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## The Ultrastructure of Five Common Pennsylvanian Pleurotomarian Gastropod Species of Eastern United States

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### ABSTRACT

The shell ultrastructure of five pleurotomarian gastropod species from the Pennsylvanian is described and variation discussed; in addition, some observations are made of three bellerophonitid species. Two thin outer shell layers previously unknown are analyzed. The outermost of these is fibrous and about  $10\ \mu$  thick; it appears to be the only one that is actually involved in the topographic expression of growth. The two principal layers of the species studied are an outer complex prismatic layer and a thicker inner nacreous layer. There is an innermost complex prismatic unit which is variable in development and may be absent in some species. Several types of pallial myostracum are present in all species examined. The importance of shell structure in elucidating the origin and phylogeny of molluscan groups is briefly discussed. Most variation of ultrastructure appears to occur within or between species and is quite conservative between larger taxonomic units.

### INTRODUCTION

The study of microscopic elements of gastropod calcified walls has had a long history with the work of Carpenter (1844) serving as a base. Recently, there has been an increased interest in calcified tissue studies stimulated by the development of the stereoscan electron microscope (Wise, 1969). Fossil gastropod wall structure has, in general, not attracted many students

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and most work has been ancillary to a study of modern families (see Bøggild, 1930). Copeland MacClintock (1967) in his important study of patellid gastropods, included a careful study of several species of bellero-phontid gastropods and established the basic structural types for Paleozoic archeogastropods. Importantly, his work is one of the first to elucidate the topography of first order crossed-lamellar structure in relation to the surface of the layers.

The purpose of the present study is to initiate a description of the walls found in Paleozoic pleurotomarian species and to investigate variation within ultrastructure. The ultimate goal, as the study continues, is to attempt to utilize ultrastructure data as an additional morphological dimension in the evolution, systematics, and, perhaps, paleoecology of fossil gastropods. It is not the present purpose to discuss the origin, chemistry, crystallography or function, in a precise sense, of fossil gastropod ultrastructure.

### FOSSIL PRESERVATION AND OCCURRENCE

Initial interest in the study of fossil gastropod ultrastructure was developed by the discovery that almost perfectly preserved molluscs and other organisms can be found in a number of Pennsylvanian horizons in a widespread area of the eastern United States. The first well-preserved fossils from this region were reported by Newell (1938) and Stehli (1956) from the Kendrick Shale (Pottsville Group of the Lower Pennsylvanian) in the type area of eastern Kentucky. The most prolific and largest exposure of the Kendrick Shale is found in a strip mine near Pikeville, Kentucky (AMNH Loc. 2093). (See pp. 6–7 for other localities.)

The Pennsylvanian molluscs discussed herein occur in black organic, rich marine shales that may be found with marine limestones and which directly overlie coal deposits associated with cyclic strata. In general, the greatest number of fossils have been completely recrystallized. In most instances, large calcite crystals stained with, or incorporating what appears to be, siderite, seem to indicate that the original structure was gradually replaced with calcite. This is reinforced by the observation that many specimens show a range of preservation from complete recrystallization to almost perfect preservation in a single specimen. Usually, wall recrystallization is progressive toward the early ontogenetic whorls and, invariably, the associated matrix is progressively reinforced by siderite. The matrix in the early whorls is, in fact, a dense siderite nodule. As yet, no tests have been made to identify the calcium carbonate mineral type. It is hoped that a microprobe analysis will be made to resolve this problem. Stehli (1956) and Yochelson, White, and Gordon (1967) have shown that



FIG. 1. *Shansiella carbonaria* (Norwood and Pratten), AMNH 29222. From Wewoka Formation (Pennsylvanian) at Holdenville, Oklahoma.  $\times 2$ .

aragonite is preserved in Kendrick Shale gastropods belonging to the same species. In addition, many of the wall structure types described below are identical with those of living forms which have been shown to be composed of aragonite. We will therefore make the assumption that: (1) the original structural types described below were aragonite; and (2) those structures which are illustrated herein are not appreciably recrystallized, except where noted.

In most specimens, secondary deposits of calcite have invaded the wall structure to some extent (fig. 21).

It must be emphasized that it has not been possible to recognize organic matrix or cement even in the best preserved nacre (the nacreous layer tends to have more organic matrix than other wall structure types in recent specimens) (fig. 28). Additionally, some leaching may take place along with the breakdown of the organic component (fig. 5). The best wall preservation is found in specimens that are white and chalky in appearance; this may be due to leaching of the outermost layer (fig. 2). Rarely, specimens show little or no leaching and these have a cream color with details of ornament more sharply visible. The better preserved specimens are usually found in freshly exposed shale in coal strip mines. In older strip mines, specimens are nearly completely leached (due to sulphuric acid corrosion derived ultimately from pyrite-rich layers). Bellerophonitids generally tend to be better preserved than other molluscs, with the murchisonid and euomphalid gastropods least likely to retain adequate preservation.

The scarcity of well-preserved material is illustrated by the fact that of the 27 specimens of *Shansiella carbonaria* (Norwood and Pratten) collected for this study, only seven were usable. Of thousands of snails collected, fewer than 100 specimens were adequately preserved. Only five pleurotomarian species were found: *Glabrocingulum* (*Glabrocingulum*)

*grayvillensis* (Norwood and Pratten), 1855; *Phymatopleura nodosa* (Girty), 1911; *Worthenia tabulata* (Conrad), 1835; *Trepostira illinoiensis* (Worthen), 1884; and *Shansiella carbonaria* (Norwood and Pratten), 1855. Of these, *S. carbonaria* was best preserved and had the thickest walls (thin-walled forms rarely are well preserved).

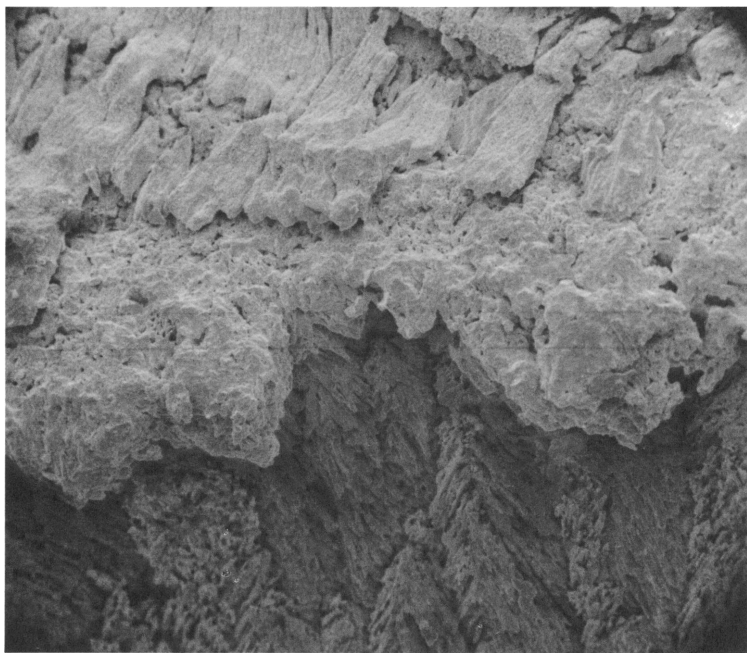


FIG. 2. *Shansiella carbonaria*, AMNH 29223. From Putnam Hill Shale (Pennsylvanian), Smith Township, Ohio. AMNH Loc. 3084. A fragment near aperture, taken from third spiral rib above selenizone. This is a vertical cross section of outer layers. Note flaring of each bundle of fibrous blades composed presumably of aragonite crystals.  $\times 1150$ .

As the wall structure types are basically similar, detailed discussion will involve the seven specimens of *S. carbonaria* and comparisons will be made with other species where appropriate. A few observations will be made of other species of archeogastropods such as the bellerophonitids.

