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PART N, REVISED, VOLUME 1, CHAPTER 2A: BIVALVE SHELL MICROSTRUCTURE AND MINERALOGY: SHELL MICROSTRUCTURE TERMINOLOGY

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INTRODUCTION

A standardized terminology is necessary to succinctly and unambiguously describe shell microstructure and to incorporate its data into taxonomic, phylogenetic, and evolutionary studies. The variable nature of microstructure terminology can be illustrated by recent applications of the term composite prismatic. Bøggild (1930, p. 249) proposed this term for "...larger prisms (prisms of the first order) each of them being composed of fine prisms (of the second order) arranged in a feathery manner, like the axes of fig. 1." His figure 1 depicts optical crystallographic axes diverging within each first-order prism toward the depositional surface from a central, longitudinal axis. Bøggild described this microstructure for *Nucula* Lamarck, 1799, wherein the composite prisms are radially oriented and comprise a shell layer that is one prism thick. He indicated that a transition from composite prismatic to common prismatic microstructure can occur in the form of "...a layer of fine prisms, mostly orientated [*sic*] horizontally in the radial plane, and possessing a feathery arrangement only in the radial section, whereas, in the horizontal section, they are perfectly parallel." Bøggild (1930, p. 287) called this transitional microstructure "prisms in a feathery arrangement," e.g., the outer shell layer of the venerids *Tapes decussata* [=*Ruditapes decussatus* (Linnaeus, 1758)], and *Tapes pullastra* [=*Venerupis corrugata* (Gmelin, 1791)]. In these two species, the outer shell layer is presently described as finely nondenticular composite prismatic with prisms secreted on a strongly reflected shell margin. Taylor, Kennedy, and Hall (1973, table 15) used "composite prismatic" for both the composite prismatic and transitional microstructures described by Bøggild. Carter and Clark (1985) and Carter and others (1990) differentiated first-order composite prisms that reflect coarse shell marginal denticles (denticular composite prisms, as in *Nucula*) from those that do not (nondenticular composite prisms or NDCP), as in *Ruditapes* Chiamenti, 1900 and *Venerupis* Lamarck, 1818 in 1818–1822. They subdivided the category of NDCP prisms into radial, compound, and crossed NDCP. Carter and others (2012) added radial lamellar NDCP. Hikida (1996) used Type I, Type II, and Type III composite prismatic for radial, radial lamellar, and crossed NDCP, respectively. Popov's (1985, 1986, 1992, 2014) terminology includes denticular composite prismatic, fibrous composite prismatic with or without megaprisms, and four types of compound composite prisms: irregular, with plates, and with or without megaprisms.

Lack of uniformity in shell microstructure terminology can be confusing. It can also lead to contradictory evolutionary interpretations. For example, Hayami (1988) hypothesized that propeamussiid foliated

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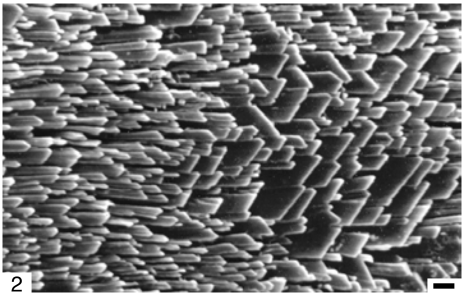

FIG. 1. Depositional surface of calcitic middle shell layer near posterior margin in adult right valve of propeamussiid *Parvamussium pourtalesianum* (DALL, 1886), showing transition from radial, lath-type fibrous prismatic (left) to semi-foliated microstructure (right), north of Glover Reef, Yucatan, Mexico, YPM 8408, posterior shell margin toward right, scale bar, 2 µm (Carter, new).

microstructure originated indirectly from calcitic simple prisms through an intermediate fibrous prismatic microstructure. He cited as evidence the difference in optical crystallography between calcitic simple prisms and foliated laths, plus intergradations between these laths and fibrous prisms. CARTER (1990a,1990e) added that propeamussiids have in their right valve a simple prismatic outer shell layer and a middle shell layer with irregular spherulitic prisms and fibrous prisms, with the latter grading laterally into foliated microstructure (according to the present terminology, through an intermediate semi-foliated microstructure; Fig. 1). The simple prisms in the right valve are discontinuous with the middle shell layer. The outer shell layer in the left valve is similar to the middle shell in the right valve. Contrary to HAYAMI and CARTER, WALLER (1976) and ESTEBAN-DELGADO and others (2008) concluded that propeamussiid foliated microstructure developed directly from simple prisms. However, their conclusion reflects the fact that, unlike HAYAMI (1988) and CARTER (1990a,1990e), they did not distinguish between propeamussiid fibrous prismatic and foliated microstructures. The fossil record suggests that the pathway for the evolution of foliated microstructure varies from group to group within the Pteriomorphia. It appears to have developed directly from calcitic fibrous prisms independently in Pectinoidea and Limoidea, from calcitic simple prisms in Anomioidea, from calcitic simple prisms or from calcitic homogeneous microstructure in Aviculopectinoidea and Pseudomonotoidea, and from calcitic homogeneous, or, less likely, nacre or aragonitic crossed lamellar microstructure in Ostreoidea (CARTER, 1990a, p. 215, 229, 254, 256; see also MCROBERTS & CARTER, 1994).

HISTORY

The earliest references to molluscan shell microstructure used nacreous and porcelaneous as textural terms. HATCHETT (1799, p. 316) noted that, “The greater part, if not all, of marine shells, appear to be of two descriptions, in respect to the substance of which they are composed. Those which will be first noticed, have a porcellaneous [*sic*] aspect, with an enamelled surface, and, when broken, are often in a slight degree of fibrous texture. The shells of the other division have generally, if not always, a strong epidermis under which is the shell, principally or intirely [*sic*] composed of the substance called *nacre* [italics *sic*] or mother of pearl.” Hatchett used nacreous in a wider sense than modern authors, applying this term to both nacreous and foliated shell layers.

GRAY (1824, p. 216) proposed the term periostracum (originally as periostraca) for the layer secreted at the margin of a mollusk shell, with “no cretaceous matter deposited in it, or only a very small quantity.” HATCHETT (1799) had called this layer the epidermis. According to GRAY (1833, p. 789), “Shells exhibit, when examined, two very distinct kinds of structure: in the one case the calcareous particles of which they are formed are crystallized, in the other they are granular.” He noted that the crystalline and granular structures correspond with HATCHETT’s (1799) porcelaneous and nacreous textures, respectively. GRAY described crystalline structure as consisting of rhombic or prismatic crystals. The rhombic crystalline structure is now called crossed lamellar, and the prismatic crystalline structure is now called regular simple prismatic or fibrous prismatic. GRAY indicated that some granular nacreous shell layers are concretionary, as in the mother-of-pearl of unionids and pinnids, whereas others are foliaceous, as in anomiids, ostreids, and pectinids.

CARPENTER's (1845, 1848) shell microstructure terminology reflects his belief that shells represent mineralized mantle epithelial cells that "...seem to have the power of consolidating themselves by drawing calcareous matter into their interior (1848, p. 98)." CARPENTER examined residues of decalcified shells in the belief that he was observing these cell membranes. He explained apparently homogeneous shell layers, in which decalcified cell membranes are not visible, by suggesting that in the final process of consolidation, the cell walls had a tendency to liquify or dissolve away. In 1845, CARPENTER proposed that nacre and corrugated (crossed lamellar) microstructures reflect distorted cell membranes. In 1848, he revised his explanation of corrugated microstructure, suggesting that it represents mineralized long prismatic cells that obliquely cross each other. CARPENTER used sub-nacreous for foliated and certain nacreous shell layers lacking the typical iridescence of nacre; prismatic cellular for the simple prismatic outer shell layer in *Pinna* LINNAEUS, 1758 and *Solemya* LAMARCK, 1818 in 1818–1822; and fusiform cellular for the prismatic outer shell layer in *Tellina* LINNAEUS, 1758. CARPENTER (1845, p. 13) proposed the term tubular structure, i.e., the shell Kanälen of EHRENBAUM (1884) and the shell tubules of OBERLING (1964).

FISCHER (1880, p. 17) used nacreous and porcelaneous in a textural sense and added the textural terms fibrous, corneous, vitreous, and translucid. NATHUSIUS-KÖNIGSBORN (1877) used Durchsichtige prismatische for myostracal irregular simple prismatic microstructure. TULLBERG (1882) called the fibrous prisms in the outer shell layer of *Mytilus* LINNAEUS, 1758 Kalkstäbchen (calcareous rods). EHRENBAUM's (1884) terminology includes regelmässig prismatische (regular prismatic), faserigen prismatische (fibrous prismatic), Backsteinbau-ähnlicher nacre (brick-wall type nacre), lamelläre Struktur mit Blättern (crossed lamellar microstructure with leaves, i.e., lamellae), körnigen (grained), and Stalaktiten (stalactites, i.e., pillar irregular simple prisms).

THIELE (1893) used the term periostracum and proposed the new terms ostracum and hypostracum. He defined ostracum and hypostracum as microstructurally distinct, outer and inner layers, not necessarily separated by the pallial line. In his example of *Arca* LINNAEUS, 1758, the ostracum included the shell between the periostracum and the outer margin of the pallial and adductor myostracum *sensu* OBERLING (1955), i.e., the outer and middle shell layers as presently defined, and the hypostracum included the inner shell layer plus the myostracum. For *Meleagrina* LAMARCK, 1818 in 1818-1822 (i.e., *Pinctada* RÖDING, 1798), the ostracum was restricted to the prismatic outer shell layer, and the hypostracum included the nacreous middle and inner shell layers plus the myostracum. For *Unio* PHILIPSSON in RETZIUS, 1788, THIELE regarded the intergrading periostracum and prismatic outer shell layer as essentially parts of the same layer, so he excluded the latter from the ostracum, used ostracum for the nacreous middle and inner shell layers, and restricted the hypostracum to the adductor myostracum. This latter example influenced NEWELL (1938) and LUCAS (1952) to restrict hypostracum to muscle attachment deposits. THIELE's microstructure terms include Prismen (columnar prisms), Perlmutter (nacre), Bandstruktur (crossed lamellar microstructure), and Stäbchenschicht (rod layer, i.e., a myostracal, irregular simple prismatic layer).

DOUVILLÉ (1907) divided shell microstructures into two categories, prismatic and lamellar, with the latter including nacreous, porcelaneous, and foliated. In subsequent papers, DOUVILLÉ (1912, 1913) described the directional nature of microstructure evolution in this class, writing (1913, p.

435–436, presently translated): "I have shown that the ancient forms were nacreous, and that they became porcelaneous as a result of evolution. It will not be possible, therefore, to interpose nacreous forms between porcelaneous forms in one and the same branch. I do not know of any regression: the extant nacreous forms resemble the primitive forms by a continuous series of equally nacreous forms." NEWELL (1969, p. 210, fig. 101) summarized DOUVILLÉ's (1912, 1913) ideas by superimposing the categories prismato-nacreous, non-nacreous (i.e., porcelaneous), and foliate over a simplified version of DOUVILLÉ's (1913, p. 466) evolutionary tree for the Bivalvia. Paleontological evidence is compatible with the hypothesis that porcelaneous and foliated shell layers were preceded by nacreous ones in the Bivalvia, but the evidence additionally suggests that nacreous layers were preceded by non-nacreous, non-porcelaneous, non-foliated layers in Cambrian mollusks (RUNNEGAR, 1983; RUNNEGAR & BENTLEY, 1983; RUNNEGAR & POJETA, 1992; VENDRASCO, CHECA, & KOUCHINSKY, 2011). NEWELL's (1969) three microstructure categories are actually oversimplified. Some bivalve shells are nacreous and porcelaneous, e.g., the Devonian cyrtodontid *Ptychodesma knappianum* HALL & WHITFIELD, 1872 (see CARTER & TEVESZ, 1978b); the Recent mytilid *Crenella decussata* (MONTAGU, 1808) (CARTER, LUTZ, & TEVESZ, 1990, p. 407); the Recent thraciid *Thracia pubescens* PULTENEY, 1799 (see CARTER & LUTZ, 1990, pl. 2); and some Recent Poromyidae (Fig. 100). Other bivalve shells are nacreous and foliated, e.g., some Triassic Gryphaeidae (MCROBERTS & CARTER, 1994); or nacreous, porcelaneous and foliated, e.g., Carboniferous *Limipecten morsei* NEWELL, 1938 (see CARTER, 1990e, p. 367); or porcelaneous and foliated, e.g., many Pectinidae (TAYLOR, KENNEDY, & HALL, 1969; WALLER, 1971, 1972, 1976; CARTER, 1990a, 1990e).

BØGGILD's (1930) study of a wide variety of Recent and fossil mollusks marks the starting point for modern shell microstructure terminology. He defined some of his terms on the basis of morphology alone, and others on the basis of morphology and optical crystallography (Table 1). As an example of the latter, BØGGILD (1930, p. 245) described that in homogeneous microstructure, "In ordinary light we see, in typical forms, no structure at all, whereas, with crossed nicols [i.e., in crossed polarized light], we find an [optical] extinction in one direction in such a manner that the main axes are parallel through large parts of the shell." BØGGILD added that "...as we see no [structural] elements at all in the typical homogeneous structure, it is impossible to tell what form the single individuals possess. They may be prismatic or lamellar or, perhaps, otherwise arranged. In many instances, however, we find transitions from that structure to various others, giving indications, in such instances, of the real structure."

Subsequent works on bivalve shell microstructure largely abandoned optical crystallography. This is unfortunate, because pteriomorphian calcitic simple prisms have phylogenetically significant optical crystallographic variations. For example, the calcitic simple prisms in most Pterioidea show irregular, wavy optical extinction, whereas those in Pinnoidea and its putative ancestral family Pterineidae show homogeneous extinction, and those in the morphologically similar Inoceramidae and Retroceramidae show granular extinction (BØGGILD, 1930; CARTER, 1990c).

NEWELL (1938) adopted THIELE's (1893) terms ostracum and hypostracum, but used ostracum for all subperiostracal shell layers except for the hypostracum, which he restricted to muscle attachment deposits. His microstructure terminology includes (with present equivalents in parentheses): prismatic (simple prismatic and composite prismatic), nacreous, foliaceous (foliated), concentric crossed lamellar (commarginal crossed lamellar and commarginal crossed foliated), homogeneous (mosaic homogeneous), and radial crossed lamellar (radial fibrous prismatic and irregular spherulitic prismatic).

NEWELL (1942, p. 33) subsequently indicated that his 1938 "radial crossed lamellar" is actually radial fibrous prismatic. NEWELL and BOYD (1975) replaced hypostracum with OBERLING's (1955) term myostracum. NEWELL and BOYD (1989) called the inner shell layer hypostracum, and used the microstructure terms irregular simple prismatic, crossed-foliate (commarginal crossed foliated), and irregular complex foliate (irregular complex crossed foliated and mosaic homogeneous).

LUCAS (1952) reviewed bivalve shell microstructure, using the terms nacreous, homogeneous (*sensu* BØGGILD, 1930), fibrous, prismatic (i.e., columnar prismatic), lamellar (i.e., regularly foliated), and porcelaneous (i.e., crossed lamellar and crossed foliated). Like NEWELL (1938), LUCAS used hypostracum (spelled hypoostracum) and hyaline layers for muscle attachment deposits.

OBERLING (1955) proposed the terms myostracum for muscle attachment deposits and palliostracum for the rest of the shell. He subdivided the palliostracum into periostracum, ectostracum, mesostracum, and endostracum, with the last three corresponding with the outer, middle, and inner shell layers as presently defined. Microstructurally identical outer and middle shell layers were called mesectostracum, and microstructurally identical middle and inner shell layers were called mesendostracum. OBERLING (1964) adopted BØGGILD's (1930) microstructure terminology, but he did not use optical crystallography. His 1964 work proposed the new terms fibrillar (fibrous prismatic) and flabellate (irregular spherulitic prismatic). OBERLING (1955, 1964) recognized three shell microstructure groups: nacroprismatic, foliated, and complex-lamellar. Nacroprismatic shells have nacreous and prismatic shell layers; foliated shells have one or more foliated shell layers; and complex-lamellar shells have crossed lamellar and complex crossed lamellar shell layers.

COX, NUTTALL, and TRUEMAN (1969, p. 73–74) rejected the terms ostracum and hypostracum, and used OBERLING's (1955) myostracum for muscle scar deposits. Their microstructure terminology includes: nacreous, prismatic, crossed-lamellar (with aragonitic and calcitic analogs), complex ("resembling [aragonitic] crossed-lamellar structure except that it is more intricate"), foliated ("more or less parallel leaves of the mineral [calcite], but it is coarser, less regular [than nacre], and without luster"), and homogeneous (*sensu* BØGGILD, 1930).

TAYLOR, KENNEDY, and HALL (1969, 1973) published the first broad survey of bivalve shell microstructure to incorporate electron microscopy. They adopted much of BØGGILD's (1930) terminology, but abandoned all of his morphological/optical crystallographic terms except for homogeneous (Table 1). TAYLOR, KENNEDY, and HALL (1969, p. 64) used electron microscopy to describe homogeneous microstructure as a very fine aggregate of granules. Subsequently, TAYLOR (1973, p. 521) described this as a fine-grained microstructure with no particular crystal form. In their microstructure summaries, TAYLOR, KENNEDY, and HALL (1969, 1973) applied homogeneous in the sense of BØGGILD (1930), i.e., to any microstructure that is too finely textured to be discernible by light microscopy. For example, the homogeneous shell layers they indicated for *Arctica islandica* (LINNAEUS, 1767 in 1766–1770) are now known to include finely homogeneous, irregular simple prismatic, irregular spherulitic prismatic, fibrous prismatic, fine nondenticular composite prismatic, diffuse crossed lamellar, crossed acicular, and irregular complex crossed lamellar microstructures (JONES, 1980, ROPES & others, 1984, DUNCA & others, 2009).

The microstructure diagnoses in TAYLOR, KENNEDY, and HALL (1969, 1973) should be regarded as based on light microscopy unless electron microscopy is specifically referenced or illustrated. This is clear in the case of several mytilids they described as having a nacreous outer shell layer. Contrary to their diagnoses, *Modiolus capax* (CONRAD, 1837)

TABLE 1. Correspondence between shell microstucture terminology in BØGGILD (1930) and TAYLOR, KENNEDY, and HALL (1969, 1973). Terms defined by both morphology and optical crystallography are italicized.

Bøggild (1930)	**Taylor, Kennedy, & Hall (1969, 1973)**
Homogeneous aragonite or calcite	*Homogeneous* aragonite
Grained	Not used
Homogeneously grained	Not used
Regular prismatic	Simple prismatic or just prismatic
Cellular	Prismatic (*Solemya* outer shell layer)
Irregular prismatic	Irregular prismatic, myostracal-type prismatic
Homogeneously prismatic	Not used
Dependent prismatic	Not used
Finely prismatic	Finely prismatic
Normal prismatic	Not used
Complex prismatic	Not used
Composite prismatic	Composite prismatic
Nacreous	Nacreous
Foliated	Foliated
Homogeneously foliated	Not used
Crossed lamellar aragonite	Crossed lamellar aragonite
Crossed lamellar calcite	Foliated
Complex crossed lamellar aragonite	Complex crossed lamellar aragonite
Complex crossed lamellar calcite	Complex crossed lamellar calcite
Complex (coarse complex crossed lamellar plus irregular simple prismatic)	Not used
Vesicular	Not used
Chalky	Chalky

actually has a calcitic outer shell layer with an outer sublayer of finely homogeneous to irregular simple prismatic microstructure, an inner sublayer of irregular simple prismatic to fibrous prismatic microstructure, and an aragonitic mosaicostracum (CARTER, 1980b; CARTER, LUTZ, & TEVESZ, 1990, p. 402; CARTER & LUTZ, 1990, pl. 116, fig. A); *Septifer bilocularis* (LINNAEUS, 1758) has an aragonitic, finely homogeneous to irregular simple prismatic outer shell layer (CARTER, LUTZ, & TEVESZ, 1990, p. 411); *Perumytilus purpuratus* (LAMARCK, 1819) has an aragonitic, finely homogeneous, irregular simple prismatic and irregular fibrous prismatic outer shell layer (CARTER, LUTZ, & TEVESZ, 1990, p. 399); and *Perna viridis* (LINNAEUS, 1758) has an aragonitic, finely prismatic outer shell layer (XU JUN & ZHANG, 2014, fig. 2m). Three other mytilids that TAYLOR, KENNEDY, and HALL (1969) described as having a nacreous outer shell layer should be restudied using SEM: *Brachidontes citrinus* (RÖDING, 1798) [=*Brachidontes modiolus* (LINNAEUS, 1767 in 1766–1770)], *Mytilus arciformis* (DALL, 1909) [=*Mytella charruana* (D'ORBIGNY, 1842 in 1841–1853)], and *Stavelia horrida* (DUNKER, 1857) [=*Stavelia subdistorta* (RÉCLUZ, 1852)].

The microstructure terminology in TAYLOR, KENNEDY, and HALL (1969, 1973) corresponds with this chapter as shown in Table 2. One important difference is that TAYLOR, KENNEDY, and HALL (1969) classified

Table 2. Correspondence between shell microstructure terminology in Taylor, Kennedy, & Hall (1969, 1973) and terms used here.

Taylor, Kennedy, & Hall (1969, 1973)	**Present terminology**
Homogeneous aragonite, not laminated	Superficially homogeneous aragonite
Homogeneous aragonite, laminated (*Solemya*)	Finely homogeneous aragonite, fine complex crossed lamellar, diffuse irregular complex crossed lamellar, dissected crossed prismatic, or solemyid-type laminar
Simple prismatic	Columnar regular simple prismatic or columnar nondenticular composite prismatic
Irregular prismatic, myostracal-type prismatic	Irregular simple prismatic
Finely prismatic	Fibrous prismatic
Composite prismatic	Denticular composite prismatic; or either nondenticular composite prismatic or spherulitic prismatic on a strongly reflected shell margin
Sheet nacreous	Sheet nacreous
Lenticular nacreous	Columnar nacreous with tapering columns and tablets with wavy surfaces
Foliated	Regularly foliated, crossed foliated, complex crossed foliated
Finely foliated (Limidae)	Fibrous prismatic, crossed bladed, transitional fibrous prismatic/crossed foliated
Commarginal crossed lamellar aragonite	Commarginal crossed lamellar with reclined to vertical first-order lamellae
Radial crossed lamellar aragonite	Commarginal crossed lamellar with horizontal first-order lamellae
Complex crossed lamellar aragonite	Irregular complex crossed lamellar, cone complex crossed lamellar, helical complex crossed lamellar, crossed-matted lineated complex crossed lamellar
Fine complex crossed lamellar aragonite	Fine complex crossed lamellar
Chalky	Chalky

prismatic microstructures with a primary emphasis on prism orientation instead of second-order structure. For example, they called prisms with a fanlike, second-order structure simple when vertically oriented, but composite when horizontally oriented. In addition, they used only the general term foliated for regularly foliated, crossed foliated, and complex crossed foliated microstructures.

Kobayashi's (1964–1996) shell microstructure terminology is summarized in Table 3. He proposed the new terms pellucid layer, trans-prismatic, and pseudo-crossed lamellar. In his later papers, Kobayashi replaced pseudo-crossed lamellar with finely crossed lamellar, complex with complex crossed lamellar, and prismatic with simple prismatic. Like Bøggild (1930), Kobayashi used crossed lamellar for both aragonitic and calcitic microstructures.

Popov (1970–2014) contributed a detailed classification of composite prismatic microstructures based on orientation and second-order structure (Table 4). He also proposed the new terms pinnate, megaprism, blocky, and tangled lamellar. Popov used crossed lamellar for both aragonitic and calcitic microstructures, foliated for a variety of foliated microstructures, and finely foliated and fibrous prismatic for calcitic fibrous prismatic microstructures.

Carter (1976–1990), Carter and Clark (1985), and Carter and others (1990) separated morphology from optical crystallography in their microstructure terminology, applied homogeneous at the

Table 3. Correspondence between shell microstructure terminology in Kobayashi (1964a, 1964b, 1966, 1967, 1969, 1971, 1975, 1976a, 1976b, 1979a, 1979b, 1980a, 1980b, 1981, 1991, 1996) and terms used here.

Kobayashi, 1964–1996	**Present terminology**
Homogeneous	Superficially homogeneous
Prismatic (1964–1971)	Regular simple prismatic
Simple prismatic (1976–1996)	Regular simple prismatic
Pellucid	Myostracal irregular simple prismatic
Trans-prismatic	Aragonitic irregular simple prismatic not very translucid in thin sections and acetate peels
Fibrous prismatic	Fibrous prismatic
Composite prismatic	Composite prismatic
Nacreous	Nacreous
Foliated	Regularly foliated, crossed foliated, complex crossed foliated
Crossed lamellar	Crossed lamellar with relatively large, linear first-order lamellae
Pseudo-crossed lamellar (1964–1971)	Crossed lamellar with relatively small, irregularly shaped first-order lamellae
Finely crossed lamellar (1996)	Crossed lamellar with smaller, commonly more irregularly shaped first-order lamellae
Complex (1964–1971)	Complex crossed lamellar
Complex crossed lamellar (1976–1996)	Complex crossed lamellar

level of electron microscopy, and classified prismatic microstructures on the basis of both prism width (e.g., fibrous versus simple and composite prisms) and second-order structure (e.g., simple versus composite prisms). Following MacClintock (1967), they restricted crossed lamellar and complex crossed lamellar to aragonitic microstructures and used crossed foliated and complex crossed foliated for the calcitic analogs.

Carter (1976, 1980a) and Carter and Clark (1985) adopted several terms from the literature of non-Bivalvia skeletal microstructure. These include Armstrong's (1969) crossed bladed; Mano's (1971) simple lamellar (as simple lamellar fibrous prismatic); Flajs' (1972) spherulitic; Fenninger and Flajs' (1974) granular; Mutvei's (1964) spherulitic prismatic; Batten and Dumont's (1976) asymmetric prismatic; Bandel's (1977) blocky prismatic; MacClintock's (1967) regularly foliated, crossed foliated, and complex crossed foliated; Bé, MacClintock, and Currie's (1972) helical; Erben's 1971 überkreuzt nadelig (as crossed acicular); and Erben's (1972) lamello-fibrillar. They also adopted Wise's (1970a, 1970b) columnar nacreous and row stack nacreous. New terms include radially elongate simple prismatic; lath-type, rod-type, and anvil-type fibrous prismatic; dissected crossed prismatic; denticular composite prismatic; nondenticular composite prismatic (NDCP); crossed composite prismatic; compound composite prismatic; irregular complex crossed lamellar; irregular complex crossed foliated; cone complex crossed lamellar; cone complex crossed foliated; semi-foliated; semi-nacreous; crossed-matted/lineated; and several varieties of crossed lamellar microstructure.

Carter and others (1990) added Sandberg's (1977, 1983) planar spherulitic, Prezant and Tan-Tiu's (1986a, 1986b) spiral crossed lamellar (as spiral cone complex crossed lamellar), and Schein-Fatton's (1988) pavimental prismatic (as pavement simple prismatic). New microstructure terms in Carter and others (1990) include lathic

Table 4. Correspondence between shell microstructure terminology in Popov (1970, 1973, 1974, 1976, 1977, 1985, 1986, 1992, 2014) and terms used here.

Popov (1970–2014)	**Present terminology**
Simple prismatic	Vertical, relatively large, polyhedral, first-order prisms separated by thick, interprismatic organic matrix, either simple prismatic or composite prismatic
Irregular prismatic	Irregular simple prismatic, irregular spherulitic prismatic
Fibrous prismatic	Reclined fibrous prismatic, reclined irregular spherulitic prismatic
Acicular prismatic (also called pinnate structure)	Spherulitic prismatic, nondenticular composite prismatic
Compound prismatic	Nondenticular composite prismatic
Composite prismatic	Nondenticular and denticular composite prismatic; radial fibrous prismatic secreted on a reflected shell margin
Acicular composite prismatic	Denticular composite prismatic with second-order prisms generally 1–10 μm wide
Fibrous composite prismatic with or without megaprisms	"Without megaprisms" = fibrous prismatic on a strongly reflected shell margin; "with megaprisms" = denticular composite prismatic
Compound composite prismatic with megaprisms	Compound nondenticular composite prismatic
Compound composite prismatic without megaprisms	Nondenticular composite prismatic on a strongly reflected but not coarsely denticulated shell margin
Compound composite prismatic with plates	Radial lamellar nondenticular composite prismatic
Sheet nacreous	Sheet nacreous
Row stack nacreous	Row stack nacreous
Columnar (or lenticular) nacreous	Columnar nacreous
Foliated	Regularly foliated, complex crossed foliated
Finely foliated	Calcitic, lath-type and rod-type fibrous prismatic
Crossed lamellar	Crossed lamellar, crossed foliated.
Complex crossed lamellar	Complex crossed lamellar
Irregular complex crossed lamellar ("blocky")	Irregular complex crossed lamellar
Tangled lamellar	Intermixed crossed lamellar and irregular complex crossed lamellar
Homogeneous	Superficially homogeneous in earlier works; very finely textured homogeneous in later works
Granular	Finely homogeneous with basic structural units 0.3–4.0 μm wide, i.e., smaller than the present granular microstructure
Irregular homogeneous	Very finely textured homogeneous, with irregularly shaped, basic structural units 0.5–3.0 μm wide
Crossed acicular homogeneous	Crossed acicular
Chalky	Chalky

simple prismatic, matted, and plywood microstructure.

Carter and others (2012) subdivided homogeneous into homogeneous *sensu stricto* (now finely homogeneous), homogeneous mosaic (now mosaic homogeneous), and granular (now alternatively granular homogeneous). They also proposed the new terms acute columnar NDCP (now low-angle NDCP) and obtuse columnar NDCP (now high-angle NDCP); used fibrous simple prismatic for very elongate simple prisms; and differentiated very elongate simple prisms from fibrous prisms on the basis of greater or lesser prism width, respectively.

The new terms superficially homogeneous, interlocking fibrous prismatic, and transverse fibrous simple prismatic are used here. In addition to the revisions indicated in the preceding paragraph, we adopt the following revisions: lathic simple prismatic is now lath-type simple prismatic; planar spherulitic simple prismatic is now high-angle NDCP; helical is now helical complex crossed lamellar; herringbone regularly foliated is now herringbone crossed foliated; large tablet imbricated nacre is now semi-foliated aragonite; and simple regularly foliated is now regularly foliated. Two correctons are presently made to figures in Carter and others (2012): figure 138 should be semi-foliated simple prismatic, and figure 206 should indicate that the upper crossed lamellar layer is inductural.

METHODS OF SHELL MICROSTRUCTURAL AND MINERALOGICAL ANALYSIS

DIAGNOSING SHELL MICROSTRUCTURE

The earliest studies of molluscan shell microstructure were limited to light microscopy of shell surfaces and fracture sections and normal and polarized light microscopy of thin sections. The later introduction of acetate peels represented an improvement over thin sections in terms of image clarity. Acetate peels also provided a relatively large field of view that is useful for revealing spatial relationships among shell layers and microstructural variations within layers. Actetate peels have traditionally been made with paper-thin, sheet acetate. Thin acetate peels are sometimes perforated when replicating a section with considerable porosity, and they are prone to buckling. These problems can be solved by making acetate slides from thicker acetate sheets, as described in Appendix A. The appendix also describes the procedure for making thin sections.

Transmission electron microscopy (TEM) was first used to study bivalve shell microstructure by Grégoire, Duchâteau, & Florkin (1949). However, TEM was not widely used for this purpose until the mid-1960s, and by the mid-1970s, it had already been largely replaced by scanning electron microscopy (SEM). More recently, electron backscatter diffraction and Raman spectroscopy have been added as tools for analyzing crystallographic orientations and shell mineralogy (Checa, Okamoto, & Ramirez, 2006; Checa, Esteban-Delgado, & Rodrígues-Navarro, 2007; Frenzel, Harrison, & Harper, 2012; Checa & others, 2013).

The difference in resolution and depth of field between acetate peels and SEM can be illustrated by two radial views of the outer shell layer of the glossid *Meiocardia vulgaris* (Reeve, 1845). The acetate peel shows only indistinct, reclined lineations, whereas the SEM reveals a finely homogeneous to irregular fibrous prismatic outer sublayer and a finely homogeneous to spherulitic prismatic inner sublayer (Fig. 2).

Shell microstructure studies should consider the possibility of spatial variation within a layer. For example, the outer shell layer in *Arca zebra* (Swainson 1833 in 1820–1833) varies from radial fibrous prismatic to radial crossed lamellar (Fig. 3); the outer shell layer in the hard substrate borer *Parapholas californica* (Conrad, 1837) changes from coarsely columnar prismatic posteriorly to finely non-columnar prismatic anteriorly (Fig. 4); and *Thracia pubescens* (Pulteney, 1799) shows an ontogenetic change in its middle shell layer from nacreous to porcelaneous (Carter & Lutz, 1990, pl. 2; present observations). This ontogenetic change recapitulates an apparent evolutionary trend in Thraciidae from nacreous to porcelaneous (Taylor, Kennedy, & Hall, 1973; Taylor, 1973, p 527; Runnegar, 1974; Checa, Harper, & Willinger, 2012).

Left/right shell microstructural asymmetry should also be considered, especially among members of Pteriomorphia (Newell & Boyd, 1985a). The left/right difference can be minor, as in a more prominent simple prismatic outer shell layer in the right valve of *Pteria colymbus* (Röding, 1798), or major, as in Propeamussiidae (see *Introduction,* p. 1–2). In the Aviculopectinidae, nacre sometimes persists in the right valve after it has been replaced evolutionarily by crossed lamellar microstructure in the left valve (Carter, 1990a, fig. 39). Left-right microstructural asymmetry in the orders Ostreida (inclusive of Pterioidea) and Pectinida commonly reflects longer evolutionary persistence of flexible, simple prisms in the outer shell layer in the right valve, and its earlier replacement by more rigid homogeneous, fibrous prismatic, and/or foliated microstructures in the outer shell layer in the left valve (Carter, 1990a, p. 261). Flexible shell margins can be adaptive for excluding predators and maximizing water retention in intertidal species (Carter & Tevesz, 1978b), but they have a dampening effect on the evolution of shell sculpture (Waller, 1972), and they limit the size of marginal mantle structures (Carter, 1990a, p. 234). Within the order Pectinida, the evolutionary change from flexible to rigid shell margins correlates with the development of stronger anti-predation sculpture and more complex mantle margins (Carter, 1990a, p. 235).

OBTAINING MICROSTRUCTURAL INFORMATION FROM ALTERED SHELLS

In Ordovician–Permian faunas, calcitic shell layers are commonly preserved, but aragonitic shell layers are generally dissolved

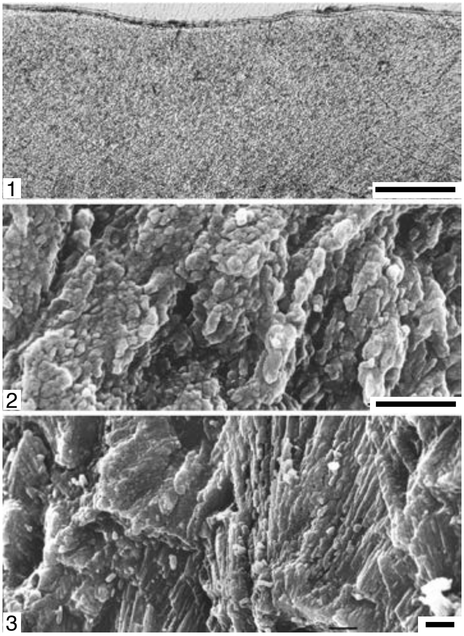

Fig. 2. Outer shell layer of glossid *Meiocardia vulgaris* (Reeve, 1845), China, YPM 9718. *1,* Radial acetate peel, with shell exterior up and shell margin toward left, also showing outer part of crossed lamellar middle shell layer (near bottom); *2–3,* SEM of radial fracture through same outer shell layer with same orientation, showing finely homogeneous to irregular fibrous prismatic outer part (*2*) and finely homogeneous to irregular spherulitic prismatic inner part (*3*); scale bars, 100 µm (Carter, new).

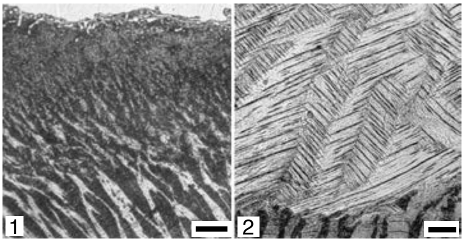

Fig. 3. Variation in shell microstructure within same aragonitic outer shell layer of arcid *Arca zebra* (Swainson 1833 in 1820–1833), Florida, USA, YPM 6170, in acetate peels of radial, vertical sections, with shell exterior up and posterior shell margin toward right. *1,* Radial fibrous prismatic outer shell layer (above) and underlying commarginal crossed lamellar shell layer; *2,* radial crossed lamellar outer shell layer (above) and underlying commarginal crossed lamellar shell layer; scale bars, 50 µm (Carter, new).

