

How a Clam Builds Windows: Shell Microstructure in *Corculum* (Bivalvia: Cardiidae)

by

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Abstract. *Corculum* is unusual among bivalves because it, like the closely related genus *Fragum* and their distant relative *Tridacna*, possesses endosymbiotic dinoflagellates. But *Corculum* does not expose its algae-laden tissues directly to the sunlight. Instead, the shell of *Corculum* incorporates several unique features that have been interpreted as adaptations to permit passage of incident light through the shell to algae-bearing mantle and gill tissue encased within. These shell modifications in *Corculum* shell include: postero-anterior compression (resulting in a prominently keeled shell with a flattened upper surface), posterior thinning of the shell, and unique transparent "windows" radially arrayed on the shell posterior.

The windows are present only on the posterior (upper) surface, are triangular in outline, and are constructed by expansion and elaboration of the outermost, fibrous prismatic layer of the shell microstructure. A concomitant reduction in pigmentation enhances transparency. Direct measurements of light transmission through the *Corculum* shell show the windows transmit an order of magnitude more light than either the other portions of the shell posterior or the shell's anterior.

INTRODUCTION

TWO BIVALVE lineages, the tridacnids and the Fraginae (including *Corculum*, the heart cockle, and the closely related genus *Fragum*), have independently evolved symbiotic relationships with dinoflagellates, or zooxanthellae (KAWAGUTI, 1950, 1983). Although both bivalve groups are assigned to the Cardiacea, or cockles, they have evolved very different sets of adaptations to accommodate their symbionts. Unlike its distant cousin *Tridacna*, *Corculum* has received little scientific attention. Consequently, its biology is not well known.

Unlike tridacnids, *Corculum* does not gape to expose its zooxanthellae to light. In fact, it cannot employ gaping to expose the algae because the shell's umbos restrict the bivalve's gape to only a few degrees. RAUP (1966) noted the severe valve overlap in *Corculum*, and observed that the two umbos are slightly offset to permit the clam to open. The zooxanthellae are situated within the mantle and gills and are densely packed in the anterior mantle epithelia (KAWAGUTI, 1950, 1966). Under the posterior (upper) valve regions, the algae are stacked in two layers: a thin covering in the posterior mantle and a dense population in the directly subjacent gills (KAWAGUTI, 1966).

Except for the narrow peripheral mantle fringe, the gills and mantle tissue containing the zooxanthellae are

always covered by the shell. Instead of direct exposure, *Corculum* appears to employ a "windows" strategy to culture its symbionts, utilizing a unique set of shell modifications to enhance light penetration through the posterior shell surface (KAWAGUTI, 1950; SEILACHER, 1972, 1973). The animals are noticeably compressed in the antero-posterior direction (Figures 1, 2) and the posterior region of the shell is thin. Located in the posterior region are numerous transparent areas arranged in radial rows. SEILACHER (1972) and VOGEL (1975) suggested that the roughly triangular to dendritic clear areas function not only as transparent windows, but also as optical lenses providing maximum light diffusion.

The purpose of this investigation was to examine the structure and properties of these putative windows and to learn how they might have evolved through modification of pre-existing shell microstructure. Preliminary investigation suggested two possible origins for the windows. Modifications of the aragonite microstructure that constitutes the shells might account for the shape and nature of the windows. Secondly, concomitant changes in shell pigmentation may enhance the transparency of the windows. We also examined the light transmission properties of the shells in order to determine whether the windows afforded any significant increase in light transmitted to the shell interior.

MATERIALS AND METHODS

Specimens of *Corculum cardissa* (Linnaeus, 1758) and *Fragum fragum* (Linnaeus, 1758) were provided by the California Academy of Sciences. Additional specimens of *Corculum* were collected live at the Motupore Island Research Center (9°32'S; 147°16'E) in Papua New Guinea. The shells were in good condition, with clean, unmarred surfaces. For preliminary observations, petrographic slides of radial sections of *C. cardissa* and *F. fragum* were prepared and studied under a polarizing microscope. For scanning electron microscopy (SEM), shells were sectioned and fractured in radial, oblique, and tranverse orientations. Sectioned specimens were then polished and etched in dilute hydrochloric acid. Specimens were mounted, coated with gold/palladium, and examined with a Hitachi S-450 Scanning Electron Microscope housed in the Geology Department at the University of California, Davis. Further SEM work was done in the laboratory of J. G. Carter at the University of North Carolina, Chapel Hill.