#### METHODS

To interpret properly the nature of gastropod ultrastructure, it is essen-



tial to use a variety of techniques to obtain a four-dimensional concept. For general orientation, thin sections or etched and stained polished sections were studied at low magnification using an optical microscope. The latter type of section was prepared with the combination carbonate

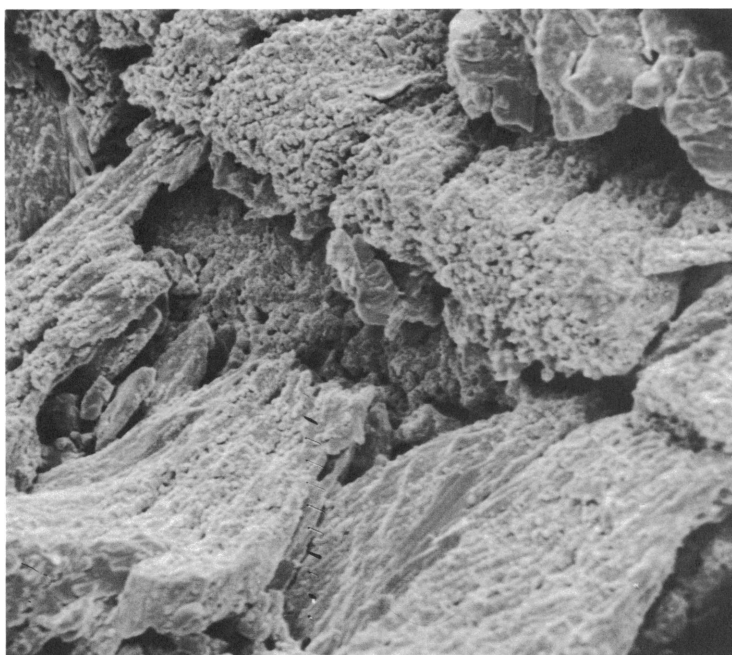


FIG. 3. *Shansiella carbonaria*. An enlargement of an area just to the right of center along top margin of figure 2, showing flaring of fibers in each bundle.  $\times 2100$ .

stain described by Katz and Friedman (1965) and studied using epillumination.

Broken fragments of shells were initially studied with an optical microscope and after orientation and selection of areas on the shell that were best preserved, the fragments were mounted on standard SEM (Scanning Electron Microscope) specimen stubs and shadowed in vacuum with gold or gold-palladium. Polished and etched wall sections for use on the SEM were prepared in the same way (Wise and Hay, 1968). Transmission electron microscopy essential to the study of crystal and intercrystal growth as well as for organic matrix observations was not used as the preservation of the material did not warrant such study.



FIG. 4. *Shansiella carbonaria*. Same fragment as figure 2. Looking down on surface of shell between ribs. Bottom half of photograph showing outer two layers with growth lines, only a small portion of second platy layer visible as a granular area just to right of center. Note that platy layer and underlying elongate complex prismatic layer show no growth increments. First order elongate prisms (see p. 11 for discussion) are dipping at an angle to surface causing an asymmetrical appearance to second order blades. Outermost fibrous layer is leached, so that growth imbrications are overemphasized.  $\times 75$ .

#### LOCALITIES<sup>1</sup>

(All localities are in the Pennsylvanian)

AMNH Loc. 2093. Kendrick Shale (Pottsville Group): 3 to 5 feet above coal in high wall of abandoned strip mine, 500 yards SE emergency landing strip at about the 1480-foot contour line. On road branch about  $1\frac{1}{2}$  mi. by road from the confluence of road branch and Island Creeks south of Pikeville, Kentucky. Locality discovered by Donald Alvord of the United States Geological Survey and marked on the geological quadrangle sheet of Pikeville, 1965 edition.

AMNH Loc. 3003. Vanport Shale (Allegheny Group): Keller Strip mine; spoil banks of shale 100 yards SE from corner of Oyster and Greenbower (Middletown) roads, about 2 mi. NE Alliance, Ohio, in NE  $\frac{1}{4}$  north central sec. 18 and

<sup>1</sup> The abbreviation AMNH refers to the American Museum of Natural History.

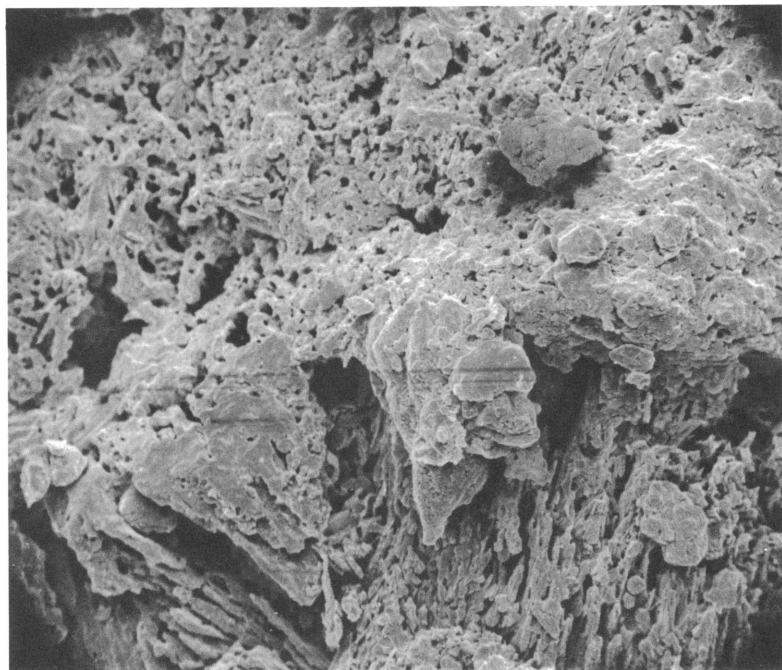


FIG. 5. *Shansiella carbonaria*. Side view of same fragment as in figure 2. Photo taken from center of figure 4. Note plates or tiles, which are essentially vertical, of second platy layer. Triangular blade cluster just to left of center is not in place.  $\times 1150$ .

SE  $\frac{1}{3}$  south central sec. 7, T 18 N, R6W Alliance 7.5' Quad. sheet (Topographic). Locality discovered by William Augur.

AMNH Loc. 3084. Putnam Hill Limestone (Allegheny Group): Spoil banks of abandoned strip mine  $\frac{1}{2}$  mi. NE junction of Martin and Middletown roads west central  $\frac{1}{2}$  Sec. 8, Smith Township, Mahoning County, Ohio. Locality discovered by Myron Sturgeon.

AMNH Loc. 2098. Brush Creek Shale (Conemaugh Group): Large road outcrop on west side of secondary paved road going north from Route 422 about 0.45 mile west of intersection of Routes 422 and 156. Collected from shale 1 foot above limestone at base of section, near Shelocta, Pennsylvania.

#### ACKNOWLEDGMENTS

I thank Prof. H. K. Erben of the University of Bonn for his most generous help and advice. He began the SEM study that forms the nucleus of this report and made important observations that guided this study in many ways. Dr. Erben supplied the SEM photographs for figures 7 and 29.



FIG. 6. *Cellana testudinaria*, AMNH 29224. A recent patelloid. Fragment from innermost layer showing a second order complex crossed-lamella, as defined by MacClintock. Second order lamellae that make up first order are represented by elongated blade seen best at right side of cone.  $\times 200$ .

However, I accept full responsibility for the content of this report.

Drs. H. B. Rollins and Myron Sturgeon contributed important specimens used herein. Dr. Sturgeon generously spent time in the field with me at many Ohio fossil localities which he discovered. Drs. Copeland MacClintock, N. D. Newell, Niles Eldredge, and H. B. Rollins, along with Mrs. Patricia Shaikh, all provided stimulating and useful discussion. Mrs. Shaikh and Mr. Michael P. Dumont aided me in sample preparation and in the operation of the SEM. Most of the SEM photographs were taken on the Cambridge Stereoscan of Lamont-Doherty Geological Observatory. I thank Drs. Andrew MacIntyre and Allan Bé, Mr. Stanley Harrison, and Mrs. Diane Currie of Lamont-Doherty Geological Observatory for their generous cooperation and help during the course of this study.