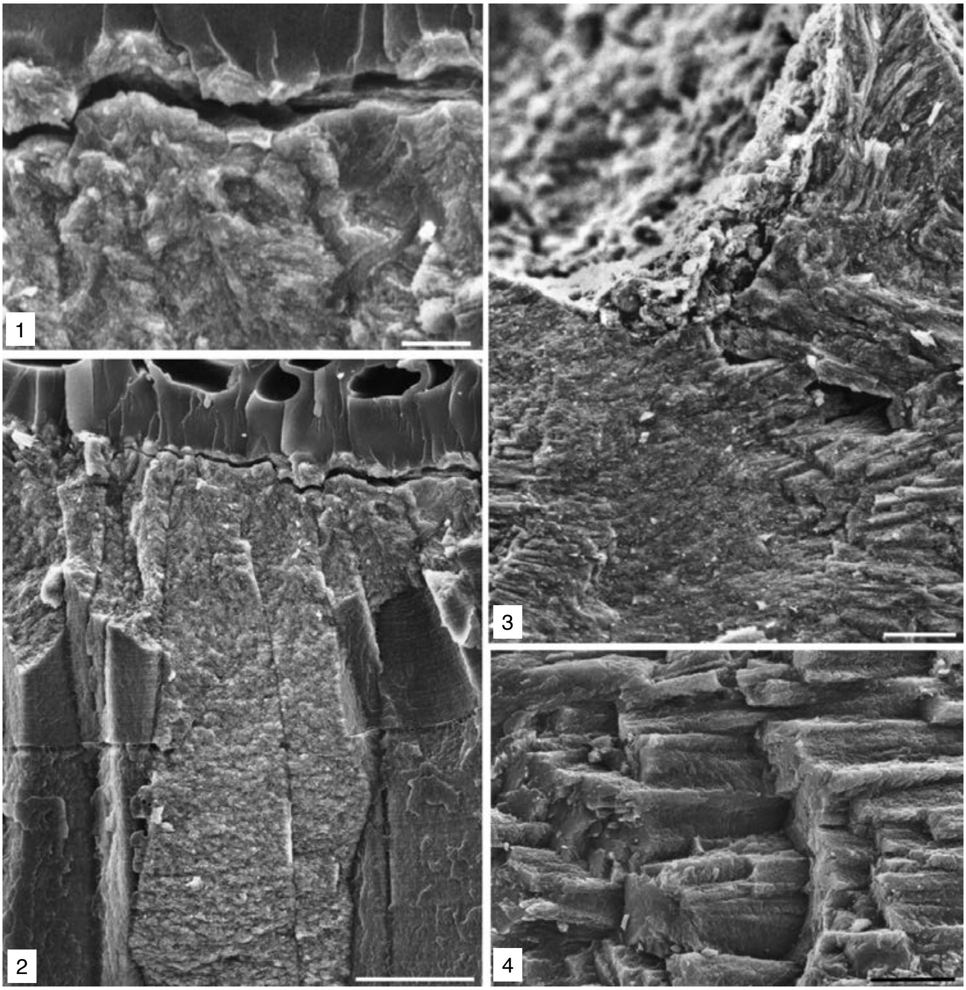

FIG. 4. Variations in shell microstructure within the aragonitic outer shell layer of pholadid *Parapholas californica* (CONRAD, 1837), Monterey Bay, California, USA, YPM 10258. SEM of radial, vertical fractures through shell posterior (*1–2*) and shell anterior (*3–4*), with shell exterior up and shell margin toward right. *1,* Periostracum (above) and underlying initial, nondenticular composite prismatic portion of columnar prisms in shell posterior; *2,* same fracture section as *1,* showing nondenticular composite prismatic grading inward into simple prismatic within a columnar prism; *3,* anterior part of outer shell layer, with rasping spine at upper right, showing variably oriented nondenticular composite prisms plus some finely homogeneous microstructure; *4,* higher magnification of nondenticular composite prisms in *3,* with prism second-order structure not visible due to fractures following the first-order prism boundaries; scale bars, 5 µm in *1* and *4;* 25 µm in *2–3* (Carter, new).

or diagenetically altered. This is because calcite is thermodynamically more stable and hence more resistant to dissolution and recrystallization than aragonite near the earth's surface (WRIGHT & CHERNS, 2009). In the exceptional cases in which Paleozoic aragonite is preserved, the mineral has probably been isolated from the catalytic action of groundwater. Wet aragonite will stabilize at a very high hydrostatic pressure, but such pressures are not likely to be attained in sedimentary rocks (JAMIESON, 1953; HALL & KENNEDY, 1967). Dry aragonite is less likely to invert to calcite, and it might survive almost indefinitely (Brown, Fyfe, & Turner, 1962). Paleozoic rocks with original shell aragonite are typically relatively impermeable by virtue of being clay-, bituminous-, or asphalt-rich (Switzer & Boucot, 1955; Stehli, 1956; Hallam & O'Hara, 1962; Runnegar, 1985). Under these conditions, the aragonite might be protected by a hydrophobic coating of amino acids derived from the shell's organic matrix (Hall & Kennedy, 1967).

Balthasar and others (2011) reported inclusions of original shell aragonite within calcite-replaced, Ordovician and Silurian brachiopods. Similar early Paleozoic occurrences of aragonite are not yet documented for the Bivalvia. However, complete, or nearly complete, aragonitic shell layers are preserved in some Bivalvia in the Middle Devonian Weatherall Formation of Arctic Canada (Johnston & Goodbody, 1988); the Pennsylvanin, Upper Oil Shale Group of Scotland (Hallam & O'Hara, 1962); the Pennsylvanian Boggy Formation (Buckhorn Asphalt) of Oklahoma (Switzer & Boucot, 1955; Stehli, 1956; Grégoire, 1959; Grégoire & Telheus, 1965; Squires, 1973; Heaney, 1998; Vendrasco & others, 2018); the Pennsylvanian Four Corners Formation (Breathitt Formation, Kendrick Shale) of Kentucky (Stehli, 1956; Yochelson, White, & Gordon, 1967; Brand, 1981, 1983; Brand & Morrison, 1987; Carter, 1990a, 2004); the Pennsylvanian Brush Creek Formation of Ohio and Pennsylvanian (Brand, 1989); and the Late Permian Wutonggou Formation of Xinjiang, China (Yochelson, 1989; Brand, Yochelson, & Eager, 1993).

Microstructural information can sometimes be retrieved from fully calcitized, originally aragonitic shell layers in acid-etched, polished sections. In these cases, the replacement calcite is commonly darkly colored, suggesting that micro-inclusions of degraded organic matrix (amino acids?) have caused defects in the calcite crystal lattice that are revealed by etching. The microstructural relicts are sometimes so distinct that they have been mistaken for original calcite, as in the case of the crossed lamellar layer in a Permian *Pseudomonotis* described by Newell and Boyd (1989; corrected by Carter, 1990e, p. 372). This kind of relict preservation has been documented for bivalves in the upper Silurian Mulde Formation of Gotland, Sweden (Carter, 2001), the Middle Devonian Hamilton Group of central New York (Carter & Tevesz, 1978a, 1978b; Carter, 1990a, 2001), and the lower Permian Wandagee Formation of Western Australia (Newell & Boyd, 1989).

Some Cambrian and Ordovician bivalves have left detailed impressions of their aragonitic and calcitic microstructures on phosphatic coatings or phosphatic internal molds (Runnegar & Jell, 1976; Runnegar, 1983, 1985; Runnegar & Bentley, 1983; Runnegar & Pojeta, 1992; MacKinnon, 1985; Kouchinsky, 1999, 2000; Vendrasco, Checa, & Kouchinsky, 2010, 2011; Vendrasco, Checa, & Heimbrock, 2019; Vendrasco, & others, 2010) (Fig. 64.1). In extraordinary cases, microstructural elements are replicated in three dimensions in calcium phosphate, e.g., nacre tablets in the Late Ordovician Maquoketa Shale of Iowa (Mutvei, 1983a, 1983b; Vendrasco & others, 2013). Phosphatic impressions and replicas of shell microstructure are largely, if not entirely, restricted to the early Paleozoic, probably because of a global decrease in the rate of secondary phosphatization in the marine realm after the Ordovician (Vendrasco, Checa, & Heimbrock, 2019).

Calcitic shell layers are not known to be retained in Cambran bivalves, but they are commonly retained in post-Cambrian bivalves. Ordovician and Silurian bivalves with original shell calcite generally show some alteration of the microstructure, whereas many later Paleozoic bivalves have excellently preserved calcitic shell layers. Calcitic microstructures are rarely replicated by replacement silica in Paleozoic bivalves, e.g., in the middle Permian Lower Getaway Limestone of west Texas (Newell & Boyd, 1985b, fig. 3).

FIG. 5. Feigl-stained depositional surface of left valve of plicatulid *Plicatula gibbosa* LAMARCK, 1801, St. Thomas, Virgin Islands, YPM 9631, showing unstained (*white*) calcite and stained (*black*) aragonite. The aragonitic middle and inner shell layers and myostracum are stained black, whereas the largely calcitic outer shell layer is unstained except for minute, radially elongate patches of aragonite. Maximum horizontal dimension is 23 mm (adapted from Carter, Barrera, & Tevesz, 1998, fig. 6,*4*).

DETERMINING SHELL MINERALOGY

Shell mineralogy is determined by X-ray diffraction of powdered samples, by Feigl's stain (FEIGL, 1937; FRIEDMAN, 1959) or Meigen's stain (HOLMES, 1921), by electron backscatter diffraction, or by Raman spectroscopy (HOPE, WOODS, & MUNCE, 2001; NEHRKE & NOUET, 2011; NEHRKE & others, 2012; ROGER & others, 2017). The two mineral stains utilize the higher solubility of aragonite relative to calcite. The increased solubility of a very finely textured, calcitic microstructure might therefore cause it to stain positively for aragonite (DICKSON, 1985). Vaterite, a very metastable polymorph of calcium carbonate, will also stain positively for aragonite, but vaterite is not known to comprise an entire molluscan shell layer. It can, however, be the first mineral deposited during shell repair, and it rarely comprises abnormal shell thickenings, as in the freshwater genus *Corbicula* MEGERLE VON MÜHLFELD, 1811 (see WOLF & others, 2000; SPANN, HARPER, & ALDRIGE, 2010; FRENZEL & HARPER, 2011). Vaterite might become stabilized in some bivalve shells by a covering of aragonite, as in the chondrophore of a *Laternula* RÖDING, 1798 studied by NEHRKE and others (2012).

Feigl's stain is useful for revealing the spatial distribution of calcite and aragonite on shell surfaces and sections (CARTER, 1980b, 1980c; CARTER, 1990e, fig. 3–5) (Fig. 5). Meigen's stain is sometimes preferred because it tends to produce smaller stain crystals that are less likely to obscure the microstructure under SEM examination (SUZUKI, TOGO, & HIKIDA, 1993).

GENERAL TERMS

General descriptive terms are defined as follows for organic-rich and strongly mineralized shell layers. Terms, when first defined, appear in bold in the following pages. Abbreviations for specimen repositories cited in the accompanying figure captions are found on p. 70. Illustrated species are extant unless indicated otherwise.

ORGANIC-RICH SHELL LAYERS

The more organic-rich parts of a bivalve shell (excluding the ligament) are the periostracum, pseudoperiostracum, and conchiolin sublayers.

The periostracum is the non-mineralized or discretely mineralized, outermost part of a shell initiated in the mantle groove adjacent to the shell margin and secreted by the inner surface of the outer mantle fold—and in some cases, also by the outer surface of the middle mantle fold (SALEUDDIN, 1979, p. 48; SALEUDDIN & PETIT, 1983; HAAS, 1981, p. 405; CARTER & ALLER, 1975; CARTER & others, 1990, p. 652; TAYLOR, GLOVER, & WILLIAMS, 2005; CHECA & SALAS, 2017). The periostracum sometimes extends inward as an incursion into the outer shell layer as a consequence of strong mantle withdrawal, but its internal growth bands remain discontinuous with those of the outer shell layer.

Discrete mineralization of the periostracum was first recognized by CARTER and ALLER (1975). For over a century, authors had described minute, aragonitic spikes and granules on the exterior of anomalodesmatan shells, but these were regarded as part of the subperiostracal shell. ALLER (1974) noted that these spikes in *Laternula* are initiated distal to the solid shell margin, but he was unaware that similar structures can be imbedded within the periostracum. Carter and Aller (1975) pointed out that periostracal mineralization is genetically distinct from the subperiostracal shell and that it can differ mineralogically and microstructurally from the outer shell layer. Mineralized periostracal structures are usually aragonitic, e.g., in trigoniids (Fig. 11), some mytilids (Fig. 13, Fig.18), gastrochaenids (Carter, 1978), venerids (Fig. 14, Fig.16), and anomalodesmatans (Fig. 17, Fig. 19). They are uniquely calcium phosphatic in some lithophaginid mytilids (Carter, 1990a, fig. 54) (Fig. 12, Fig.15) (Waller, 1983; Carter, 1990a, p. 281).

Periostracal mineralization can be intraperiostracal, extraperiostracal, or infraperiostracal. **Intraperiostracal** structures are entirely embedded within the organic periostracum, with the possible exception of their proximal ends cementing to the outer shell layer. **Infraperiostracal** structures differ in having their proximal ends embedded within the outer shell layer. **Extraperiostracal** structures extend from the interior of the periostracum beyond its outer surface (Checa & Harper, 2010; Carter & others, 2012). When infraperiostracal structures are embedded in the outer shell layer, their internal growth bands are discontinuous with that layer. The three categories of periostracal mineralization are not mutually exclusive. For example, aragonitic periostracal spikes can be simultaneously extraperiostracal and infraperiostracal in the gastrochaenid *Spengleria rostrata* (Spengler, 1793) (Carter, 1978, fig. 17–21; Carter & others, 2012, fig. 143; Checa & Harper, 2012).

Periostracal mineralization is sometimes accompanied by minute pores extending vertically outward from the inner surface of the periostracum. The pores can be accompanied by calcium phosphatic (Fig. 12, Fig. 15) or aragonitic mineralization (Glover & Taylor, 2010, fig. 6F–7F) (Fig. 16). Accumulations of calcium phosphate around some pores (Fig. 15) suggest that they supply mineralizing fluids to the periostracum. However, individual pores do not generally associate with a single, mineralized periostracal structure (Fig. 12, Fig. 16).

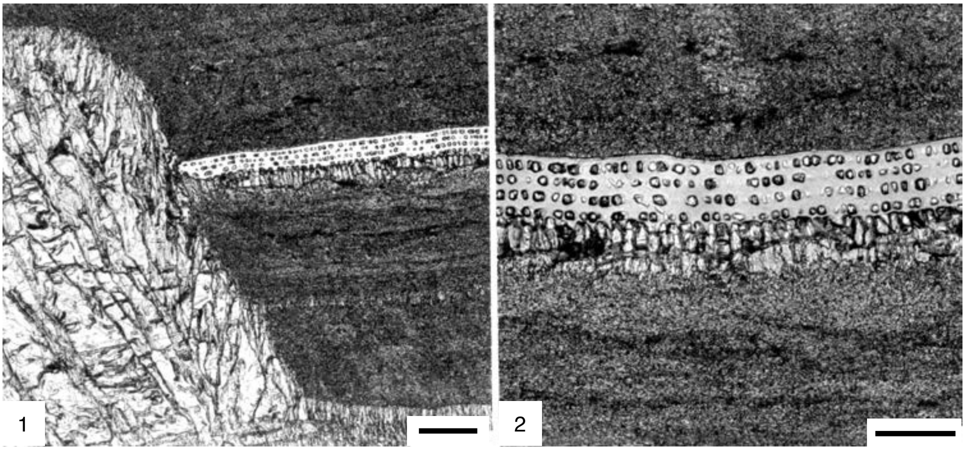

Fig. 6. Pseudoperiostracum with aragonitic granules, butting against the adductor myostracum in lucinid *Lucina pensylvanica* (Linnaeus, 1758), Florida, USA, YPM 10017, radial acetate peel with shell exterior up and posterior shell margin toward right. *1,* Pseudoperiostracum and overlying and underlying middle shell layer on right, prismatic adductor myostracum on left; *2,* higher magnification showing horizontal rows of aragonitic granules in pseudoperiostracum, and gradation from these granules into an underlying irregular simple prismatic sublayer in middle shell layer; scale bars,100 µm in *1,* 50 µm in *2* (Carter, new).

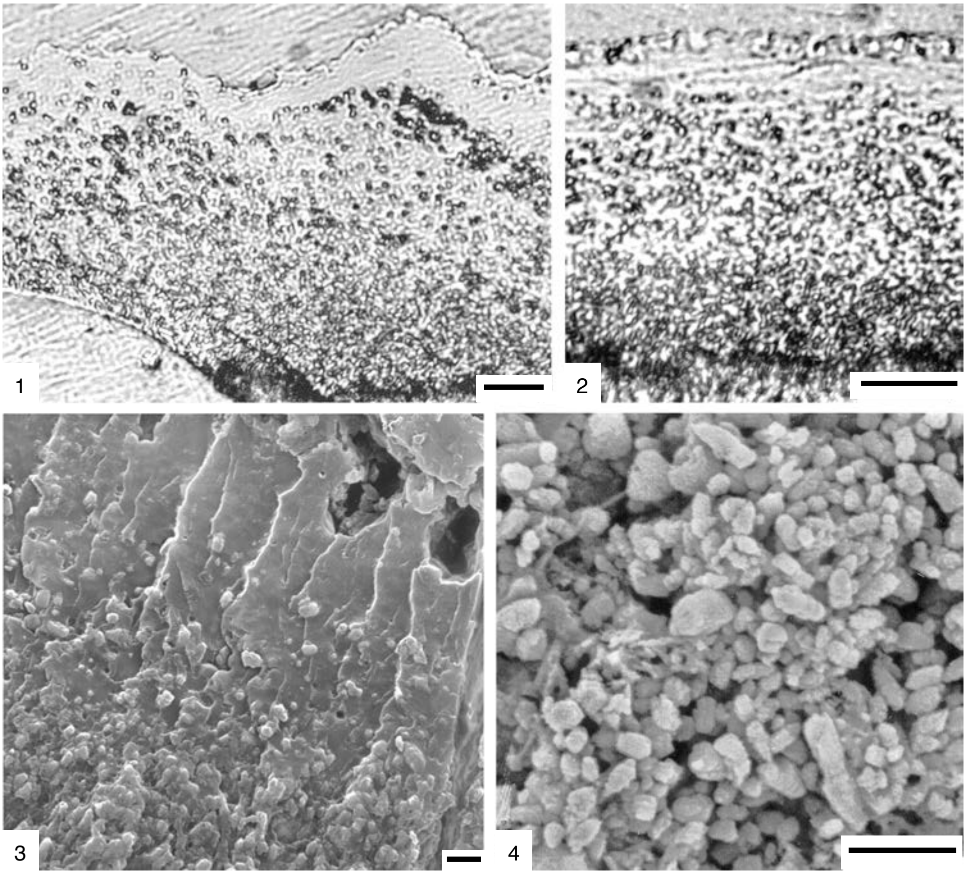

FIG. 7. Pseudoperiostracum with aragonitic granules in astartid *Astarte undata* GOULD, 1841, Maine, USA, YPM 9727. *1–2,* Radial, vertical acetate peel with posteroventral shell margin toward left and shell exterior up, showing non-mineralized, true periostracum (clear layer, above) and underlying pseudoperiostracum (granular layer, middle) and prismatic outer shell layer (extreme bottom); *3,* SEM of radial, vertical fracture through periostracum (top right) and discretely mineralized pseudoperiostracum (bottom, left), with shell exterior up; *4,* aragonitic granules freed from pseudoperiostracum by digestion of organic material in sodium hypochlorite; scale bars, 10 µm in *1* and *2;* 1 µm in *3* and *4* (Carter, new).

CARTER and others (2012, p. 146) proposed **pseudoperiostracum** for a non-mineralized or discretely mineralized, organic-rich sublayer secreted by the outer surface of the outer mantle fold and by the lateral mantle epithelium between the shell margin and the pallial myostracum. Pseudoperiostracum differs from periostracum in having internal growth bands that can be continuous with those in another subperiostracal shell layer. It differs from a conchiolin sublayer in not extending into the inner shell layer position. Discrete mineralization of the pseudoperiostracum is sometimes intergradational with an adjacent prismatic sublayer, as in *Lucina pensylvanica* (LINNAEUS, 1768 in 1766–1770) (Fig. 6.2). TAYLOR and others (2004) called the pseudoperiostracum in *Lucina pensylvanica* calcified periostracal lamellae. The true periostracum in that species is a very thin, non-mineralized layer overlying the outer surface of the shell and the distal margin of the pseudoperiostracum. CARTER and others (2012, fig. 247) illustrated aragonitic, irregularly shaped granules isolated from the pseudoperiostracum of

Lucina pensylvanica. Tulip-shaped, mineralized spherulites are present in the pseudoperiostracum of *Pleurolucina harperae* Glover & Taylor, 2016 (see Glover & Taylor, 2016).

Discrete mineralization of the pseudoperiostracum also occurs in the astartid *Astarte undata* Gould, 1841 (Fig. 7) and in the corbulid *Caryocorbula nasuta* (G. B. Sowerby I) (Fig. 8).

Conchiolin sublayers resemble periostracum and pseudoperiostracum in being largely or entirely organic, but differ in being restricted to the inner or middle and inner shell layers. The term conchiolin was proposed by Frémy (1855) for the water-, alcohol-, and ether-insoluble residue of molluscan shells remaining after dissolution of its mineral content in hydrochloric acid. Conchiolin sublayers are commonly secreted in response to irritation of the mantle accompanying shell breakage, penetrative corrosion or abrasion, or parasitic infestation. Other conchiolin sublayers are formed to seal the shell margins against unfavorable environmental conditions, as in many corbulids, or are secreted as **prophylaxis sublayers** in anticipation of predatory drilling or other shell penetration, as in some unionids, lucinids, and corbulids (Tevesz & Carter, 1980; Lewy & Samtleben, 1979; Araujo, Delvene, & Munt, 2014; Glover & Taylor, 2016).

STRONGLY MINERALIZED SHELL LAYERS

The more strongly mineralized shell layers are called outer, middle, inner, myostracum, ligostracum, mosaicostracum, and inductura. The outer shell layer comprises most of the shell's thickness at its distal margins, whereas the inner shell layer comprises most of its thickness near the umbos. The pallial and (usually contiguous) adductor myostracum marks the boundary between the middle and inner shell layers.

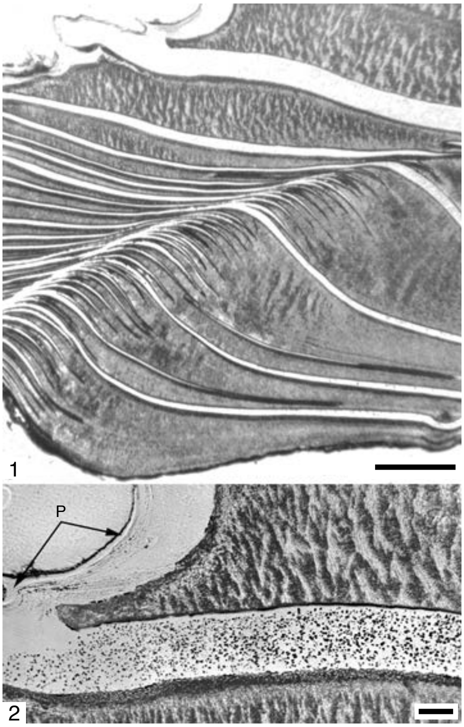

Fig. 8. Periostracum (*P*) and much thicker pseudoperiostracum (granular layer) in corbulid *Caryocorbula nasuta* (G. B. Sowerby I, 1833b), Zorritos, Peru, UNC 16033. Acetate peel of radial, vertical section through posterior shell margin, with shell exterior up and shell margin toward left. Outer and middle shell layers also visible. *1,* Lower magnification showing entire shell margin; *2,* higher magnification of upper part of *1,* showing aragonitic granules in pseudoperiostracum; scale bars, 500 µm in *1,* 50 µm in *2* (Carter, new).

Oberling (1955, p. 128) proposed myostracum for shell material secreted at sites of shell-muscle attachment. Smith (1983) broadened this definition to include shell material secreted at sites of non-muscle mantle attachment. Smith's definition is preferred because both kinds of mantle attachment typically result in the same irregular simple prismatic microstructure. Vendrasco, Checa, and Heimbrock (2019, p. 661) described the adductor myostracum in the Late Ordovician praenuculid *Homilodonta* Cope, 1997 sp. as having a terraced surface, which they interpreted as the impression of stair-step nacre. However, definitive impressions of nacre tablets were not present. The surface of the adductor myostracum in modern *Arca zebra* (Swainson 1833 in 1820–1833) shows polygonal areas 10–15 µm wide, which CARTER (1990c, p. 323) interpreted as impressions of mantle cells. In this species, the underlying microstructure is the usual myostracal irregular simple prismatic. This raises the possibility that the myostracum in *Homilodonta* was similarly structured.

The outer shell layer is positioned directly below the periostracum or directly below any mosaicostracum that might be present. It differs from periostracum in being secreted by the outer surface of the outer mantle fold. The middle shell layer is positioned between the outer shell layer and the pallial (and generally also) adductor myostracum. The boundary between the outer and middle shell layers can be sharp or gradational. When a shell is microstructually uniform between the periostracum and the pallial myostracum, this is referred to as outer and middle shell layer undifferentiated. The inner shell layer is positioned proximal to the pallial myostracum, and it includes microstructurally similar parts of the hinge. The inner shell layer differs from the outer and middle shell layers in thickenning toward instead of away from the beaks.

The terms outer, middle, and inner are used instead of MACCLINTOCK's (1967) numerical system because the latter typically results in unlikely homologies among layers. For example, consider two species, A and B, both with a simple prismatic shell layer directly below the periostracum and a homogeneous shell layer proximal to the pallial myostracum. Species A has crossed lamellar microstructure grading inward into crossed acicular between the simple prismatic layer and the pallial myostracum, whereas species B has only crossed lamellar microstructure in this position. According to MACCLINTOCK's system, the simple prismatic, crossed lamellar, and crossed acicular layers in species A would be designated M+3, M+2, and M+1, respectively, with M representing the pallial myostracum. The prismatic and crossed lamellar layers in species B would be designated M+2 and M+1, respectively. The numerical system suggests that the simple prismatic shell layer in species A has no homolog in species B, and that the crossed lamellar shell layer in species A is homologous with the simple prismatic shell layer in species B. It is more reasonable to conclude that the two simple prismatic layers are homologous, and that the crossed lamellar and crossed acicular layers in species A are homologous with the crossed lamellar layer in species B.

Identifying a shell layer as outer versus middle can be complicated by ontogenetic attenuation of an early post-larval outer shell layer, thereby causing an early post-larval middle shell layer to occupy an outer layer position in the adult stage. This occurs in many Pectinidae, wherein the simple prismatic outer shell layer is restricted to the first few millimeters of shell growth. In such cases, to maintain homologies with shell layers in other Pectinoidea with a persistent prismatic outer shell layer, the early ontogenetic middle shell layer should also be identified as middle near the adult shell margin.

In a few bivalves, the middle/inner shell layer boundary is obscured by a discontinuous pallial myostracum or, as in most oysters, by the absence of a pallial myostracum (DOUVILLÉ, 1907; STENZEL, 1971, p. 968). In such cases, the middle/inner shell layer boundary may be marked by a distinct change in shell microstructure. Failing this, comparison can be made with closely related species with an intact pallial myostracum, as in the oyster *Saccostrea* DOLLFUS & DAUTZENBERG, 1920. Alternatively, one can indicate "middle and inner shell layer undifferentiated."

CARRIKER and PALMER (1979, p. 691) proposed the term ligostracum for a very thin, mineralized sublayer binding the ligament to the shell. CARRIKER (1979) broadened this definition to include a thin sublayer binding the periostracum to the shell. CARRIKER and PALMER's (1979) definition is preferred because HAMILTON (1969) had earlier proposed mosaicostracum for the periostracal attachment layer. Ligostracum is usually aragonitic and fibrous prismatic, with

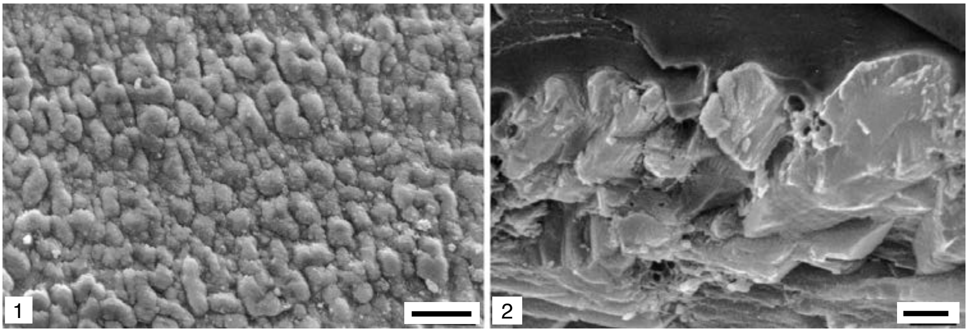

FIG. 9. Calcitic mosaicostracum with pustular surface texture in mytilid *Mytilus galloprovincialis* LAMARCK, 1819, South Africa, UNC 15415. *1,* SEM of external surface of mosaicostracum, with periostracum removed by digestion in sodium hypochlorite; *2,* SEM of radial, vertical fracture showing finely homogeneous to granular homogeneous microstructure of mosaicostracum (middle), the overlying periostracum (above) and the calcitic, fibrous prismatic outer shell layer (below); scale bars,10 μm in *1,* 1 μm in *2* (Carter, new).

prisms oriented parallel with the fibers in the adjacent fibrous sublayer of the ligament. In bivalves without a preserved ligament, the ligostracum can indicate the attachment site and orientation of the ligament fibers.

Mosaicostracum is a very thin, microstructurally distinct, mineralized sublayer binding the periostracum to the shell (HAMILTON, 1969). Mosaicostracum has been described for some members of Solemyidae, Mytilidae, Tellinidae, and Veneridae, e.g., *Solemya pusilla* (GOULD, 1861) (SATO & others, 2013, fig. 6*a–c,* identified as part of the prismatic outer shell layer). Hamilton named five mosaicostracal textures based on scanning electron microscopy of shell exteriors exposed by chemical removal of the periostracum: crystalline, pustular, linear, mosaic, and planar. These textures do not necessarily indicate the microstructure of the mosaicostracum. For example, the pustular mosaicostracum in *Mytilus galloprovincialis* LAMARCK, 1819, consists of finely homogeneous to granular homogeneous microstructure (Fig. 9).

MOORE (1941, p. 139) adopted KNIGHT's (1931, p. 180) term **inductura** for shell material secreted over the normal exterior surface of the shell by a reflected mantle margin. GRAY (1833, p. 792) correctly inferred the genesis of this layer in cypraeid gastropods, and he noted that its microstructure resembles the underlying shell layer. In some Cardiidae, the inductura forms a patchy or persistent, later ontogenetic addition to the shell. It is especially thick in Late Cretaceous *Protocardia* (*Pachycardium*) *stantoni* (WADE, 1926), where it locally obscures the underlying sculpture (SCHNEIDER & CARTER, 2001, fig. 5,*2*). Because inductura is initiated after the prodissoconch-dissoconch transition, its persistence into the adult stage can give the false impression of an early juvenile prismatic outer shell layer submerging, during shell growth, into a crossed lamellar middle shell layer, as in *Acanthocardia aculeata* (LINNAEUS, 1758) (Fig. 10).

DESCRIPTIVE TERMINOLOGY

Bivalve shell microstructures are classified into nine categories based on periostracal *versus* non-periostracal mineralization and major structural organization: periostracal mineralization, homogeneous, spherulitic, prismatic, laminar, reticulate, crossed, chalky, and vesicular.

Structural elements are described as **radial** when perpendicular to the shell margin or to a former shell margin at the point of observation, **commarginal** when parallel to the shell margin or to a former shell margin at the point of observation, **reclined** when radial and dipping away from the beak,

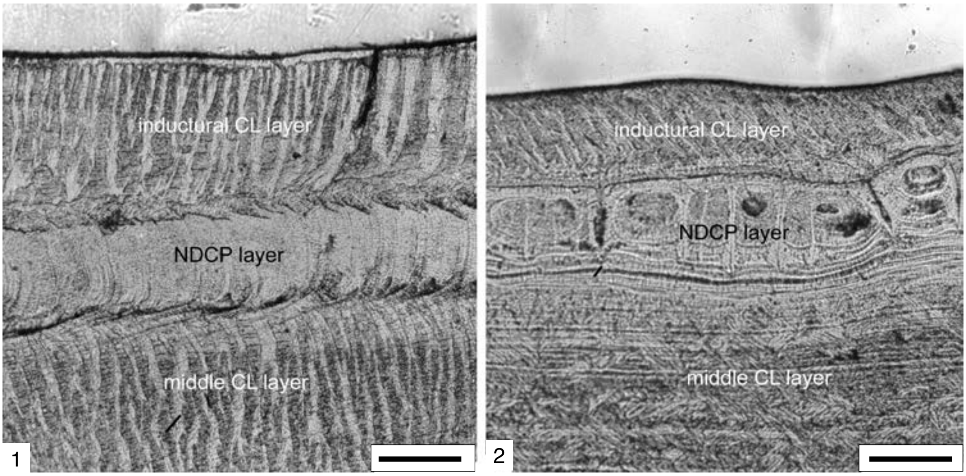

FIG. 10. Inductural and outer and middle shell layers in cardiid *Acanthocardia aculeata* (LINNAEUS, 1758), YPM 15376, acetate peels. *1,* Radial section, with shell exterior up and distal margin toward right, showing the nondenticular composite prismatic (*NDCP*) outer shell layer, the crossed lamellar (*CL*) middle shell layer, and the crossed lamellar inductura; *2,* commarginal, vertical section through same part of shell, with shell exterior up; scale bars, 100 µm (adapted from Schneider & Carter, 2001, fig. 6,*1*–6,*2*).

inclined when radial and dipping toward the beak, **horizontal** when parallel with the plane of the shell layer, and **vertical** when perpendicular to the plane of the shell layer.

A **radial** section is a vertical section that is perpendicular to growth lines at the point of observation. A **commarginal** section is a vertical section that is parallel with growth lines at the point of observation. Some authors use **antimarginal** instead of radial because bivalve shell growth is conispiral, not planispiral.

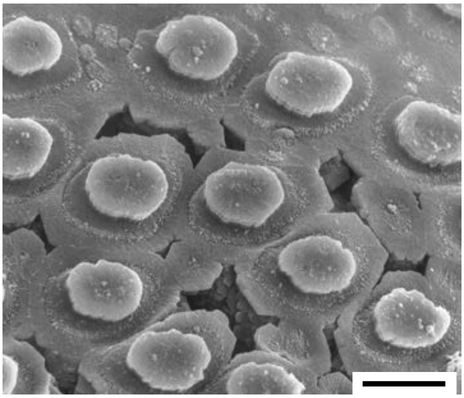

FIG. 11. Aragonitic intraperiostracal bosses in trigoniid *Neotrigonia gemma* IREDALE, 1924, Sydney, Australia, UNC 5427, underlain by columnar prismatic outer shell layer. Organic parts of periostracum and outer shell layer removed by digestion in sodium hypochlorite, SEM of exterior shell surface, scale bar, 5 µm (Carter, new).

I. PERIOSTRACAL MINERALIZATION

Bosses. Flattened, rounded to polygonal, disk-shaped, mineralized, intraperiostracal structures, in some cases cemented to the outer surface of the outer shell layer, and sometimes but not always positioned at the outer end of a columnar prism in the outer shell layer, e.g., in the trigoniid *Neotrigonia gemma* IREDALE, 1924 (Fig. 11).

Cylinders. Columnar, typically polygonal, mineralized intraperiostracal structures, e.g., hexagonal and fluorapatitic in the mytilid *Lithophaga nigra* (D'ORBIGNY, 1853 in 1841–1853) (Fig. 12).

