig. 33.** Finger-like projection of ventral portion of byssal gland cup. Horizontal field width = 0.8 mm.

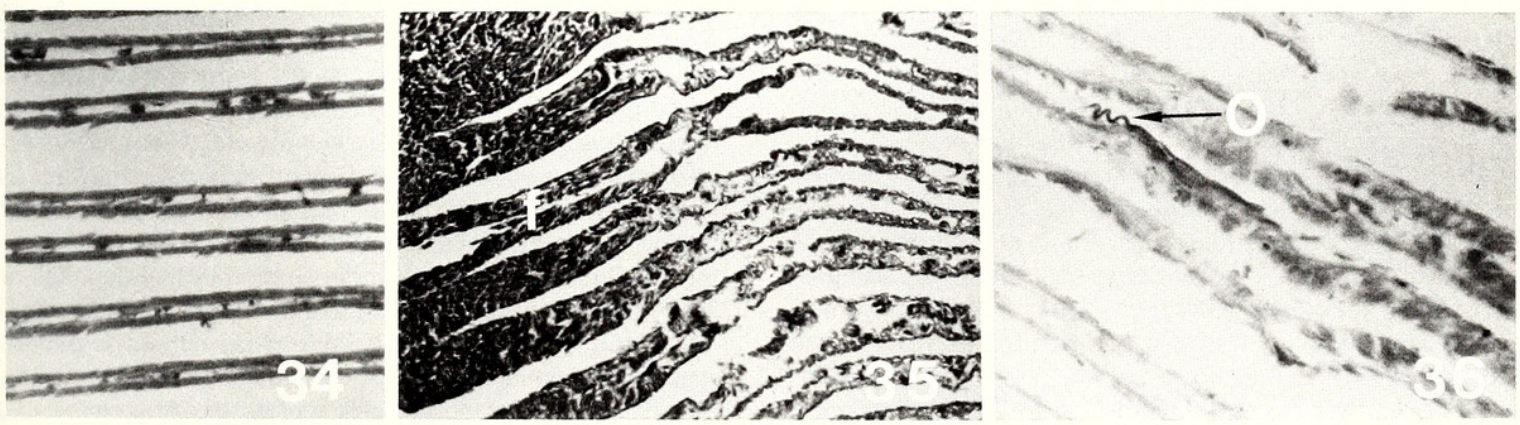

Fig. 34. Histological section through folds of byssal gland. Modified Pantin. Horizontal field width = 340 μm. **Fig. 35.** Histological section through byssal gland showing infiltration of muscle fibers (f) within gland folds. Modified Pantin. Horizontal field width = 510 μm. **Fig. 36.** Histological preparation showing organic ribbons (O) between folds of byssal gland. Toluidine blue. Horizontal field width = 185 μm.

DISCUSSION

Highly folded byssal glands in a cup-like retainer have also been found in some scallops (Gruffydd, 1978) but in these the gland produces a series of flattened ribbons of a protein or mucopolysaccharide nature. In *Amonia simplex* the gland produces a calcified byssus composed of two basic microstructural and often mineralogical forms.

Contrary to initial hypotheses, the byssal gland produces a basically calcitic byssus column. Based on histological sections it appears that each calcified lamella may have an organic core or matrix. Gland lamellae often show an organic ribbon-like secretion between adjacent folds (i.e. site of calcified lamellae secretion). Following treatment of the byssus with an organic solvent *in vitro,* "dissolved" interlamellar regions are evident in areas apparently beneath the reach of byssal gland tissue. Deposition of the basal (i.e. plaque) calcite also appears to be dependent upon initial production of an organic sheet. Presence of an organic matrix or nucleation layer may regulate calcification (Degens, 1965). Hare (1963) suggests that certain side chains, possibly acid mucopolysaccharides bound to proteins by specific amino acid side chains (Wada, 1964a, b), may concentrate and localize calcium and carbonate ions and provide the impetus for calcification and nucleation. Wada and Furuhashi (1971) suggest that sulfated acid mucopolysaccharides act as calcium carriers providing calcium concentrations high enough to initiate mineralization. Wheeler et al. (1981), however, have found a protein in the soluble organic shell matrix of *Crassostrea virginica* that binds calcium and suppresses calcium carbonate nucleation and crystal growth.