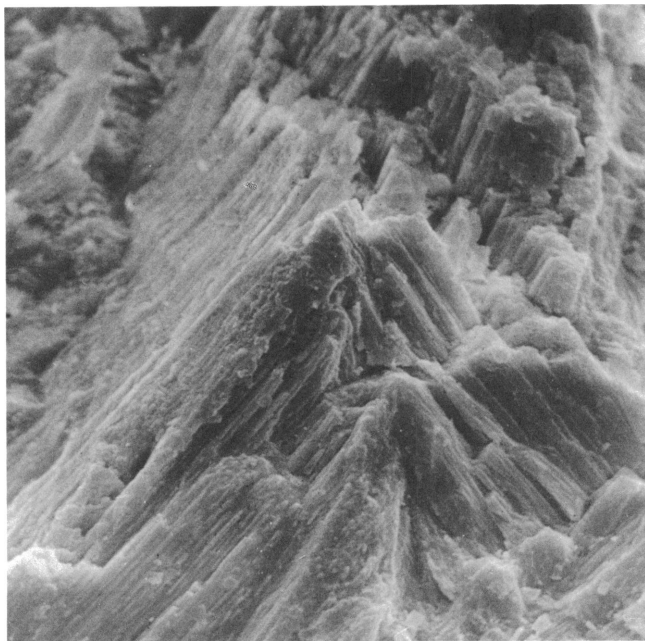


FIG. 7. *Cellana testudinaria*, another specimen, Bonn Univ. 9498. Vertical cross section showing detail of second order lamella. Note lack of any regular subdivision of blades. SEM photography courtesy of H. K. Erben.  $\times 2000$ .

#### SUPERFAMILY PLEUROTOMARIACEA SWAINSON, 1840

##### FAMILY PORTLOCKIELLIDAE BATTEN, 1956

##### *Shansiella carbonaria* (Norwood and Pratten), 1855

*Shansiella* is a portlockiellid pleurotomarian, which ranges in age from the Lower Carboniferous into the Permian. It is virtually cosmopolitan, found principally in marine shales and limestones. The genus is relatively conservative and generally an inconspicuous element in most faunas. It tends to be somewhat more common locally, as in the Brush Creek Shale near Shelocta, Pennsylvania (AMNH Loc. 2098), and in the Vanport shale near Alliance, Ohio (AMNH Loc. 3003).

*Shansiella carbonaria* is characterized by having globose whorls with rather coarse spiral ribbing becoming progressively finer from the upper suture to the base (fig. 1). The shell is quite gross by virtue of a rather thick shell and by possessing a large columellar callus and a parietal inductura.



FIG. 8. *Shansiella carbonaria*, AMNH 29225, AMNH Loc. 2093. Fragment (somewhat leached) from upper whorl at suture near aperture of a mature specimen. Looking down on a small portion of upper surface of innermost complex prismatic layer, showing top of several first order spherulitic complex prisms.  $\times 1050$ .

#### DESCRIPTION AND DISCUSSION OF WALL STRUCTURE

**OUTERMOST THIN LAYERS:** Two extremely thin outermost layers (about  $25\ \mu$  total) were identified in a fragment taken from the junction of the upper and outer whorl surfaces, about three spiral ribs above the selenizone and from near the aperture of a mature specimen, recovered from the Putnam Hill shale (AMNH Loc. 3084) (figs. 2, 3). The outermost of these two layers consists of a series of laterally directed fibrous bundles which appear to be flattened cones. Each unit of bundles represents a growth increment and the broad terminal face of each represents a growth line. The units are imbricate with the apex of each bundle terminating under the preceding unit (fig. 3). The axes of the bundles are normal to the growth lines; thus, the boundaries between each bundle are normal to



FIG. 9. *Shansiella carbonaria* same fragment as figure 2. Upper left is surface of shell with growth lines, showing relative thickness of outer two layers in relation to much thicker, elongate complex prismatic layer. Lower half is vertical broken edge of shell, showing outermost elongate complex prismatic layer. In lower far right corner is horizontal upper surface of stacked nacreous layer.  $\times 115$ .

the direction of growth. This fibrous layer conceivably is similar to that described in patelloids by MacClintock (1967, p. 14) as fibrillar structure. His fibrillar structure appears to be composed of elongate crystals uniform in thickness and in parallel arrangements. The diameter of the fibrils is of the same magnitude as the fibers under discussion. Also, the fibrillar layer is restricted to the outer two layers in the patelloids. However, it is much thicker—several hundred microns—than the fibrous layer under discussion. The fibrous layer, which is about  $10\ \mu$  thick, is the only one that reflects growth increments. The surface of all other layers does not show any evidence of growth phenomena (fig. 4). Thin sections cut parallel to growth, of course, do show growth lines as has been demonstrated by Pannella and MacClintock (1968), and others.

The next thin layer beneath the fibrous layer is about  $15\ \mu$  thick and is made up of a series of plates or tiles that are vertically arranged and appear



FIG. 10. *Glabrocingulum* (*Glabrocingulum*) *grayvillensis*, AMNH 29226, AMNH Loc. 2093. Fragment near aperture and just beneath selenizone, showing top surface of outermost elongate complex prismatic layer.  $\times 610$ .

to be placed at about 45 degrees to the growth lines (fig. 5). The exact nature of this platy layer is unknown as it was observed on the single fragment under discussion. It does not appear to reflect surficial growth phenomena as does the fibrous layer. Despite attempts to etch or break the walls of other specimens, these two outer layers were observed only once. I have examined a number of specimens of recent snails in an attempt to discover the exact relationship between the actual growth increment and the outermost wall layer, but thus far have not been successful. In general, recent wall structure does not fragment so well as fossils, possibly owing to the organic matrix which may serve as a cement. These layers together may be the homogenous layer described by Bøggild (1930) and may be similar in part to the distal layer of Wise and Hay (1968, p. 421) in that the crystals are oriented at about 45 degrees to the growth lines.





FIG. 11. *Shansiella carbonaria*, AMNH 29227, AMNH Loc. 3003. Looking down on eroded surface of outer elongate complex prismatic layer, showing fanning out of first order prisms in a localized area near aperture and about midway between suture and selenizone.  $\times 50$ .

## OUTERMOST COMPLEX PRISMATIC LAYER

### INTRODUCTION

Bøggild (1930) and others have described a wall type as complex or compound prismatic, consisting of a series of aragonite blades or fibers generally radially arranged about essentially vertical axis (Wise and Hay, 1968, p. 425; note that their orientation of the wall is such that the outermost layer is down). MacClintock (1967, p. 106) has interpreted the prismatic layer in the bellerophonitid *Pharkidonotus* and other snails as being complex crossed-lamellar, based partly on the observation that the inner layer of the recent patelloid, *Cellana testudinaria* Linnaeus, 1758, has stacks of cones vertically arranged and composed of aragonitic blades forming a rather solid sheet (figs. 6, 7). He regarded the individual cones as first order lamellae and the aragonite blades as second order lamellae. He has shown that the aragonite blades were further subdivided into units with the elongate axis vertical, that is, parallel to the main axis of the cones (MacClintock, 1967, p. 34).

Specimens of *Cellana testudinaria* recently examined with the SEM at much higher magnification than MacClintock had available, clearly show

that the first order cones are indeed subdivided into second order structures. But I have not been able to recognize the third order structures which should appear as regular rhomboidal prisms (fig. 6). Instead, the second order structures appear to be composed of acicular microcrystals,



FIG. 12. *Shansiella carbonaria*, AMNH 29228, AMNH Loc. 2093. Fragment near aperture and suture. Eroded surface of elongate complex prismatic layer showing abrupt change in direction (spiral and parallel to suture) of first order prisms.  $\times 180$ .

which is the condition to be expected in the complex prismatic structure. Therefore, I will consider such layers as complex prismatic reserving the term complex crossed-lamellar to those layers having third order rhomboid prisms such as in the living *Nerita* (fig. 30).

Erben, Flajs, and Siehl (1968) have shown that the complex prismatic layer at its base is composed of vertical aragonite blades which gradually bend inward to form the characteristic patterns of blades which are grouped about an axis and radiate outward and downward (fig. 8). In addition, Erben and Krampitz (In press) have shown that in living *Pleurotomaria* the complex prismatic layers change ontogenetically.