Granules. More or less equidimensional, mineralized, intraperiostracal structures, e.g., aragonitic and cemented to the outer shell layer in the thraciid *Thracia morrisoni* PETIT, 1964, or aragonitic and embedded within the periostracum (along with some

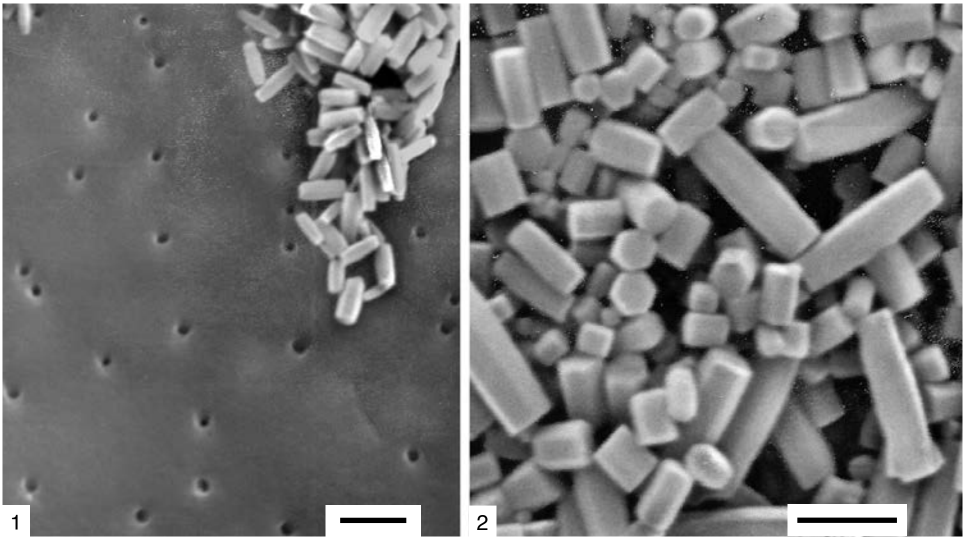

FIG. 12. Intraperiostracal, fluorapatitic cylinders in mytilid *Lithophaga nigra* (D'ORBIGNY, 1853 in 1841–1853), Bermuda, UNC 13147. *1,* Exterior view of inner sublayer of periostracum, with outer sublayer removed by digestion in sodium hypochlorite, also showing openings of periostracal pores; *2,* higher magnification of cylinders, with orientations randomized by absence of surrounding organic periostracum; scale bars, 1 µm (adapted from Carter, 1990a, fig. 54A–B).

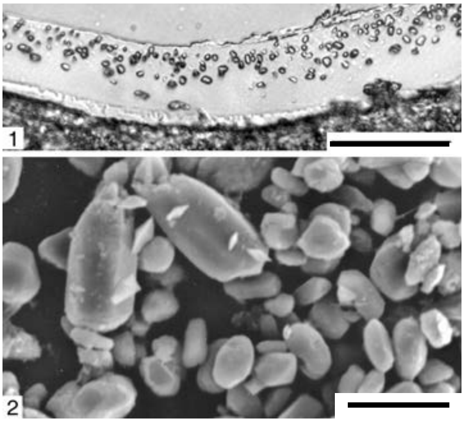

FIG. 13. Aragonitic intraperiostracal granules and spikes in mytilid *Trichomya hirsuta* (LAMARCK, 1819), western Pacific, YPM 10124. *1,* Acetate peel of radial, vertical section through periostracum and outer shell layer, with shell exterior up, scale bar, 50 µm; 2, SEM of granules and a few spikes freed from periostracum by digestion in sodium hypochlorite, scale bar, 10 µm (Carter & others, 2012, fig. 223).

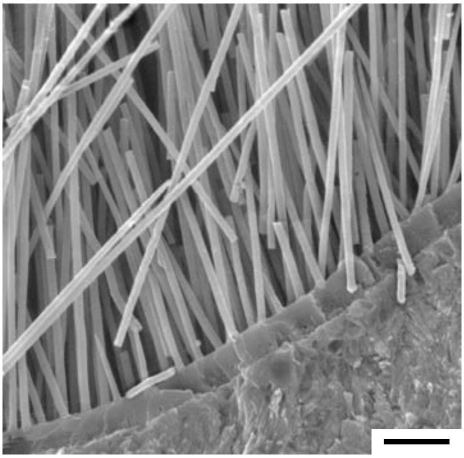

FIG. 14. Aragonitic extraperiostracal needles in venerid *Tivela* (*Tivela*) *byronensis* (GRAY, 1838), Guaymas, Gulf of California, Mexico, YPM 9737, also showing the organic periostracum and outer shell layer, SEM of vertical fracture, with shell exterior up, scale bar, 10 µm (Carter & others, 2012, fig. 225).

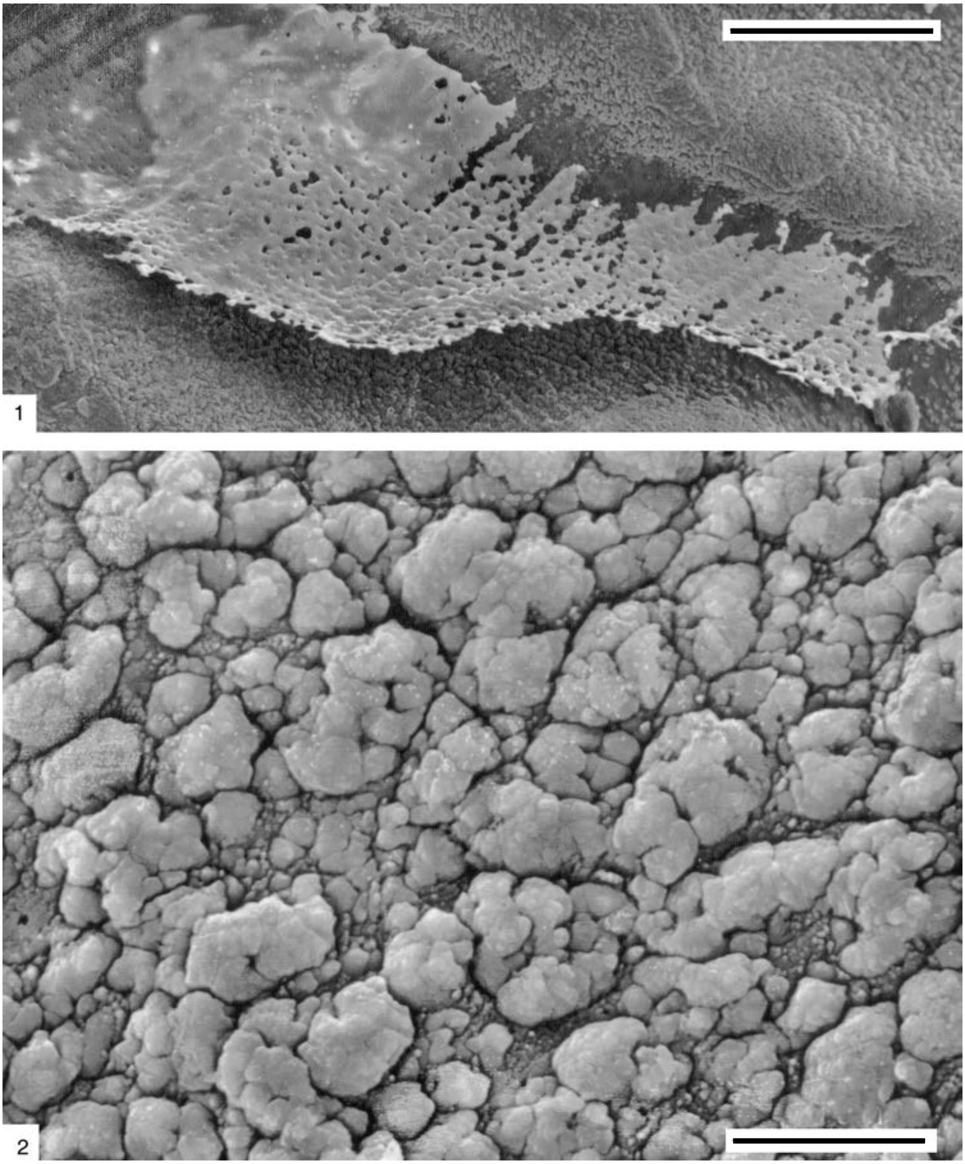

FIG. 15. *1,* Exterior view of fluorapatitic to carbonate fluorapatitic, intraperiostracal irregular masses in lithophaginid *Lithophaga antillarum* D'ORBIGNY, 1853 in 1841–1853, Bahamas, UNC 13150, locally agglomerated into a sheetlike sublayer, outer sublayer of periostracum removed by digestion in sodium hypochlorite, also visible are openings of several pores extending from inner surface of periostracum and penetrating some of the irregular masses, scale bar, 100 µm; *2,* higher magification, scale bar, 10 µm (Carter & others, 2012, fig. 224).

aragonitic spikes) in the mytilid *Trichomya hirsuta* (LAMARCK, 1819) (Fig. 13).

Needles. Distally tapering, vertical to oblique, very elongate, mineralized, generally extraperiostracal structures less than 3 µm wide, with average length/height ratio greater than 35, i.e., narrower than a spike or stud, more elongate than a pin, e.g., aragonitic in the venerid *Tivela (Tivela) byronensis* (GRAY, 1838) (Fig. 14). They were called periostracal spines by CARTER and LUTZ (1990, p. 23, pl. 97,*C*) for *Tivela trigonella* (LAMARCK, 1818) and needles by OHNO (1996) and GLOVER and TAYLOR (2010).

Irregular masses. Mineralized, intraperiostracal structures without regular shapes, sometimes nodular, sometimes agglomerated into a discontinuous sublayer, e.g., fluorapatitic to carbonate fluorapatitic in the lithophaginid *Lithophaga antillarum* D'ORBIGNY, 1853 in 1841–1853 (Fig. 15).

Pins. Distally tapering to blunt-ended, more or less vertical, moderately elongate, mineralized, extraperiostracal structures less than 3 µm wide, with average length/height ratio from between 5 and 35, i.e., narrower than a spike or stud, less elongate than a needle, e.g., aragonitic in the venerid *Pitar trevori* LAMPRELL & WHITEHEAD, 1990 (Fig. 16). GLOVER and TAYLOR (2010) applied this term to narrow, elongate, mineralized periostracal structures less than 20 µm long, without specifying width.

Plaques. Subovate to subrectangular, flattened, mineralized, intraperiostracal structures cemented to the outer shell layer, commonly with length axes more or less commarginally aligned, e.g., anteriorly in the myochamid *Myadora complex* IREDALE, 1924, and in the thraciid *Thraciopsis angustata* (ANGAS, 1868) (CHECA & HARPER, 2010, figs. 2E, 2F) (Fig. 17).

Spikes. Distally tapering, more or less pointed, moderately elongate, mineralized periostracal structures more than 3 µm wide, e.g., aragonitic intra-, extra-, and infraperiostracal spikes in the gastrochaenid *Spengleria rostrata* (SPENGLER, 1783) (CARTER, 1978, fig. 17–22) and aragonitic intraperiostracal spikes in the mytilid *Gregariella* sp. (Fig. 18).

Studs. Distally flat, columnar, mineralized, generally intraperiostracal structures more than 3 µm wide, e.g., aragonitic and cemented to the outer shell layer in the verticordiid *Euciroa elegantissima* (DALL, 1881) (Fig. 19).

II. HOMOGENEOUS (HOM).

An aggregation of minute, more or less equidimensional, irregularly shaped and

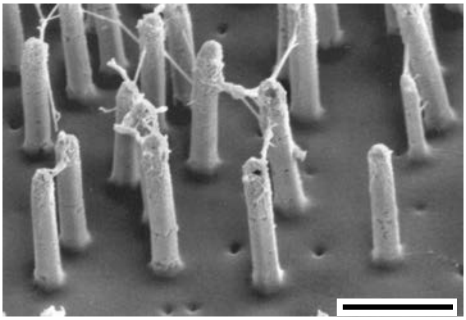

FIG. 16. Aragonitic extraperiostracal pins and openings of periostracal pores in venerid *Pitar trevori* LAMPRELL & WHITEHEAD, 1990, Moreton Bay, Queensland, Australia; scale bar, 2 µm (adapted from Glover & Taylor, 2010, fig. 6F, courtesy of Oxford University Press).

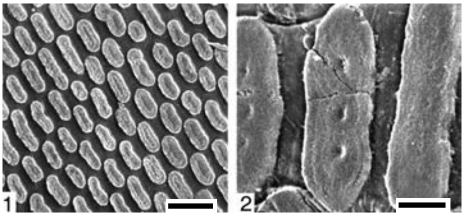

FIG. 17. Exterior view of aragonitic intraperiostracal plaques cemented to outer shell layer in two anomalodesmatans. *1,* Myochamid *Myadora complexa* IREDALE, 1924, scale bar, 50 µm; *2,* thraciid *Thraciopsis angustata* (ANGAS, 1868), scale bar, 5 µm (adapted from Checa & Harper, 2010, fig. 2E–F; courtesy of Marine Biological Laboratory, Woods Hole, Massachusetts, USA).

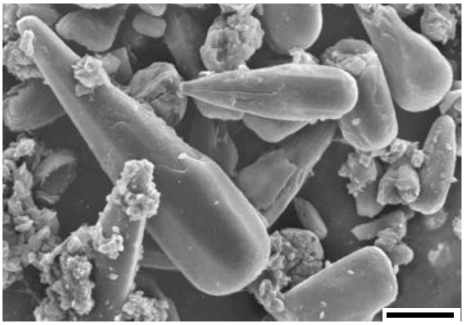

FIG. 18. Aragonitic, intraperiostrcal spikes and small granules isolated from periostracum of mytilid *Gregariella* sp., South Pacific, UNC 13148, by digestion of organic part of periostracum in sodium hypochlorite, scale bar, 10 µm (Carter & others, 2012, fig. 228).

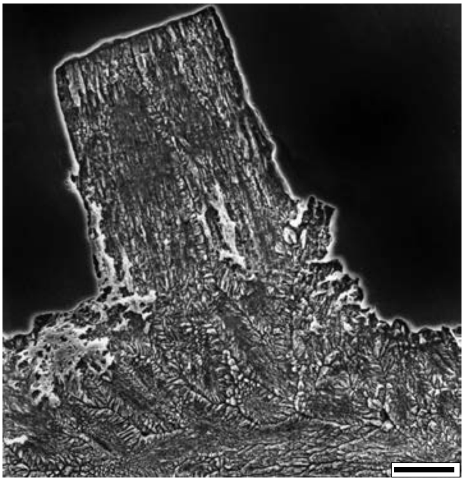

FIG. 19. Aragonitic intraperiostracal stud cemented to outer shell layer of verticordiid *Euciroa elegantissima* (DALL, 1881), Caribbean, YPM 9653, SEM of acid-etched, radial section, with shell exterior up and ventral shell margin toward right, scale bar, 25 µm (Carter, new).

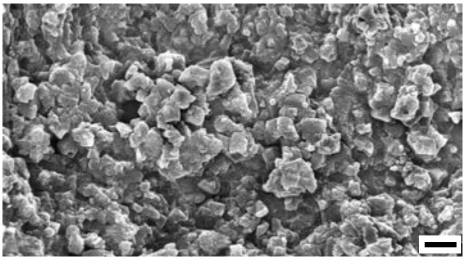

FIG. 20. Finely homogeneous microstructure in aragonitic middle shell layer of hiatellid *Cyrtodaria siliqua* (SPENGLER, 1793), SEM of radial, vertical fracture, scale bar, 1 µm (adapted from Carter & Lutz, 1990, pl. 15B).

oriented, basic structural units (CARTER & CLARK, 1985; CARTER & others, 1990, p. 612, 643). Varieties include finely homogeneous, granular homogeneous, and mosaic homogeneous.

Superficially homogeneous refers to any of several microstructures comprised of basic structural units too small to be characterized by light microscopy, e.g., finely homogeneous, matted, crossed acicular, and fine complex crossed lamellar.

Finely homogeneous (finely HOM). A homogeneous microstructure with basic structural units less than 5 µm in average maximum dimension, e.g., parts of the aragonitic middle shell layer in the hiatellid *Cyrtodaria siliqua* (SPENGLER, 1793) (Fig. 20) and the calcitic partitions separating vesicles in the gryphaeid *Hyotissa hyotis* (LINNAEUS, 1758) (Fig. 116.2).

Granular homogeneous (granular HOM, or just granular). A homogeneous microstructure with basic structural units greater than 5 µm in average maximum dimension and not showing a coarse, mosaic-like pattern in vertical sections, e.g., the outer sublayer of the aragonitic outer shell layer of the laternulid *Laternula* cf. *L. elliptica* (KING, 1832) (Fig. 21) (CARTER, 1980a). See also the intermediate granular homogeneous/prismatic parts of the aragonitic outer shell layer of the hiatellid *Cyrtodaria siliqua* (SPENGLER, 1793) (Fig. 22). "Granular" has been used as a textural term since GRAY (1833, p. 789). It was first used in the context of electron microscopy, for hydrozoan skeletons, by FENNINGER and FLAJS (1974), and subsequently applied to bivalve shells by SUZUKI (1979) and CARTER (1980a, p. 649).

Mosaic homogeneous (mosaic HOM). A coarsely textured, calcitic homogeneous microstructure with basic structural units greater than 5 µm in average maximum dimension, and showing a mosaic-like pattern in vertical sections, e.g., the calcitic outer shell layer in the left valve of the Late Triassic gryphaeid *Gryphaea* (*Gryphaea*) *nevadensis* MCROBERTS, 1992 (Fig. 23) (MCROBERTS & CARTER, 1994). This can appear similar to diagenetic calcite, but its original nature is indicated by uniformity throughout the shell layer and the presence of other well-preserved, originally calcitic microstructures in the same shell. TSCHELTSOVA (1969) used the term "furcillate" for a mixture of this microstructure and reclined, irregular simple prisms in *Gryphaea sensu stricto.*

III. SPHERULITIC

Spherical, subspherical, and/or or flattened aggregates of elongate structural units radiating in all directions from a central nucleation site or spindle (Mutvei, 1964; Flajs, 1972; Carter, 1980a, fig. 16–18; Carter & others, 1990, p. 660), e.g., the aragonitic outer shell layer in the lucinid *Anodontia* (*Pegophysema*) *bialata* (Pilsbry, 1895) (Fig. 24). Not to be confused with spherulitic prismatic, wherein the elongate structural units radiate toward the depositional surface. The term **planar spherulitic** is used when the spherulites are distinctly flattened (Sandberg, 1977, 1983; Carter & others, 1990, p. 652).

IV. PRISMATIC

A non-laminar microstructure comprised of mutually parallel, short to elongate, first-order structural units. The prisms are called **regular prismatic** when their cross-section shapes are more or less uniform (Fig. 25), and **irregular prismatic** when their cross-section shapes are highly variable (Fig. 26). Prisms with maximum width greater than 5 µm can be **spherulitic prismatic, simple prismatic,** or **composite prismatic.** Prisms with maximum width less than 5 µm wide are **fibrous prismatic**, regardless of their degree of elongation (not to be confused with fibrous simple prismatic, wherein the prisms are very elongate and have maximum width greater than 5 µm).

Spherulitic prismatic (SphP). Prisms with second-order structural units radiating toward the depositional surface from a single point, initial spherulite, or spindle (Mutvei, 1964). This is most commonly **irregular spherulitic prismatic** in the Bivalvia,

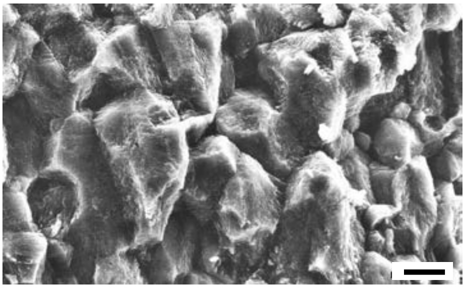

Fig. 21. Granular homogeneous microstructure in outer part of aragonitic outer shell layer of laternulid *Laternula* cf. *L. elliptica* (King, 1832), Holocene, Kerguelen or Gough Island, YPM 4956, SEM of radial, vertical fracture; scale bar, 20 µm (Carter, new).

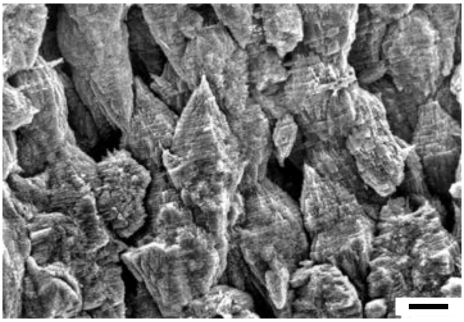

Fig. 22. Intermediate granular homogeneous/prismatic microstructure in aragonitic outer shell layer of hiatellid *Cyrtodaria siliqua* (Spengler, 1793), SEM of vertical, radial fracture, with shell exterior up; scale bar, 10 µm (Carter & others, 2012, fig. 312).

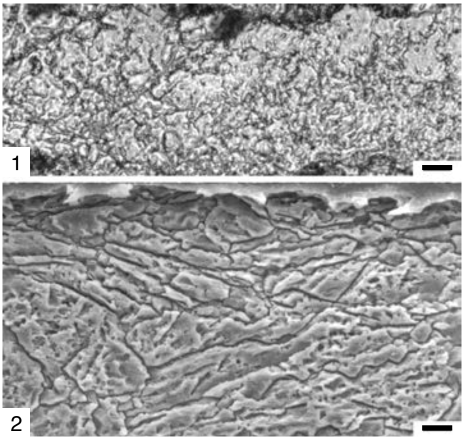

Fig. 23. *For explanation, see adjacent column.*

Fig. 23. Mosaic homogeneous microstructure in calcitic outer shell layer in left valve of Late Triassic gryphaeid *Gryphaea* (*Gryphaea*) *nevadensis* McRoberts, 1992, lower member of Luning Formation, Pilot Mountain, west-central Nevada, UNC 15004. *1,* Radial acetate peel, with shell exterior up; *2,* SEM of acid-etched, radial section through same shell layer, with shell exterior up; scale bars, 10 µm (Carter, new).

i.e., with variably shaped, strongly laterally interdigitating first-order prisms, e.g., in the aragonitic outer shell layer of the lucinid *Divalucina cumingi* (ADAMS & ANGAS, 1864) (Fig. 27). It is less commonly **regular spherulitic prismatic**, i.e., with rather uniformly shaped, non-interdigitating, first-order prisms. In the Bivalvia, regular spherulitic prisms rarely comprise an entire shell layer, e.g., in the margaritiferid *Margaritifera margaritifera* (LINNAEUS, 1758) (RÖMER, 1903; BIEDERMANN, 1913, fig. 159). They more commonly occur in the initial part of a columnar, otherwise simple or composite prism, as in the unionid *Elliptio complanata* (LIGHTFOOT, 1786). Regular spherulitic prisms comprise an entire outer shell layer in some Monoplacophora (ERBEN, FLAJS, & SIEHL, 1968; CARTER & others, 2012, fig. 295). Spherulitic prismatic is not to be confused with spherulitic microstructure.

Simple prismatic (SP). Prisms greater than 5 µm in maximum width, without diverging or radiating, elongate, second-order structural units. Very elongate simple prisms are called **fibrous simple prisms**, e.g., the lath-type, fibrous simple prisms in the outer shell layer of the Eocene eligmid *Nayadina* (*Exputens*) sp. (Fig. 29). Fibrous simple prisms are not to be confused with fibrous prisms, which by definition have narrower widths.

Columnar calcitic simple prisms can be optically homogeneous or optically heterogeneous when viewed in vertical thin sections in crossed polarized light. **Optically homogeneous** simple prisms behave as a single, optical crystallographic entity, as in the outer shell layer of some Pterineidae and most Pinnoidea. **Optically heterogeneous** simple prisms consist of multiple, optical crystallographic entities, and they may appear irregular wavy or granular in crossed polarized light. **Irregular wavy extinction** is characterized by several elongate, more or

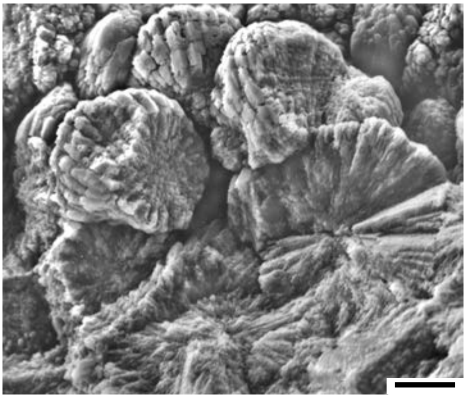

FIG. 24. Spherulitic microstructure in aragonitic outer shell layer of lucinid *Anodontia* (*Pegophysema*) *bialata* (PILSBRY, 1895), tidal sand flat, Tsingtao, China, YPM 8963, SEM of a radial, vertical fracture, with shell exterior up, scale bar, 10 µm (Carter, new).

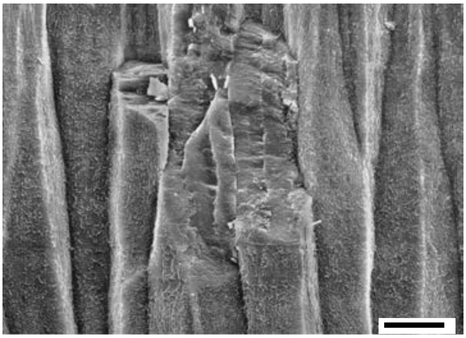

FIG. 25. Regular simple prismatic, calcitic outer shell layer in right valve of anomiid *Anomia simplex* D'ORBIGNY, 1853 in 1841–1853, New Haven, Connecticut, YPM 9715, SEM of vertical fracture, with shell exterior up, scale bar, 10 µm (Carter & others, 2012, Fig. 259). See Fig. 38 for higher magnification.

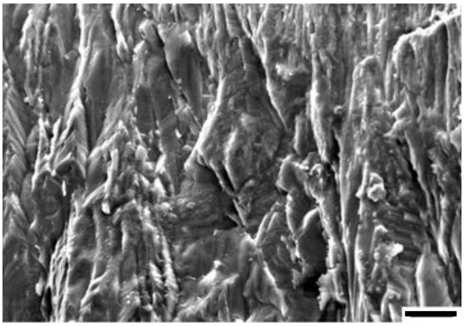

FIG. 26. *For explanation, see adjacent column.*

FIG. 26. Irregular simple prismatic, aragonitic inner shell layer of lucinid *Divalucina cumingi* (ADAMS & ANGAS, 1864), New Zealand, YPM 9065, SEM of vertical fracture, with shell exterior up, scale bar, 10 µm (Carter & others, 2012, fig. 152).

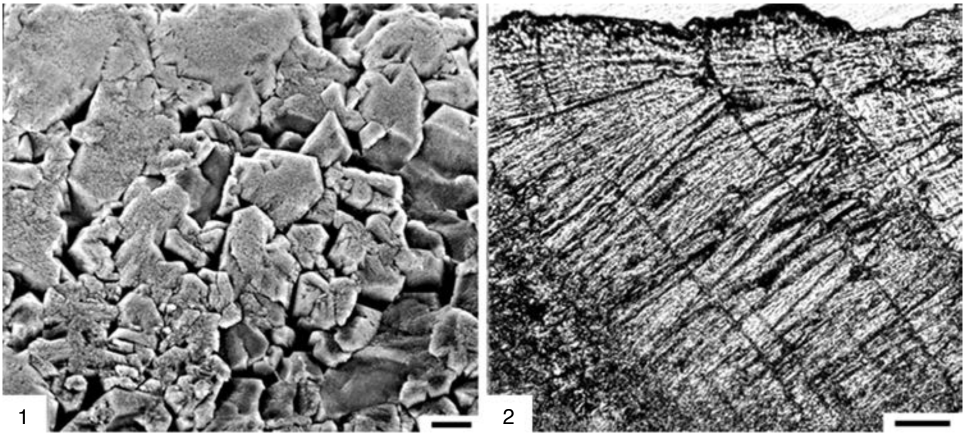

FIG. 27. Aragonitic, irregular spherulitic prismatic outer shell layer of lucinid *Divalucina cumingi* (ADAMS & ANGAS, 1864). *1,* SEM of depositional surface; *2,* radial, vertical acetate peel, with shell margin toward left; scale bars, 10 µm in *1,* 50 µm in *2* (Carter & others, 2012, fig. 294).

less length-parallel, optically homogeneous subunits, e.g., the outer shell layer of most Pteriidae, Ostreidae, and some Pterineidae. **Granular extinction** is characterized by minute (micron scale), more or less equidimensional, optical crystallographic entities, and is characteristic of Inoceramidae and Retroceramidae.

Columnar, aragonitic simple prisms occur in the aragonitic outer shell layer of some Trigoniida, Unionida, and Pholadoidea, e.g., in posterior parts of the prismatic outer shell layer in the pholadid *Parapholas californica* (CONRAD, 1837) (Fig. 4.1–4.2; Fig. 35). In this species, the columnar prisms change inwardly from nondenticular composite prismatic to simple prismatic. A similar change occurs within the columnar prisms in the outer shell layer of some Unionidae, e.g., in *Obliquaria reflexa* RAFINESQUE, 1820 (Fig. 52). The optical extinction axis in these aragonitic columnar prisms is sometimes parallel with the prism length axis, with extinction moving from left to right, or vice versa, as the microscope stage is rotated.

Varieties of simple prisms are defined on the basis of shape and orientation, or on the basis of second-order structure, as follows.

Simple prism varieties based on shape and orientation:

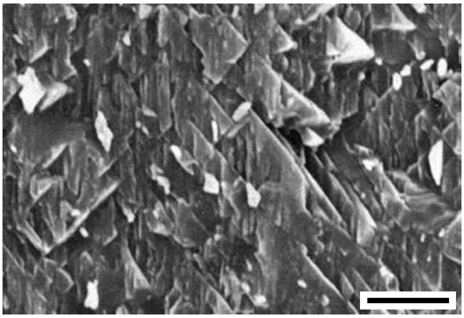

Fig. 28. Dissected crossed irregular simple prisms in aragonitic shell "window" in cardiid *Corculum cardissa* (LINNAEUS, 1758), Indo-Pacific Ocean, UNC 8291, SEM of radial, vertical fracture, with shell exterior up, scale bar, 5 µm (Carter, new).

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1) **Columnar simple prismatic** (columnar SP). Vertical or slightly oblique simple prisms that are longer than wide, and not crossed by one or more oblique, second-order structural trends, e.g., the calcitic outer shell layer in the right valve of the anomiid *Anomia simplex* D'ORBIGNY, 1853 in 1841–1853 (Fig. 25, Fig. 38), parts of the aragonitic, posterior outer shell layer of the pholadid *Parapholas californica* (CONRAD, 1837) (Fig. 4.2; Fig. 35, middle and bottom of figure), and the calcitic outer shell layer in the right valve of the propeamussiid *Propeamussium dalli* (E. A. SMITH, 1885) (Fig. 37).

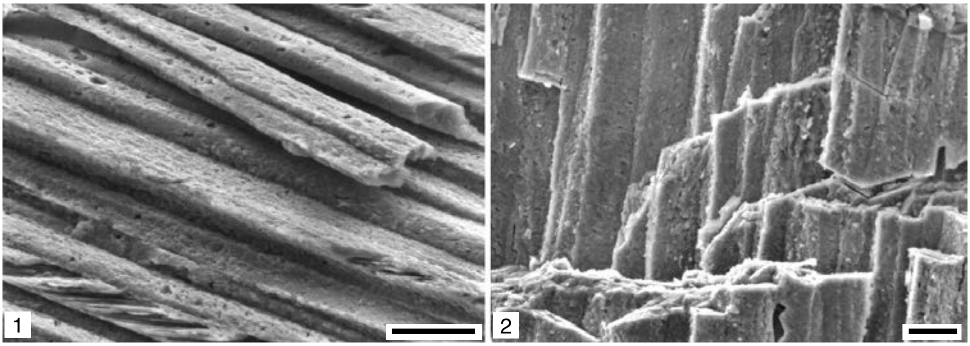

FIG. 29. Reclined, lath-type, fibrous simple prisms in calcitic outer shell layer of right valve in eligmid *Nayadina* (*Exputens*) sp., middle Eocene, Castle Hayne Limestone, Atlantic Limestone Quarry, Duplin County, North Carolina, USA, UNC 9687. *1,* SEM of radial, vertical fracture, with shell exterior up; *2,* SEM of slightly oblique, nearly horizontal fracture perpendicular to flat surface of laths; scale bars, 10 µm (Carter, new).

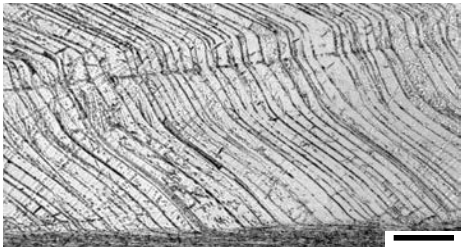

FIG. 30. Reclined, lath-type, fibrous simple prisms in calcitic outer shell layer of ostreid *Flemingostrea sub spatulata* (FORBES, 1845), interrupted by a thin sublayer of vertical, regular simple prisms, Late Cretaceous, Prairie Bluff Chalk, southeastern Alabama, USA, UNC 8049, radial acetate peel through inner part of outer shell layer in left valve, with shell exterior up and shell margin toward right, also showing the regularly foliated middle shell layer at bottom, scale bar, 100 µm (Carter, new).

2) Dissected crossed simple prismatic (dissected crossed SP). Simple prisms with one or more oblique, second-order structural trends (CARTER & others, 1990, p. 612; CARTER & SCHNEIDER, 1997). Examples include the aragonitic shell "windows" in the cardiid *Corculum cardissa* (LINNAEUS, 1758) (Fig. 28) and parts of the aragonitic inner shell layer of the astartid *Astarte* (*Astarte*) *undata* GOULD, 1841 (CARTER & others, 2012, fig. 95).

3) Lath-type simple prismatic (lath-type SP). Typically strongly reclined, blade-like simple prisms, e.g., parts of the calcitic outer shell layer in the Late Cretaceous ostreid *Flemingostrea subspatulata* (FORBES, 1845) (Fig. 29) and most of the calcitic outer

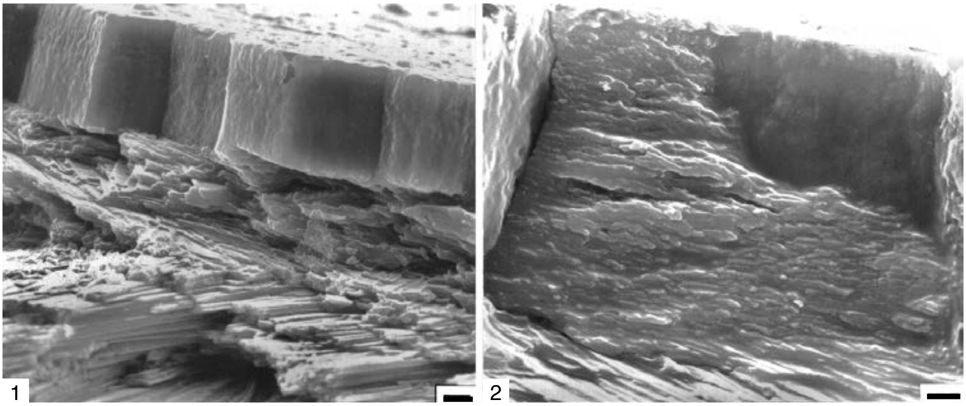

FIG. 31. Pavement simple prisms in early post-larval, calcitic outer shell layer in right valve of pectinid *Leopecten diegensis* (DALL, 1898), California, USA, YPM 7856. SEM of vertical fracture, with shell exterior up. *1,* Prismatic layer and underlying crossed foliated outer part of middle shell layer; *2,* oblique fracture through a pavement simple prism, showing semi-foliated second-order structure; scale bars, 1 µm (adapted from Carter, 1990a, fig. 48a–b).

shell layer in the Eocene eligmid *Nayadina* (*Exputens*) sp. (Fig. 30).

4) **Pavement simple prismatic** (pavement SP). More or less vertical simple prisms that are shorter than they are wide, and not elongated in the radial or commarginal direction, e.g., the early post-larval, calcitic outer shell layer in the right valve of the pectinid *Leopecten diegensis* (DALL, 1898) (Fig. 31).

5) **Commarginally elongate simple prismatic** (CESP). More or less vertical simple prisms that are shorter than they are wide, and commarginally elongated, e.g., the calcitic outer shell layer in the right valve of the cyclochlamydid *Chlamydella favus* (HEDLEY, 1902) (Fig. 32).

6) **Radially elongate simple prismatic** (RESP). More or less vertical simple prisms that are shorter than they are wide, and elongated in the radial direction, e.g., the aragonitic outer shell layer in the solemyid *Solemya* (*Zesolemya*) *parkinsoni* E. A. SMITH, 1874 (Fig. 33). The calcitic outer shell layer in the right valve of many propeamussiids has commarginal bands of radially elongate simple prisms alternating with commarginal bands of pavement simple prisms (WALLER, 1971, 1972; NEWELL & BOYD, 1985a; CARTER, 1990a, p. 257).

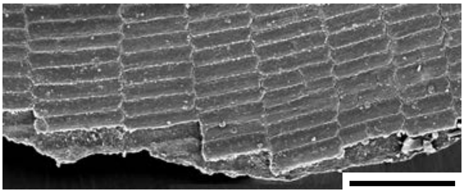
FIG. 32. Commarginally elongate simple prisms in calcitic outer shell layer in right valve of cyclochlamydid *Chlamydella favus* (HEDLEY, 1902); exterior of shell with ventral margin down, scale bar, 100 µm (DIJKSTRA & BEU, 2018, fig. 21J; courtesy of Records of the Australian Museum).