The possibility that composition of the organic matrix controls mineralogy has been examined by many authors (Beedham, 1958; Watabe and Wilbur, 1960; Simkiss, 1965; Wilbur, 1964; Grégoire and Lorent, 1972; Weiner and Hood, 1975; Nakahara et al., 1980). Many organisms with calcium carbonate skeletons have crystals closely associated with an organic matrix (Watabe, 1974) that may serve as a crystal nucleation site (Watabe, 1981). This being the case, the matrix may exert a primary influence on mineralogy. Distinct chemical differences have been found in the matrix of calcitic and aragonitic shell layers.Different amino acids, for example, have been reported in the organic matrices of the two primary biological calcium carbonate morphs (calcite and aragonite) by Roche et al. (1951), Tanaka et al. (1960), and Hare (1963). Differences in amino acid composition, however, may not readily explain "mineral selection" since Travis et al. (1967) discovered variations in amino acid composition in different layers of monomineralogic shells that vary as much as or more than the differences seen in adjacent layers of bimineralogic shells. Insoluble and soluble portions of the molluscan organic matrix are usually present. These components, varying in composition, may be found in different places within the shell matrix milieu. Krampitz et al. (1976) identified calcium ligands in the water-soluble matrix of some gastropods. This ligand may stimulate mineralization. The soluble fraction of the matrix, proportionally less abundant than the insoluble fraction, may be confined within crystals or in or on the insoluble, interlamellar matrix (for review see Watabe, 1981).

Further evidence of the role that organic layers or matrices may play in control of calcium carbonate deposition and mineralogy resides in potential influence of periostracum. In molluscs with well developed bimineralogic (aragonite and calcite) shells, initial calcification may occur on the periostracum and was thought to be calcite (Kennedy et al., 1969). Carriker (1979), however, described the mosaicostracum of *Mytilus edulis* and suggested that this "attachment" layer was aragonitic. Kennedy et al. (1969) claim that "The role of periostracum and/or organic matrix in initiating calcification, and thus controlling the deposition of either aragonite or calcite, cannot be doubted. . . ." During shell regeneration, some molluscs may first form a thin, organic sheet, similar to periostracum, before initiating calcification (Kawaguti and Ikemoto, 1962).

The thin organic ribbons often seen between byssal gland folds in *A. simplex* may be precursors of calcification of the byssal lamellae. Organic byssal threads of *Chlamys islandica* are produced by a similar byssal gland (Gruffydd, 1978). Here glycine composes 11.0–15.5% of the byssal amino acids (Gruffydd, 1978). Glycine is also not an uncommon amino acid in the decalcified byssus of *A. simplex* (J. H. Waite; personal communication, 1983).

The step between producing proteinaceous byssal threads and altering the chemistry of those threads sufficiently to initiate calcification may not have been a "complex" evolutionary change. Organic byssal ribbons of *A. simplex* probably function as might the organic templates described earlier. The organic sheet laid down in front of the calcified basal byssal plaque also indicates the possible role in nucleation played by organic structures during and preceding calcification. Organic ribbons or sheets act as nucleation sites that may favor the production of calcite. Since very thick oyster shells are mainly calcitic, seawater is saturated with calcite, and calcite is the least soluble and most stable of the biogenic calcium carbonate morphs, it might be predicted that crystallization of this mineral type is a simple process (Simkiss, 1965). This is not the case. Calcium carbonate crystals are not easily precipitated from natural seawater and when it does precipitate, it is usually in the form of aragonite (Gee et al., 1937). Naturally occurring orthophosphates and other phosphatic compounds in seawater seem to interfere with calcite precipitation (Simkiss, 1965). Several naturally occurring marine cations (i.e. Mg, Mn, Cu, Zn) also seem to inhibit calcite precipitation (Milliman, 1974).