FIG. 13. *Shansiella carbonaria*. Same view, same specimen as figure 2 but with magnification  $\times 220$ .

#### DESCRIPTION

Beneath the two thin outer layers there is a rather prominent complex prismatic layer about 0.4 mm. in thickness (fig. 9). This layer is quite different from the complex prismatic layers described in the past by various workers. In this case, the layer is composed of a series of complex prisms that appear to be identical with that of radial complex prisms as seen in cross section. However, instead of the aragonite blades being arranged about an axis, they are arranged along a plane that is almost vertical (with some exceptions; figs. 4, 10). I will term this type elongate complex prismatic.

Seen from above, the prisms appear to be superficially like first order crossed-lamellar; the main difference is that the "second order" prisms are arranged downward and outward and are not solid lamellae. They do not alternate in opposing dips as does crossed-lamellar structure. The topography of the first order prisms is much like that of first order crossed-lamellae (fig. 11). It is quite variable in some species (such as in *Shansiella carbonaria*) and conservative in others (such as *Worthenia tabulata*). In

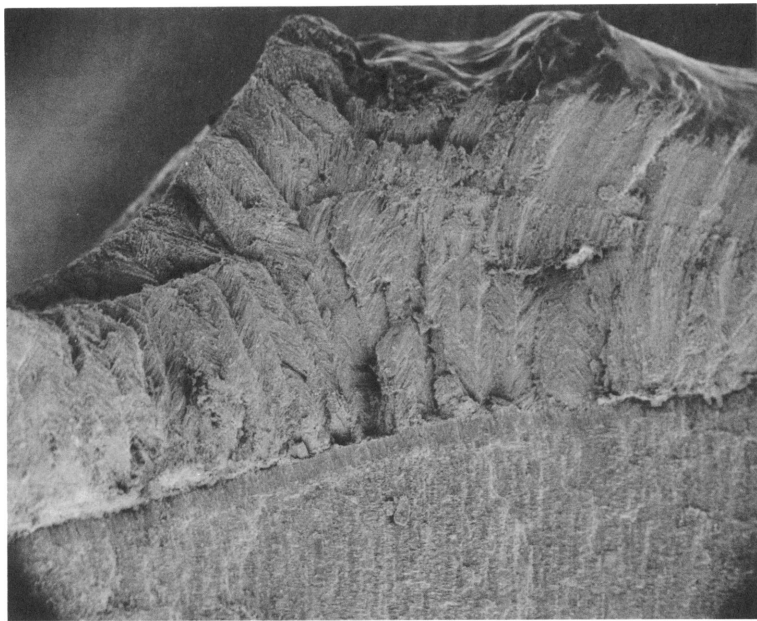


FIG. 14. *Shansiella carbonaria*, AMNH 29229, AMNH Loc. 2093. Fragment from aperture of a mature specimen showing cross section of spiral rib; note that complex prisms bend in order to retain a normal relationship with outer surface.  $\times 118$ .

*Glabrocingulum* (*Glabrocingulum*) *grayvillensis* and *W. tabulata*, first order prisms tend to be oriented spirally on the base and over most of the upper whorl surface. But in the alveozone just beneath the selenizone they swing around and are parallel to the growth lines. First order prisms continue to be parallel to the growth lines in the selenizone and the area immediately above the selenizone. In *S. carbonaria*, the first order prisms are predominantly spirally directed from suture to umbilicus, except where noted below. Immediately adjacent to the umbilicus, in all species examined, the trend of the first order prisms changes again, swinging upward into the umbilicus and becoming parallel to the axis of coiling on the inside of the shell. This distribution pattern of first order elements has also been observed in almost every recent genus examined that possesses crossed-lamellar walls. Also, all callus, parietal, and funicle deposits in and around the umbilicus in the species studied are exclusively complex prismatic of the elongate type discussed above.

The trends of first order prisms are not so constant as that observed in crossed-lamellar structure; almost all specimens studied show sudden

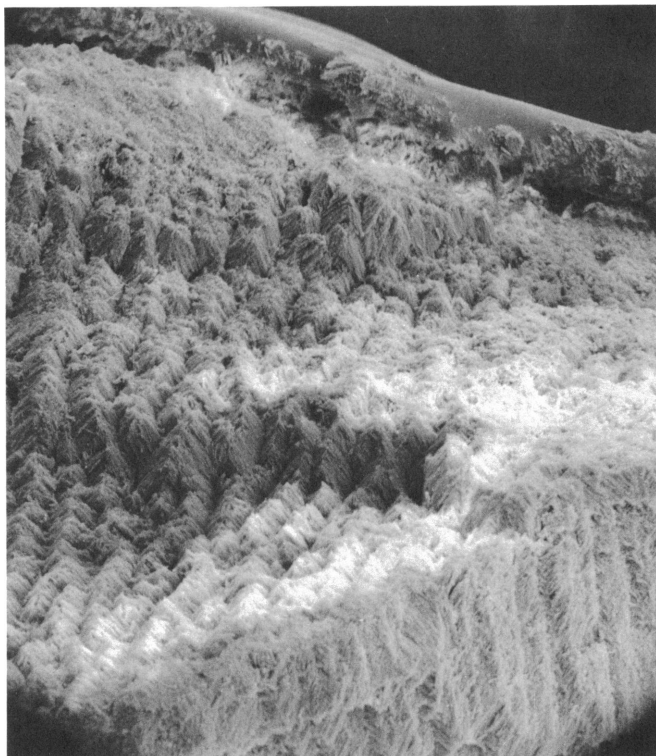


FIG. 15. *Worthenia tabulata*, AMNH 29230, AMNH Loc. 2093. Fragment from columellar lip of final whorl. Oblique view of broken surface showing vertical fracture in lower right side and elongate complex prisms three dimensionally. Note that break has produced cap-shaped projections along axis of a first order prism with some second order blades bending around cones; see also figure 11.  $\times 120$ .

directional and dip changes in localized areas. These changes are expressed by the fanning out of first order prisms (fig. 11), or by abrupt nearly right-angled change (fig. 12).

Two other types of changes were observed in both the spherulitic (to be discussed later) and elongate complex prismatic layers. Usually, the planes of first order prisms are almost normal to the surface (fig. 10), but in regions near the selenizone they appear to be inclined (fig. 13). It has not been possible to trace first order prisms over a sufficient enough area to be able to comment on how extensive the areas of the inclined planes might be or if there is any pattern to their distribution. In most wall layers, which have a vertical component to subsidiary structures, such as

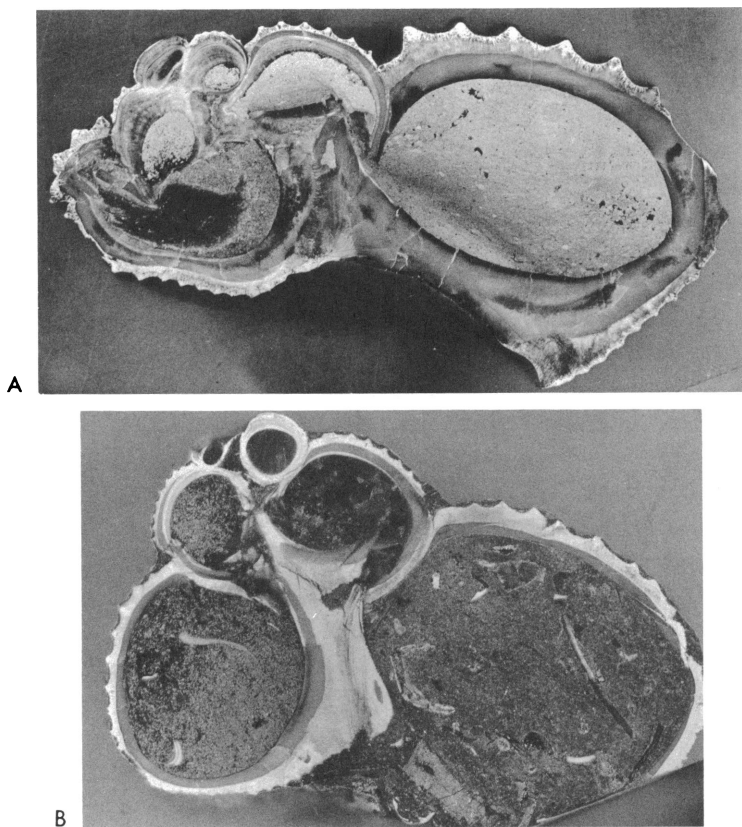


FIG. 16. *Shansiella carbonaria*, AMNH Loc. 2093. A. AMNH 29231. Polished axial section showing gradual thickening of innermost spherulitic complex prismatic layer. Light-colored layers are complex prismatic; dark layer is nacreous. B. AMNH 29232. Polished section of another specimen from same locality. Note much thinner innermost complex prismatic layer and irregular thickness of walls in both specimens from one region of shell to another. Note gradual thickening of nacreous layer toward aperture, reverse of innermost complex prismatic layer. Both  $\times 5$ .

complex prisms and prismatic nacre stacks, there is a change in attitude in the vicinity of ribs, the selenizone, the periphery, or at any abrupt whorl change. This attitude is seen as a bending of the planes so that the planes remain normal to the surface (fig. 14).