Two additional techniques were utilized to examine shell microstructure. Pieces of shell were embedded in lucite plugs and sectioned in radial, oblique, and tranverse orientations. Acetate peels were then prepared from the polished and etched sections and examined under a light microscope. Embedded sections were also mounted, coated and examined under SEM. These techniques are detailed in CARTER (1980a).

Measurements of light transmission characteristics of different parts of the *Corculum* shell were obtained using a microspectrophotometer. Pieces of shell were mounted on glass slides, with cover slips, in an embedding wax. The percent light transmission was then measured for the anterior region of the shell, the posterior non-window portion, and the windows. Measurements were taken every 10 nm at wavelengths from 420 to 700 nm. Measurements are given as percent of incident light at the specified wavelength transmitted through the shell, relative to that transmitted through the glass slide, cover slip, and mounting medium.

RESULTS

Anterior Shell Microstructure of *Corculum*

The region of the *Corculum* shell anterior to the pronounced medial keel is composed of three types of microstructure arranged in layers. (Terminology for microstructure employed here follows CARTER, 1980a.) The relatively thin outer layer of the shell consists of fibrous prismatic crystals (Figure 3). Previous workers (TAYLOR *et al.*, 1973) have found cardiacean shells to be entirely aragonitic, and the morphology of the fibrous prismatic crystals and of crystals forming the other shell layers is consistent with that observation (for comparisons, see CARTER, 1980a). The prisms are oriented in a plumose

pattern, running parallel to the shell surface and then radiating away from the central axis toward the interior and exterior surfaces of the shell. The central plane of this layer tends to form a natural breakage plane parallel to the surface of the shell. Throughout the layer, the prisms have identical ratios of length to width.