7) **Pillar simple prismatic** (pillar SP). Vertical or nearly vertical, irregular simple prisms mutually isolated within a matrix of non-prismatic microstructure, e.g., in parts of the aragonitic inner shell layer in

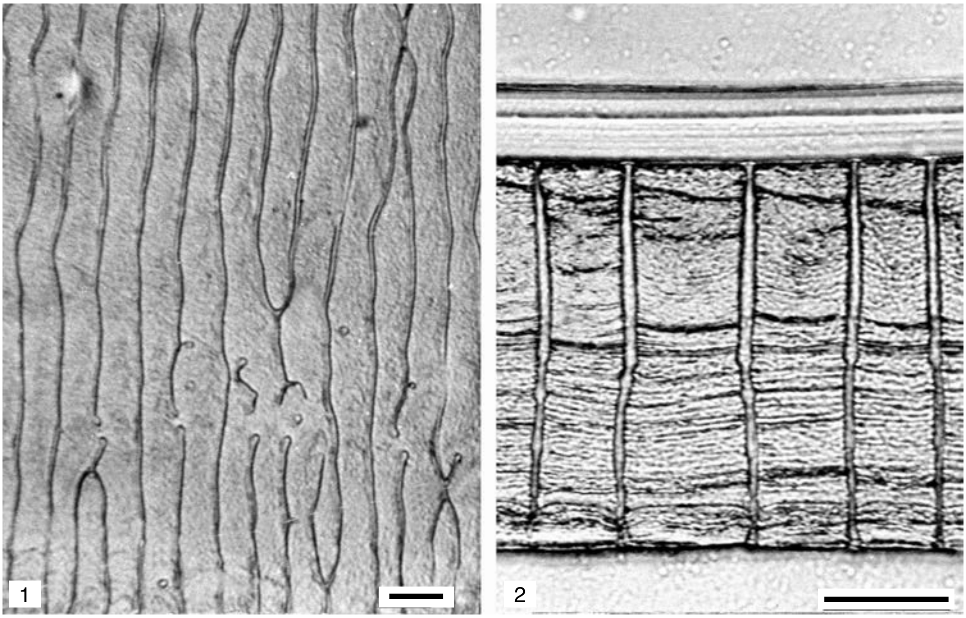

FIG. 33. Radially elongate simple prismatic, aragonitic outer shell layer of solemyid S*olemya (Zesolemya) parkinsoni* E. A. SMITH, 1874, Ararua Bay, New Zealand, YPM 5364, acetate peels. *1,* Horizontal section, with ventral margin down; *2,* commarginal, vertical section, with shell exterior up, also showing the two-layered periostracum (at top); scale bar, 50 µm in *1* and *2* (adapted from Carter & Lutz, 1990, pl. 20E–F).

the astartid *Astarte undata* GOULD, 1841, which is otherwise complex crossed lamellar (Fig. 34).

Simple prism varieties based on substructure:

8) Homogeneous simple prismatic (hom SP). Simple prisms with a finely homogeneous second-order structure, e.g., the later-formed parts of the columnar, regular simple prisms posteriorly in the aragonitic outer shell layer of the pholadid *Parapholas californica* (CONRAD, 1837) (Fig. 35) and the aragonitic, radially elongate simple prisms in the outer shell layer of the solemyid *Solemya* (*Zesolemya*) *parkinsoni* E. A. SMITH, 1874 (Fig. 33, Fig. 36).

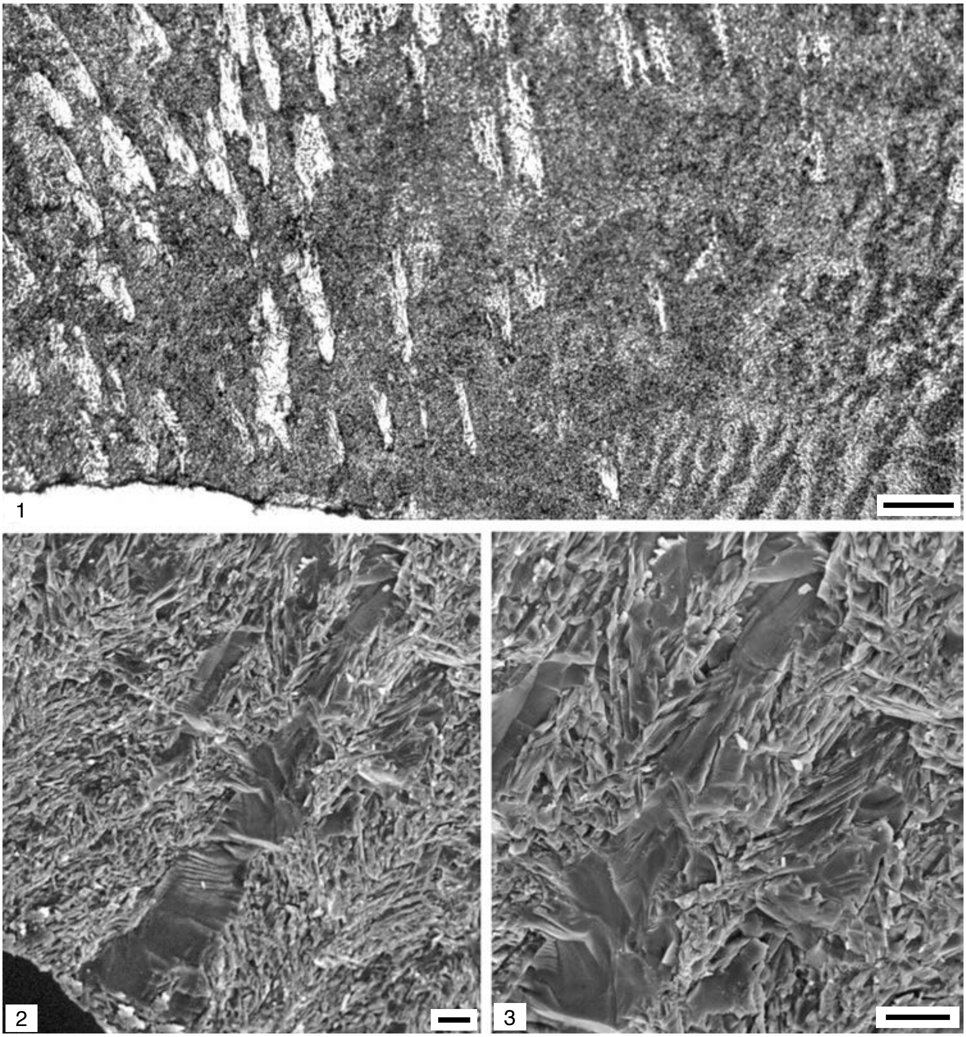

FIG. 34. Pillar simple prisms within a matrix of irregular complex crossed lamellar microstrucure in aragonitic inner shell layer of astartid *Astarte undata* GOULD, 1841, Maine, USA, YPM 9727, with shell exterior up. *1,* Acetate peel of radial, vertical section, with pillar simple prisms appearing as bright areas, and with a branching crossed lamellar part of inner shell layer visible on right; *2–3,* SEM of radial, vertical fracture, showing conchoidal fractures through pillar simple prisms; scale bars, 50 µm in *1,* 10 µm in *2–3* (Carter, new).

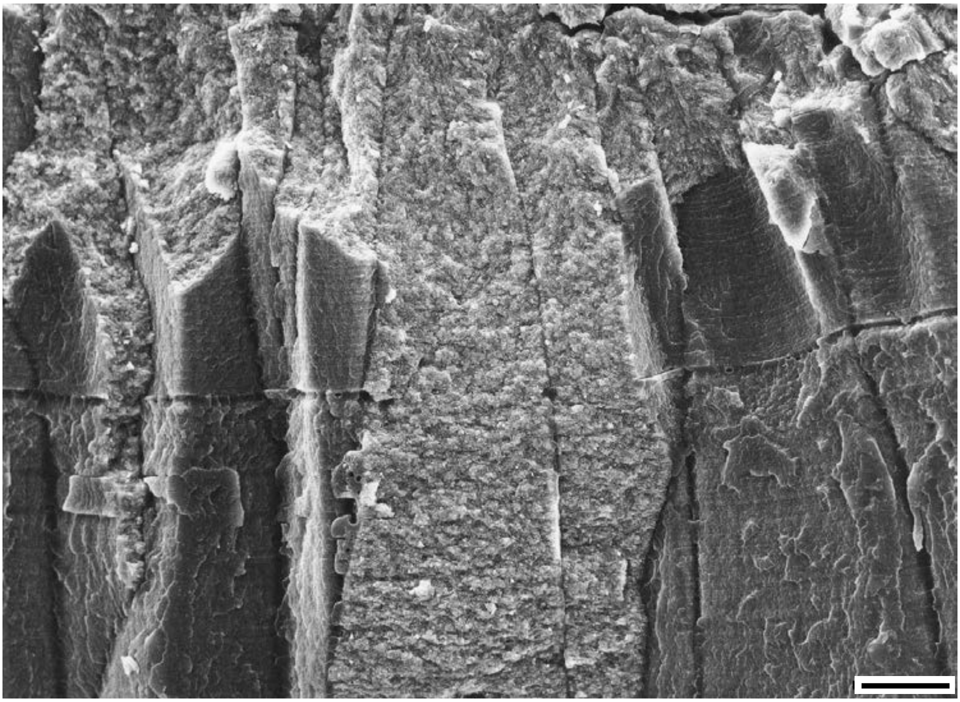

Fig. 35. Columnar prisms in posterior part of aragonitic outer shell layer of pholadid *Parapholas californica* (Conrad, 1837), YPM 10258, Monterey Bay, California, USA; SEM of radial fracture, with shell exterior up. Prisms are initially nondenticular composite prismatic (near top) but for most of their length regular simple prismatic with homogeneous second-order structure (middle and bottom); scale bar, 20 µm (Carter, new). See Fig. 4.1 for higher magnification of nondenticular composite prismatic portion.

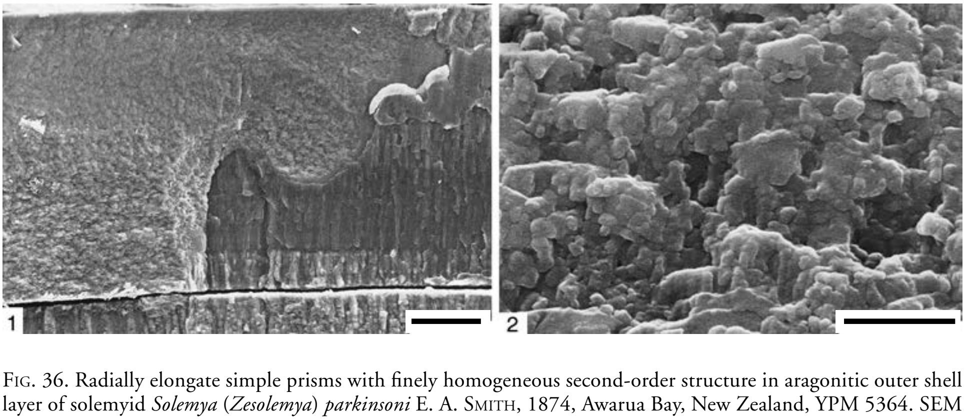

Fig. 36. Radially elongate simple prisms with finely homogeneous second-order structure in aragonitic outer shell layer of solemyid *Solemya* (*Zesolemya*) *parkinsoni* E. A. Smith, 1874, Awarua Bay, New Zealand, YPM 5364. SEM of vertical, nearly radial fracture, with shell exterior up. *1,* interior of one prism (on left) and interprismatic organic matrix (on right), also showing solemyid-type laminar microstructure locally developed in inner shell layer (at bottom, below horizontal fracture); *2,* higher magnification of finely homogeneous second-order structure in *1;* scale bar, 2 µm in *1,* 1 µm in *2* (Carter, new). See Fig. 33 for lower magnification of this shell layer.

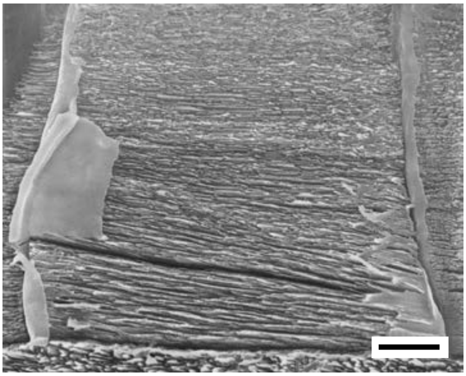

FIG. 37. Semi-foliated regular simple prism in calcitic outer shell layer in right valve of propeamussiid *Propeamussium dalli* (E. A. SMITH, 1885), west of Martinique, Windward Islands, YPM 8387, also showing a fibrous prismatic portion of calcitic middle layer (at bottom), SEM of acid-etched, radial section, with shell exterior up, scale bar, 5 µm (Carter & others, 2012, fig. 274).

9) Semi-foliated simple prismatic (semi-foliated SP). Simple prisms with a semi-foliated second-order structure, e.g., the calcitic, pavement simple prismatic outer shell layer in the early post-larval, juvenile right valve of the pectinid *Leopecten diegensis* (DALL, 1898) (Fig. 31); the calcitic simple prismatic outer shell layer in the right valve of the propeamussiid *Propeamussium dalli* (E. A. SMITH, 1885) (Fig. 37); the calcitic, regular simple prismatic outer shell layer in the right valve of the anomiid *Anomia simplex* D'ORBIGNY, 1853 in 1841–1853 (Fig 38); and the calcitic simple prismatic outer shell layer in some Malleidae and Pteriidae (CARTER & LUTZ, 1990, pl. 25B,C; ESTEBAN-DELGADO & others, 2008, fig. 2J).

10) Transverse fibrous simple prismatic (transverse fibrous SP). Simple prisms with

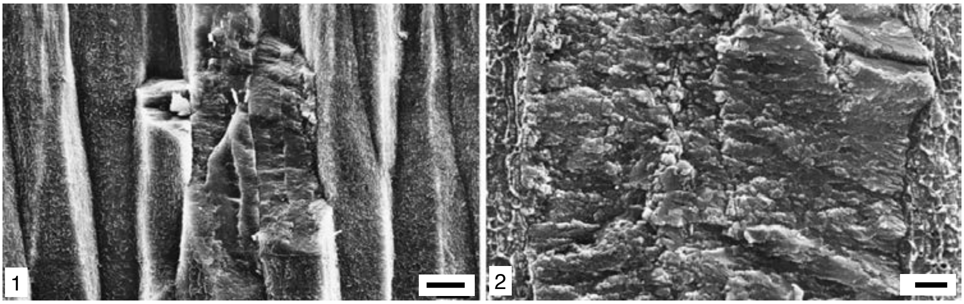

FIG. 38. Semi-foliated regular simple prism in calcitic outer shell layer in right valve of anomiid *Anomia simplex* D'ORBIGNY, 1853 in 1841–1853, New Haven, Connecticut, USA, YPM 9715; SEM of radial, vertical fracture, with shell exterior up, at lower (*1*) and higher (*2*) magnifications; scale bar, 10 µm in *1,* 1 µm in *2* (Carter, new).

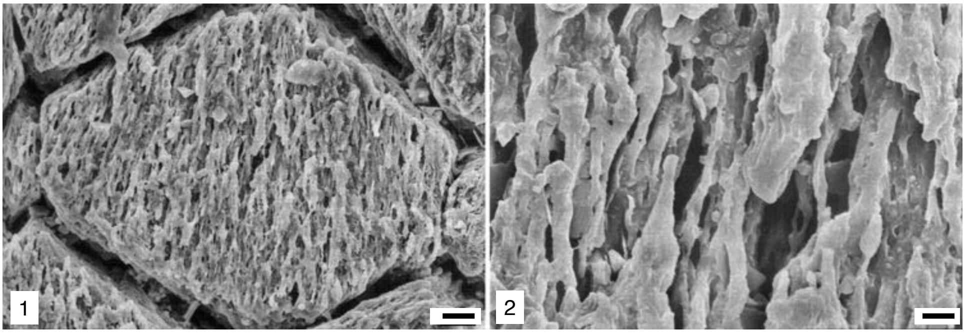

FIG. 39. Depositional surface of transverse fibrous simple prisms in calcitic outer shell layer of an inoceramid, Maastrichtian, Late Cretaceous, Basque Country, France, SEM at lower (*1*) and higher (*2*) magnifications; scale bar, 10 µm in *1,* 2 µm in *2* (adapted from Elorza & García-Garmilla, 1998, fig. 6c–6d).

a second-order structure of horizontal, more or less mutually parallel, irregular fibrous prisms, e.g., the calcitic outer shell layer in most Inoceramidae and Retroceramidae (Fig. 39). Not to be confused with fibrous simple prismatic (very elongate simple prisms) or fibrous prismatic (narrower than simple prisms).

Fibrous prismatic (FP). Prisms narrower than 5 μm in maximum width and generally, but not necessarily, very elongate. Fibrous prisms are narrower than fibrous simple prisms, but they can be similarly elongate. Not to be confused with transverse fibrous simple prismatic, which refers to the second-order structure of a simple prism. Fibrous prisms typically have a finely homogeneous second-order structure. **Simple lamellar fibrous prismatic** refers to mutually parallel, aragonitic fibrous prisms arranged into more or less planar, mutually parallel, first-order lamellae with the same dip direction and dip angle, e.g., in the outer shell layer of the arcid *Barbatia virescens* (Reeve, 1844) and in the dreissenid *Dreissena polymorpha* (Pallas, 1771) (Archambault-Guezou, 1982, p. 329, fig. 6, as "simple lamellar;" Carter & Clark, 1985; Carter & others, 2012, fig. 112). The prisms comprising this microstructure are commonly continuous with third-order lamellae in an adjacent crossed lamellar microstructure.

Fibrous prisms are classified as regular or irregular depending on their uniform *versus* variable cross-section shapes, respectively.

1) **Irregular fibrous prismatic** (irregular FP). Fibrous prisms with variable cross-section shapes (Carter & Clark, 1985; Carter & others, 1990, p. 610, 645), e.g., parts of the aragonitic outer shell layer of the venerid *Cyclina sinensis* (Gmelin, 1791), also the second-order prisms in the aragonitic denticular composite prismatic outer shell layer in the nuculid *Nucula proxima* Say, 1822 (Fig. 40).

2) **Regular fibrous prismatic** (regular FP). Fibrous prisms with uniform cross-section shapes. Varieties include lath-type, rod-type, and interlocking fibrous prisms.

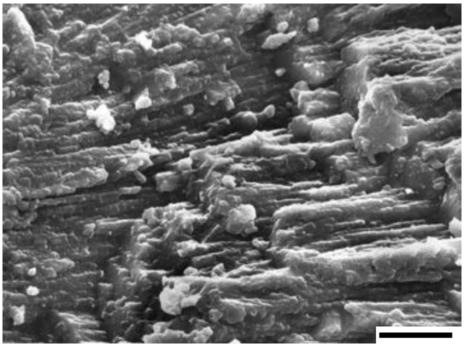

Fig. 40. Irregular fibrous prisms comprising a single denticular composite prism in aragonitic outer shell layer of nuculid *Nucula proxima* Say, 1822, Long Island Sound, New York, USA, YPM 10014; SEM of radial fracture, with shell exterior up and shell margin toward right; scale bar, 5 μm (adapted from Carter & Lutz, 1990, pl. 19B).

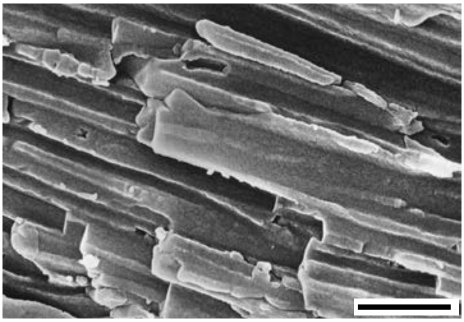

Fig. 41. Radial, lath-type fibrous prisms in calcitic outer shell layer in left valve of propeamussiid *Propeamussium dalli* (E. A. Smith, 1885), 1250 meters depth, west of Martinique, Windward Islands, YPM 8387; SEM of horizontal fracture, with ventral shell margin toward lower right; scale bar, 1 μm (Carter, new). This shell layer is also locally irregular spherulitic prismatic and complex crossed foliated.

a) **Lath-type fibrous prismatic** (lath-type FP). More or less flat regular fibrous prisms with margins not regularly interlocking with laterally adjacent prisms (Carter & others, 1990, p. 610), e.g., parts of the calcitic outer shell layer in some Limidae. Also locally present in the calcitic outer shell layer in the left valve (Fig. 41) and locally in the calcitic middle shell layer in the right valve of some Propeamussiidae (Fig. 1, left side) (Carter, 1990e, p. 375). Lath-type fibrous

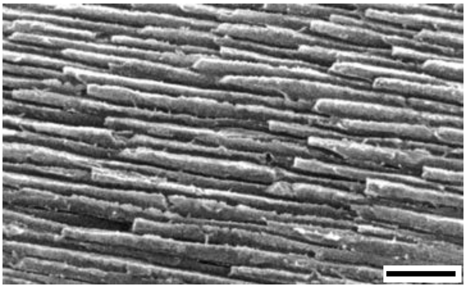

FIG. 42. Rod-type fibrous prisms in inner part of calcitic outer shell layer of mytilid *Adula falcata* (GOULD, 1851); SEM of acid-etched, radial section, with shell exterior up and posterior shell margin toward right, scale bar, 1 µm (Carter, new).

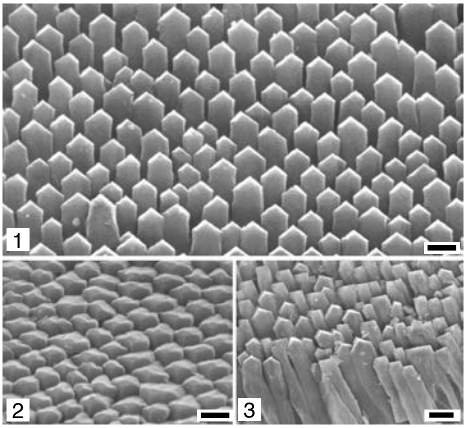

FIG. 43. Anvil-type interlocking fibrous prismatic microstructure in calcitic outer shell layer of *Mytilus. 1, Mytilus edulis* LINNAEUS, 1758, Rock, England, UK, UNC 15424, depositional surface showing terminations of reclined fibrous prisms; *2, Mytilus galloprovincialis* LAMARCK, 1819, Rock, England, UK, UNC 15422, depositional surface tilted 27° to show ends of fibrous prisms; *3,* same shell layer as in *2,* showing depositional surface (above) and fracture along prism length axes (below); scale bars, 1 µm in *1,* 5 µm in *2,* 1 µm in *3* (Carter, new).

prisms have narrower maximum widths than lath-type simple prisms (see Fig. 29–30, for the latter).

b) Rod-type fibrous prismatic (rod-type FP). Regular fibrous prisms with more or less equidimensional cross-sections and with margins not interlocking with adjacent prisms (CARTER & CLARK, 1985; CARTER & others, 1990, p. 610), e.g., parts of the calcitic outer shell layer in the mytilid *Adula falcata* (GOULD, 1851) (Fig. 42).

c) Interlocking fibrous prismatic (interlocking FP). Regular fibrous prisms with two sets of opposed margins and with all four margins inserted between laterally adjacent prisms. Two wider opposing surfaces contact two superadjacent and two subadjacent prisms, e.g., most of the calcitic outer shell layer in the mytilids *Mytilus edulis* LINNAEUS, 1758 and *Mytilus galloprovincialis* LAMARCK, 1819 (Fig. 43). Called anvil-type interlocking fibrous prismatic by CARTER and others (1990, p. 629) and CARTER and others (2012).

Composite prismatic (CP). Prisms with a second-order structure of smaller prisms radiating in three dimensions from a central longitudinal axis or core toward the depositional surface or toward the sides of the first-order prism. If a central longitudinal core is present, this may be length-parallel fibrous prismatic, finely homogeneous, or fine complex crossed lamellar. Fibrous prisms radiating in only two dimensions by virtue of deposition on a strongly reflected shell margin do not comprise a composite prism. Fibrous prisms radiating in three dimensions by virtue of deposition on a shell marginal denticle comprise a denticular composite prism (DCP), whereas fibrous prisms radiating in three dimensions and deposited on a flat or finely hummocky depositional surface comprise a nondenticular composite prism (NDCP). NDCP prisms radiating in three dimensions by virtue of deposition on a shell marginal denticle comprise a compound NDCP prism. The organizing influence of a marginal denticle on prismatic structure is illustrated by the venerid *Mercenaria mercenaria* (LINNAEUS, 1758) (Fig. 44–45).

Denticular composite prismatic (DCP). First-order composite prisms comprised of second-order fibrous prisms with a three-dimensional, fan-like arrangement by virtue of deposition on a shell margin denticle (CARTER, 1980a; CARTER & CLARK, 1985; CARTER & others, 1990, p. 637), e.g., the

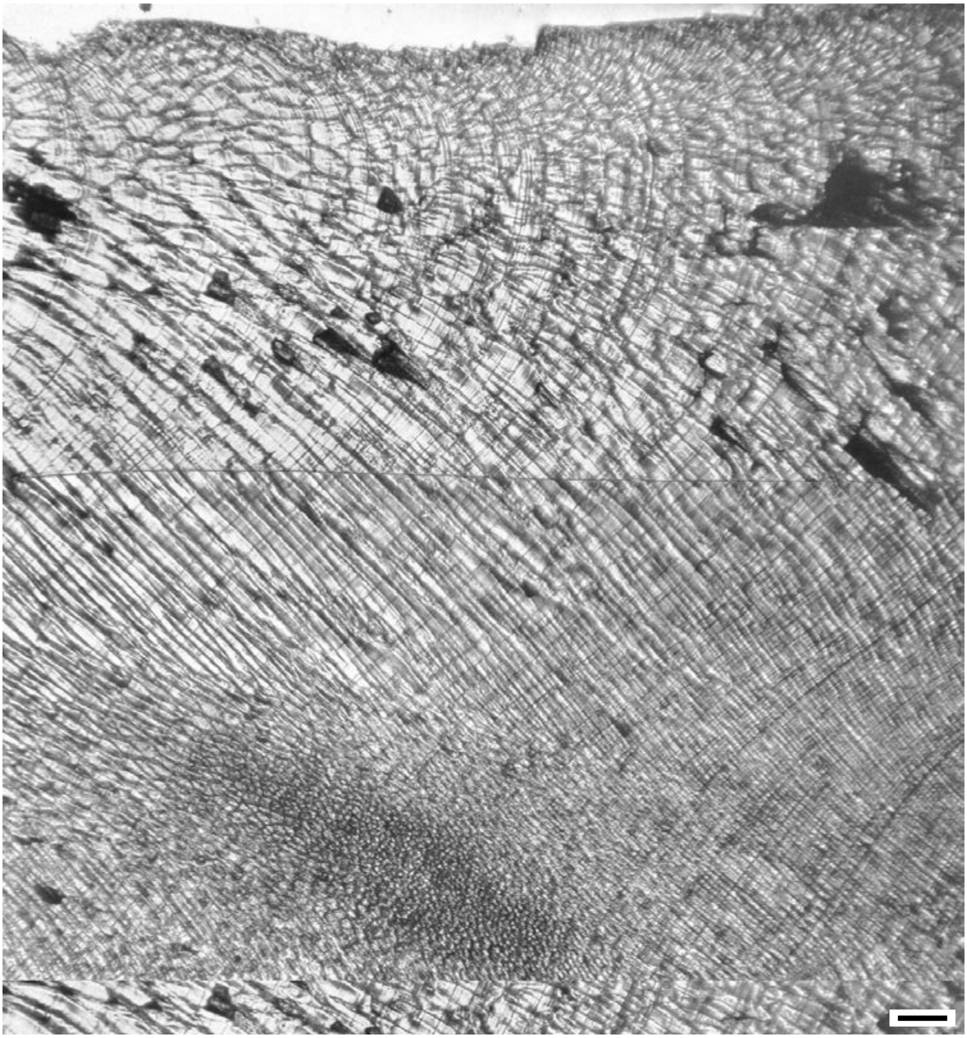

Fig. 44. Aragonitic prismatic outer shell layer of venerid *Mercenaria mercenaria* (Linnaeus, 1758), western Atlantic, YPM 3029 (same shell layer as in Fig. 45), radial, vertical acetate peel (two photographs), with shell exterior up and posterior shell margin toward right. The upper two-thirds is radial NDCP and radial lamellar NDCP, and the lower third is radial NDCP and compound NDCP. The middle shell layer is visible at the extreme bottom. The dark, elliptical area in the inner sublayer shows NDCP prisms turned toward the viewer as a consequence of secretion on the flank of a denticle. Not visible in this figure (but visible in Fig. 45.1–45.2) is a very thin, outermost sublayer of radial fibrous prisms. Scale bar, 100 µm (Carter, new).

outer shell layer of the nuculid *Nucula proxima* Say, 1822 (Fig. 46).

Nondenticular composite prismatic (NDCP). First-order composite prisms comprised of second-order fibrous prisms deposited on a smooth or finely hummocky but not denticulated depositional surface (Carter, 1980a; Carter & others, 1990, p. 650). Nondenticular composite prisms can be low-angle, high-angle, or dendritic NDCP, depending on the arrangement of their second-order prisms.

1) **Low-angle nondenticular composite prismatic** (low-angle NDCP). Nondenticular composite prisms comprised of second-order fibrous prisms diverging at a

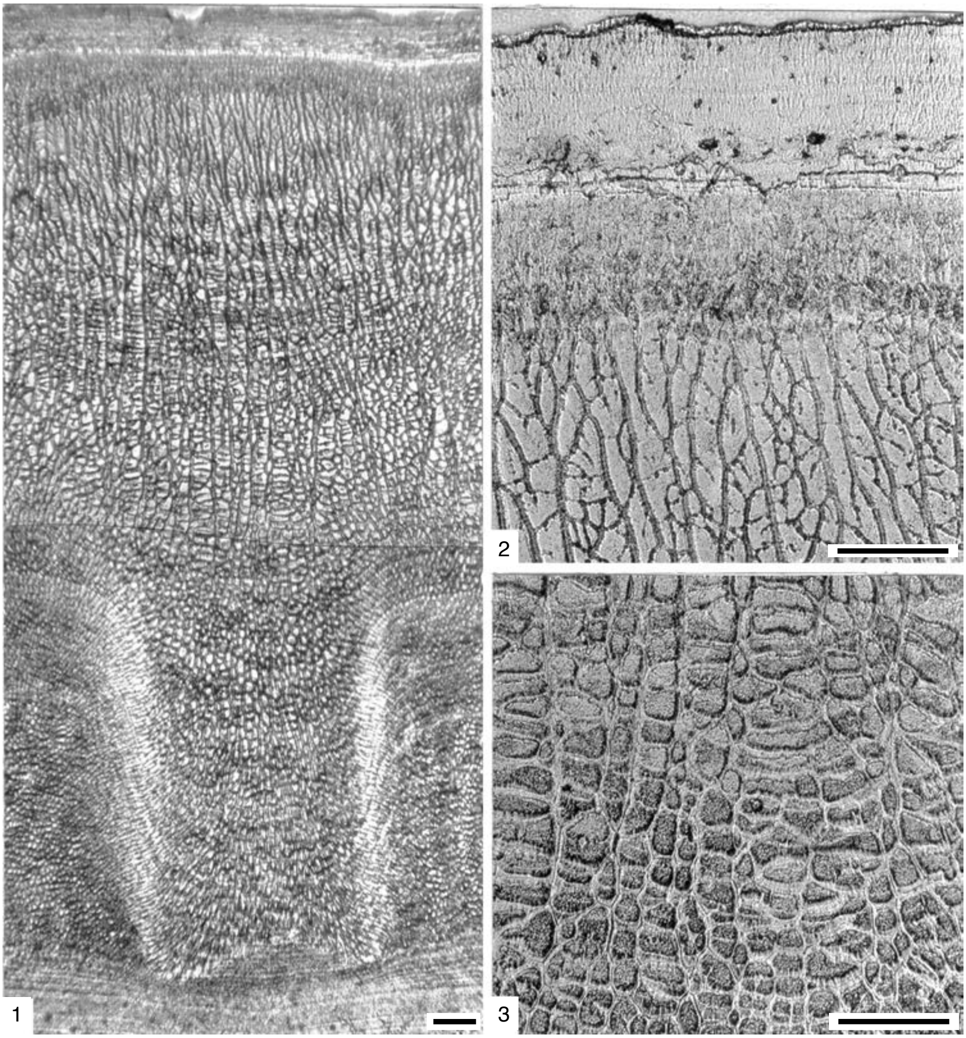

FIG. 45. Aragonitic prismatic outer shell layer of venerid *Mercenaria mercenaria* (LINNAEUS, 1758), western Atlantic, YPM 3029 (same shell layer as in Fig. 44), commarginal, vertical acetate peel, with shell exterior up. *1,* Entire prismatic layer, showing thin, outer sublayer of radial fibrous prisms (extreme top), underlain by radial lamellar NDCP and radial NDCP (between outer sublayer and top of denticle), underlain by radial NDCP to compound NDCP (at level of denticle). The non-prismatic, middle shell layer is visible at extreme bottom; *2,* outer part of prismatic outer shell layer, showing radial fibrous prisms (individual fibrous prisms not distinguishable at this magnification) underlain by radually oriented, radial lamellar NDCP with irregular prism cross-sections; *3,* higher magnification of the NDCP prisms comprising the compound NDCP prism; scale bars, 100 µm (Carter, new).

mutual angle less than 90° from the central, longitudinal, first-order prism axis. Low-angle NDCP prisms comprise most of the prismatic outer shell layer in the venerid *Mercenaria campechiensis* (GMELIN, 1791), where they vary from laterally equidimensional (Fig. 47) to laterally compressed, and are locally organized into larger scale, compound NDCP prisms (Fig. 45). More or less equidimensional, low-angle NDCP prisms comprise the compound NDCP prisms in the outer shell layer of the donacid *Donax variabilis* SAY, 1822 (Fig. 48).

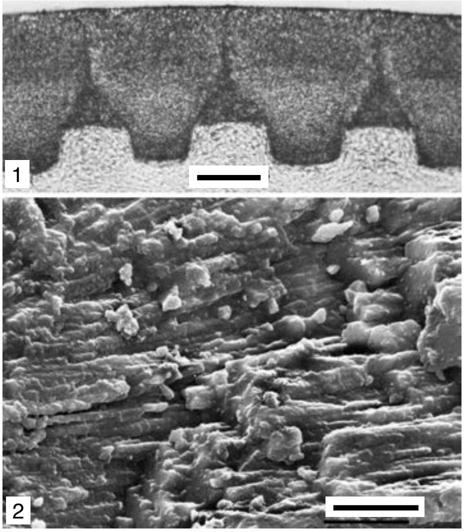

FIG. 46. Denticular composite prismatic, aragonitic outer shell layer in nuculid *Nucula proxima* SAY, 1822, Long Island Sound, New York, USA, YPM 10014. *1,* Commarginal, vertical acetate peel showing four denticular composite prisms and underlying nacreous middle shell layer; *2,* SEM of radial, vertical fracture, showing second-order, irregular fibrous prisms comprising a denticular composite prism, with shell exterior up and shell margin toward right, scale bar in 1, 50 µm, scale bar in 2, 5 µm (Carter & others, 2012, fig. 93).

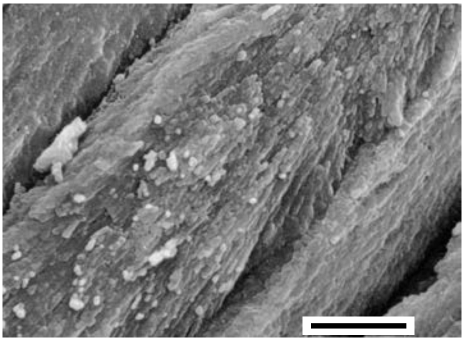

FIG. 47. Low-angle, nondenticular composite prisms in aragonitic outer shell layer of venerid *Mercenaria campechiensis* (GMELIN, 1791), Sanibel, Florida, USA, UNC 8495, SEM of radial, vertical fracture, with shell exterior up and shell margin toward left, scale bar, 5 µm (Carter, new).

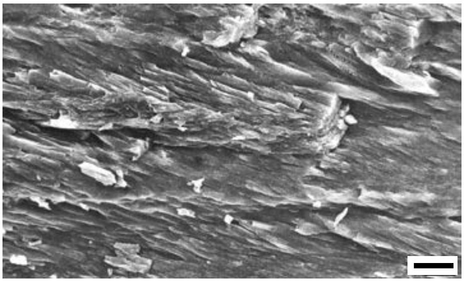

FIG. 48. Low-angle, nondenticular composite prisms comprising a compound NDCP prism in aragonitic outer shell layer of donacid *Donax variabilis* SAY, 1822, Sanibel, Florida, USA, YPM 10074, SEM of radial, vertical fracture, with shell exterior up and posterior shell margin toward left; scale bar, 5 µm (Carter, new).