There appears to be some intergradation between the spherulitic and elongate complex prismatic layers. In general, either of the types are consistently found in a particular layer, but in some cases, particularly

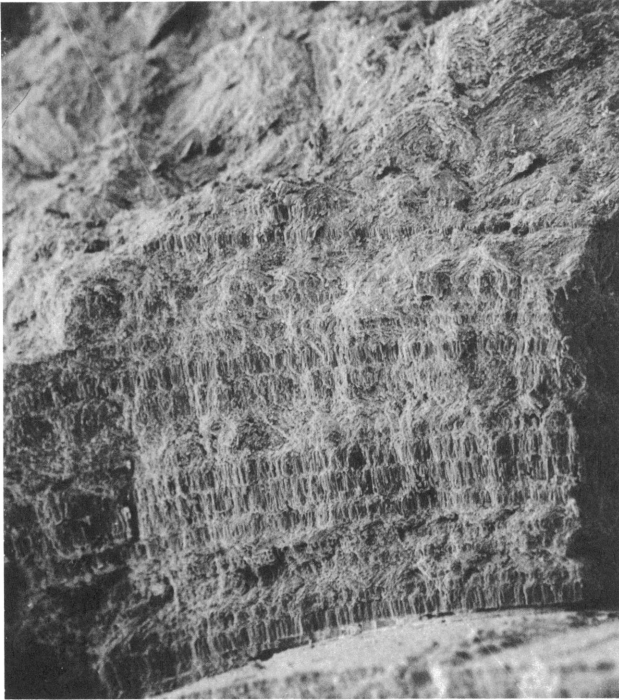


FIG. 17. *Shansiella carbonaria*, AMNH 29233, AMNH Loc. 3003. Fragment from third whorl showing cross section of innermost complex prismatic layer. Note episodic spacing of myostracal layers, and that the axes of first order spherulitic complex prisms are interrupted by myostracal layers, but appear to be continuous crystallographically. Inner shell surface just below final myostracum at bottom of micrograph.  $\times 238$ .

involving the elongate type, there are areas where there is a change in orientation of second order blades along the plane (fig. 15 of *W. tabulata*). MacClintock (1967, p. 36) has shown that there is an analogous condition of intergradation between the complex crossed-lamellar and crossed-lamellar structure.

In the pleurotomarian species thus far examined, the elongate type is invariably an outer layer, and this is also true in three bellerophonitid species examined: *Pharkidonatus percarinatus* (Conrad), 1842; *Pharkidonatus labioreflexus* Sturgeon, 1964; and *Retispira tenulineata* (Gurley), 1884. Beneath the outermost prismatic layer is the nacreous layer, the thickest layer of most pleurotomarian species; it is discussed in a later section.

## INNERMOST COMPLEX PRISMATIC LAYER

The innermost of the principal layers is a complex prismatic layer of the spherulitic type (figs. 8, 17, 19, 27). This layer is usually absent in the final whorls, but gradually becomes thicker toward the earlier whorls and may



FIG. 18. *Shansiella carbonaria*, AMNH 29234, AMNH Loc. 3003. Section of final whorl of a mature specimen taken just above selenizone, showing contact of outermost elongate complex prismatic layer and Vertikalschichtung nacreous layer. These layers are separated by the thin pallial myostracum. Note that just to left of center and right of white triangular area, the vertical prisms of myostracum are continuous with the blades of the complex prismatic layer and at about 45 degrees to them; see also figure 26.  $\times 570$ .

completely seal off the nuclear whorls in shells that have thick initial walls (fig. 16A, B). It has been suggested that this deposit is secondarily formed by the mantle, but MacClintock (personal commun.) has pointed out that it may result from continuous deposition of the mantle and should not be identified as secondary. However, the layer does not seem to be continuously secreted but rather at irregular intervals or in some type of episode (fig. 17).



There is some variability in the thickness of the innermost layer and in the position of its margin toward the aperture. This is in contrast to the other two principal layers which are much more conservative. In most of the seven specimens of *S. carbonaria* examined, there was a considerable

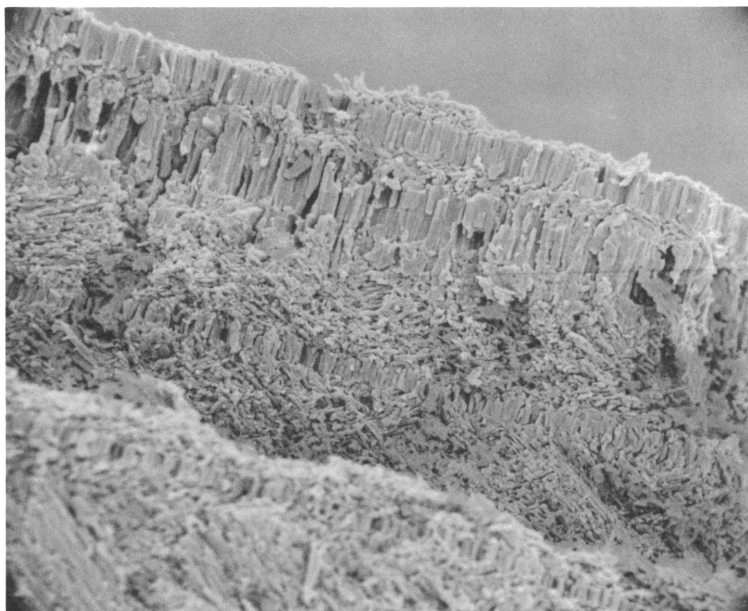


FIG. 19. *Shansiella carbonaria*, AMNH 29235, AMNH Loc. 3003. Fragment from third whorl, cross section showing thin pallial myostracum forming a "wash" on floor of whorl. Layer just below it is spherulitic complex prismatic with another thin pallial myostracum above. Inner shell surface at top of micrograph.  $\times 900$ .

amount of deposition, but the thickness varied from specimen to specimen (fig. 16A, B). Except for *T. illinoiensis* all species have this layer developed, but it rarely extends much beyond the first two to three whorls. Furthermore, the spherulitic layer does not close off the early whorls, as it does in *S. carbonaria*. There does not seem to be any particular relationship between the thickness of the other layers and the thickness of the innermost layer, except perhaps in *S. carbonaria* (again compare fig. 16A and B). The inner layer in recent pleurotomarians is far more complicated, consisting of simple prismatic, crossed-blocky and crossed-platy types which appear to change ontogenetically [see Erben and Krampitz (In press)]. Furthermore, there is interfingering of this layer with the nacreous layer.



FIG. 20. *Shansiella carbonaria*, same fragment as in figure 2. Stacked nacre layer is the middle thick one, and is corroded. Sloping surface near base of layer represents nacre which has less well-defined stacks.  $\times 48$ .