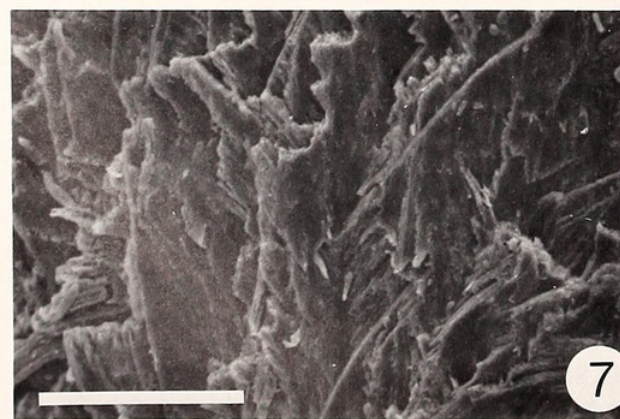
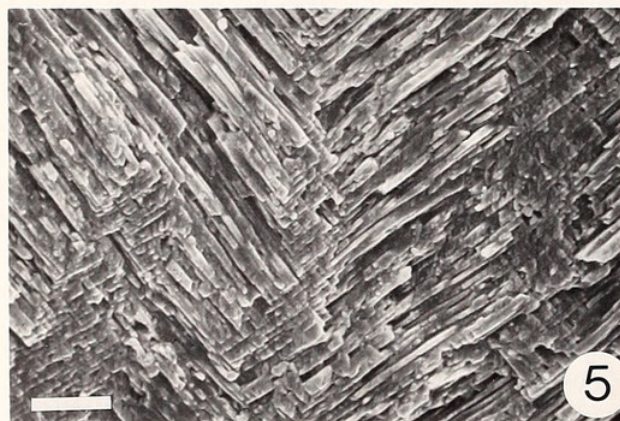
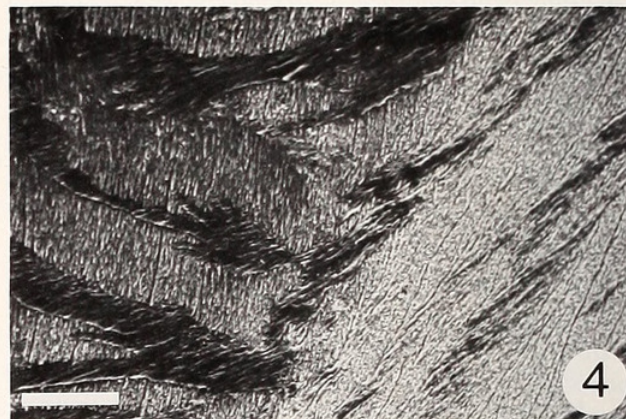
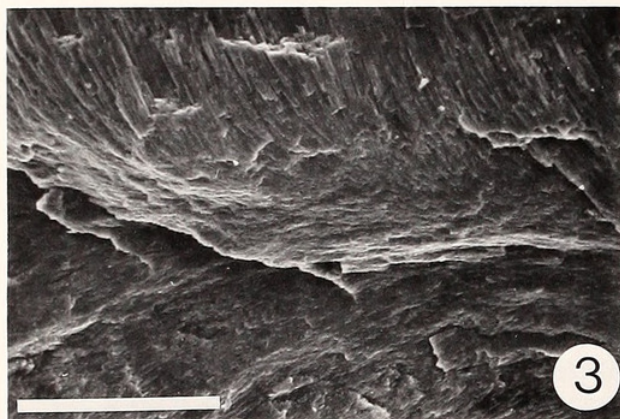
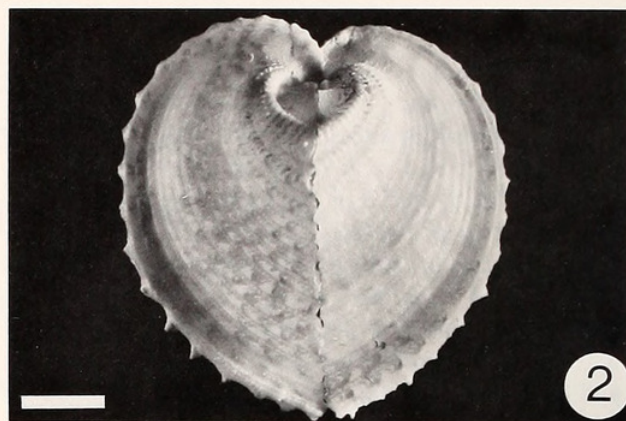
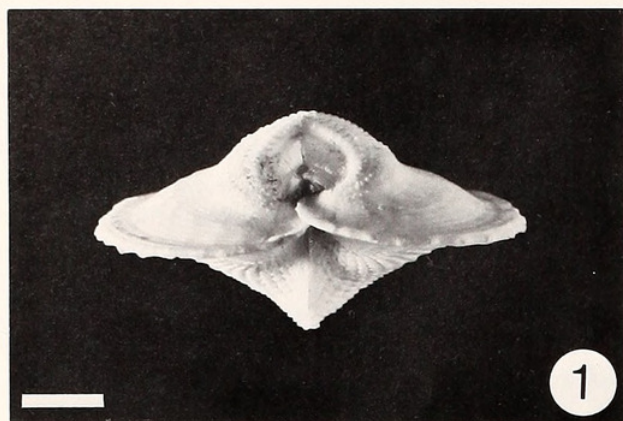
Directly underlying the fibrous prismatic layer is a thick layer of irregular complex crossed-lamellar shell material. This microstructure is an irregular three-dimensional arrangement of aragonite crystals with three or more crystal orientations. In radial section, the pattern produced by the different orientations resembles dendritic striping (Figure 4).

The innermost shell layer consists of an interdigitating cone-complex crossed-lamellar structure (Figure 5). Aragonite crystals are arranged in a pattern of stacked cones, with the crystals radiating downward from the apices of the cones. This pattern presents nearly identical appearances when viewed in any direction normal to the shell surface, thus distinguishing it from the irregular complex crossed-lamellar structure. In some places, especially where the shell is flexed by formation of a plication, the cone-complex crossed-lamellar structure grades upward into the irregular complex crossed-lamellar structure.

Posterior Shell Microstructure of *Corculum*

The shell is thinner posterior to the medial keel than in the anterior portion. Also, the microstructure is strikingly different. The outer fibrous prismatic layer is in places greatly thickened, extending through the underlying layers to the interior surface of the shell. Where the fibrous prismatic layer penetrates to the interior shell surface, the crystals are greatly elongated and oriented perpendicular to the shell surface. These elongated prisms constitute the features previously described as windows (Figure 6). Small topographic highs form on the interior shell surface where the fibrous prismatic layer reaches to the shell surface. Figure 8 presents a block diagram showing the geometric arrangement of fibrous prismatic crystals within the shell.