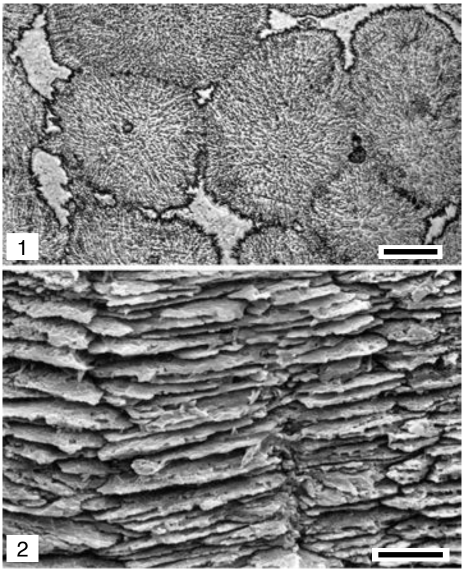

FIG. 49. High-angle nondenticular composite prisms in parts of aragonitic outer shell layer of hiatellid *Panopea generosa* GOULD, 1850, Puget Sound, Washington, USA, YPM 9746. *1,* Horizontal acetate peel showing several first-order NDCP prisms; *2,* SEM of acid-etched, vertical section, with shell exterior up; scale bars, 100 µm in *1,* 5 µm in *2* (Carter & others, 2012, fig. 231, as planar spherulitic simple prismatic).

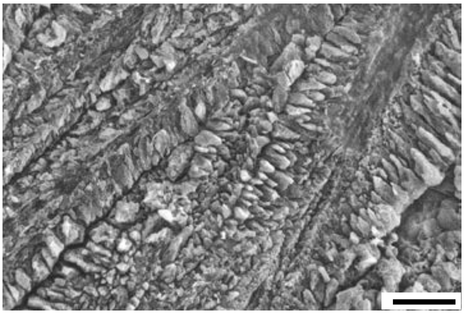

FIG. 50. Narrow-core dendritic nondenticular composite prisms in aragonitic outer shell layer of verticordiid *Euciroa elegantissima* (DALL, 1881), Caribbean, YPM 9653, SEM of acid-etched, radial, vertical section, with shell exterior up and posterior shell margin toward left, scale bar, 5μm (Carter, new).

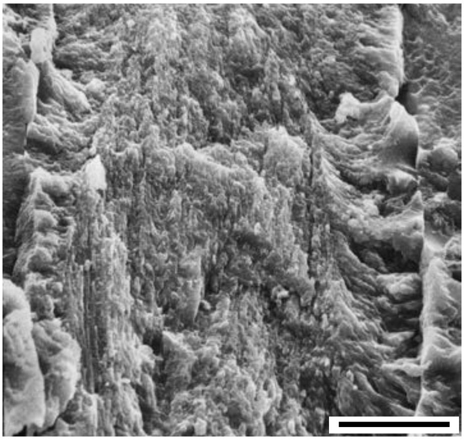

FIG. 51. Wide-core dendritic nondenticular composite prism in aragonitic outer shell layer of trigoniid *Neotrigonia gemma,* IREDALE, 1924, Sydney, Australia, UNC 5427, SEM of commarginal, vertical fracture, with shell exterior up, scale bar, 5 μm. (Carter, new).

2) **High-angle nondenticular composite prismatic** (high-angle NDCP). Nondenticular composite prisms comprised of second-order fibrous prisms diverging at a mutual angle greater than 90° near the central, longitudinal, first-order prism axis, e.g., parts of the aragonitic outer shell layer of the hiatellid *Panopea generosa* GOULD, 1850 (CARTER & LUTZ, 1990, p. 16, pl. 48, as irregular simple prismatic) (Fig. 49) and parts of the aragonitic outer shell layer of the thraciid *Thracia pubescens* (PULTENEY, 1799) (CARTER & LUTZ, 1990, p. 16, pl. 52, as weakly regular simple prismatic).

3) **Dendritic nondenticular composite prismatic** (dendritic NDCP). Nondenticular composite prisms comprised of second-order, elongate structural units (commonly fibrous prisms) diverging from a central, longitudinal core (instead of from a central, longitudinal axis) toward the sides of the first-order prism. The central, longitudinal core can be relatively narrow or relatively wide, i.e., creating two further types of NDCP—narrow-core or wide-core dendritic, and it can be fine CCL, finely homogeneous, or comprised of mutually parallel to slightly diverging fibrous prisms.

a) **Narrow-core dendritic nondenticular composite prismatic** (narrow-core dendritic NDCP). Dendritic NDCP prisms with a relatively narrow, central, longitudinal core. Locally present in the aragonitic outer shell layer of the verticordiid *Euciroa elegantissima* (DALL, 1881) (Fig. 50). Also locally present in parts of the aragonitic outer shell layer in the thraciids *Thracia pubescens* (PULTENEY, 1799) and *Thracia similis* COUTHOUY, 1839 (see CHECA, HARPER, & WILLINGER, 2012, for the latter), in the thyasirid *Thyasira flexuosa* (MONTAGU, 1803) and in some Mesozoic Pleuromyidae.

b) **Wide-core dendritic nondenticular composite prismatic** (wide-core dendritic NDCP). Dendritic NDCP prisms with a relatively wide, central, longitudinal core. Locally present in the aragonitic outer shell layer of the trigoniid *Neotrigonia gemma* IREDALE, 1924 (Fig. 51). Also locally present in the outer shell layer of the unionid *Obliquaria reflexa* RAFINESQUE, 1820 (Fig. 52) where the prisms are also locally simple prismatic; in the aragonitic outer shell layer of the venerid *Leukoma staminea* (CONRAD, 1837) (Fig. 53); and in the aragonitic outer shell layer of the verticordiid *Euciroa elegantissima* (DALL, 1881).

4) **Compound nondenticular composite prismatic** (compound NDCP). Radially oriented, zeroth-order prisms comprised

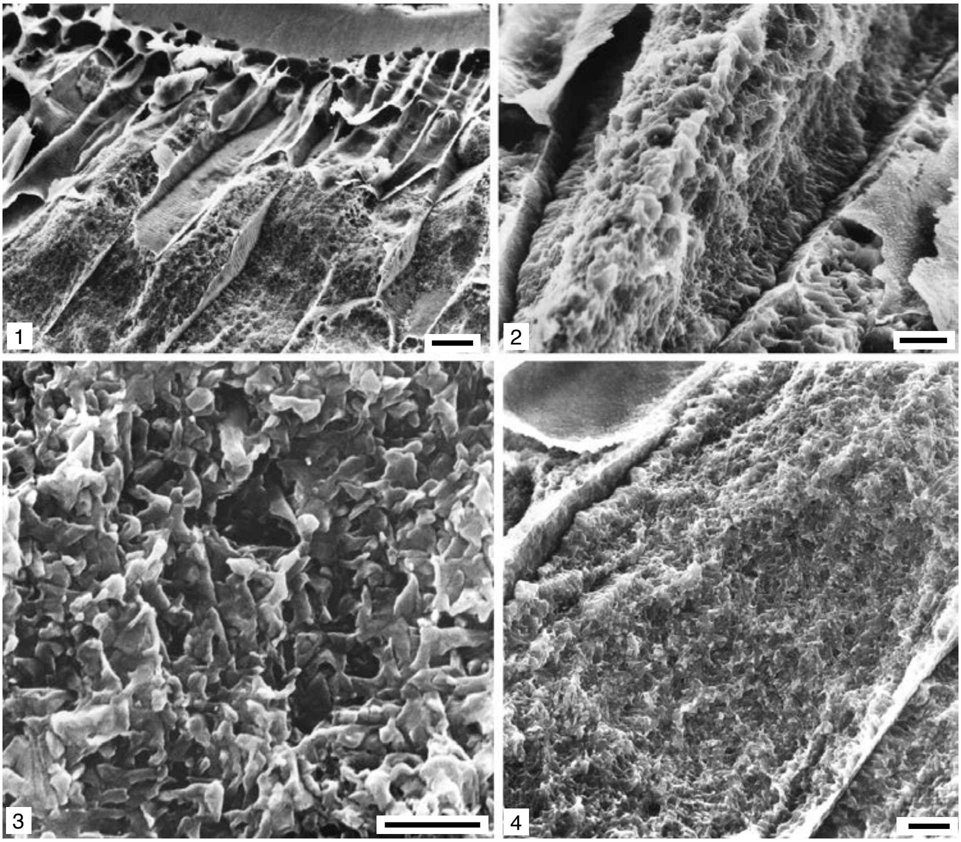

FIG. 52. Wide-core dendritic nondenticular composite prismatic to regular simple prismatic, aragonitic outer shell layer in unionid *Obliquaria reflexa* RAFINESQUE, 1820, Meramec River, St. Louis, Missouri, USA; YPM 97490; SEM of acid-etched radial, vertical section, with shell exterior up and shell margin toward left. *1,* Entire thickness of prismatic layer, with periostracum at top; *2,* wide-core dendritic nondenticular composite prism with a finely homogeneous central core flanked by narrow zone of radiating, second-order prisms; *3,* fine CCL central, longitudinal core of a wide-core dendritic nondenticular composite prism; *4,* a wide-core dendritic nondenticular composite prism with a very narrow, marginal zone of radiating second-order prisms; scale bars, 10 µm in *1,* 2 µm in *2,* 1 µm in *3,* and 2 µm in *4* (Carter, new). These columnar prisms are locally simple prismatic (not shown here).

of first-order nondenticular composite prisms with a three-dimensional, fanlike arrangement by virtue of deposition on a shell marginal denticle, e.g., comprising the denticles in the prismatic outer shell layer of the venerid *Mercenaria mercenaria* (LINNAEUS, 1758) (Fig. 44–45) and comprising the entire outer shell layer in the donacid *Donax variabilis* SAY, 1822 (Fig. 54).

5) **Radial lamellar nondenticular composite prismatic** (radial lamellar NDCP). Radially oriented, zeroth-order, vertical stacks (lamellae) of variably laterally compressed first-order NDCP prisms deposited on a strongly reflected shell margin, e.g., in the outer part of the aragonitic prismatic outer shell layer in the venerid *Mercenaria mercenaria* (LINNAEUS, 1758) (Fig. 44, upper part of figure; Fig. 45.1, upper part of figure). The constituent first-order NDCP prisms sometimes have highly irregular cross-section shapes (Fig. 45.2, lower part of figure). Also present in the aragonitic prismatic outer shell layer in the venerid *Tapes* (*Tapes*) *literata* (LINNAEUS, 1758) (Fig. 55) and in the outer part of the aragonitic prismatic outer shell

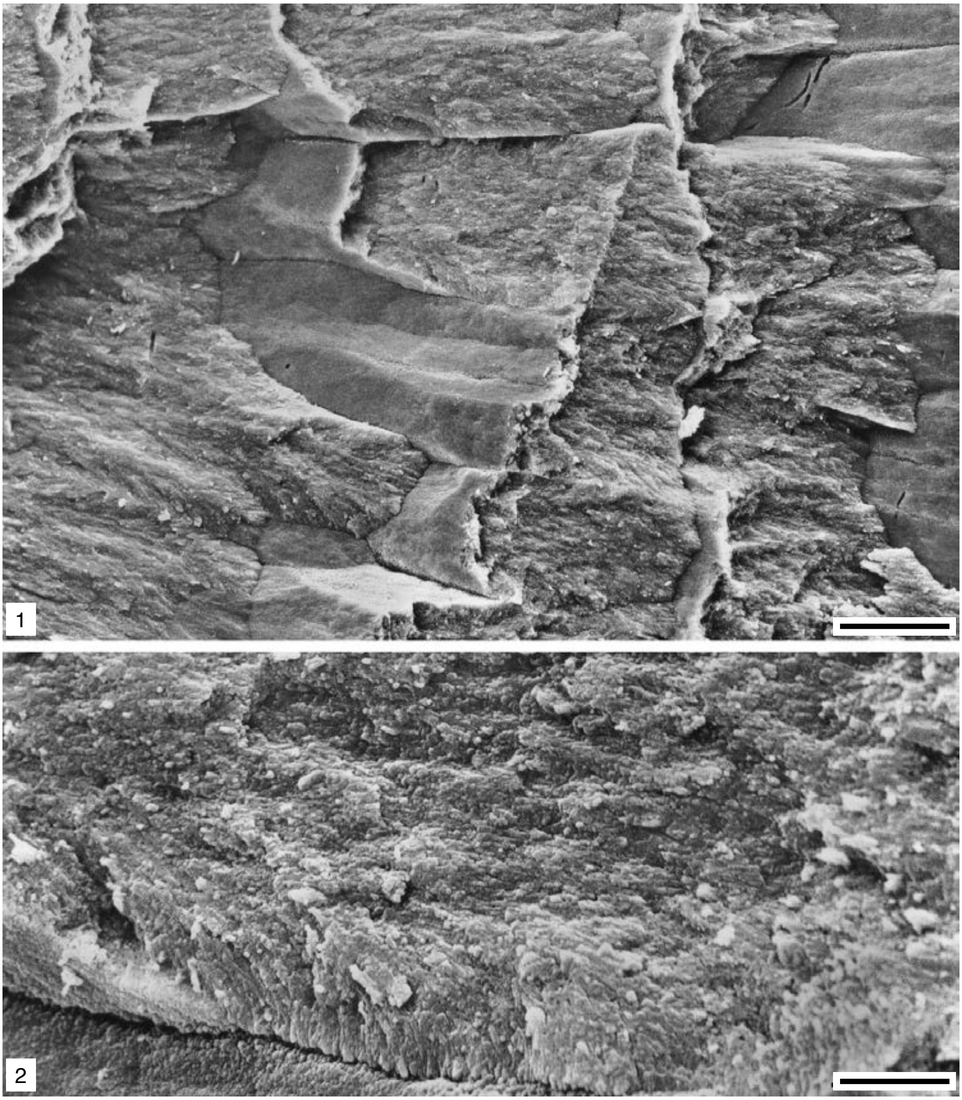

FIG. 53. Wide-core dendritic nondenticular composite prisms in aragonitic outer shell layer of venerid *Leukoma staminea* (CONRAD, 1837), Salmon Bay, Puget Sound, Washington, USA, YPM 9678. SEM of radial, vertical fracture with shell exterior up and posterior shell margin toward right. *1,* Several dendritic NDCP prisms; *2,* part of a dendritic NDCP prism with a very narrow, marginal zone of second-order prisms flaring toward its side; scale bar, 20 µm in *1,* 2 µm in *2* (Carter, new).

layer in the venerid *Dosinia (Asa) troscheli* LISCHKE, 1873 (Fig. 56).

6) Crossed nondenticular composite prismatic (crossed NDCP). Planar to slightly convex aggregations (zeroth-order lamellae) of mutually parallel, first-order NDCP prisms, with each zeroth-order lamella having the thickness of one NDCP prism, and with adjacent zeroth-order lamellae showing alternating, non-radial orientations of their NDCP prisms (CARTER & others, 1990, p. 636), e.g., the inner sublayer of the aragonitic prismatic outer shell layer in the venerid *Dosinia* (*Asa*) *troscheli* LISCHKE, 1873 (Fig. 56–57).

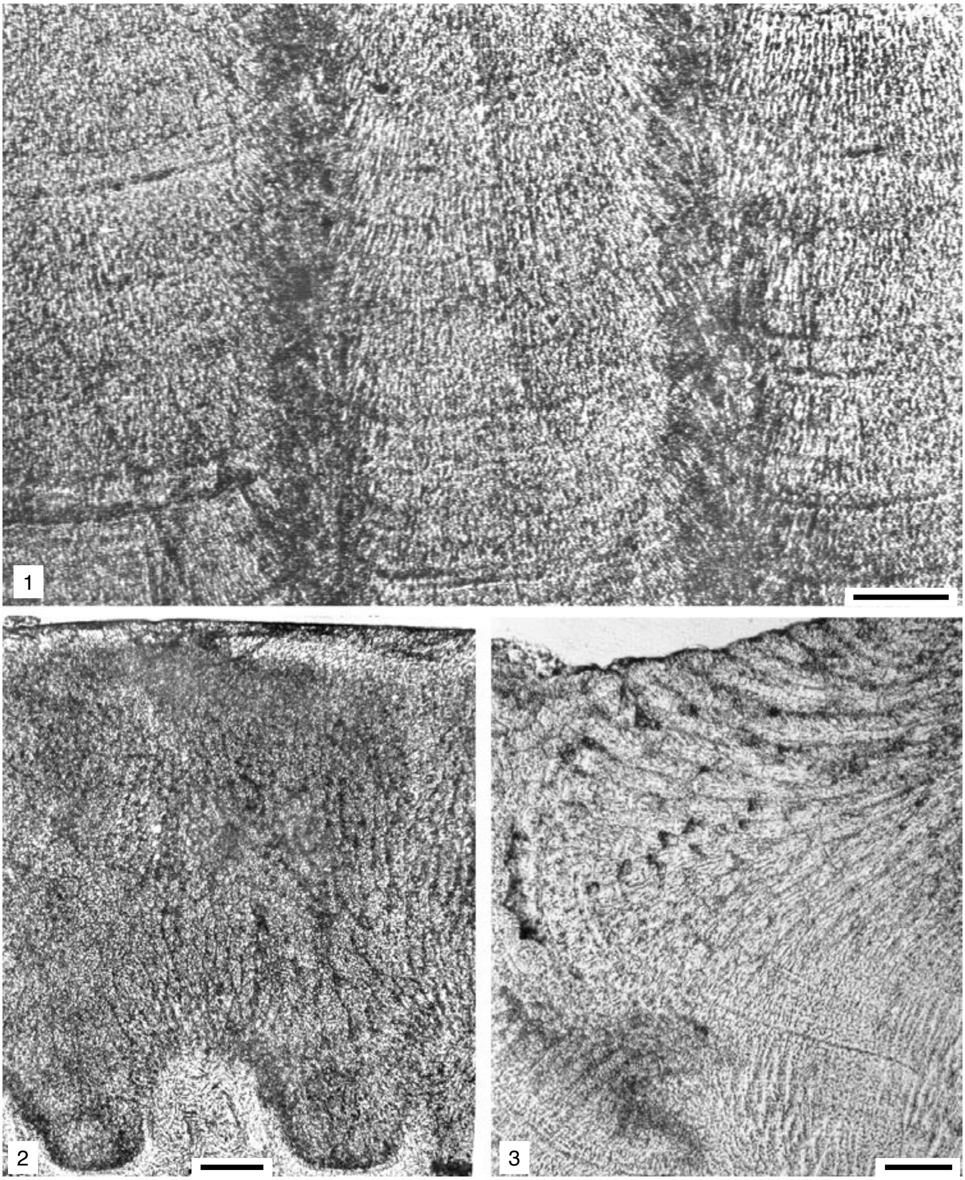

FIG. 54. Compound nondenticular composite prisms in aragonitic outer shell layer of donacid *Donax variabilis* SAY, 1822, Sanibel, Florida, USA, YPM 10074; acetate peels. *1,* Horizontal section through middle of prismatic layer, with posterior shell margin down; *2,* commarginal, vertical section with shell exterior up; *3,* radial, vertical section, with shell exterior up and posterior margin toward left; the outer part of the crossed lamellar middle shell layer is visible at the bottom of *2* and *3;* scale bars, 50 µm (Carter, new).

V. LAMINAR

Non-prismatic, non-crossed microstructures comprised basic structural units arranged into horizontal or imbricated sublayers (laminae). This includes nacreous, semi-nacreous, regularly foliated, semi-foliated, solemyid-type laminar, crossed-bladed, lamello-fibrillar, and matted microstructures.

Nacreous. An aragonitic, laminar microstructure comprised of mutually parallel,

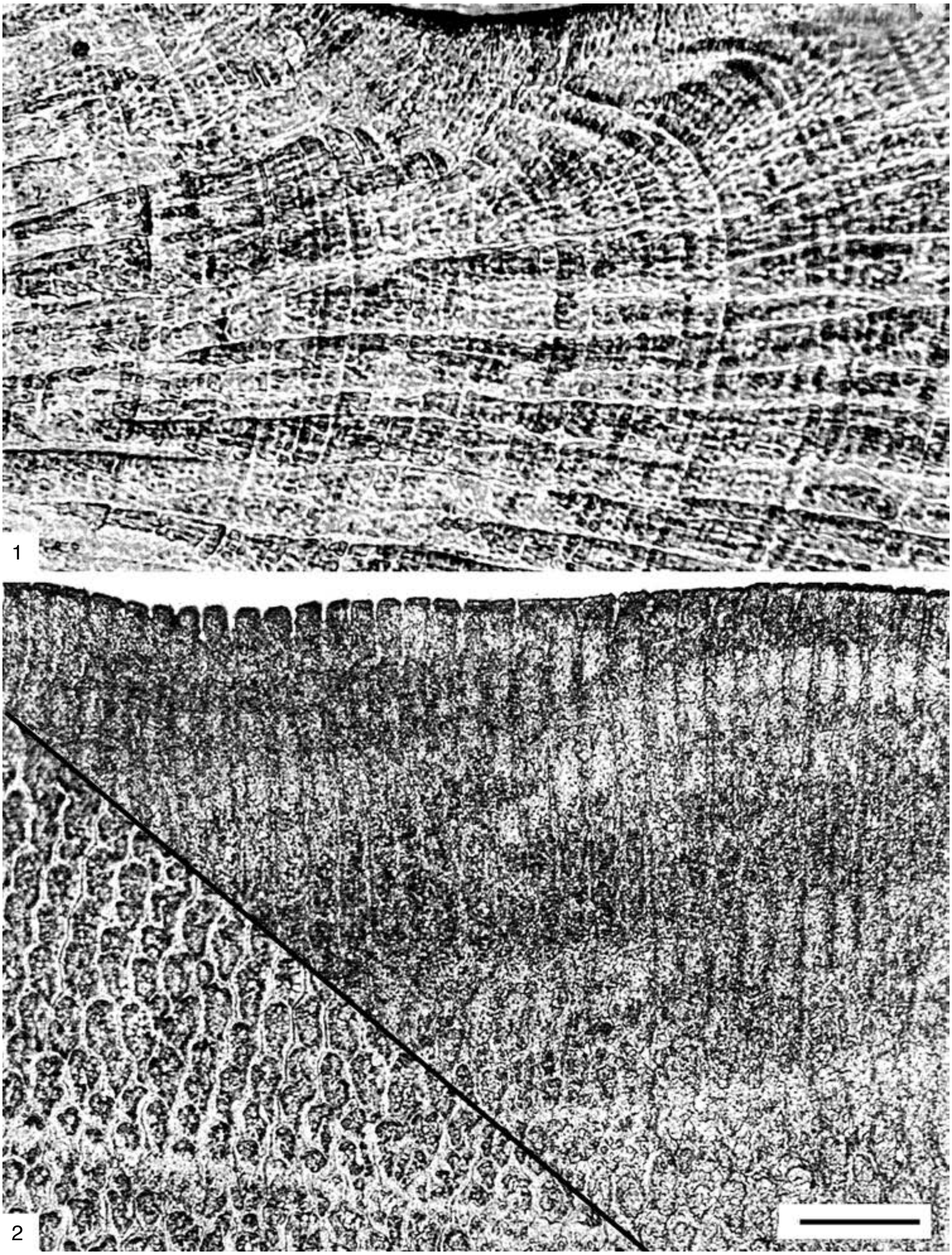

FIG. 55. Radial lamellar nondenticular composite prisms in aragonitic outer shell layer of venerid *Tapes (Tapes) litterata* LINNAEUS, 1758, the Philippines, YPM 9679, acetate peels. *1,* Radial, vertical section, with shell exterior up and shell margin toward right; *2,* commarginal, vertical section showing outer (upper right) and inner (bottom left) parts of prismatic layer; scale bar, 50 µm, applies to both photographs (adapted from Carter & others, 2012, fig. 254).

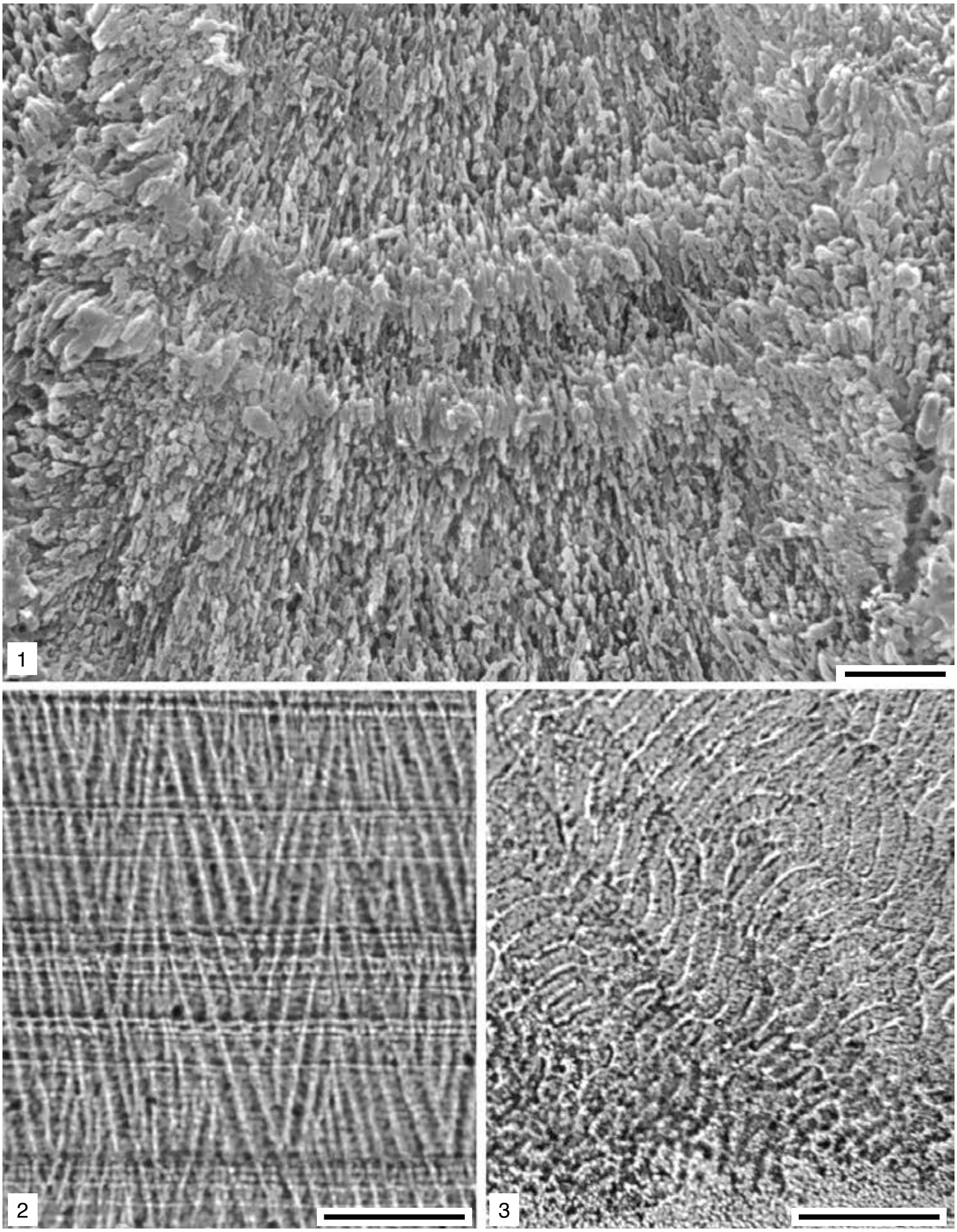

FIG. 56. Crossed nondenticular composite prismatic microstructure in inner sublayer of aragonitic NDCP outer shell layer of venerid *Dosinia* (*Asa*) *troscheli* LISCHKE, 1873, Pei-Tei-Ho, north coast of China, USNM 344529. *1,* SEM of acid-etched, horizontal section, with shell margin down, showing a low-angle NDCP prism within the crossed NDCP microstructure; *2*, horizontal acetate peel, with shell margin down, showing several zeroth-order lamellae; *3*, horizontal acetate peel near contact with underlying crossed lamellar layer (extreme bottom of photograph), showing slightly convex zeroth-order lamellae; scale bars,1 µm in *1,* 100 µm in *2–3* (Carter, new).

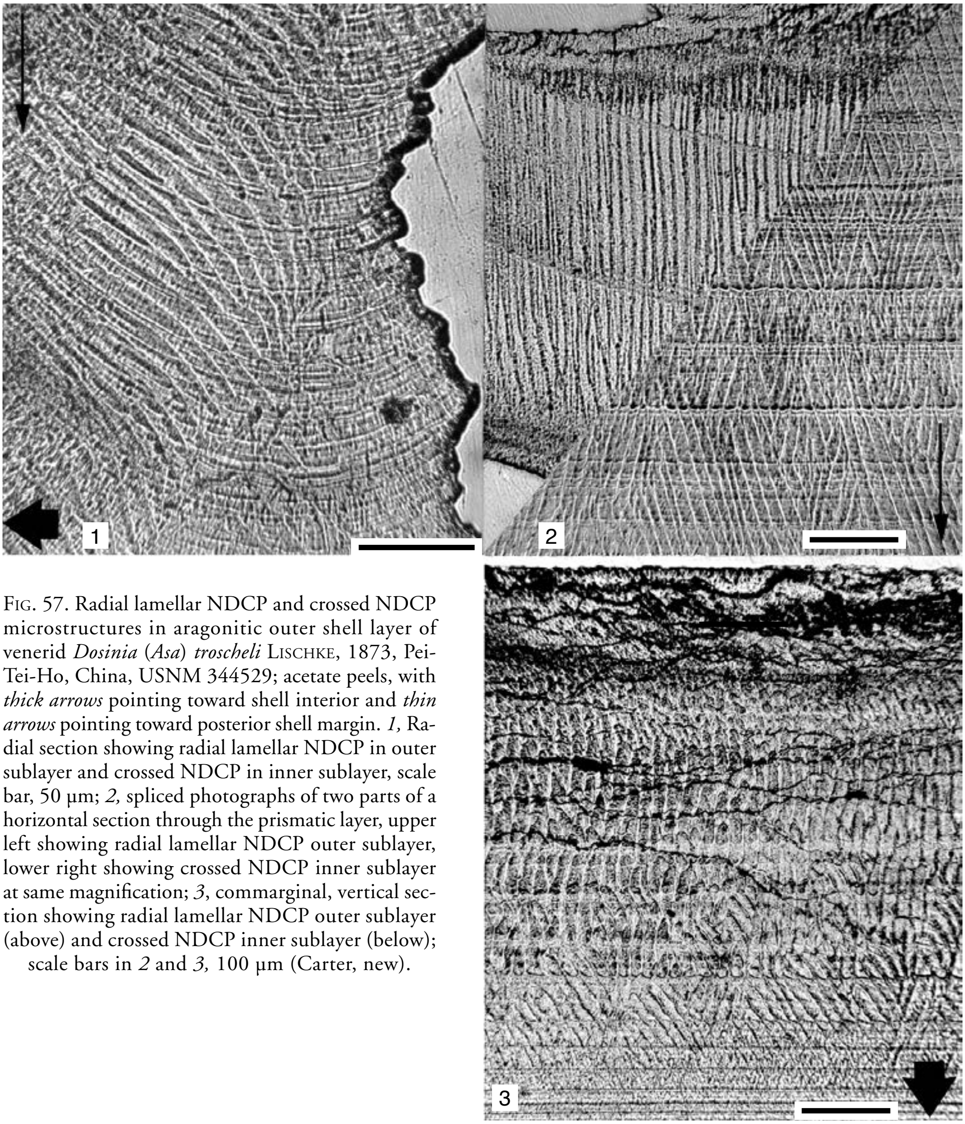

FIG. 57. Radial lamellar NDCP and crossed NDCP microstructures in aragonitic outer shell layer of venerid *Dosinia* (*Asa*) *troscheli* LISCHKE, 1873, Pei-Tei-Ho, China, USNM 344529; acetate peels, with *thick arrows* pointing toward shell interior and *thin arrows* pointing toward posterior shell margin. *1,* Radial section showing radial lamellar NDCP in outer sublayer and crossed NDCP in inner sublayer, scale bar, 50 µm; *2,* spliced photographs of two parts of a horizontal section through the prismatic layer, upper left showing radial lamellar NDCP outer sublayer, lower right showing crossed NDCP inner sublayer at same magnification; *3,* commarginal, vertical section showing radial lamellar NDCP outer sublayer (above) and crossed NDCP inner sublayer (below); scale bars in *2* and *3,* 100 µm (Carter, new).

horizontal or slightly imbricated tablets arranged into laterally continuous laminae, with irregular (brickwall), stair step, row stack, or columnar stacking of the tablets. The tablets generally show few screw dislocations. Columnar tablet stacking probably enhances maximum shell layer accretion rate (WISE, 1970a), whereas row stacking enhances directional flexing of the shell layer (CARTER & TEVESZ, 1978b).

1) Sheet nacreous. A nacreous microstructure with irregular (brick wall) and/or stair-step stacking of the tablets (TAYLOR, KENNEDY, & HALL, 1969), e.g., irregular stacking in the inner shell layer of the malleid *Malleus candeanus* (D'ORBIGNY, 1853 in 1841–1853), the pteriid *Pinctada imbricata* RÖDING, 1798, and the trigoniid *Neotrigonia gemma* IREDALE, 1924 (Fig. 58–59); stair-step stacking in the middle shell layer of the

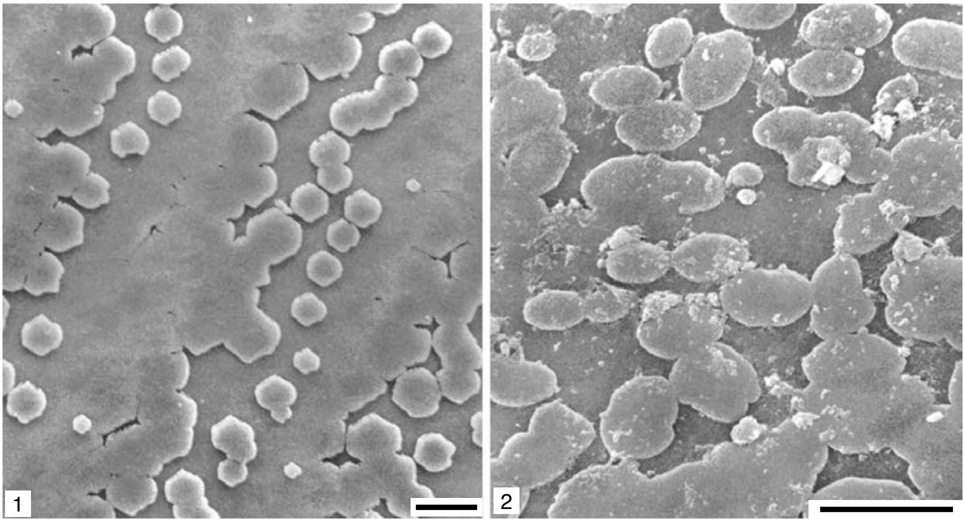

Fig. 58. Sheet nacreous microstructure; SEM of depositional surfaces. *1*, Malleid *Malleus candeanus* (d'Orbigny, 1853 in 1841–1853), inner shell layer, Big Pine Key, Florida, USA, UNC 15431; *2*, trigoniid *Neotrigonia gemma* Iredale, 1924, inner shell layer; scale bars, 5 µm (Carter, new).

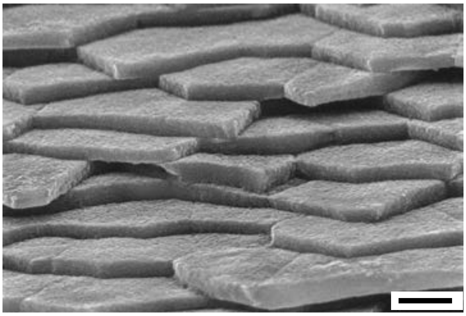

Fig. 59. Sheet nacreous microstructure with irregular tablet stacking. SEM of oblique fracture through inner shell layer of pteriid *Pinctada imbricata* Röding, 1798, Bimini, Bahamas, YPM 6889, scale bar, 10 µm (Carter & others, 2012, fig. 280).

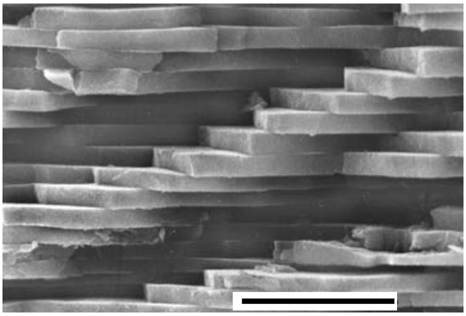

Fig. 60. Sheet nacreous microstructure with stair step tablet stacking. SEM of middle shell layer of unionid *Elliptio complanata* (Lightfoot, 1786), Sangerfield River, Hamilton, New York, USA, YPM 4923, scale bar, 5 µm (Carter & others, 2012, fig. 299).

unionid *Elliptio complanata* (Lightfoot, 1786) (Fig. 60).