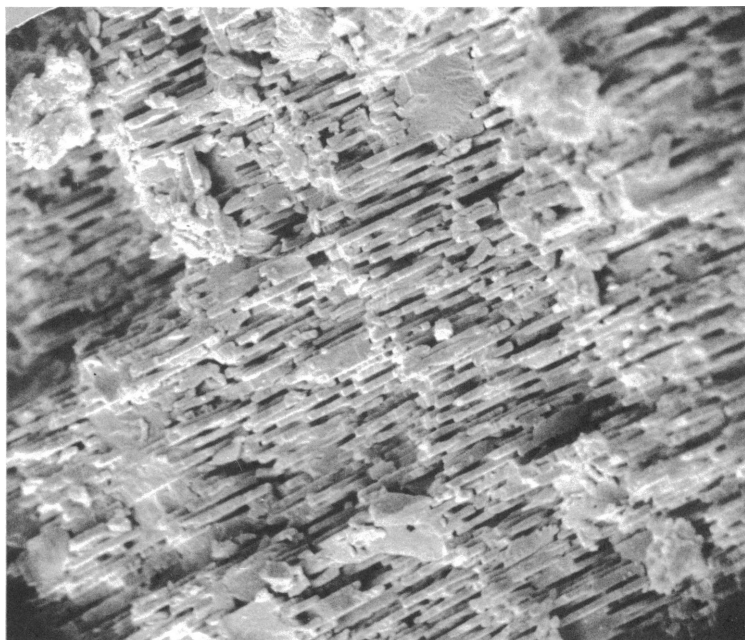


FIG. 21. *Worthenia tabulata*, AMNH 29236, AMNH Loc. 2093. Fragment from beneath selenizone near aperture. Note irregular stock of nacre laths; this area is near base of nacreous layer.  $\times 2080$ .

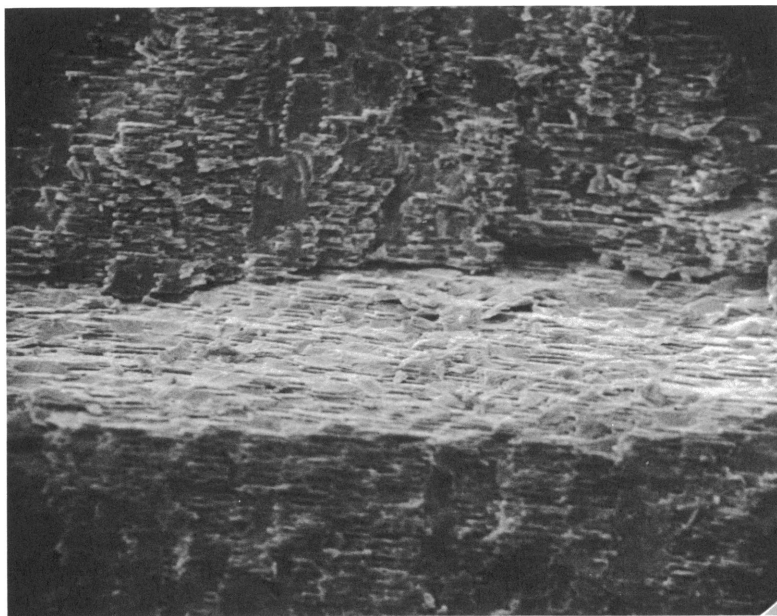


FIG. 22. *Shansiella carbonaria*, AMNH Loc. 2093. Fragment from middle of upper whorl face, with view of lower portion of nacreous layer same as figure 2. Light-colored wedge apparently has different-sized laths compared with stacks above and below it. Note slight angular discordance between wedge and stacks above and below it.  $\times 620$ .

#### PALLIAL MYOSTRACUM

There is a series of very thin layers, ranging from about 5 to 50 microns in thickness, which appear to be composed of either very fine prisms or more commonly blades (figs. 18, 19). MacClintock (personal commun.) has pointed out that the prisms or blades in the layers tend to be converted from blades of contiguous aragonite layers such as the complex prismatic layer in the case where the two structures are in contact (figs. 18, 27). The thinness, uniformity, and type of blade or prism seem to be almost identical with the myostracum found in the Bivalvia. It has been demonstrated that bivalve myostracum is formed by the mantle or, commonly, by the musculature. Because of the distribution of these layers in gastropods I believe that most of them must be formed by the mantle as pallial myostracum. In general, the retractor muscle is the only muscle directly attached to the shell in orthostrophic gastropods and it usually is restricted to the columella and/or to the inner portion of the upper whorl surface. In only a single specimen of *S. carbonaria* on the upper surface of the



FIG. 23. *Shansiella carbonaria*, same specimen, same position as in figure 20. Left center of view shows corroded stacked nacre; gentler slope on right side appears to be wedge of less well-defined stacked nacre.  $\times 230$ .

penultimate whorl is there a rather thin lenticular myostracum that could have been formed by the retractor muscle. It is more likely that the mantle periodically became attached to the inner shell surface and deposited essentially all the myostracal layers we have observed in the course of this study.

The pallial myostracum in the bellerophontid and pleurotomarian species examined is found in three regions of the wall:

1. Separating thicker, primary layers as in figure 18. In this case, the pallial myostracum is quite uniform in thickness (the usual case) and continuously separates the layers throughout the entire shell. For example, in all pleurotomarian species examined, the myostracum separates the outermost and innermost prismatic layers from the nacreous layer.

2. The myostracal layer usually forms the basal "wash" that coats most of the inner surface of the shell much as the homogenous layer does in many advanced gastropods (figs. 17, 19). This coating is uniform in thickness all over the shell but varies in thickness between the species (fig. 25 of *W. tabulata*, and fig. 19).

3. The pallial myostraca may occur as multiple episodic layers within the innermost complex prismatic layer (fig. 17). Each layer is rather

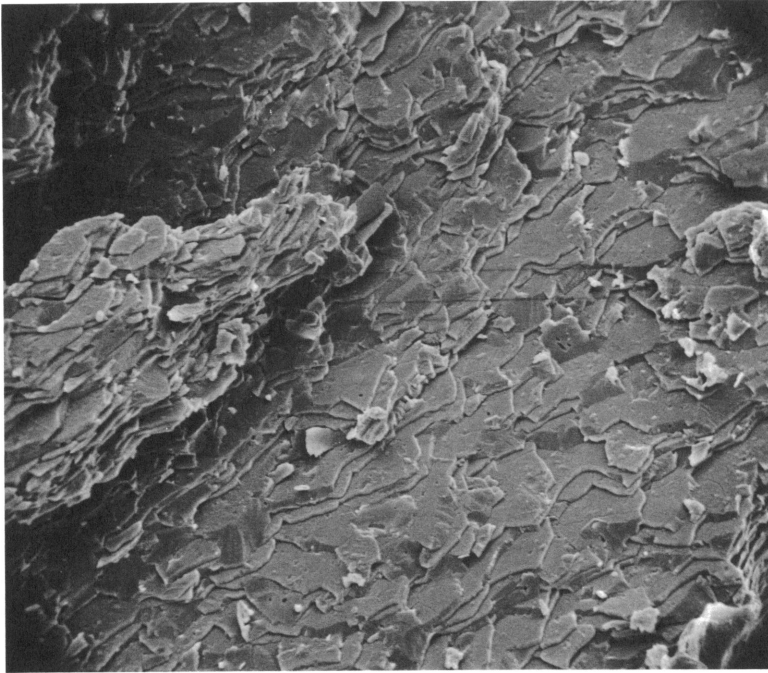


FIG. 24. *Worthenia tabulata*, same specimen as in figure 21. Looking down at gently sloping surface of wedge described in figure 21. Note that some laths have been obscured by secondary calcite impregnation.  $\times 940$ .

uniform in thickness but again there is variability between layers (fig. 19), and it appears not to have a rhythmic pattern. It is interesting to note that the myostracal layers do not seem to interrupt or affect unit crystallization of first order complex prisms (figs. 17, 19). Again, note the very similar appearance of this layer type between major molluscan groups. For example, compare the blades seen in *Euphemites vittatus* (a bellerophonitid) in figure 29 with that of *S. carbonaria*, figure 19.

The most obvious variation in the pallial myostracum is in the relative width of the blades and in the thickness of the layer (fig. 19).