The non-window matrix of the shell posterior is composed of irregular complex crossed-lamellar microstructure and a very reduced layer of cone-complex crossed-lamellar structure. Our observations of petrographic slides of *Corculum* under polarized light indicate windows contain unpigmented growth lines. In contrast, non-window areas do contain pigment, suggesting pigmentation is suppressed during window formation. The combination of pigmentation and type of microstructure undoubtedly contributes to the visually obvious variation in translucency of the *Corculum* shell posterior. Interestingly, there are also relatively translucent areas in the shell anterior, though these areas are not as pronounced as the windows. There is no variation in microstructure associated with these patches, suggesting the effect is due entirely to pigmentation.



Shell Microstructure of *Fragum fragum*

There is no significant differentiation of the microstructure in the anterior and posterior parts of the *Fragum fragum* shell. The shell is also less compressed, thicker, and visibly more opaque. The *Fragum* shell contains a more diverse suite of microstructure; four types of microstructure are found in contrast to the three occurring in *Corculum* (Figure 7). The outermost shell layer is composed of relatively thin, fibrous prismatic aragonite. Underlying this layer is a thin, irregular complex crossed-lamellar layer. Subjacent to this is a relatively thick, extensive layer of simple crossed-lamellar microstructure. This microstructure, not found in *Corculum*, consists of laths of aragonite arranged in two orientations within parallel primary sheets, with adjacent sheets having alternate lath orientations. The innermost layer is a relatively thick layer of cone-complex crossed-lamellar structure that occurs dorsal to the pallial line and is separated from the overlying layer by a thin pallial myostracum.

Light Transmission Characteristics of the *Corculum* Shell

Windows transmit as much as 40% of incident light, and a full order of magnitude more light than either posterior shell matrix or anterior portions of the shell. Light transmission is relatively poor in the shorter wavelengths, but increases rapidly through the greens, yellows, and reds (Figure 9). At the long end of the spectrum, transmission is again reduced. The windows provide significant increases in light transmission at wavelengths important for photosynthesis.

Compared with the anterior part of the shell, the relatively thin posterior shell matrix transmits more light, but the maximum transmission is only a few percent of incident light (Figure 9).

DISCUSSION

Our results indicate that a combination of pigmentation and shell microstructure greatly increases the intensity of light transmitted to the shell interior of *Corculum*. Presumably, this is an adaptation for the benefit of the symbiotic dinoflagellates inhabiting the clam's tissues. The evolutionary pathways followed in development of the unique windows of *Corculum* can be inferred from com-

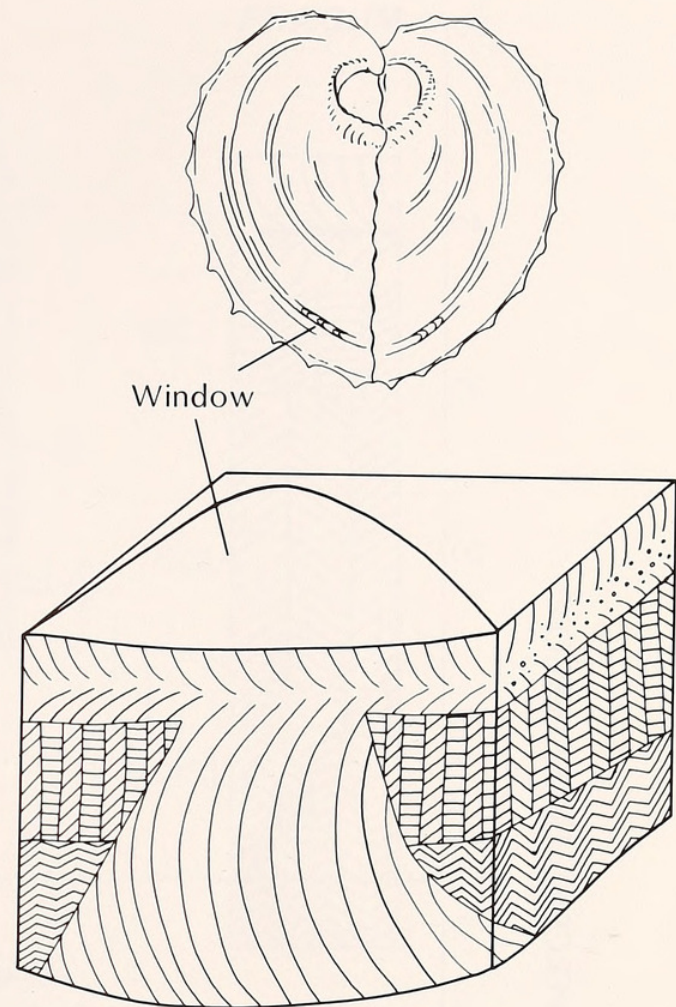


Figure 8

Block diagrams showing the geometric arrangement of the three microstructural layers that constitute the posterior portion of the shell of *Corculum*. Expansion of the fibrous prismatic layer and penetration of the prisms to the inner shell wall form light-transmitting structures, or windows. Drawn approximately to scale.

parison of character states present in *Corculum* and *Fragum*.