2) **Columnar nacreous**. A nacreous microstructure with laterally more or less equidimensional (i.e., not greatly elongated) tablets arranged into vertical stacks. Columnar nacre is well developed in the haliotid gastropod *Haliotis rufescens* Swainson, 1822 in 1820–1833 (Fig. 61) but generally weakly developed, if at all, in nacreous bivalves, e.g., in parts of the nacreous middle shell layer in the trigoniids *Neotrigonia margaritacea* (Lamarck, 1804) (Dauphin, Cuif, & Salomé, 2014) and *Neotrigonia gemma* Iredale, 1924 (Fig. 62). Columnar nacre also occurs in some Nuculoidea, Mytiloidea, Unionoidea, and Pandoroidea, usually in the more rapidly growing, distal parts of the nacreous layer. Taylor, Kennedy, and Hall (1969, p. 28) used the term lenticular nacre

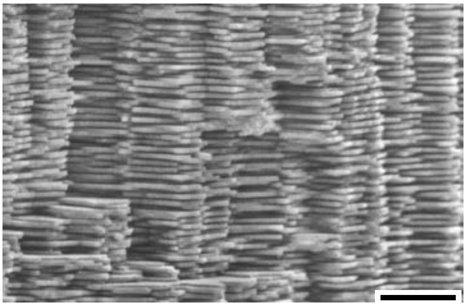

Fig. 61. Columnar nacre with well developed tablet stacking in middle shell layer of haliotid gastropod *Haliotis rufescens* Swainson, 1822 in 1820–1833, California. USA, UNC 8803; SEM of vertical fracture, with shell exterior up, scale bar, 10 µm (Carter, new).

for columnar nacre in which the tablets have wavy surfaces and comprise tapering columns.

3) **Row stack nacreous.** A nacreous microstructure comprised of elongated tablets arranged in mutually parallel rows, with each row representing a stack of tablets (Wise, 1970b; Carter, 1980a). Present in the posterior part of the nacreous shell layer in some Pinnidae, where the row stacks are oriented roughly perpendicular to the medioposterior shell margin (Fig. 63).

Semi-nacreous. An aragonitic or calcitic, laminar microstructure comprised of subhexagonal, rhombic, and/or irregularly

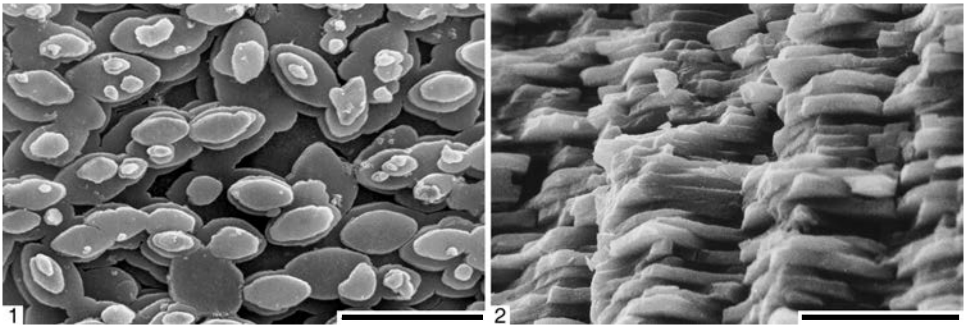

Fig. 62. Columnar nacre in outer part of middle shell layer of trigoniid *Neotrigonia gemma* Iredale, 1924, Sydney, Australia, UNC 5427, SEM. *1*, Depositional surface, with shell margin up; *2*, vertical fracture through same shell layer, slightly closer to shell margin; scale bars, 5 µm (Carter, new).

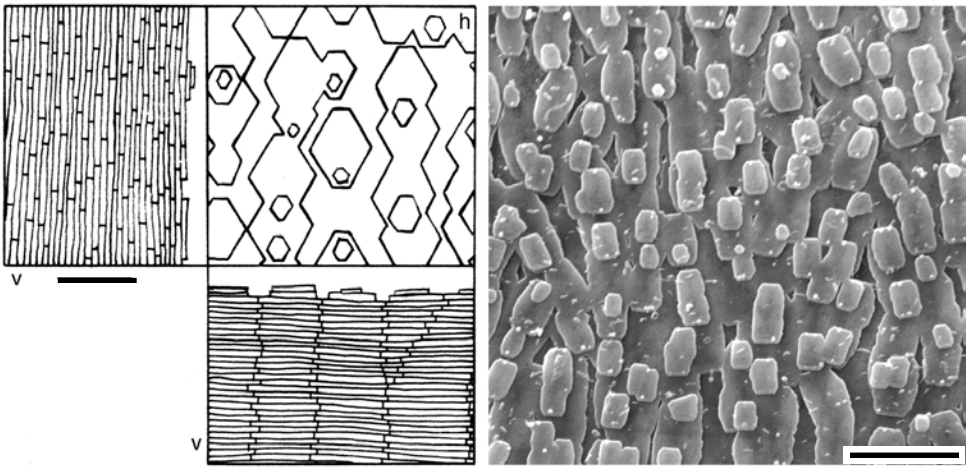

Fig. 63. Row stack nacre in pinnid *Atrina rigida* (Lightfoot, 1786), UNC unnumbered specimen, Beaufort, North Carolina, USA. Left, diagram illustrating depositional surface (*H,* horizontal) and two mutually perpendicular, vertical (*V*) sections, scale bar 10 µm (adapted from Carter & others, 1990, p. 618); right, SEM of depositional surface in a different part of the same shell layer, scale bar, 10 µm (Carter & others, 1990, p. 618; 2012, fig. 267).

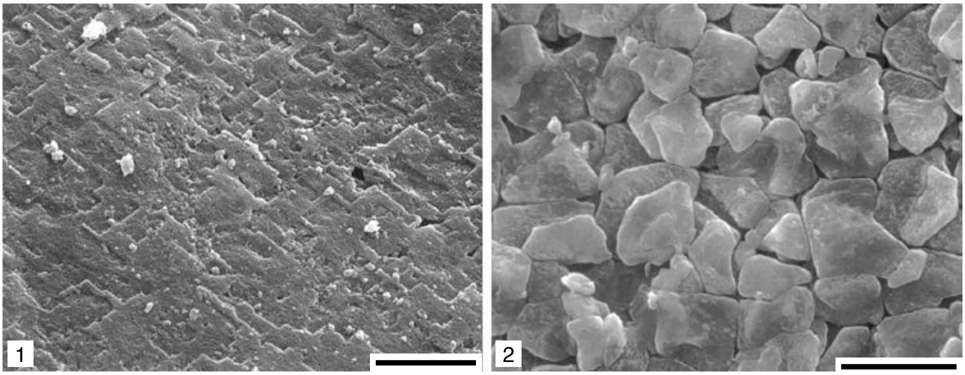

FIG. 64. Calcitic (*1*) and aragonitic (*2*) varieties of semi-nacre. *1,* Rhombic semi-nacre in inner shell layer of Middle Cambrian stenothecid monoplacophoran *Anabarella simesi* MACKINNON, 1985, SEM of impression of inner shell layer on phosphatic internal mold (adapted from Vendrasco, & others, 2010, pl. 2,*11*); *2,* semi-nacre in left valve of Pennsylvanian limipectinid *Acanthopecten carboniferous*? (STEVENS, 1858), Magoffin Member, Four Corners Formation, milepost 55 on Daniel Boone Parkway, west of Hazard, Kentucky, USA, UNC 13724b, horizontal fracture through middle shell layer, adjacent to a well-preserved, irregular simple prismatic pallial myostracum (Carter, 1990a, fig. 43C). Scale bars, 10 µm in *1,* 5 µm in *2*.

shaped tablets arranged in horizontal or slightly imbricated, laterally discontinuous layers (CARTER & CLARK, 1985). Some semi-nacre shows more abundant screw dislocations than nacre. Semi-nacre is only rarely approximated in the Bivalvia, e.g., irregular semi-nacre in the middle and/or inner shell layers of the Carboniferous limipectinid *Acanthopecten carboniferous*? (STEVENS, 1858) (CARTER, 1990a, fig. 43; 1990e, p. 364–365) (Fig. 64.2) and in the Carboniferous mytilid "*Modiolus* or *Volsellina*. cf. *Modiolus* (*Modiolus*) *radiatus* HOARE, STURGEON, AND KINDT, 1978" of CARTER, LUTZ, & TEVESZ (1990, fig. 3G). Bivalve shell semi-nacre might represent an evolutionary transition between nacre and matted microstructure. Calcitic, rhombic semi-nacre is present in the Middle Cambrian, laterally compressed, stenothecid monoplacophoran *Anabarella simesi* MACKINNON, 1985 (VENDRASCO & others, 2010) (Fig. 64.1). Semi-nacre is well developed in many cranioidean brachiopods and cyclostomatid bryozoans (ROSS, 1977; WEEDON & TAYLOR, 1995).

Regularly foliated (RF). A calcitic, laminar microstructure comprised of mutually parallel laths arranged in laterally extensive laminae dipping at the same angle and in the same general, non-radial direction over a large portion of the shell layer (MACCLINTOCK, 1967, p. 18; CARTER, 1980a; CARTER & CLARK, 1985, CARTER & others, 1990, p. 611, 656). Present in the middle shell layer of the ostreids *Dendostrea frons* (LINNAEUS, 1758) (Fig. 65) and *Crassostrea virginica* (GMELIN, 1791) (Fig. 66) and in the outer shell layer in the right valve of the anomiid *Enigmonia aenigmatica* (HOLTEN, 1802) (Fig. 67). This differs from calcitic lath-type fibrous prismatic in being laminar and in having wider elongate structural units.

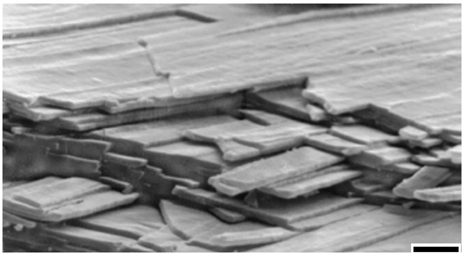

FIG. 65. Regularly foliated microstructure near dorsoposterior margin in calcitic middle shell layer in left valve of ostreid *Dendostrea frons* (LINNAEUS, 1758), Florida, USA, YPM 7017, SEM of oblique fracture, with shell exterior up, scale bar, 1 µm (Carter, new).

Semi-foliated. An aragonitic or calcitic, laminar microstructure comprised of horizontal or slightly imbricated, mutually parallel,

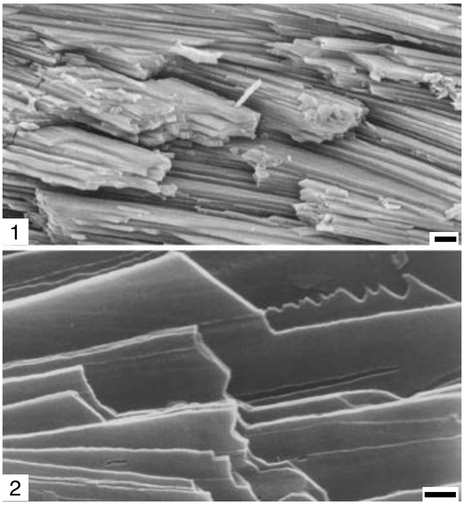

FIG. 66. Regularly foliated microstructure in calcitic middle shell layer of ostreid *Crassostrea virginica* (GMELIN, 1791), SEM of nearly vertical fracture with shell exterior up (*1*) and of horizontal fracure (*2*); scale bars, 1.0 µm (Carter, new).

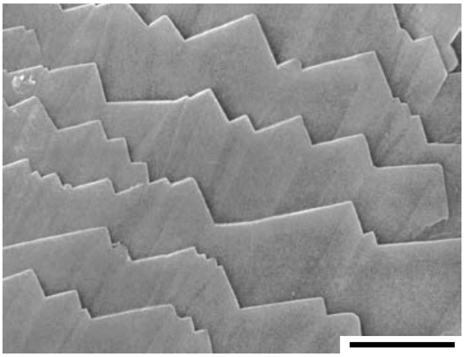

FIG. 67. Regularly foliated microstructure in calcitic outer shell layer in right valve of anomiid *Enigmonia aenigmatica* (HOLTEN, 1802), the Philippines, YPM 10160, SEM of depositional surface, scale bar, 5 µm (Carter, new).

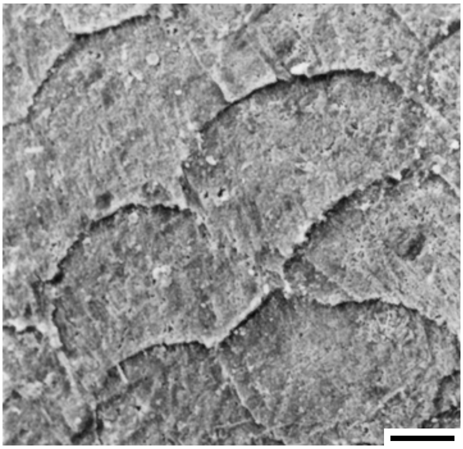

FIG. 68. Semi-foliated microstructure in (originally) aragonitic inner shell layer of lower Cambrian fordillid *Pojetaia runnegari* JELL, 1980, near top of Ajax Limestone, Mount Scott Range, Flinders Ranges, South Australia, SEM of impression of depositional surface on phosphatic internal mold, scale bar, 10 µm (adapted from Runnegar, 1983, fig. 10B, as "cast of shell prisms") (courtesy of Geoscience Australia).

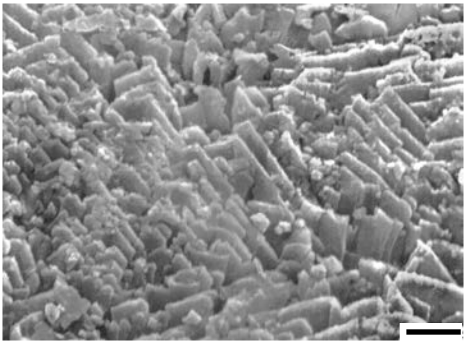

FIG. 69. Semi-foliated microstructure in calcitic middle shell layer of ostreid *Crassostrea virginica* (GMELIN, 1791), Ocean Isle, North Carolina, USA, UNC 12823, SEM of depositional surface of right valve, in transition zone between regularly foliated and chalky microstructure, scale bar, 2 µm (Carter, new).

horizontally flattened, equidimensional or slightly elongate, basic structural units arranged into laterally discontinuous laminae that dip at the same low angle and in the same general direction over a large portion of the shell layer. The terminations of the basic structural units may be flat, rounded, angular, or irregular, and the laths are sometimes longitudinally creased or keeled (CARTER & CLARK, 1985; CARTER & others, 1990, p. 612, 657).

Aragonitic semi-foliated microstructure is present in the inner shell layer of the Early Cambrian fordillids *Fordilla troyensis*

Barrande, 1881, and *Pojetaia runnegari* Jell, 1980 (Runnegar & Bentley, 1983, fig. 4a) (Fig. 68). It is also present in some tryblidiid monoplacophorans (Checa, & others, 2009; Checa, Sánchez-Navas, & Rodríguez-Navarro, 2009, as foliated aragonite).

Calcitic semi-foliated microstructure is present in the transition zone between regularly foliated and chalky microstructures in the ostreid *Crassostrea virginica* (Gmelin, 1791) (Fig. 69), and locally in the middle shell layer in the right valve of the propeamussiid *Parvamussium pourtalesianum* (Dall, 1886) (see Fig. 1, right side).

Solemyid-type laminar. An aragonitic, laminar microstructure comprised of horizontally flattened, irregularly shaped, slightly to moderately elongate, mutually length-parallel structural units with long axes commarginally aligned and comprising laterally continuous or discontinuous laminae. Locally developed in the inner shell layer of the solemyid *Acharax japonica* (Dunker, 1882), where this grades laterally into fine CCL and/or irregular CCL microstructure with similar basic structural units (Sato & others, 2013, fig. 8c, 12g) (Fig. 70). Solemyid-type laminar microstructure is also locally present in the inner shell layer of *Solemya* (*Zesolemya*) *parkinsoni* E. A. Smith, 1874 (Fig. 36.1, Fig. 71), not to be confused with matted microstructure, wherein the basic structural units are not preferentially commarginally aligned.

Crossed bladed. A calcitic, laminar microstructure comprised of aggregations of mutually parallel laths, with lath orientations differing in superadjacent and subadjacent, laterally discontinuous laminae. Rarely developed in the Bivalvia, e.g., in parts of the middle and inner shell layers of the middle Eocene eligmid *Nayadina* (*Exputens*) sp. (Fig. 72.2), and in parts of the outer shell layer of the limid *Ctenoides scaber* (Born, 1778) (Fig. 73). Crossed bladed microstructure is well developed in many strophomenid brachiopods, e.g., in Ordovican *Strophomena planumbona* Hall, 1847, presently illustrated for comparison (Fig. 74).

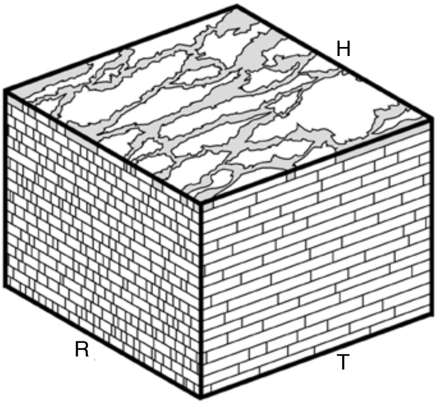

Fig. 70. Diagram of solemyid-type laminar microstructure as seen in horizontal (*H*), radial (*R*), and transverse (*T*) sections (adapted from Sato & others, 2013, fig. 12g).

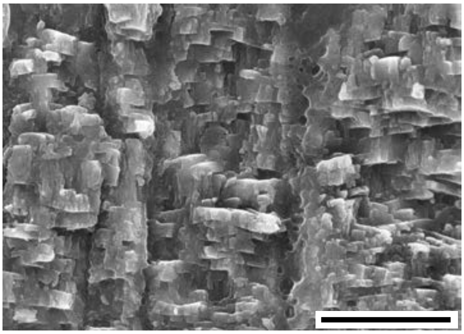

Fig. 71. Solemyid-type laminar microstructure locally developed in aragonitic inner shell layer of solemyid *Solemya* (*Zesolemya*) *parkinsoni* E. A. Smith, 1874, Awarua Bay, New Zealand, YPM 5364, SEM of commarginal, vertical fracture, scale bar, 5 µm (Carter, new). See also Fig. 36.1.

Lamello-fibrillar. An aragonitic microstructure comprised of horizontal or slightly imbricated, mutually parallel laminae, with each lamina consisting of mutually parallel fibrous prisms, with the prisms differently oriented in adjacent laminae (Erben, 1972, p. 28), e.g., the inner shell layer of the Early Cambrian, stenothecid monoplacophorans *Watsonella* Grabau, 1900 and *Anabarella plana* Vostokova, 1962 (Fig. 75) (Kouchinsky, 1999, p. 177, as "stepwise texture"). Not known to occur in the Bivalvia, but possibly an evolutionary precursor to Bivalvia nacre.

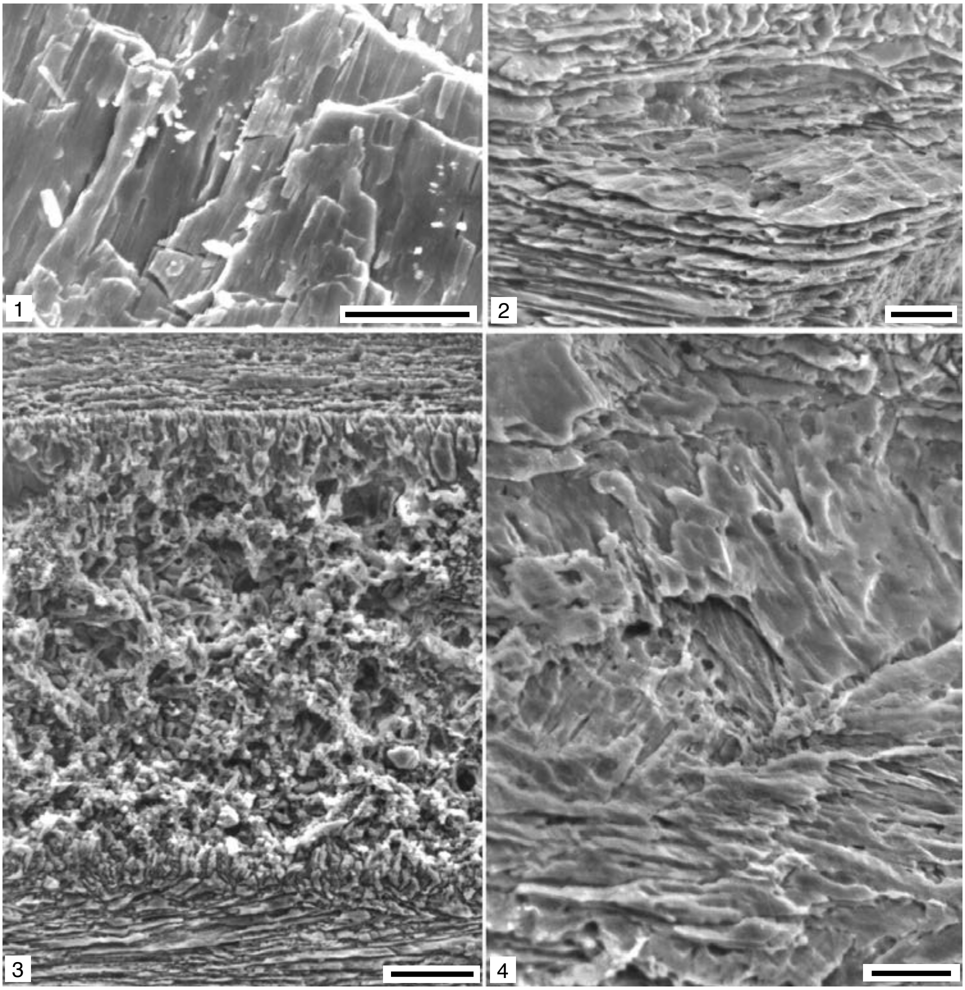

Fig. 72. SEM of middle and inner calcitic shell layers in right valve of eligmid *Nayadina* (*Exputens*) sp., middle Eocene, Castle Hayne Limestone, southeastern North Carolina, USA. *1,* Horizontal fracture showing lath-type fibrous prismatic outer part of middle shell layer, Atlantic Limestone quarry, 4 km SSE of Magnolia, North Carolina, USA, UNC 9687; *2–4,* acid-etched, vertical sections, Magnolia or Castle Hayne, North Carolina, USA, UNC 14947; *2,* middle shell layer, with small, horizontal fracture showing surface of crossed bladed microstructure; *3,* middle shell layer, showing crossed bladed microstructure (above and below) separated by thick sublayer of chalky microstructure (middle), with upper and lower boundaries of the latter marked by very thin sublayer of vertical, irregular simple prisms; *4,* coarsely textured, irregular complex crossed foliated microstructure in inner shell layer; scale bars, 10 µm in *1–3,* 20 µm in *4* (Carter, new).

Matted. An aragonitic microstructure comprised of slightly elongate, irregularly shaped, horizontally flattened structural units arranged into horizontal laminae, without a preferential orientation within each lamina (CARTER & others, 1990, p. 612). Present in the inner shell layer of the Pennsylvanian edmondiid *Edmondia gibbosa* (MCCOY, 1844) (Fig. 76).

VI. RETICULATE

An aragonitic microstructure comprised of a matrix (B-unit) of vertical to steeply reclined, very narrow (less than 1 µm), short, irregular, nodular fibrous prisms and finely homogeneous microstructure enveloping aggregations (A-units) of similar basic structural units, with the A-units showing both reclined and inclined long axes in radial sections, more or less horizontal long axes in commarginal sections, and highly irregular orientations in horizontal sections. The B-unit matrix diminishes in thickness between the A-units toward the inner part of the shell layer, and the A-units diminish in size toward the inner part of the layer. The A-units acid-etch more slowly than the B-unit matrix and in horizontal sections appear irregularly V-shaped to irregularly hexagonal in the outer part of the layer, irregularly trapezoidal in the middle part of the layer, and irregularly rhomboidal in the inner part of the layer (SATO & others, 2013). Present in the outer shell layer of the solemyid *Acharax johnsoni* (DALL, 1891) (Fig. 77–78).

VII. CROSSED

Non-laminar, non-prismatic microstructures comprised of elongate structural units dipping in two or more directions relative to the depositional surface and shell margin (CARTER & others, 1990, p. 612).

Crossed acicular (CA). An aragonitic, crossed microstructure comprised of narrow, elongate structural units dipping in predominantly two and only two opposite or oblique directions and not aggregated into first-order or second-order lamellae (CARTER & others, 1990, p. 612). In Protobranchia, the elongate structural units are generally poorly defined, as in the diffuse crossed acicular middle shell layer of the malletiid *Malletia obstusa* (G. O. SARS, 1872) (Fig. 79), whereas in Heteroconchia they are generally more distinct, as in the crossed acicular middle shell layer of the arcticid *Arctica islandica* (LINNAEUS, 1767 in 1766–1770) (Fig. 80). Radial, vertical fractures through diffuse, commarginal, crossed acicular microstructure can appear identical to finely homogeneous microstructure (Fig. 79.1).

Crossed lamellar (CL, or simple CL). An aragonitic crossed microstructure comprised

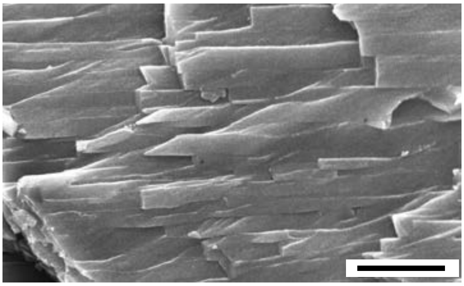

FIG. 73. SEM of horizontal fracture through crossed bladed microstructure in inner part of calcitic outer shell layer of limid *Ctenoides scaber* (BORN, 1778), Big Pine Key, Florida, USA, UNC 6841, scale bar, 5 µm (Carter, new).

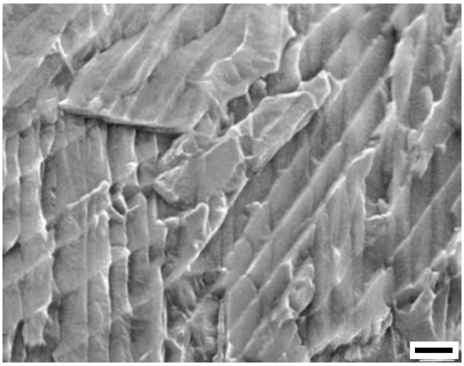

FIG. 74. Crossed bladed microstructure in Late Ordovician strophomenid brachiopod *Strophomena planumbona* HALL, 1847, Richmondian, Ohio, USA, UNC 7173, SEM of horizontal fracture of calcitic inner shell layer in pedical valve, scale bar, 2 µm (Carter, new).

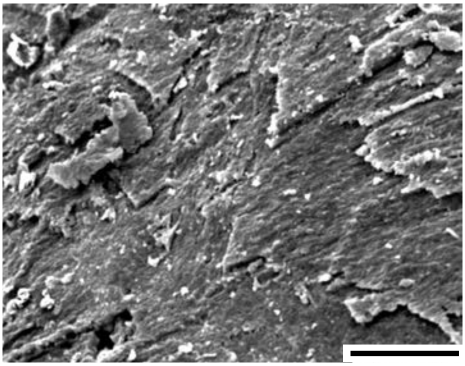

FIG. 75. Lamello-fibrillar microstructure in (originally) aragonitic inner shell layer of lower Cambrian stenothecid monoplacophoran *Anabarella plana* VOSTOKOVA, 1962, Siberian Platform, replicated on phosphatic, internal mold, scale bar, 5 µm (adapted from Kouchinsky, 1999, fig. 2E).

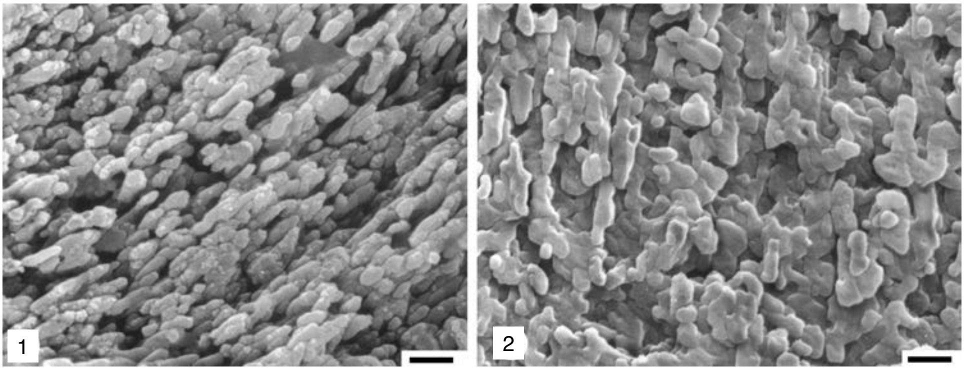

FIG. 76. Matted microstructure in aragonitic inner shell layer of Pennsylvanian edmondiid *Edmondia gibbosa* (MCCOY, 1844), Kendrick Shale Member, Four Corners Formation, Ligon, Kentucky, USA, UNC 13751b. *1,* SEM of acid-etched vertical section; *2,* horizontal fracture; scale bars, 1 µm (Carter & others, 2012, fig. 173).

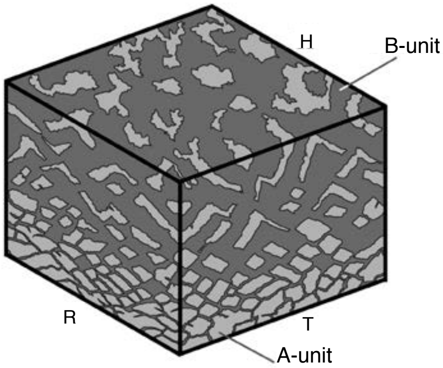

FIG. 77. Diagram of reticulate microstructure in aragonitic outer shell layer of solemyid *Acharax johnsoni* (DALL, 1891); *H,* horizontal, *R,* radial, *T,* transverse (commarginal) section (adapted from Sato & others,

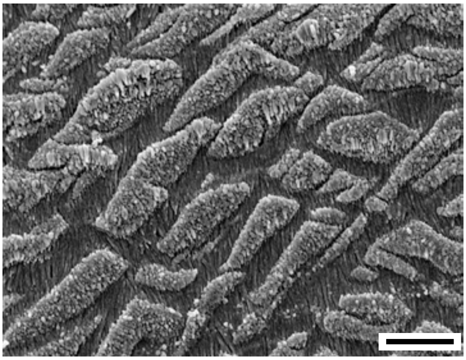

FIG. 78. Reticulate microstructure in aragonitic outer shell layer of solemyid *Acharax johnsoni* (DALL, 1891), acid-etched, radial section with shell exterior up and shell margin toward right, scale bar, 10 µm (adapted from Sato & others, 2013, fig. 9C).

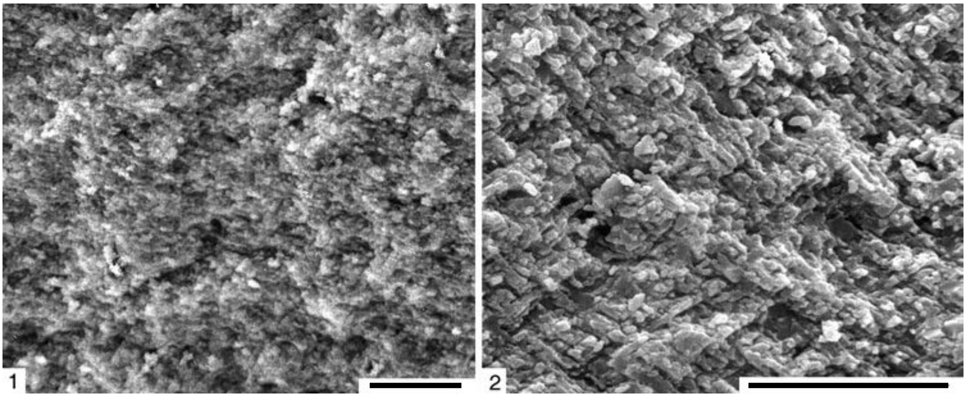

FIG. 79. Diffuse crossed acicular microstructure in aragonitic middle shell layer of malletiid *Malletia obtusa* (G. O. SARS, 1872), U. S. Fish Commission Station 2221, Atlantic Ocean, SEM. *1,* Radial, vertical fracture with shell exterior up; *2,* commarginal, vertical fracture, with shell exterior up; scale bar in *1,* 10 µm, scale bar in *2,* 5 µm (adapted from Carter, 2001, fig. 1,*1–1,2*).

of aggregates (first-order lamellae) of more or less mutually parallel, elongate basic structural units dipping in predominantly two and only two opposite or oblique directions in adjacent first-order lamellae. When the elongate basic structural units are arranged into mutually parallel laminae (second-order lamellae), the structural units are called third-order lamellae (BØGGILD, 1930, p. 251; WISE, 1968, p. 325; CARTER, 1980a; CARTER & CLARK, 1985). The elongate basic structural units may be lath-type, rod-type, or irregular fibrous prisms (Fig. 81). Also called **simple crossed lamellar** (WISE, 1968, p. 325; CARTER & CLARK, 1985; CARTER & others, 1990, p. 612) to distinguish this from complex crossed lamellar.

When second-order lamellae are not developed, the microstructure is called **rod-type crossed lamellar** (CARTER & CLARK, 1985; CARTER & others, 1990). Rod-type CL is common in the Polyplacophora but is only rarely present in the Bivalvia, e.g., in parts of the pallial myostracum of the Late Triassic myophoriid *Costatoria ornata* (MÜNSTER, 1841).

FIG. 80. Crossed acicular microstructure in aragonitic middle shell layer of arcticid *Arctica islandica* (LINNAEUS, 1767 in 1766–1770), SEM of acid-etched, radial section; scale bar, 5 µm (Carter & others, 2012, fig. 76).

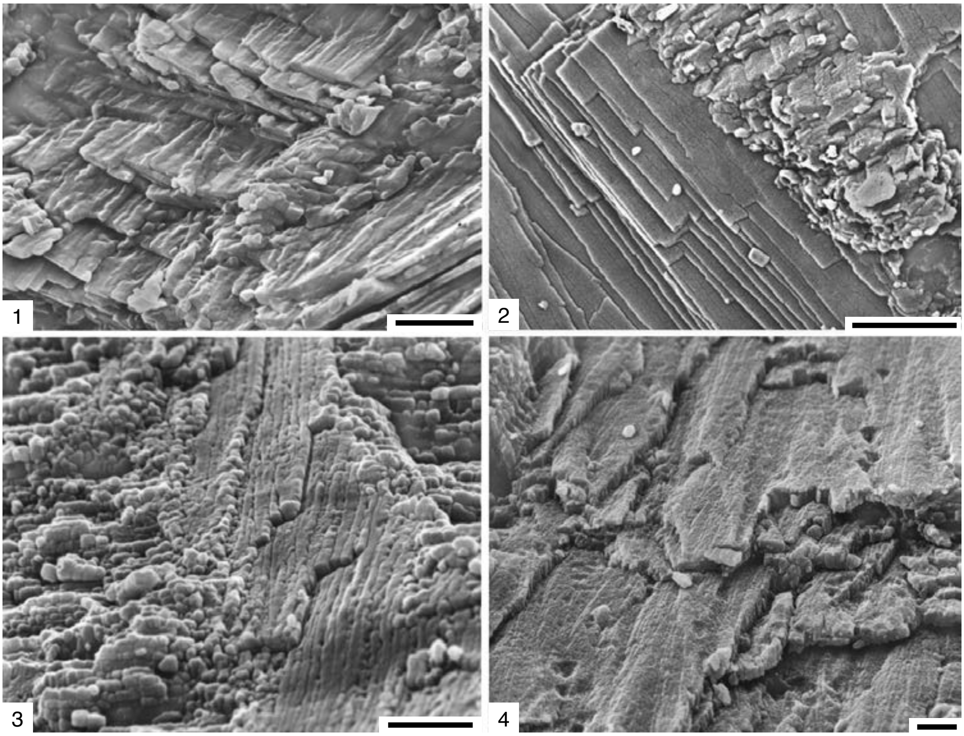

FIG. 81. Second- and third-order lamellae in various aragonitic crossed lamellar middle shell layers; SEM of radial, vertical fractures, with shell exterior up. *1*, Arcid *Barbatia virescens* (REEVE, 1844), Japan, YPM 6420; *2*, plicatulid *Plicatula gibbosa* LAMARCK, 1801, St. Thomas, Virgin Islands, YPM 9631; *3,* anomiid *Anomia simplex* D'ORBIGNY, 1853 in 1841–1853, New Haven, Connecticut, YPM 9715; *4,* venerid *Cyclina sinensis* (GMELIN, 1791), Japan, YPM 9695; scale bars, 1 µm (Carter, new).