#### NACREOUS LAYER

Wise (1970, pp. 783, 789) stated that all gastropod nacre is composed of the stacked crystal type (I will term *Vertikalschichtung*) (fig. 14 or 26) whereas that of the bivalves is chiefly *Treppen* (stepped) or *Backsteinbau* (brick) patterns (these terms were proposed by Schmidt in 1923). The

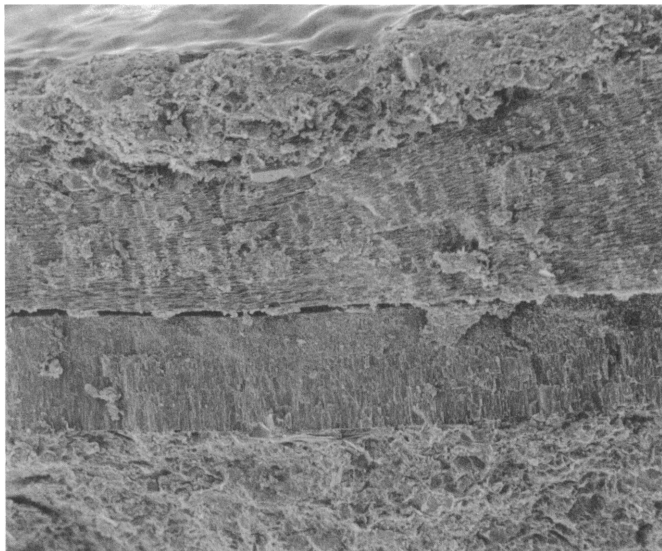


FIG. 25. *Worthenia tabulata*, same specimen as in figure 21. Portion of nacreous layer and thick pallial myostracum forming floor of whorl; selenizone and shoulder at right.  $\times 210$ .

results of a study of the five Pennsylvanian pleurotomarian species basically support his findings. The Vertikalschichtung of these species is, with some exceptions, fairly conservative between genera, with the columns being about the same width (approximately  $10\ \mu$ , except for *Trepostira illinoensis* where the columns are about  $20\ \mu$  wide). There appears to be some variability in the precision of crystal stacking and, in some walls, crystal widths (fig. 26). The term "crystal" used here is as defined by Wise, (1970, p. 781), that is, the smallest nacre unit which can be discerned in a given structure at magnifications greater than 100. The term is equivalent to "lath" used by Taylor, Kennedy, and Hall (1969).

Despite excellent preservation of the study material, there has been some alteration of the walls. The most obvious alteration is the absence of organic matrix; corrosion or secondary calcite implantation are common (figs. 18, 20). The variability in the Vertikalschichtung described below may partly be an artifact of diagenesis. I believe I have observed the following types of variation:

1. As small random and irregular patches involving portions of the columns, where the boundaries between stacks are uneven (fig. 21 of *W. tabulata* and 28 of *S. carbonaria*).



FIG. 26. *Phymatopleura nodosa*, AMNH 29237, AMNH Loc. 3003. Cross section view of contact between uppermost complex prismatic layer and Vertikalschichtung nacreous layer, from just under selenizone on base (inside of whorl in upper right of picture). Note less well-defined stacking near top of nacreous layer.  $\times 580$ .

2. As lenticular wedges of stacked nacre where the columns are arranged at a slightly different angle to subjacent and superjacent Vertikalschichtung in the main body of the layer (fig. 22 of *S. carbonaria*). These wedges tend to occur near, but not at, the bottom or top of the nacreous layer. Additionally, the stacks appear less regular in vertical orientation and the crystals appear wide.

In the four specimens that have this latter feature, the wedge is preserved differently in that it consistently fractures into a gentle slope in a layer where the stacked nacre fractures into vertical surfaces (figs. 20 and 23 of *S. carbonaria*). This difference in expression might be due to uneven developments of the stacks. This does appear likely as stack boundaries are difficult to detect. However, there is a possibility that the wedges may be produced by diagenetic effects. In other wall structures described



FIG. 27. *Trepostora illinoiensis*, AMNH 29238, AMNH Loc. 3003. Cross section view of lower contact between nacreous layer and a very thin spherulitic complex prismatic layer. Section is near selenizone on base of a mature specimen. Note continuity of blades between pallial myostracum and spherulitic complex prismatic layer. Inside of shell is toward top. Inner myostracal "wash" not preserved in this view.  $\times 680$ .

above the walls may be unevenly preserved. In many specimens, the entire wall may be badly corroded or recrystallized or just in irregular patches of varying sizes. In other specimens a given layer may be altered, whereas an adjacent layer is relatively free from either corrosion or added calcite (fig. 23). Therefore, there is a possibility that the wedges are in fact areas of alteration. In the case of figure 23 the crystal boundaries may have been obliterated, in part, by the addition of calcite. When one looks down on the top of the wedge, the crystal boundaries appear in some areas to be obscure (fig. 24). As Wise (1970, p. 786) has shown, Vertikal-schichtung is very difficult to identify unless it is seen in a vertical fracture or etched section. Because all the wedges identified, outcrop as gentle slopes on fractured surfaces, it may be that the vertical stacks cannot be seen. Nonetheless my interpretation is that these are real entities, pending further observations.

3. The crystals appear to become larger, or the boundaries between



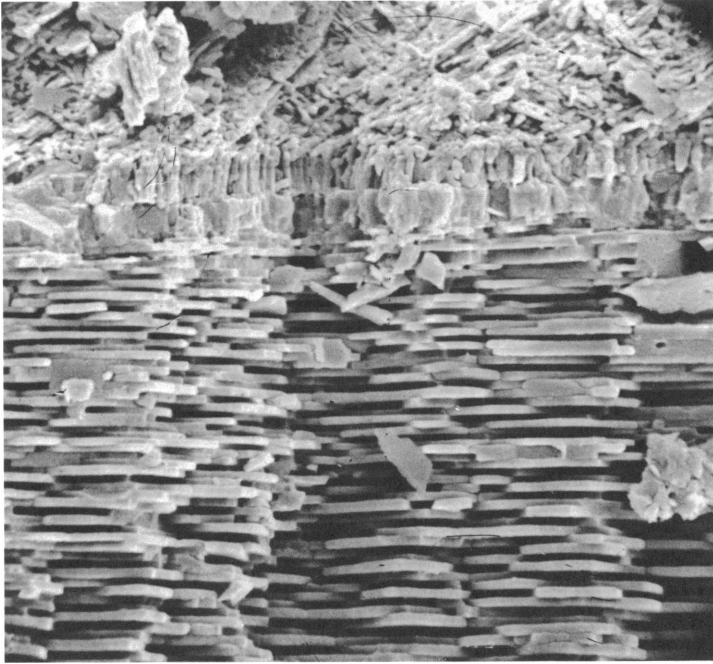


FIG. 28. *Shansiella carbonaria*. Same specimen as in figure 2. Note slight angular unconformity between pallial myostracum and stacks of nacre laths.  $\times 1750$ .

stacks become less well defined, near the top or base of the layer (figs. 25 of *W. tabulata* and 26 of *P. nodosa*). Wise (1970, p. 787) mentioned a similar pattern in the pelecypod genus *Pinna*.

The Vertikalschichtung layer in the pleurotomarian species is, with some exceptions, the thickest portion of the wall. In *Trepostira illinoensis*, it is the dominant layer, with the innermost pallial myostracum and the outermost complex prismatic layer represented by thin "washes" (fig. 27). Little ontogenetic change in wall structure has been observed in this species. However, in *Shansiella carbonaria*, *Worthenia tabulata*, *Phymatopleura nodosa*, and *G. (Glabrocingulum) grayvillensis* the nacreous layer becomes proportionally thicker with age, at the expense of the outer complex prismatic layer which becomes progressively thinner (fig. 16A, B, of *S. carbonaria*). Without exception the nacreous layer in the five species is bounded by a pallial myostracum that in most cases grades into complex prismatic structure (figs. 18 of *S. carbonaria* and 27 of *T. illinoensis*).