The role of pigmentation in enhancing shell transparency is not entirely clear from our results, nor is the general phenomenon of shell pigmentation well understood. Research to date (for review, see CRENSHAW, 1980) sug-

Figure 1. Ventral view of *Corculum cardissa*. Scale bar = 2 cm.

Figure 2. Posterior view of *C. cardissa*. Scale bar = 2 cm.

Figure 3. Outermost, fibrous prismatic microstructural layer of anterior shell of *C. cardissa*. Scanning electron micrograph of fractured radial section. Scale bar = 50 μ m.

Figure 4. Irregular complex crossed-lamellar microstructure of anterior shell of *C. cardissa*. Scanning electron micrograph of polished and etched oblique section. Scale bar = 50 μ m.

Figure 5. Innermost cone-complex crossed-lamellar microstructure layer of posterior portion of *C. cardissa* shell. Scanning electron micrograph of fractured radial section. Scale bar = 5 μ m.

Figure 6. Expanded, window-forming fibrous prismatic microstructure of posterior shell of *C. cardissa*. Scale bar = 5 μ m.

Figure 7. Simple complex crossed-lamellar microstructure of *Fragum fragum*. Scanning electron micrograph of fractured transverse section. Scale bar = 50 μ m.

Explanation of Figures 1 to 7

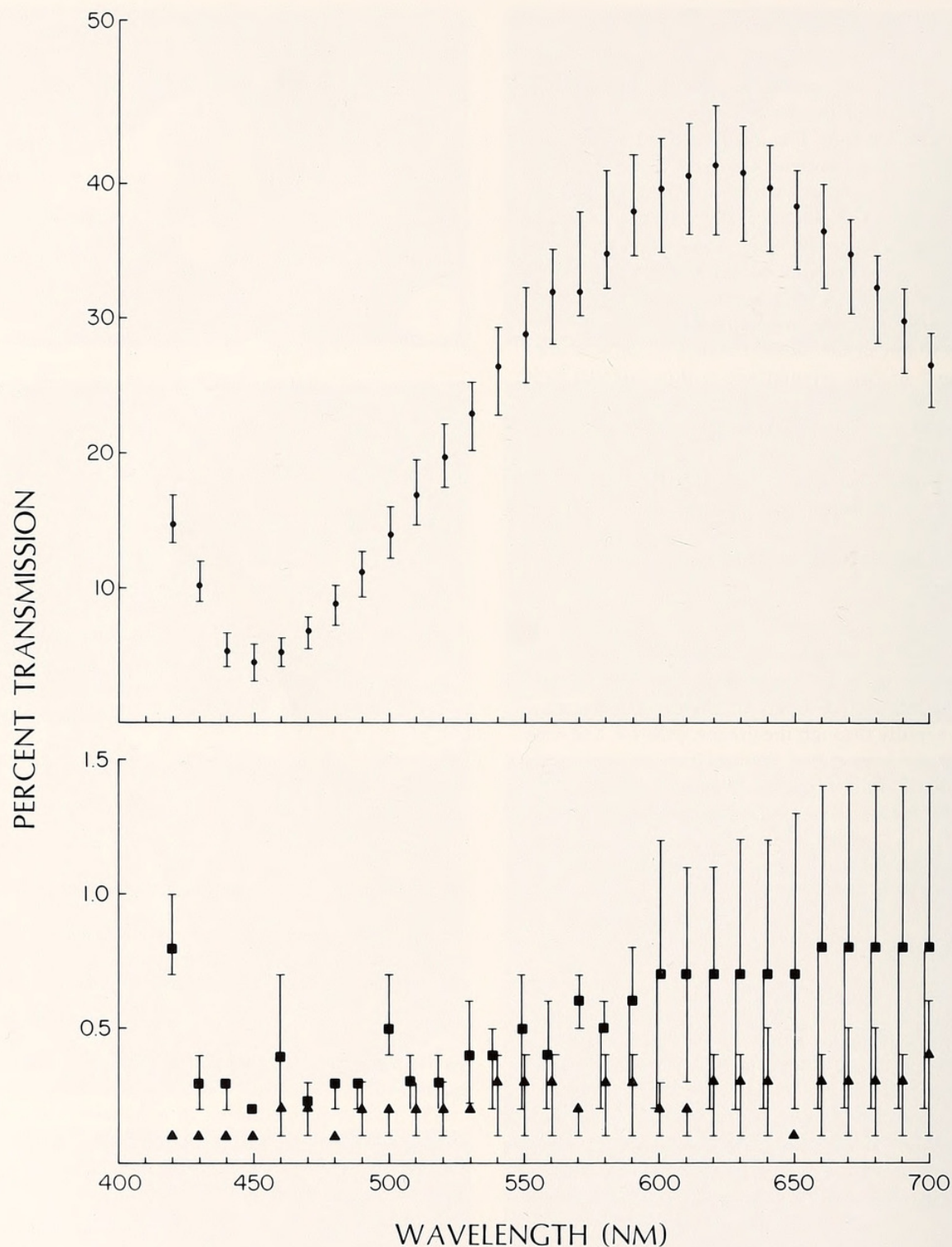


Figure 9

Transmission characteristics of the shell of *Corculum cardissa*. Circles indicate mean value for four windows, lines indicate range of readings. Squares indicate values for four readings on the shell matrix of the shell posterior, and triangles indicate percent transmission for four areas of the anterior shell of *Corculum*. Lines above and below squares and triangles represent ranges of values obtained.

gests changes in organic content and concentration are linked to salinity fluctuations, mantle irritation, and anaerobiosis during shell deposition. It is perhaps suggestive that the prismatic layer of both the anterior and posterior

portions of *Corculum* and *Fragum* contain no pigmented growth lines. Thus, simple expansion of the prismatic layer may be sufficient to cause an increase in light transmission.

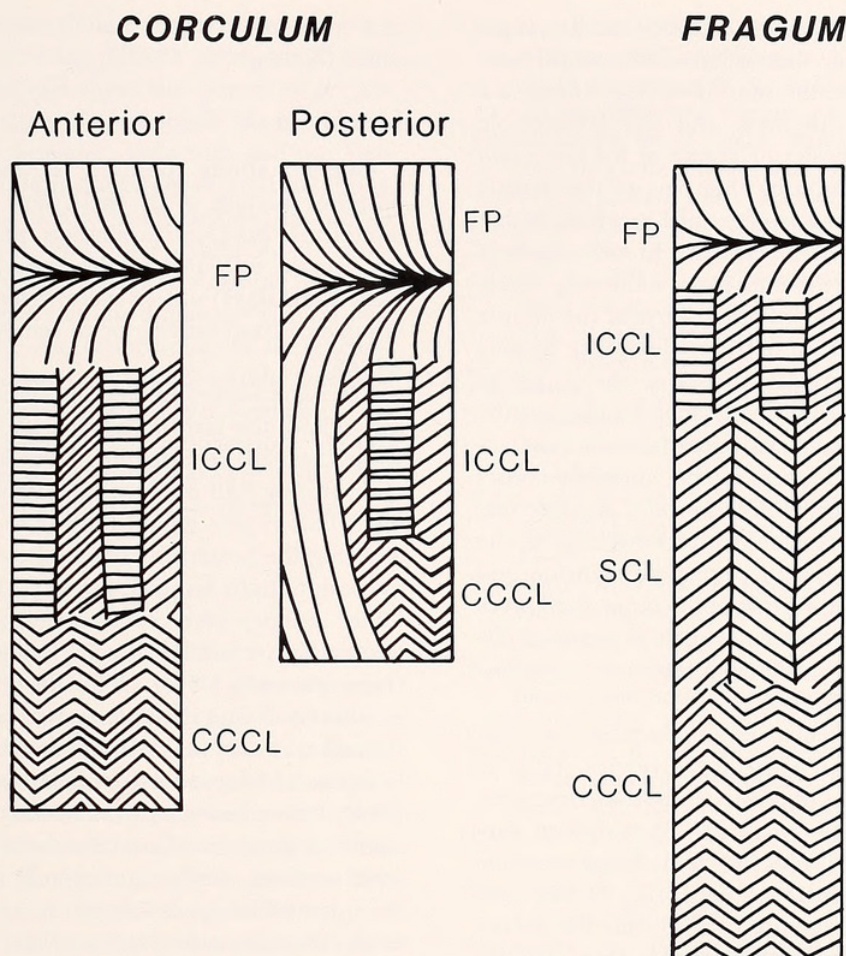


Figure 10

Comparison of shell architecture of *Fragum* and *Corculum*. Layers indicated as follows: FP, fibrous prismatic; ICCL, irregular complex crossed-lamellar; CCCL, cone-complex crossed-lamellar; and SCL, simple crossed-lamellar. Not drawn to scale.