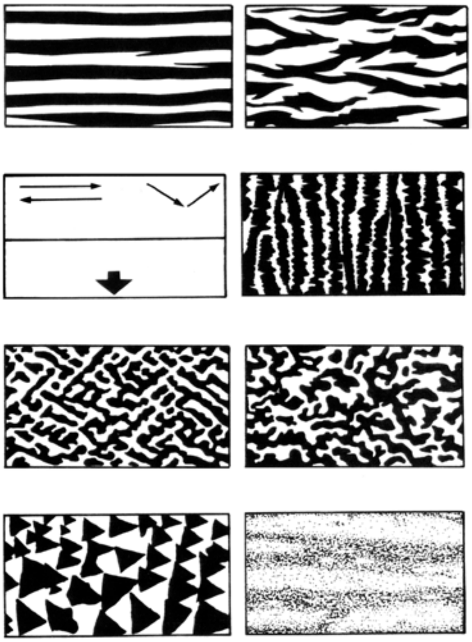

FIG. 82. Signatures of commarginal crossed lamellar microstructures as seen on the depositional surfaces and in horizontal sections, with an inset diagram showing alternative dip directions (*thin arrows*) relative to shell margin (*thick arrow*) (adapted from Carter & others, 1990, p. 621).

Crossed lamellar microstructures generally have higher dip angles and smaller first-order lamellae than crossed foliated microstructures. However, some first-order crossed lamellae approach the size of some first-order crossed folia, e.g., in the middle shell layer of the chamid *Chama limbula* LAMARCK, 1819 (CARTER & LUTZ, 1990, pl. 82B, as *Chama iostoma* CONRAD, 1837) (Fig. 83).

In **commarginal crossed lamellar** microstructure the third-order lamellae dip in two opposite commarginal directions or in two not directly opposed, oblique directions. In **radial crossed lamellar** microstructure the third-order lamellae dip in two opposite, radial directions. Radial CL is rarely present in the Bivalvia, e.g., locally in the outer shell layer of the arcid *Arca zebra* (SWAINSON, 1833 in 1820–1833) (Fig. 3.2). Radial CL commonly occurs in the Gastropoda as a sublayer between commarginal crossed lamellar sublayers, e.g., in many Conidae and Cypraeidae. Varieties of crossed lamellar microstructure are defined on the basis of their appearance (signature) on depositional surfaces and in horizontal sections. Commarginal crossed lamellae can have a variety of signatures, sometimes varying within a single shell layer (Fig. 82), whereas radial crossed lamellae are limited to branching and linear signatures.

1) **Branching crossed lamellar** (BCL). A crossed lamellar microstructure with elongate, strongly branching first-order lamellae (CARTER & CLARK, 1985). This is the most common simple crossed lamellar microstructure in Heteroconchia, e.g., in the chamid *Chama limbula* LAMARCK, 1819 (Fig. 83). Branching CL is less common in the Pteriomorphia, e.g., locally in the inner shell layer of the pectinid *Amusium pleuronectes* (LINNAEUS, 1758) (Fig. 84).

2) **Linear crossed lamellar** (LCL). A crossed lamellar microstructure with elongate, slightly branching first-order lamellae (CARTER & CLARK, 1985). Present in many Pteriomorphia, e.g., Arcoidea, Limopsoidea, Pectinoidea, Anomioidea, and Limoidea, e.g., in the limid *Ctenoides scaber* (BORN, 1778) (Fig. 85). Less common in the Heteroconchia, e.g., in the cyrenid *Batissa* sp. (CARTER & LUTZ, 1990, pl. 69).

3) **Compressed crossed lamellar** (compressed CL). A commarginal crossed lamellar microstructure with commarginally shortened, radially elongate first-order lamellae (CARTER & CLARK, 1985; CARTER & others, 1990, p. 634), e.g., part of the inner shell layer of the carditid *Carditamera* (*Carditamera*) *affinis* (G. B. SOWERBY I, 1833a) (Fig. 86) and part of the middle shell layer of the solecurtid *Solecurtus divaricatus* (LISCHKE, 1869) (Fig. 87). Not to be confused with radial crossed lamellar, wherein the dip angles of the third-order lamellae and the length axes of the first-order lamellae are both radially oriented.

4) **Irregular crossed lamellar** (irregular CL). A commarginal crossed lamellar microstructure with irregularly shaped first-order

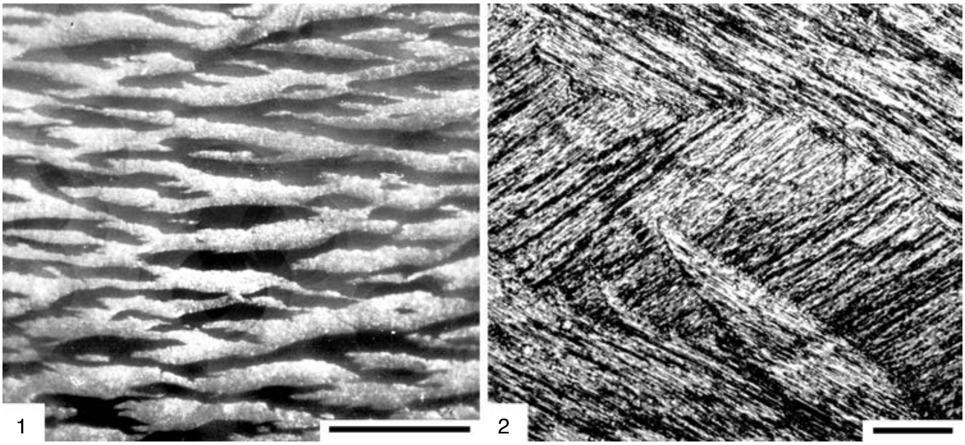

FIG. 83. Branching crossed lamellar microstructure in chamid *Chama limbula* LAMARCK, 1819, Palau, UNC 9744. *1,* Unidirectional reflected light microscopy of depositional surface of aragonitic middle shell layer, with shell margin down; *2,* acetate peel of commarginal, vertical section, with shell exterior up; scale bars, 0.5 mm in *1,* 50 µm in *2* (Carter & others, 2012, fig. 80).

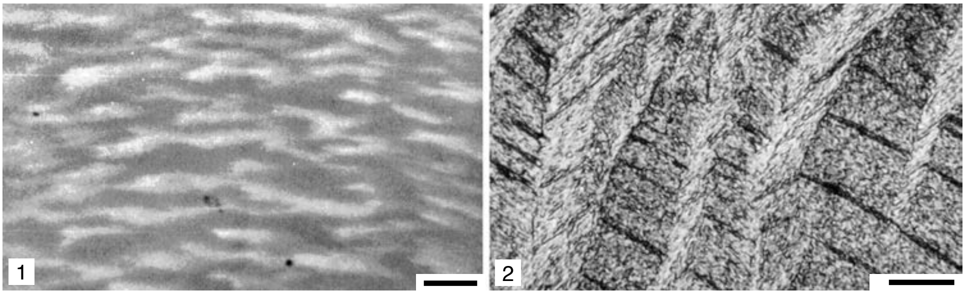

Fig. 84. Branching crossed lamellar microstructure in outer part of inner shell layer of pectinid *Amusium pleuronectes* (LINNAEUS, 1758), Indo-West Pacific, YPM 8492. *1*, Unidirectional reflected light microscopy of depositional surface between two internal ribs, with ventral shell margin up; *2*, commarginal, vertical acetate peel, with shell exterior up; scale bars, 10 µm in *1*, 50 µm in *2* (Carter, new).

lamellae, e.g., in the middle shell layer of the thyasirid *Thyasira flexuosa* (MONTAGU, 1803) (Fig. 88); also present in some Cyamiidae, Gastrochaenidae, and Tellinidae (CARTER & CLARK, 1985).

5) **Crisscross crossed lamellar** (XCL). A commarginal crossed lamellar microstructure with triangular to irregularly shaped first-order lamellae forming a crossing pattern as seen on the depositional surface and in horizontal sections (CARTER & CLARK, 1985), e.g., in the outer part of the middle shell layer posteriorly in the solecurtid *Solecurtus divaricatus* (LISCHKE, 1869) (Fig. 89) and in a similar position in the pharid *Ensis siliqua* (LINNAEUS, 1758) (Fig. 90).

6) **Triangular crossed lamellar** (TCL). A commarginal crossed lamellar microstructure with more or less triangular first-order lamellae not aligned into radial rows and not forming a criss-cross pattern as seen on the depositional surface and in horizontal sections, e.g., part of the middle shell layer of the lucinid *Pegophysema bialata* (PILSBRY, 1895) (Fig. 91). Also present in some Tellinidae and Solenidae (CARTER & CLARK, 1985).

7) **Diffuse crossed lamellar** (DCL). A commarginal crossed lamellar microstructure

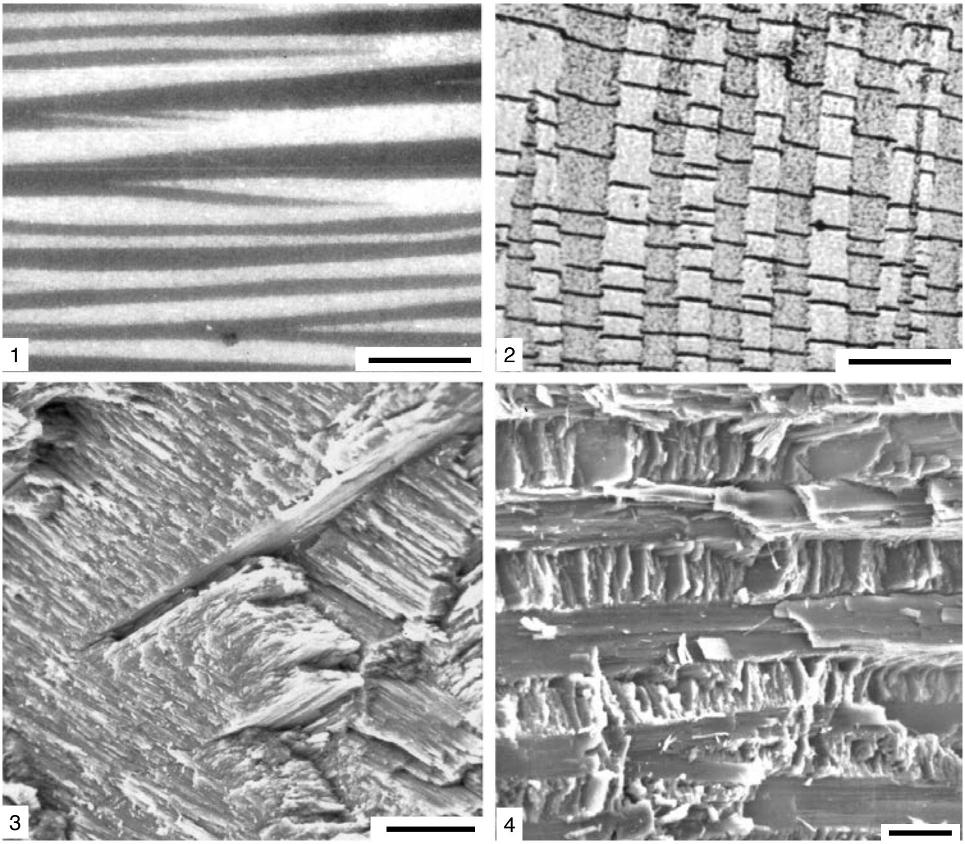

FIG. 85. Linear crossed lamellar microstructure in aragonitic middle shell layer of limid *Ctenoides scaber* (BORN, 1778), Biscayne Bay, Florida, USA, YPM 9702. *1,* Unidirectional reflected light microscopy of depositional surface, with shell margin down; *2*, radial, vertical acetate peel, with shell exterior up; *3*, SEM of vertical, slightly oblique, nearly commarginal fracture; *4*, SEM of horizontal fracture, with shell margin down; scale bars, 50 µm in *1–2*; 10 µm in *3–4* (Carter, new).

with very indistinct first-, second-, and third-order lamellae. This occurs in many porcelaneous shelled Protobranchia, where it is commonly misdiagnosed as a finely homogeneous microstructure, e.g., in the middle shell layer of the Pennsylvanian cucullellid *Palaeoneilo oweni* (MCCHESNEY, 1860) (Fig. 92). It is rarely present in Autobranchia, e.g., in the the middle shell layer of the ungulinid *Zemysina orbella* (GOULD, 1851) (Fig. 93).

Crossed foliated (CF, or simple CF). A calcitic crossed microstructure comprised of aggregates (first-order folia) of more or less mutually parallel, elongate, basic structural units dipping in predominantly two directly opposite commarginal or in two non-commarginal, oblique directions in adjacent first-order folia. When the elongate, basic structural units are arranged into mutually parallel laminae (second-order folia) within each first-order folium, the basic structural units are called third-order folia (MACCLINTOCK, 1967; CARTER, 1980a; CARTER & others, 1990, p. 621, 626). The elongate structural units are generally lath-type or rod-type fibrous prisms. Also called **simple crossed foliated** (CARTER & others, 2012) to distinguish this from complex crossed foliated. When the elongate structural units are not arranged into second-order folia, the microstructure is called **rod-type**

crossed foliated, e.g., locally in the middle shell layer in the right valve of the pectinid *Leopecten diegensis* (DALL, 1898) (Fig. 95).

Crossed foliated microstructures generally have larger first-order folia and lower dip angles than crossed lamellar microstructures. **Low-angle crossed foliated** has a maximum dip angle less than 15° relative to the depositional surface, e.g., in the middle shell layer in the left valve of the propeamussiid *Propeamussium dalli* (E. A. SMITH, 1885) (Fig. 94). **High-angle crossed foliated** has a maximum dip angle greater than 15° relative to the depositional surface, e.g., the middle shell layer of the Middle Jurassic oxytomid *Oxytoma* (*Oxytoma*) *inequivalvis* (J. SOWERBY, 1819) (Fig. 96); the middle shell layer of the Jurassic gryphaeid *Gryphaea* (*Bilobissa*) *bilobata* J. DE C. SOWERBY, 1840 (Fig. 97); and the middle shell layer of the pectinid *Amusium pleuronectes* (LINNAEUS, 1758) (Fig. 98).

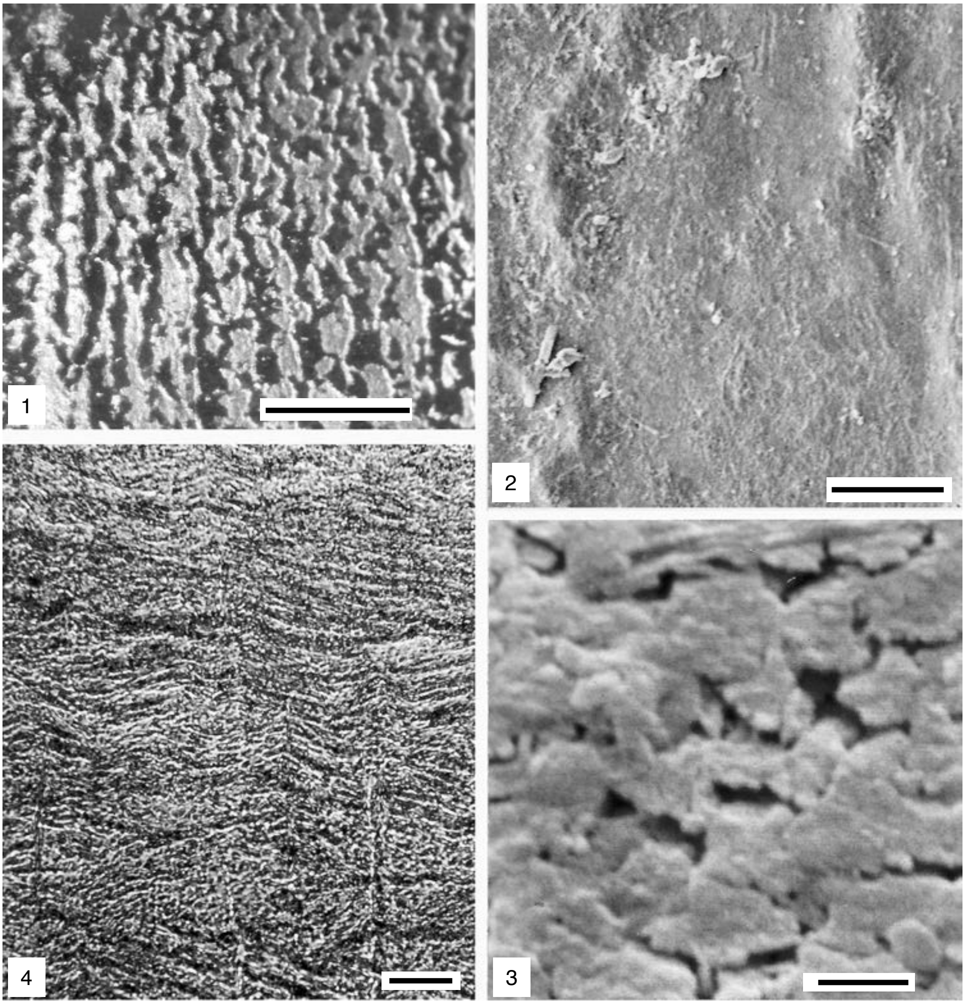

FIG. 86. Compressed crossed lamellar microstructure in outer part of inner shell layer, just proximal to pallial line, in carditid *Carditamera* (*Carditamera*) *affinis* (G. B. SOWERBY I, 1833a), Gulf of California, Mexico, YPM 4078a, outer part of inner shell layer, near pallial line. *1*, Unidirectional reflected light microscopy of depositional surface, with ventral shell margin up; *2–3,* SEM of depositional surface, same area and orientation as in *1*; *4*, commarginal, vertical acetate peel, with shell exterior up; scale bars, 500 µm in *1,* 50 µm in *2*; 1.0 µm in *3*; 10 µm in *4* (Carter, new).

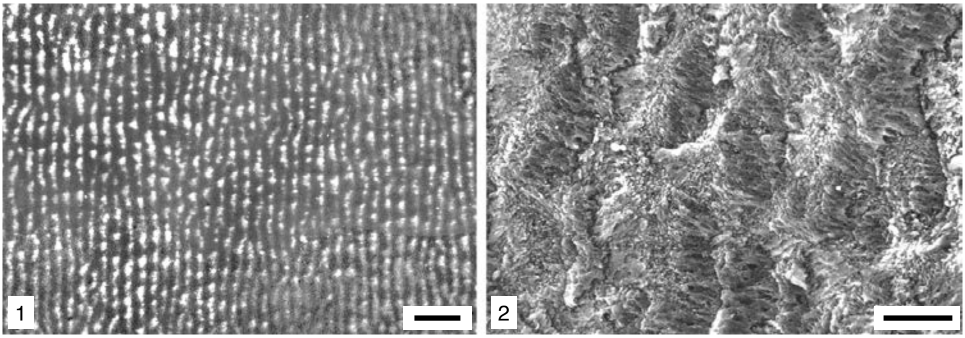

FIG. 87. Compressed crossed lamellar microstructure in middle of aragonitic middle shell layer of solecurtid *Solecurtus divaricatus* (Lischke, 1869), Japan (YPM 9608). *1*, Unidirectional reflected light microscopy of deposition surface in shell posterior, with posterior shell margin up; *2*, SEM of same depositional surface with same orientation; scale bars, 100 µm in *1*, 10 µm in *2* (Carter, new).

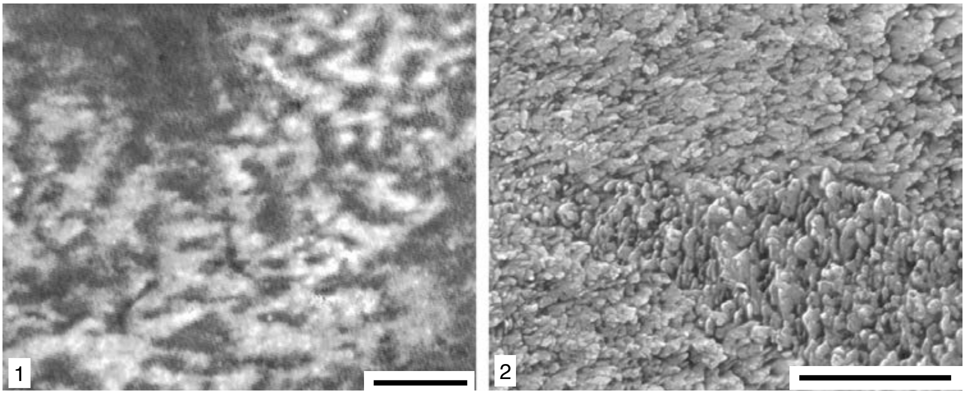

FIG. 88. Irregular crossed lamellar microstructure in aragonitic middle shell layer of thyasirid *Thyasira flexuosa* (MONTAGU, 1803), YPM 1125. *1*, Unidirectional reflected light microscopy of posteroventral depositional surface, with shell margin down; *2*, SEM of acid-etched, horizontal section, showing two first-order lamellae; scale bars, 100 µm in *1,* 5 µm in *2* (Carter, new).

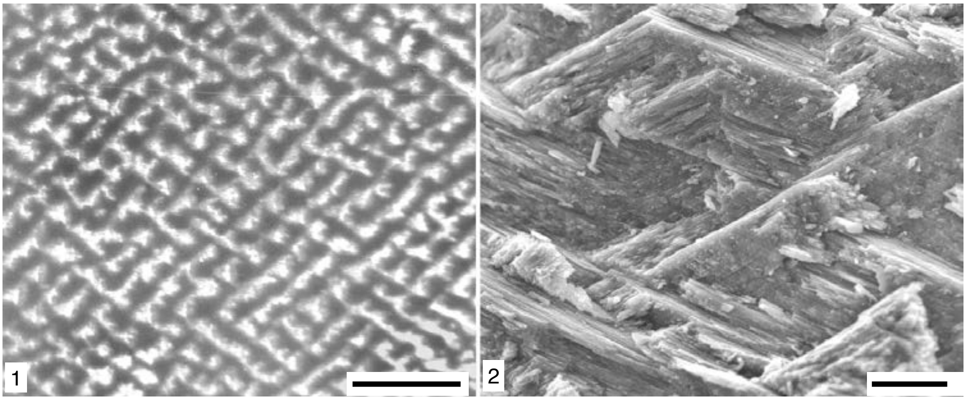

FIG. 89. Crisscross crossed lamellar microstructure in outer part of aragonitic middle shell layer posteriorly in solecurtid *Solecurtus divaricatus* (LISCHKE, 1869), Japan, YPM 9608. *1*, Unidirectional reflected light microscopy of depositional surface, with posterior shell margin up; *2*, SEM of commarginal, vertical fracture, with shell exterior up; scale bars, 100 µm in *1,* 2 µm in *2* (Carter, new)

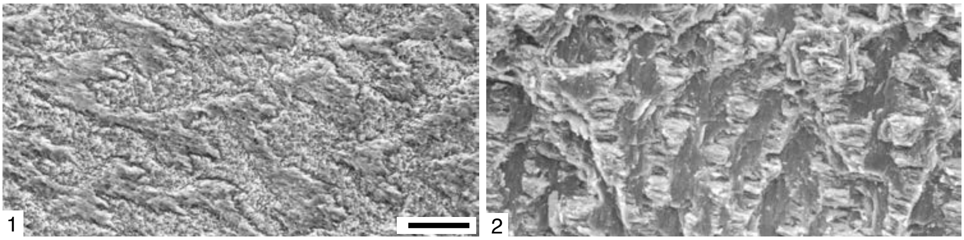

FIG. 90. Crisscross crossed lamellar microstructure in outer part of middle shell layer posteriorly in pharid *Ensis siliqua* (LINNAEUS, 1758), North Sea, west of Ameland, the Netherlands, YPM 9716, SEM; *1,* Acid-etched, horizontal section, with posterior shell margin down; *2,* nearly radial, slightly oblique fracture, with shell exterior up; scale bars, 10 µm (Carter, new).

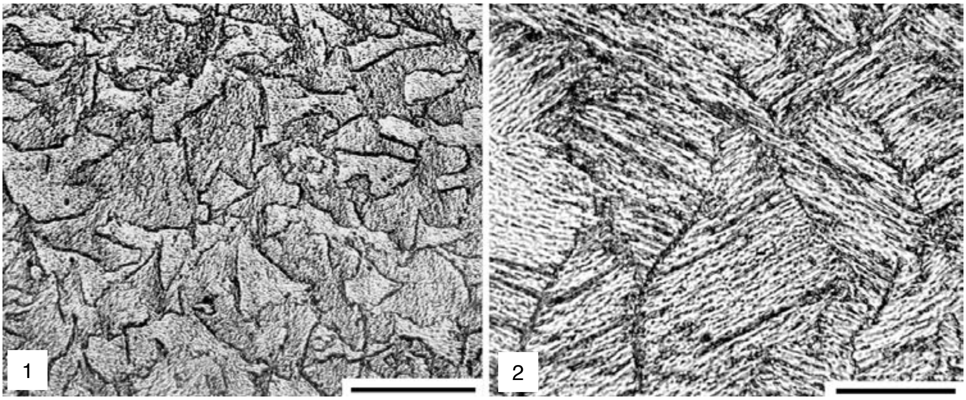

FIG. 91. Triangular crossed lamellar microstructure in posterior part of aragonitic middle shell layer in lucinid *Pegophysema bialata* (PILSBRY, 1895), Tsingtao, China, YPM 8963, acetate peels. *1,* Horizontal section, with shell margin down; *2,* commarginal, vertical section, with shell exterior up; scale bars, 50 µm (Carter, new).

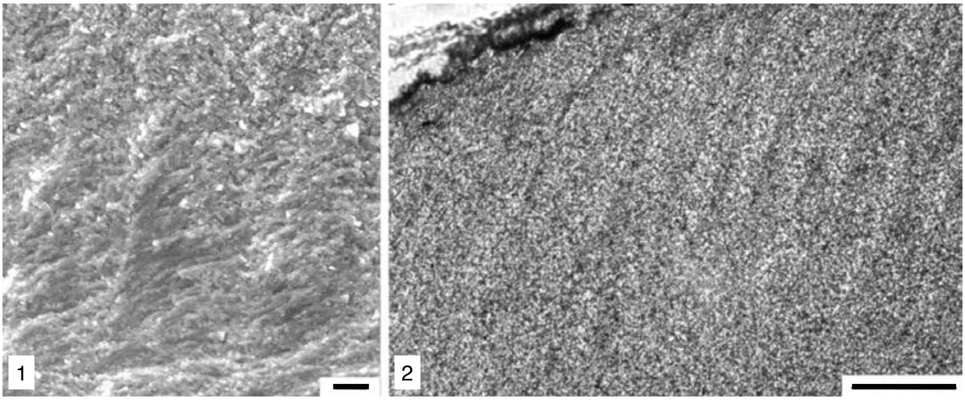

FIG. 92. Diffuse crossed lamellar microstructure in aragonitic middle shell layer of Pennsylvanian cucullellid *Palaeoneilo oweni* (MCCHESNEY, 1860), Kendrick Shale Member, Four Corners Formation, off Clear Creek, Ligon, Kentucky, USA, UNC 13758g; shell exterior is up and ventral shell margin is toward left. *1*, SEM of nearly radial, vertical fracture showing several first-order diffuse crossed lamellae; *2,* radial, vertical acetate peel of same part of shell as in *1*, showing several diffuse, first-order crossed lamellae; scale bars, 10 µm in *1*, 50 µm in *2* (adapted from Carter, 1990a, fig. 11*e–f*).

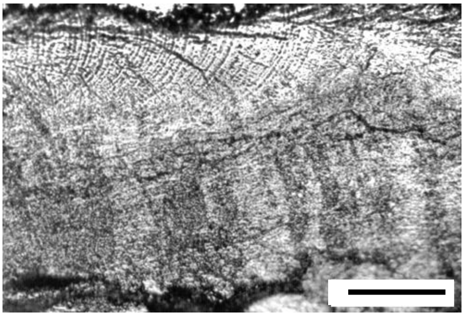

FIG. 93. Diffuse crossed lamellar microstructure in aragonitic middle shell layer (below), also showing aragonitic prismatic outer shell layer (above), in ungulinid *Zemysina orbella* (GOULD, 1851), Anaheim Bay, California, USA, YPM 1003, acetate peel of radial, vertical section, with shell exterior up and posterior shell margin toward right, scale bar, 100 µm (Carter, new).

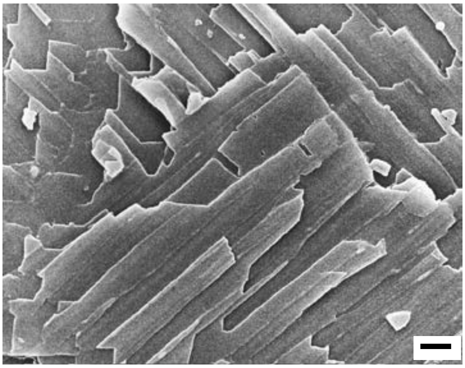

FIG. 94. *For explanation, see adjacent column.*

Crossed foliated microstructures have branching (Fig. 96, Fig. 97) or linear (Fig. 98) first-order folia signatures.

1) **Branching crossed foliated** (BCF). A crossed foliated microstructure with strongly branching first-order folia signatures, e.g., the middle shell layer of the Jurassic oxytomid *Oxytoma* (*Oxytoma*) *inequivalvis* (J. SOWERBY, 1819) (Fig. 96), and the middle shell layer of the Jurassic gryphaeid *Gryphaea* (*Bilobissa*) *bilobata* J. DE C. SOWERBY, 1840 (Fig. 97).

2) **Linear crossed foliated** (LCF). A crossed foliated microstructure with weakly branching first-order folia signatures, e.g., the middle shell layer of the pectinid *Amusium pleuronectes* (LINNAEUS, 1758) (Fig. 98).

Herringbone crossed foliated (herringbone CF). A calcitic crossed microstructure comprised of two or more regularly foliated sublayers, at least one with radially inclined third-order folia and at least one with radially reclined third-order folia, e.g., in the middle shell layer of the Liassic, Early Jurassic pectinid *Pseudopecten equivalvis* (J. SOWERBY 1816, in J. SOWERBY & J. DE C. SOWERBY,

FIG. 94. Low-angle crossed foliated microstructure in calcitic middle shell layer in left valve of propeamussiid *Propeamussium dalli* (E. A. SMITH, 1885), west of Martinique, Windward Islands, YPM 8387, SEM of horizontal fracture, with ventral shell margin down, scale bar, 1 µm (Carter, new).

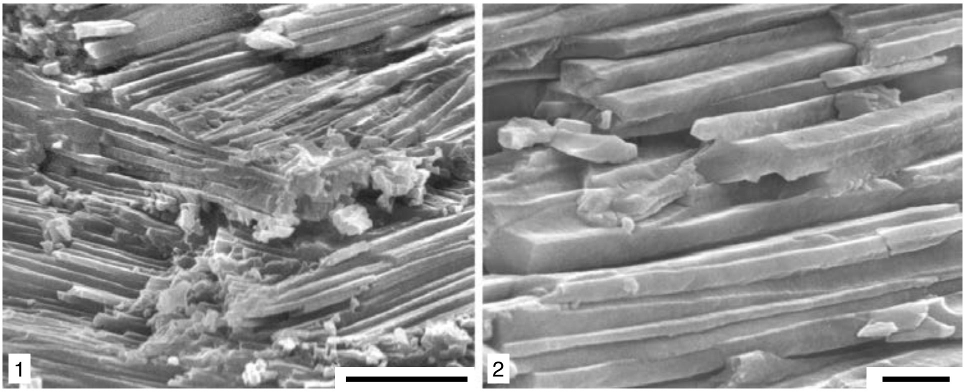

FIG. 95. Rod-type crossed foliated microstructure in calcitic middle shell layer in right valve of pectinid *Leopecten diegensis* (DALL, 1898), California, USA, YPM 7856. *1,* SEM of commarginal, nearly vertical fracture, showing two interdigitating first-order folia; *2,* higher magnification of same fracture, showing the rod-type fibrous prismatic third-order folia; scale bar, 5 µm in *1,* 1 µm in *2* (adapted from Carter, 1990a, fig. 48c).

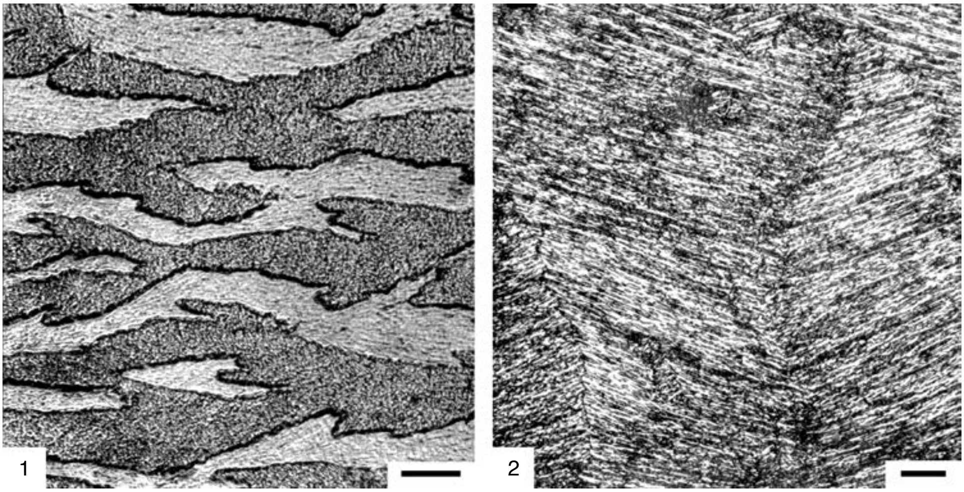

Fig. 96. High-angle, branching crossed foliated microstructure in calcitic middle shell layer of Oxfordian, Late Jurassic oxytomid *Oxytoma (Oxytoma) inequivalvi*s (J. Sowerby, 1819), Bucks, England, UK, UNC 4527, acetate peels. *1,* Horizontal section, with shell margin up; *2,* commarginal, vertical section, with shell interior up; scale bars, 50 µm (Carter & others, 2012, fig. 78).

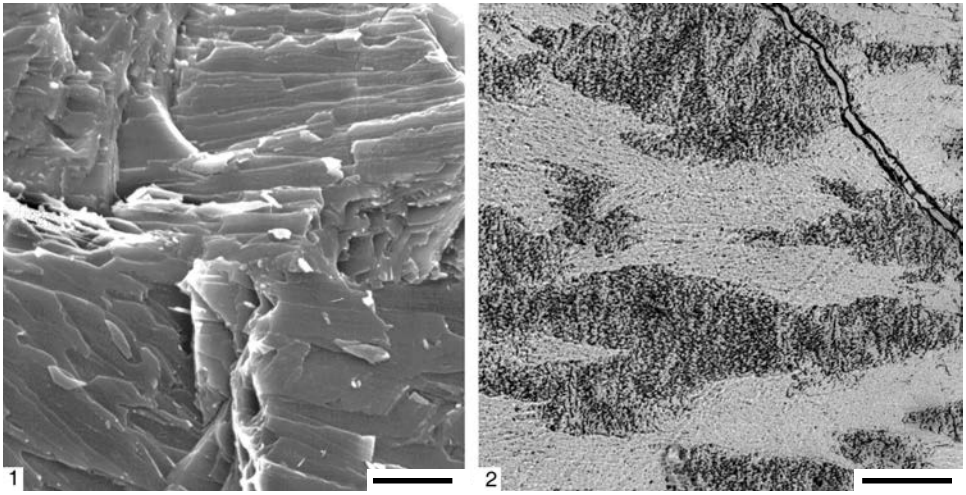

Fig. 97. High angle, branching crossed foliated microstructure in calcitic middle shell layer of Jurassic gryphaeid *Gryphaea* (*Bilobissa*) *bilobata* J. de C. Sowerby, 1840, England, UK, UNC 5525. *1,* Horizontal fracture, with shell margin down; *2,* horizontal acetate peel, with shell margin down; scale bar, 10 µm in *1,* 100 µm in *2* (Carter & others, 2012, fig. 38).

1812–1846) (Fig. 99). Bøggild (1930, p. 266–267) called this microstructure zigzag-lamellar and zigzag structure and illustrated double and triple zigzag varieties.