In most of the specimens examined, the stacks of nacre crystals are

essentially normal adjacent to the upper and lower contacts, and remain so throughout the layer. In some specimens the columns behave, as does the first order prisms of the complex prismatic layer, fanning out under ribs or the selenizone to maintain normalcy to the outer surface (fig. 25 of *W. tabulata*). In other cases they appear independent (fig. 14 of *S. car-*

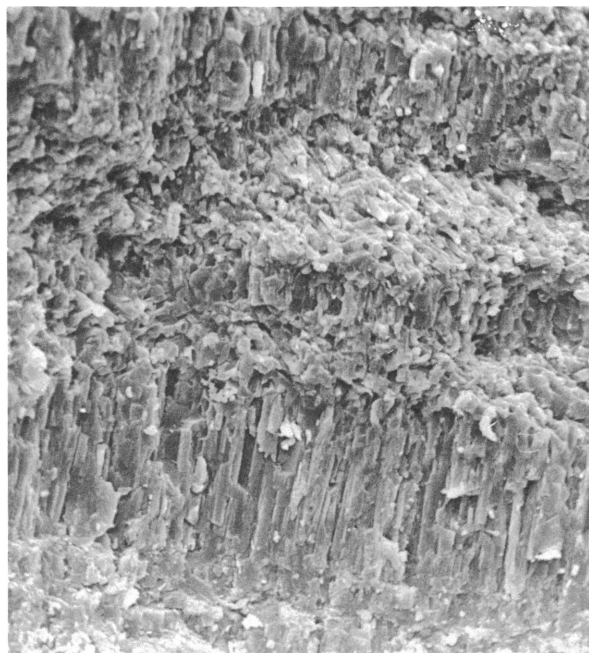


FIG. 29. *Euphemites vittatus*, Bonn Univ. 8627, AMNH Loc. 2093. Note shape of blades in lower pallial myostracum. Photograph from near inner surface of shell at selenizone. SEM photography courtesy Dr. H. K. Erben.  $\times 1050$ .

*bonaria*). In a few rare cases, the axes of the stacks appear to be at a slight angle to the contact (fig. 18 or 28). Even so, I would agree with Wise that the common relationship of the stack axes to the surface is normal in contrast to the Bivalvia. In general, the stacks are consistently vertical throughout their entire length in the species examined, but there are exceptions, such as in the specimen of *Worthenia tabulata* shown in figure 25. In two other specimens (*T. illinoiensis* and *S. carbonaria*) (figs. 27, 28) the nacre stacks appear to have a slight angular relationship with the surface but, as the nacre is covered by other layers, observations of the surface would not reveal imbrication as in the Bivalvia.



FIG. 30. *Nerita* sp., AMNH 29239, a recent specimen. Near base of a complex crossed-lamellar cone. Note third order prisms described by MacClintock.  $\times 5600$ .

#### WALL STRUCTURE AND PHYLOGENY

The problem of interpreting phylogeny based on wall structure alone cannot be resolved until much more sampling and study of both the fossil record and recent material can establish variation patterns. Wise (1970, pp. 789–794) has come to certain conclusions regarding the relative phylogenetic positions of the Monoplacophora, Bivalvia, Gastropoda, and Cephalopoda based partly on an analysis of the nacreous layer.

Wise concluded that the Bivalvia branched off the “primitive stock” earlier than did the Gastropoda and Cephalopoda. His principal reason is that both the Gastropoda and Cephalopoda possess stacked nacre, a characteristic considered to be primitive, and that the Pelecypoda evolved a more advanced type—the Backsteinbau nacre. It is probably premature to speculate about the origin of any molluscan group based on wall structure as hardly anything is known about wall structure in the early fossil record. The only firm evidence of monoplacophoran wall structure in the Paleozoic is the Gotlandian *Pilina* and *Tryblidium* which is composed of prismatic and nacreous layers (Erben, Flajs, and Siehl, 1968). I am not convinced that Bøggild’s (1930, p. 299) interpretation of “*Bellerophon*” wall structure in a specimen from the Ordovician of Bornholm is correct. He believed that the wall is composed of laminated calcite. His photograph (pl. 8, fig. 6) shows a series of growth lines but no wall structure per se and I suspect that the wall has been recrystallized to the point that no residual structure remains. One can be sympathetic to the view that morphoclines can and should be used to interpret phylogeny, but the fossil record must be investigated to increase the area of evidence. Also, all morphologic features rather than one single feature should be considered.

If all wall structure types are considered rather than a single type, one

can come to the opposite conclusion of Wise's concept, specifically, that the Cephalopoda branched off the "primitive stock" earlier than did the gastropods and bivalves. The reasoning is as follows: the Cephalopoda have only prismatic and nacreous layers, a condition shared by the Monoplacophora and so-called primitive groups of gastropods and bivalves. However, gastropods and bivalves share not only the primitive wall types but crossed-lamellar, crossed-foliate, complex crossed-lamellar, and complex crossed-foliate layers as well. It seems quite incredible that these latter four layers could have developed independently in the bivalves and gastropods and far more logical that they shared a common ancestor. It is for this kind of reasoning that I strongly believe Paleozoic groups must be studied before drawing any phylogenetic conclusions. To cite a further example, it is commonly believed that the crossed-lamellar wall is a more advanced wall type since it is most commonly associated with advanced families both in the gastropods and the bivalves. Bellerophonitids are considered by most students to be the most primitive group of snails. Some students even are of the opinion that the bellerophonitids are more likely cyclomyan Monoplacophora. Whatever the case may be, the bellerophonitids are certainly more "primitive" than any other major molluscan group. Yet it has been demonstrated that crossed-lamellar structure is present in the bellerophonitids (MacClintock, 1967, p. 95).

Thus far, none of the pleurotomarian species studied seem to show any type of phylogenetic ordering among the genera or families they represent.

Finally, with the exception of the rather stable pallial myostraca, most of the variation observed in shell ultrastructure occurs within or between species while it appears conservative between larger taxonomic units.

### SUMMARY

Two previously undescribed shell layers are defined. The outermost fibrous layer is the only one directly involved in growth increment expression on a wall layer surface. The next layer beneath shows no topographic expression of growth and is composed of vertically arranged plates distributed at an acute angle to the growth lines.

There are two types of complex prisms. An elongate type with second order prisms arranged about a vertical plane, is restricted to the outer main layer and makes up all "secondary" deposits such as the callus, parietal surface, and funicle. A spherulitic type forms a much more variable innermost layer and may be absent in some species.

The pallial myostraca are found (1) as a thin unit separating primary layers; (2) as episodic layers within the innermost complex prismatic layer; and (3) as a thin "wash" coating the inner shell surface.

The nacreous layer is, as shown by Wise (1970), of the Vertikalschichtung type essentially normal to the outer surface.

It is premature to speculate on the origin or phylogeny of the Mollusca based on wall structure alone. However, since the most primitive gastropods (the bellerophonitids) share a crossed-lamellar layer among others with the pelecypods and with more advanced gastropods, it is likely that the gastropods and pelecypods are more closely related than to other molluscs. The cephalopods probably diverged from a common ancestor prior to that of the gastropods and pelecypods.

None of the pleurotomarian species studied seem to show any type of phylogenetic ordering between genera or families they represent.

Ultrastructure apparently is more variable within or between species and more conservative between higher taxonomic levels.

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#### ADDENDUM

While this paper was in galley proof, I examined a poorly preserved *Scissurella crispata*(?) Fleming from the east of the Marianas at latitude 17°56.6' S; longitude 154°08' W. The sample (V18, 10-IX-62; B-B-O#2 Lamont-Doherty Geological Observatory) was dredged from approximately 740 meters.

The specimen is about 4 mm. in width and has a very thin transparent shell. The outermost layer is thin and not preserved. The inner layer represents about 95 percent of the shell thickness and is crossed-lamellar and of the type found in other thin-shelled gastropods, for example, the planktonic atlantid *Oxygyrus*. As far as I am aware, this is the first report of crossed-lamellar wall structure in the pleurotomarians.

The presence of a crossed-lamellar wall in the pleurotomarians is not surprising in view of the fact that it is present in the related bellerophontids, thus indicating that the pleurotomarians had the genetic potential to produce such a wall type. It is too early to speculate about the significance of this observation. However, I suggest that perhaps a thin-shelled form would benefit from the inherently strong crossed-lamellar structure.