On the other hand, several modifications of the *Corculum* shell occurred, leading to the present combination of gross morphology and the presence of windows. These include antero-posterior flattening of the shell (with a concomitant increase in the ratio of surface area to shell volume), thinning of the posterior portion of the shell through reduction in the number of shell layers and thinning of the remaining layers, and differential expansion of the fibrous prismatic layer resulting in triangular, clear windows in the posterior region of the shell. The peculiar, flattened shell of *Corculum* and the windows are unique among modern bivalves, but reduction in the numbers of microstructural layers is a common occurrence in the evolution of bivalve clades (TAYLOR *et al.*, 1973; TAYLOR, 1973; CARTER, 1980b).

Comparison of the shell microstructure of *Fragum* and *Corculum* reveals several evolutionary modifications (Figure 10). Both *Fragum* and *Corculum* have an outermost fibrous prismatic layer. However, this layer is relatively thin in *Fragum* and well developed in *Corculum*. Underlying the fibrous prismatic layer in both *Corculum* and *Fragum* is an irregular complex crossed-lamellar layer. In *Fragum* the irregular complex crossed-lamellar layer is

thinner and more variable in extent than in *Corculum*, where it represents a major microstructural component of the shell. Whereas *Corculum* lacks a simple crossed-lamellar structure, in *Fragum* it is a major component of the shell. The inner shell layer of cone-complex crossed-lamellar structure occurs in both *Fragum* and *Corculum*, but is much reduced in the posterior portion of the latter. In *Fragum*, a noticeable prismatic myostracum separates the inner cone-complex crossed-lamellar layer from the simple crossed-lamellar layer, but in *Corculum* the myostracum separating the inner cone layer from overlying irregular complex crossed-lamellar structure is prominent only in the anterior portion of the shell. Thus, the major evolutionary modifications apparent in the transition from the typical *Fragum* shell structure to that of *Corculum* are an elimination of the simple crossed-lamellar layer, an elaboration of the fibrous prismatic layer, and a differentiation of patterns of deposition between the anterior and posterior portions of the *Corculum* shell.

The absence of a pallial myostracum and reduction in the extent of the cone-complex crossed-lamellar layer in the posterior region of the *Corculum* shell suggests a significant change in the pattern of shell deposition by the

mantle. Because the cone-complex crossed-lamellar layer lies below the myostracum, the region of the mantle depositing this layer must be the mantle surface inside the pallial line. The lack of this layer and any appreciable myostracal prisms in the posterior region of the *Corculum* shell indicates that deposition by this part of the mantle must be suspended. The mantle edges of *Corculum*, which deposit the fibrous prismatic layer, must at times greatly increase the rate of deposition to form windows, while deposition continues normally at other parts of the mantle margin. This demonstrates an extreme flexibility in patterns of deposition and greatly increases the range of structures that potentially could be formed by the mantle.

CARTER (1980b) has found that expansion or contraction of shell microstructural layers during ontogeny occurs in at least three bivalve genera. *Mercenaria*, *Cerastoderma*, and *Spisula* show either occasional inter-tonguing of the outer and middle shell layers, or periodic expansion and contraction of the area of deposition of the outer shell layer in response to environmental stresses such as seasonal climatic changes and thermal shock or in response to spawning.

Observations of shell structures in *Corculum cardissa* and *Fragum fragum* reveal a greater diversity, both in variety and arrangement, of microstructure than described by earlier workers. TAYLOR *et al.* (1973) described cardiacean microstructure in general, and *Fragum unedo* (Linnaeus, 1758) in particular, as consisting of two concentric layers: an outer aragonite crossed-lamellar structure and an inner complex crossed-lamellar layer usually separated by a thin prismatic myostracum. The surprising diversity of shell microstructure now known to be present in *Corculum* and *Fragum* suggests the possibility of undiscovered diversity and variation in the microstructure of other molluscan taxa.