Complex crossed lamellar (CCL). An aragonitic crossed microstructure comprised of aggregates (first-order lamellae) of more or less mutually parallel, elongate basic structural units dipping in predominantly three or more directions relative to the shell margin. The elongate basic structural units are usually arranged into mutually parallel laminae (second-order lamellae), in which case they are called third-order lamellae. The

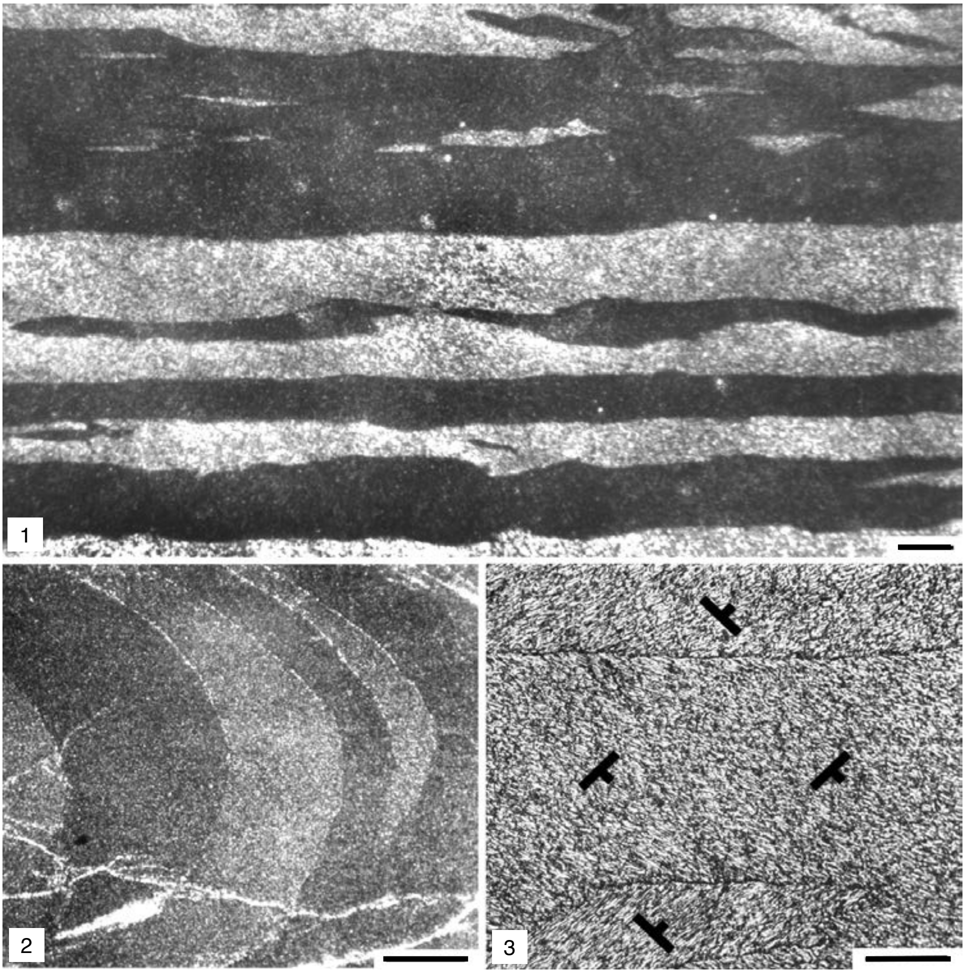

FIG. 98. High angle, linear crossed foliated microstructure in calcitic middle shell layer of pectinid *Amusium pleuronectes* (LINNAEUS, 1758), Indo-West Pacific Ocean, YPM 8492. *1*, Unidirectional reflected light microscopy of depositional surface, with ventral shell margin down, showing linear crossed foliated signature; *2*, radial acetate peel, with shell exterior up and ventral shell margin toward right; *3*, horizontal acetate peel with symbols indicating dip directions of third-order folia; scale bars, 100 µm in *1–2*, 50 µm in *3* (Carter, new).

third-order lamellae may be lath-type, rod-type, or irregular fibrous prisms. In **rod-type CCL**, the elongate basic structural units do not comprise second-order lamellae, e.g., the inner shell layer of the poromyid *Poromya* (*Poromya*) sp. (Fig. 100). Varieties include irregular, cone, fine, helical, crossed-matted/lineated, and pseudo-irregular CCL.

1) Irregular complex crossed lamellar (ICCL). A complex crossed lamellar microstructure with irregularly shaped, laterally interdigitating first-order lamellae (CARTER & others, 1990, p. 613). Commonly present in the inner shell layer of many Heteroconchia, rarely present in Anomalodesmata, e.g., the rod-type, irregular CCL inner shell layer of the poromyid *Poromya* (*Poromya*) sp. (Fig. 100).

2) Cone complex crossed lamellar (cone CCL). A complex crossed lamellar microstructure comprised of cone-in-cone or spiral-conical first-order lamellae (CARTER

& Tevesz, 1978a; Carter, 1980a; Carter & others, 1990, p. 613, 634). **Cone-in-cone CCL** is present in the inner shell layer of the trapeziid *Neotrapezium sublaevigatum* (Lamarck, 1819) (Fig. 101) and in the middle shell layer of the mactrid *Lutraria rhynchaena* Jonas, 1844 (Fig. 102). **Spiral-conical CCL** is present in the outer shell layer of the cyrenid *Corbicula* cf. *C. fluminea* (O. F. Müller, 1774) (Fig. 103).

3) Fine complex crossed lamellar (fine CCL). A complex crossed lamellar microstructure comprised of mutually isolated, elongate basic structural units not arranged into first-order or second-order lamellae. The elongate structural units may be poorly defined (**diffuse fine CCL**), as locally developed in the inner shell of the solemyid *Solemya* (*Zesolemya*) *parkinsoni* E. A. Smith, 1874 (Fig. 104), or well defined (**distinct fine CCL**), as in the inner shell layer of the venerid *Tivela* (*Tivela*) *byronensis* (Gray, 1838) (Fig. 105). As seen in vertical sections, diffuse fine CCL is easily mistaken for finely homogeneous, but SEM shows that the basic structural units are differently shaped and oriented.

Fig. 99. Herringbone crossed foliated microstructure in calcitic, middle shell layer of Liassic, Early Jurassic pectinid *Pseudopecten equivalvis* (J. Sowerby, 1816, in J. Sowerby and J. de C. Sowerby, 1812–1846); radial, vertical thin section with shell exterior up and shell margin toward right, width of image is ~1.0 mm wide (Bøggild, 1930, pl. 1,*6*).

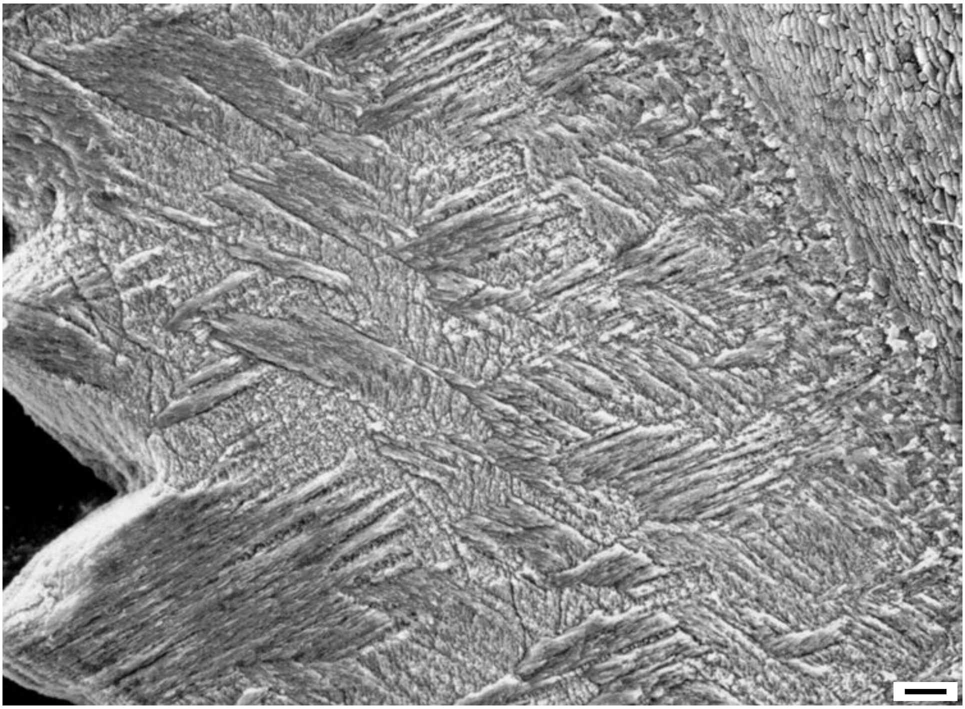

Fig. 100. Rod-type, irregular complex crossed lamellar inner shell layer (left) and nacreous middle shell layer (upper right) in poromyid *Poromya* (*Poromya*) sp., eastern Atlantic Ocean, deep sea, YPM 9636; SEM of acid-etched, nearly horizontal, slightly oblique section; scale bar, 10 µm (adapted from Carter & Lutz, 1990, pl. 10,A)

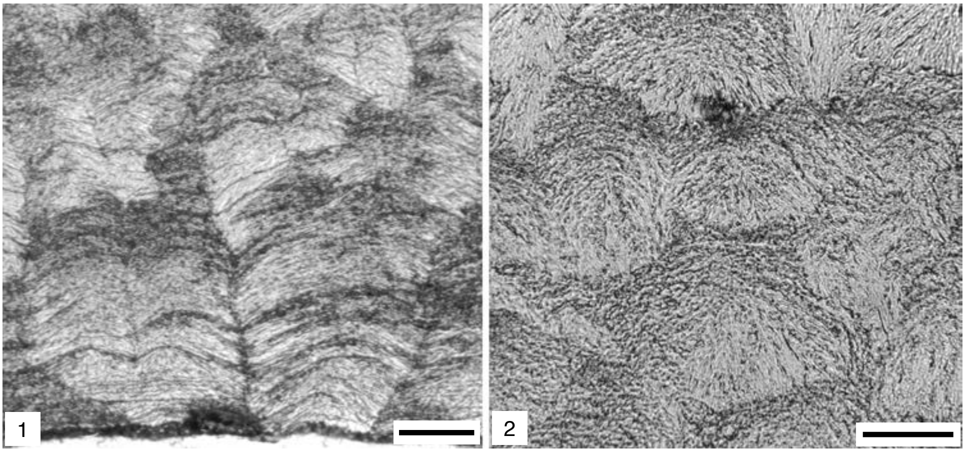

FIG. 101. Cone-in-cone complex crossed lamellar microstructure in aragonitic inner shell layer of trapeziid *Neotrapezium sublaevigatum* (LAMARCK, 1819), Bahia, the Philippines, YPM 9717; acetate peels. *1*, Radial, vertical section, with shell exterior up; *2*, nearly horizontal, slightly oblique section; scale bars, 50 µm (Carter, new).

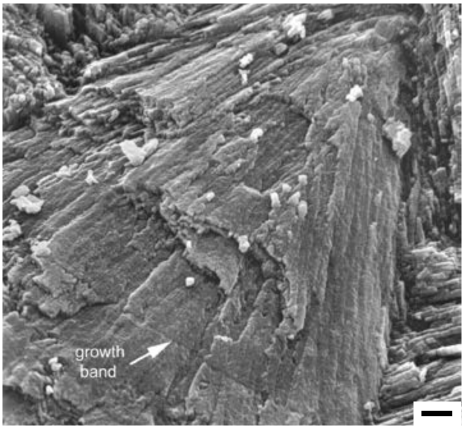

FIG. 102. Cone-in-cone complex crossed lamellar microstructure in aragonitic middle shell layer of mactrid *Lutraria rhynchaena* JONAS, 1844, Calapan, Mindoro, the Philippines, YPM 9742, SEM of vertical fracture, scale bar, 1 µm (Carter & others, 2012, fig. 73).

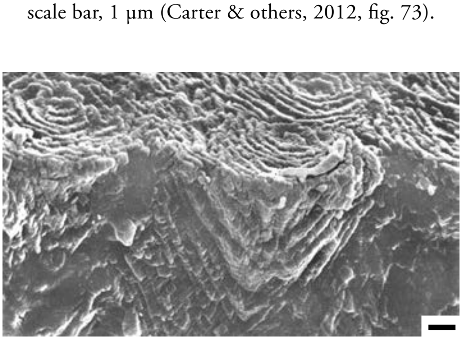

FIG. 103. *For explanation, see adjacent column.*

4) **Helical complex crossed lamellar** (helical CCL). A complex crossed lamellar microstructure comprised of vertically concatenated, spiral, elongate basic structural units. Rarely present in the Bivalvia, e.g., in the inner shell layer of the sphaeriid *Pisidium dubium* (SAY, 1817) (Fig. 106). This microstructure is well developed in many pteropod gastropods (BÉ, MACCLINTOCK, & CURRIE, 1972). In both the Gastropoda and Bivalvia, helical complex crossed lamellar generally associates with extremely thin shells.

5) **Crossed-matted/lineated complex crossed lamellar** (crossed-matted/lineated CCL). A complex crossed lamellar microstructure comprised of laterally intergrading, low-angle, rod-type irregular CCL (the crossed-matted parts) and nearly horizontal fibrous prisms (the lineated parts), e.g., the inner shell layer of the arcid *Anadara notabilis* (RÖDING, 1798) (CARTER, 1980a; CARTER & others, 1990, p. 636) (Fig. 107).

6) **Pseudo-irregular complex crossed lamellar** (pseudo-irregular CCL). A complex

FIG. 103. Spiral-conical complex crossed lamellar microstructure in aragonitic outer shell layer of cyrenid *Corbicula* cf. *C. fluminea* (O. F. MÜLLER, 1774), SEM of vertical fracture through outer part of outer shell layer, also showing depositional surface (upper part of figure), scale bar, 1 µm (adapted from Prezant & Tan-Tiu, 1986a, fig. 5).

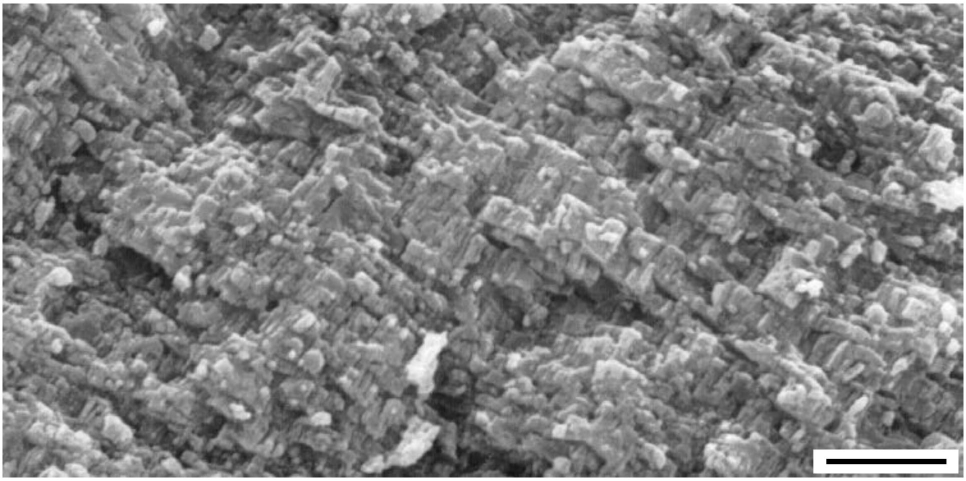

FIG. 104. Diffuse fine complex crossed lamellar microstructure locally developed in aragonitic inner shell layer of solemyid *Solemya* (*Zesolemya*) *parkinsoni* E. A. SMITH, 1874, Awarua Bay, New Zealand, YPM 5364, SEM of vertical fracture through ligament nymph, with shell exterior up, scale bar, 2 µm (Carter, new).

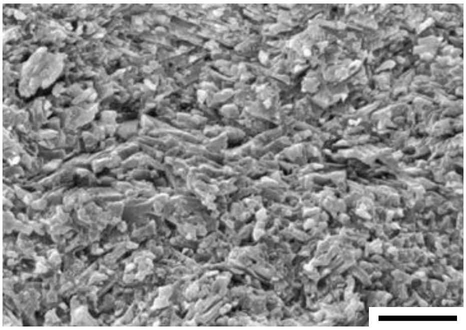

FIG. 105. Distinct fine complex crossed lamellar microstructure in aragonitic inner shell layer of venerid *Tivela* (*Tivela*) *byronensis* (GRAY, 1838), Guaymas, Gulf of California, Mexico, YPM 9737, SEM of vertical fracture, with shell exterior up, scale bar, 10 µm (Carter & others, 2012, fig. 115).

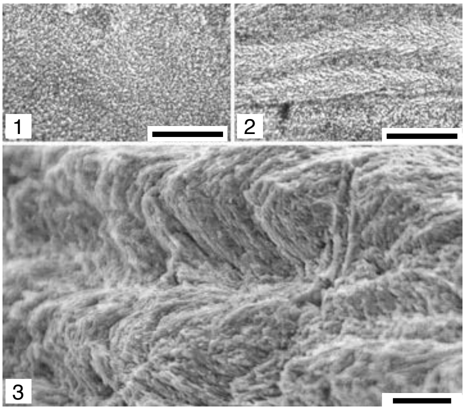

FIG. 106. Helical complex crossed lamellar microstructure in aragonitic inner shell layer of sphaeriid *Pisidium dubium* (SAY, 1817), Burton's Landing, Au Sable River, Crawford County, Michigan, USA, UNC 15044. *1–2,* Horizontal and vertical acetate peels, respectively; *3,* SEM of vertical fracture, with shell exterior up; scale bars, 50 µm in *1–2;* 10 µm in *3* (Carter & others, 2012, fig. 131).

crossed lamellar microstructure organizationally similar to irregular complex crossed lamellar, but comprised of irregularly oriented fragments of an adjacent composite prismatic microstructure, e.g., parts of the otherwise composite prismatic outer shell layer in the hiatellid *Panopea generosa* GOULD, 1850 (Fig. 108) and in the gastrochaenid *Spengleria mytiloides* (LAMARCK, 1818) (CHECA & HARPER, 2012, p. 198, fig. 3*d–f*), as "non-composite prismatic units"). Irregular CCL has a pseudopleochroic, yellowish-brown color in thin sections and in acetate peels, whereas pseudo-irregular CCL has a non-pseudopleochroic, gray appearance, like the adjacent prismatic microstructure.

Complex crossed foliated (CCF). A calcitic crossed microstructure comprised of

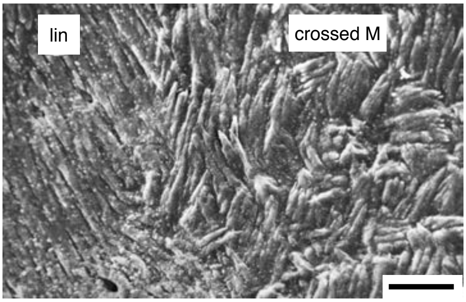

FIG. 107. Crossed-matted/lineated complex crossed lamellar microstructure in aragonitic inner shell layer of arcid *Anadara notabilis* (RÖDING, 1798), SEM of depositional surface; *lin,* lineated portion, *crossed M,* crossed-matted portion, scale bar, 10 µm (adapted from Wise, 1971, pl. 6,*6*).

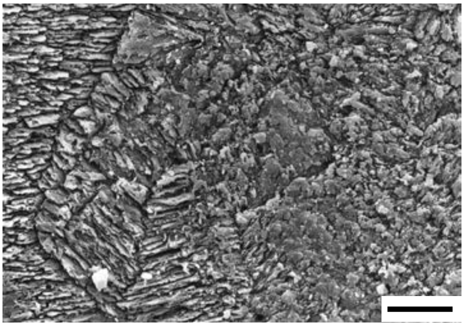

FIG. 108. Pseudo-irregular complex crossed lamellar microstructure locally present in otherwise high-angle, nondenticular composite prismatic outer shell layer of hiatellid *Panopea generosa* GOULD, 1850, Puget Sound, Washington, USA, YPM 9746, SEM of acid-etched, radial, vertical section, with shell exterior up, scale bar, 25 µm (Carter, new).

aggregates (first-order folia) of more or less mutually parallel, elongate basic structural units dipping in predominantly three or more directions relative to the shell margin (MACCLINTOCK, 1967; CARTER & others, 1990, p. 633). The elongate basic structural units are usually arranged into mutually parallel laminae (second-order folia) within each first-order folium, in which case they are called third-order folia. The structural units may be lath-type, rod-type, or interlocking fibrous prisms. When the elongate structural units are not arranged into second-order folia, the structure is called **rod-type CCF**, e.g., the inner sublayer of the foliated middle shell layer in the pectinid *Leopecten diegensis* (DALL, 1898) (Fig. 109). **High-angle complex crossed foliated** has a maximum dip angle greater than 15° relative to the depositional surface (Fig. 109). **Low-angle complex crossed foliated** has a maximum dip angle less than 15° relative to the depositional surface, e.g., parts of the inner shell layer of the Early Jurassic gryphaeid *Gryphaea (Gryphaea) arcuata* (LAMARCK, 1801) (Fig. 110, upper part of figure) and parts of the inner shell layer in the left valve of the anomiid *Enigmonia aenigmatica* (HOLTEN, 1802) (Fig. 111). Complex crossed foliated microstructure can have irregulary shaped or conical first-order folia, i.e., irregular *versus* conical complex crossed folia, respectively.

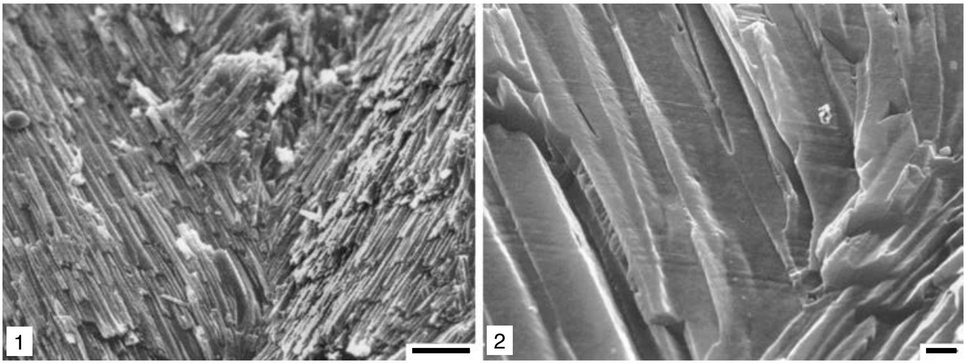

FIG. 109. High-angle, rod-type irregular complex crossed foliated microstructure in inner sublayer of calcitic middle shell layer of pectinid *Leopecten diegensis* (DALL, 1898), California, USA, YPM 7856. SEM of commarginal, vertical fracture, with shell exterior up, seen at lower (*1*) and higher (*2*) magnifications; scale bars, 10 µm in *1*, 1 µm in *2* (Carter, new).

1) Irregular complex crossed foliated (ICCF). A complex crossed foliated microstructure with laterally interdigitating, irregularly shaped first-order folia, e.g., parts of the inner shell layer of the Early Jurassic oxytomid *Oxytoma* (*Oxytoma*) *inequivalvis* (J. SOWERBY, 1819) (Fig. 112).

2) Cone complex crossed foliated (cone CCF). A complex crossed foliated microstructure with laterally interdigitating, conical first-order folia, e.g., parts of the inner shell layer of the Early Jurassic gryphaeid *Gryphaea* (*Gryphaea*) *arcuata* (LAMARCK, 1801) (Fig. 113).

3) Pseudo-irregular complex crossed foliated (pseudo-irregular CCF). A calcitic crossed microstructure comprised of elongate structural units arranged as in irregular CCF, but only as a local variation within an otherwise fibrous prismatic shell layer, e.g., parts of the outer shell layer of the mytilid *Mytilus californianus* CONRAD, 1837 (Fig. 114) and the limid *Acesta rathbuni* (BARTSCH, 1913).

VIII. CHALKY

A porous, calcitic microstructure comprised of minute, more or less mutually isolated plates, granules, fibrous prisms, and/or spherulitic prisms, developed as a local variation within another calcitic microstructure, e.g., in the

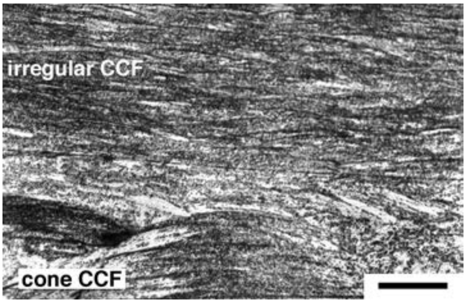

FIG. 110. Low-angle, irregular complex crossed foliated (above) and cone complex crossed foliated (below) microstructure in calcitic inner shell layer of Early Jurassic gryphaeid *Gryphaea (Gryphaea) arcuata* (LAMARCK, 1801), England, UK, UNC 5526, vertical acetate peel, with shell exterior up, scale bar, 100 µm (Carter & others, 2012, fig. 149).

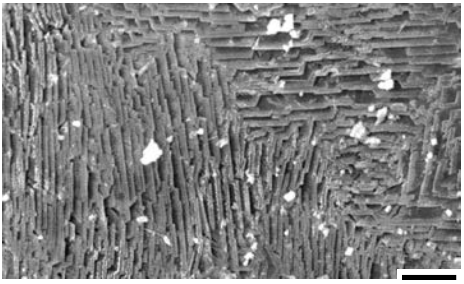

FIG. 111. Depositional surface of low-angle, irregular complex crossed foliated microstructure in calcitic inner shell layer in left valve of anomiid *Enigmonia aenigmatica* (HOLTEN, 1802) as seen in SEM, the Philippines, YPM 10160, scale bar, 10 µm (Carter, new).

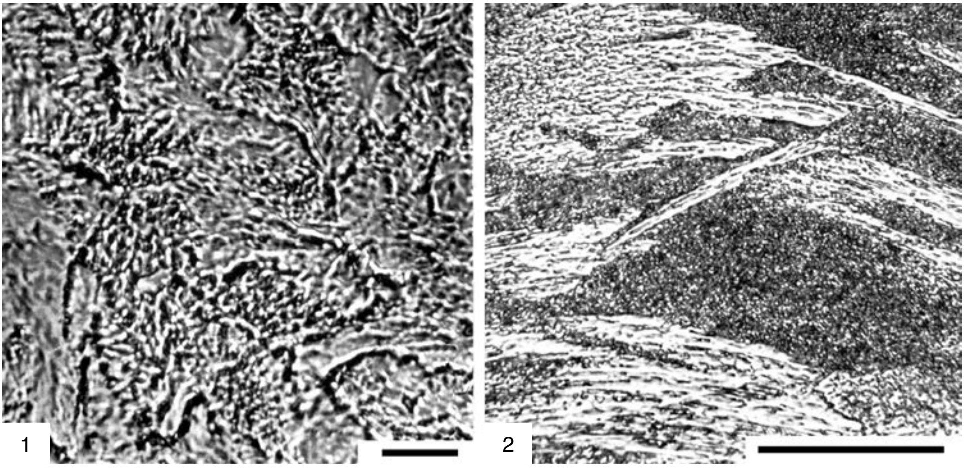

FIG. 112. Irregular complex crossed foliated microstructure in calcitic inner shell layer of Liassic, Early Jurassic oxytomid *Oxytoma (Oxytoma) inequivalvis* (J. SOWERBY, 1819), acetate peels. *1,* Horizontal section; *2,* radial section, with shell exterior up; scale bars, 50 µm (adapted from Carter & Lutz, 1990, pl. 8B).

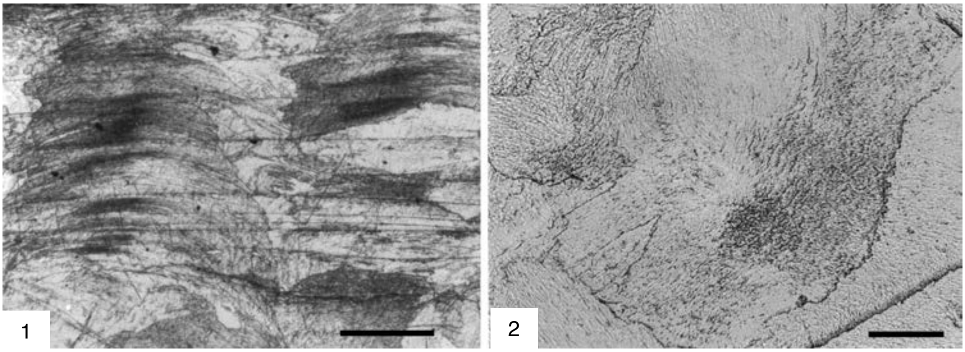

FIG. 113. Cone complex crossed foliated microstructure in calcitic inner shell layer of Early Jurassic gryphaeid *Gryphaea* (*Gryphaea*) *arcuata* (LAMARCK, 1801), England, UK, UNC 5526, acetate peels. *1,* Radial, vertical section with shell exterior up; *2,* horizontal section; scale bars, 0.5 mm in *1,* 100 µm in *2* (Carter & others, 2012, fig. 72).

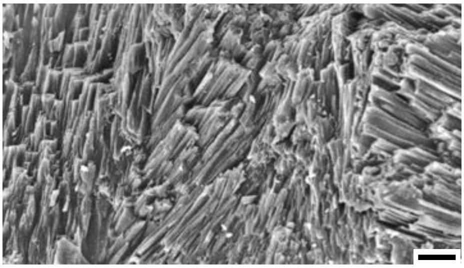

FIG. 114. Pseudo-irregular complex crossed foliated microstructure locally developed in calcitic outer shell layer of mytilid *Mytilus californianus* CONRAD, 1837, California, USA, YPM 9526, SEM of radial, vertical fracture, with shell exterior up, scale bar, 10 µm (Carter, new).

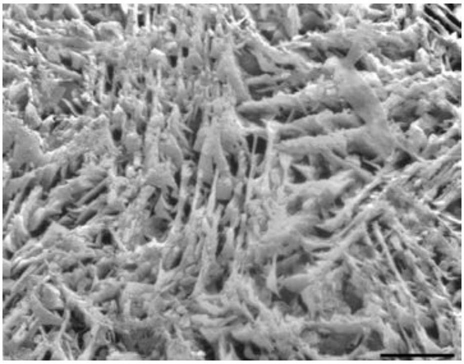

FIG. 115. Chalky microstructure locally developed in foliated, calcitic inner shell layer of ostreid *Crassostrea virginica* (GMELIN, 1791), Ocean Isle, North Carolina, USA, UNC 12823, SEM of depositional surface of right valve, scale bar, 5 µm (Carter, new).

otherwise foliated inner shell layer of the ostreid *Crassostre virginica* (GMELIN, 1791) (Fig. 115) and in the otherwise largely crossed-bladed to irregular complex crossed foliated middle shell layer of the middle Eocene eligmid *Nayadina* (*Exputens*) sp. (Fig. 72.3). MALCHUS (1990) called this microstructure mocret.

IX. VESICULAR

A strongly vacuolated microstructure comprised of thin, more or less vertical partitions (STENZEL, 1971, p. 987). Present as a sublayer in the calcitic middle and/or inner shell layers in some Gryphaeidae, e.g., *Hyotissa hyotis* (LINNAEUS, 1758), where the partitions vary from irregular fibrous prismatic to finely homogeneous calcite (Fig. 116). Also present in the calcitic outer shell layer of some rudists, where this has been called cellulo-prismatic (CAYEUX, 1916, p. 474).

APPENDIX A

PREPARATION OF ACETATE PEELS AND THIN SECTIONS

Acetate peels and thin sections are relatively inexpensive sources of shell microstructure information that require little instrumentation other than a metallurgical saw. Acetate peels provide greater clarity than thin sections, but thin sections are necessary

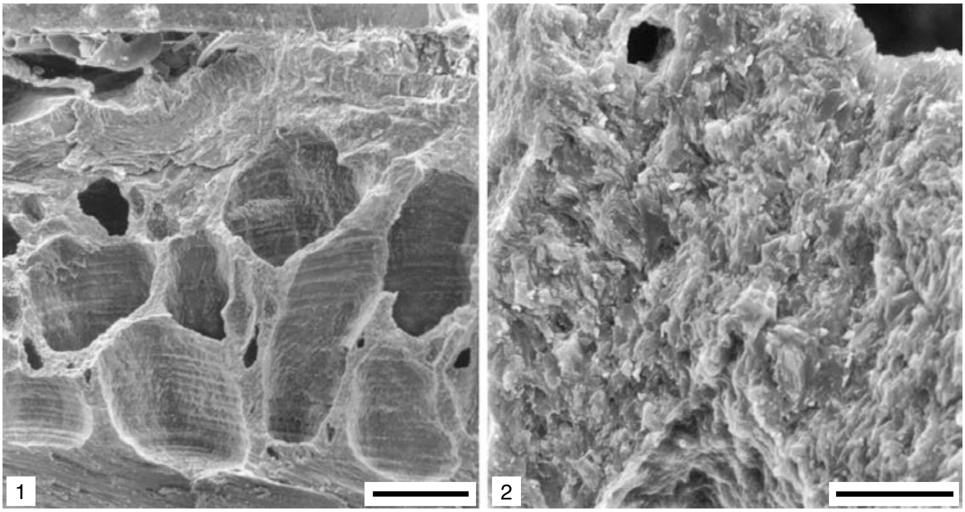

FIG. 116. Calcitic vesicular structure in left valve of gryphaeid *Hyotissa hyotis* (LINNAEUS, 1758), Key Largo, Florida, USA, YPM 7038. *1,* SEM of radial, vertical fracture through vesicular sublayer, with shell exterior up; *2,* irregular fibrous prismatic to finely homogeneous microstructure comprising a vesicle wall; scale bar, 100 µm in *1;* 5 µm in *2* (Carter, new).

for some optical crystallographic, crystal orientation, and mineralogical studies.

Acetate peels are best made from acetate slides about 1.2 mm thick. Acetate with this thickness can be purchased from some plastics companies in sheets about 50 x 100 cm. After cutting to a size compatible with your microscope, store the acetate blanks in vertical stacks under a flat, substantial weight to eliminate any initial curvature and to keep them flat. Larger shells should be cut into pieces that include all major shell layers plus the ligament, with each piece ideally fitting into a plastic peel-away boat (the kind used for making histological sections) not greater than 30 mm in maximum dimension. Larger plastic boats can complicate sectioning, smoothing, and polishing, and larger acetate peels are more likely to incorporate bubbles. Prepare the boat by pouring an epoxy floor about 4 mm thick. Fill the boat with sufficient epoxy to cover the uppermost part of the specimen with at least 4 mm of epoxy, then submerge the shell, leaving at least 4 mm clearance on all sides. This clearance will make it less likely for bubbles to form in the peel. Evacuate the specimen for 2–3 minutes, then slowly release the vacuum to force epoxy into small crevices and pores on the shell. Dislodge bubbles from the surface of the specimen, then orient it in the boat for sectioning. After the epoxy has cured, remove the boat and use a coarse file to round any sharp edges on the epoxy block. This rounding will facilitate sectioning and polishing.

Section the epoxy block with a low-speed, metallurgical saw with a gravity-fed, diamond-impregnated, wafering blade about 0.3 mm thick and 10.2 cm wide. Smooth the sections with a series of 240, 320, 400, 600 grit, water-lubricated, adhesive-backed grinding strips, polish them with 0.05 µm alumina, then etch them in 0.12 N HCl for 5–15 seconds, shorter for aragonite, longer for calcite. The shell is sufficiently etched when it first loses its polish. Longer etching can create a build-up of shell organic matrix that might interfere with the peel or create a wide gap between the polished surface of the epoxy block and the shell. Rinse the specimen in tap water and blow it dry.

Orient the specimen with its etched surface up and slightly tilted, apply a full layer of acetone using an eyedropper, and lower the acetate slide, meniscus side first, onto its surface. Do not press or apply weight to the acetate slide; doing so might cause bubbles to form in the peel. After a few seconds, the acetate will adhere firmly to the epoxy block. After several hours drying, pull the slide from the epoxy block. The slide will remain flat for several weeks. For longterm storage, keep the slide under a flat weight to prevent warping. The peeled surface can be used for SEM, thereby allowing direct comparison of light microscopic and SEM images. If a thin section is needed, save one of the polished sections for this purpose, or regrind and repolish one of the peeled sections.

To make a thin section, epoxy the polished surface of a sectioned block to a petrologic glass slide (typically 26 x 46 mm) that has been smoothed and frosted using 240 grit abrasive. Using the metallurgical saw with a chuck designed to hold a glass slide, cut away all but about 100–200 µm thickness of specimen. Using 240 grit abrasive, reduce the thickness of the specimen to 30 µm. Wash the slide in tap water, dry it, and apply a glass cover slip with a drop of glycerin. It is then ready for examination using a petrologic microscope with the capability of crossed-polarized light. If the slide is to be used for scanning electron microprobe, electron backscatter diffraction, or Raman spectroscopic analysis, remove the glass coverslip and polish its surface.

ABBREVIATIONS FOR MUSEUM REPOSITORIES

UNC: University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA. [All UNC specimens have been transferred to YPM]

USNM: United States National Museum, Washington D.C., USA

YPM: Yale University Peabody Museum, New Haven, Connecticut, USA

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