Outer granular or spindle shaped byssal deposits are likely of inorganic origin. They do not appear in all specimens examined, are aragonite (based on x-ray diffraction patterns and Feigl stain indications) and do not appear uniformly over the entire lamellar surface of the byssus. Aragonite is, as mentioned, preferentially precipitated from seawater. Spindle shaped granules on the surface of the byssus of *Anomia simplex* are also similar to crystals of high magnesium calcite that have been precipitated in the laboratory by Towe and

Malone (1970). Structurally-similar types of crystals have also been found in spine diaphragms of an archaeogastropod (Wind and Wise, 1976), the lithodesma of the anomalodesmacean bivalve *Lysonia floridana* (Prezant, unpublished data), and in regenerating shell of various species of *Tegula* (Reed-Miller, 1983 and personel communication). All of these spindloid structures might be of inorganic origin. In many Myoida, however, similar spindles occur in spaces beneath the periostracum (Carter, personel communication, 1983). These may be biogenic in origin. Inorganic precipitation of aragonite, however, on the byssal calcite base may reflect the presence of calcium that has undergone dissolution elsewhere in the byssus (Prezant, 1982). In *Tegula*, Reed-Miller (1982) suggests that areas of shell dissolution may be responsible for the aragonitic, spindloid deposits in regenerating shell. The inconsistent presence of aragonite spindles on the byssus may indicate a temporal event occurring only under appropriate micro-environmental circumstances. At present we have little understanding of what these circumstances might be although it is likely that the spindles are deposited only while the byssal gland is inactive. Thus, in *A. simplex*, when the byssal gland is not producing the calcitic byssal core, residual Ca^{2+} and CO^{2-}_3 ions may inorganically precipitate out onto the calcite lamellar base as aragonitic spindles. Macroenvironmental regimes are known to influence mineralogies of molluscan and other phyla shells (see review in Carter, 1980). It is reasonable to assume microenvironment is the final coordinator of mineralization.

The overall byssus-byssal gland system of *Anomia simplex* presents a structure well adapted to this bivalve's sessile lifestyle. The small, flexible vermiform foot likely functions to keep the peripherally exposed byssal notch area clean. The firm connection between gland and byssus is retained by the muscular extensions that run into the gland folds. Contraction of these muscle fibers will place pressure on the calcified byssal lamellae and help maintain a firm connection in the living animal. The expanded byssal plaque with an underlying organic layer, offers an expanded flattened surface for attachment to the substratum. Actual basal attachment to the substratum is probably not a structural feature of the calcified byssus but may be a chemical bond involving an organic basal portion that precedes and underlies the calcified byssal plaque. Waite (1982) and Waite and Tanzer (1981) have recently described a bonding protein system for the byssal plaque of *Mytilus edulis*.

The advantages of a calcitic (versus aragonitic) primary byssal column is uncertain. Calcite structures are generally less dense than aragonite structures (Carter, 1980). Carter (1980) suggests that a low density, porous structure in some sedentary bivalves may be associated with "crack-stopping mechanisms, economy of secretion, or rapidity of shell layer thickness increase." The byssus is the sole adhering structure that allows retention of *Anomia* on some substratum. The porous basal portion of the calcite basis of *A. simplex* is well suited for this arduous task and well adapted for fracture resistance and, perhaps, rapidity or economy of secretion.

The soft dorsal tongue-like flap of the byssal gland may be responsible for the contoured, nonlamellate basal surface of the dorsally directed byssal attachment plaque. This area is either never lamellate and the flap may be directly responsible for its production or is secondarily involved in fusion of lamellae. The subtle change from lamellae to plaque supports the latter conjecture.

Small finger-like projections along the dorsal right edge of the byssal gland may mold or contour calcareous byssal secretions as they are deposited upon an organic substrate.

Many questions concerning this system remain. The exact mode of lamellar secretion is unknown. The qualities of the organic ribbons that apparently precede calcification are unknown. The adhesive nature of the basal plaque undersurface remains to be explored as does the possible adaptive features of aragonitic surface granules. Might the aragonitic surface be deposited regularly between periods of primary calcite deposition? Since this type of inorganic precipitation of calcium carbonate is not unique to *Anomia simplex*, how common is it? It is certain that a closer look at biogenic versus nonbiogenic calcification in molluscan systems is called for.

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