Photosymbiosis in *Fragum*

KAWAGUTI (1983) has recently reported the presence of symbiotic dinoflagellates in *Fragum fragum* and *F. unedo*. In the latter species, the photosymbionts are primarily concentrated in the enlarged mantle tissues around the siphons and in the gills. Kawaguti reports that this species lives buried shallowly in the sediment, with enlarged mantle tissues around the siphons spread over the sediment. In contrast, Kawaguti reports that *F. fragum* lives with the posterior side of the shell above the sediment. This species lacks the enlarged mantle tissues and does not gape widely. (PWS confirms these observations on *F. fragum* from field and laboratory work in Guam.) In *Fragum fragum* the zooxanthellae are distributed throughout the animal, and are concentrated in the gills and mantle. In this species, light transmitted through the shell apparently sustains the enclosed zooxanthellae, as in *Corculum*. Thus, these three species seem to constitute an evolutionary series from *Fragum unedo*, which uses a *Tridacna*-like strategy of directly exposing zooxanthellae-laden tissue to light,

to *Corculum*, where the shell encloses the animal at all times (KAWAGUTI, 1983).

Life Habits of *Corculum*

One remaining question is how *Corculum* keeps the posterior surface of its shell clear of fouling and boring organisms. Surfaces in shallow marine environments do not remain unfouled in the Indo-Pacific for long (more than a few days) unless there is some mechanism to deter organisms from settling or to remove organisms that have settled.

Corculum occurs in shallow intertidal to subtidal areas throughout the Indo-Pacific region (BARTSCH, 1950). KAWAGUTI (1950) reported that *Corculum* occurs around reefs, often resting half obscured by filamentous algae and rubble. (This report would appear to contradict the suggestion that the posterior surface of the *Corculum* shell serves to conduct light to algae living within the clam's tissues.) Other authors have reported *Corculum* occurring in shallow sandy or muddy areas (Franco in BARTSCH, 1950; CERNOHORSKY, 1972). One of us (PWS) recently was able to observe living *Corculum cardissa* and *C. monstrosum* (Gmelin, 1791) at Motupore Island in Papua New Guinea. At Motupore Island, the two species occur intertidally. *Corculum monstrosum* was found living free on a sand and grass flat; *C. cardissa* was found living in a sheltered area on sandy mud among intertidal rocks on the lee side of Motupore Island. In each case, the shell posterior was exposed to the sunlight and was free of algae or fouling organisms.

Corculum maintained in aquaria will migrate within the tank from shady to sunny areas. If overturned, they will right themselves by planting the foot in the substrate and rotating the entire shell onto its anterior surface. The foot also occasionally sweeps the posterior surface of the shell, and may be the mechanism for keeping that area free of fouling organisms.

Comparison of *Corculum* and *Notoacmea*

There is an interesting morphological parallel between the *Corculum* windows and the limpet *Notoacmea persona*. LINDBERG *et al.* (1975) noted the presence of light-transmitting spots in the anterior shell of *N. persona*, and demonstrated that these spots play a role in the limpet's negatively phototropic reaction to light. The *Corculum* windows might also facilitate the bivalve's positive response to light noted above, but that was not tested. Nevertheless, the structures documented in the limpet windows by LINDBERG *et al.* (1975) and in *Corculum* (this paper) are quite distinct.

Recognition of Photosymbiosis in Fossil Bivalvia

Depending on the degree of preservation, shell modifications such as those seen in *Corculum* could be recognized in the fossil record. Unusual shell thinness, indica-

tive of translucency, would be especially obvious. Recognition of other modifications such as prismatic windows or layers would depend upon the degree of preservation, especially for aragonitic structures. Even though only two Recent bivalve lineages, tridacnids and the *Fraginae*, are known to maintain symbiotic algal associations, given the broad spectrum of Recent organisms that harbor algae we should expect to find other examples of paleophotosymbiosis in the fossil record. For example, YANCEY (1982) has recently interpreted an unusual Permian myalinid bivalve group, the Alatoconchidae, as the earliest photosymbiont-bearing bivalves. Alatoconchids resemble tridacnids in size and shell thickness, yet resemble *Corculum* in terms of antero-posterior compression, life position, and prismatic microstructure. COWEN (1983) has reviewed the evidence for photosymbiosis in bivalves and other fossil clades.

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During the course of this investigation, we learned that an independent study of *Corculum* microstructure was being conducted by Mr. Clement Counts, III, at the University of Delaware (Counts, 1981). We thank Mr. Counts for outlining his project for us, sharing his ideas on cardiacean microstructure and providing suggestions on techniques employed here.

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