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Origin and Expansion of Foliated Microstructure in Pteriomorph Bivalves

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Abstract. The ultrastructure of the calcitic prisms of the prismatic shell layers of pteriomorph bivalves was examined by scanning electronic microscopy and diffraction techniques. Results indicate that the internal structure of the prisms is noticeably different among taxa. In species belonging to the families Pinnidae, Pteriidae, and Isognomonidae (Pterioida), prisms are built up with nanometric calcite crystals. On the other hand, Pectinidae, Propeamusliidae, Anomiidae (order Pectinoidea) and the Ostreidae (Ostreoida) have prisms constituted by calcitic laths with micrometric size. These laths are indistinguishable from those constituting the foliated microstructure. In almost all cases, there is mineral continuity from the prisms to the underlying foliated layer, as confirmed by X-ray texture analyses. These findings corroborate a previous assumption that the foliated microstructure derived from calcitic prisms, particularly from those with internal foliated structure. The appearance of the foliated microstructure facilitated drastic mineralogical and microstructural changes in pteriomorph shells—for example, the development of rigid shell margins and the production of largely calcitic shells. Such changes have, no doubt, contributed to the evolutionary success of the groups, which have shown a pronounced diversification over time.

Introduction

Early bivalves built wholly aragonitic shells consisting of an external prismatic layer and middle and inner nacreous layers (Taylor, 1973). This primitive prismato-nacreous

shell is retained by some extant groups such as nuculoideans, trigonioids, unionoids, and most anomalodesmatan families (Taylor, 1973; Carter, 1990; Cope, 1997), whose origins extend far back into the Paleozoic. However, the majority of bivalves have developed new ways to organize their shells. Many bivalves evolved new aragonitic microstructures (crossed-lamellar, complex crossed-lamellar, and homogeneous); and a smaller number of taxa acquired the ability to secrete calcite in their shells as prismatic and foliated microstructures (Bøggild, 1930; Kennedy *et al.*, 1969; Taylor *et al.*, 1973; Carter, 1980, 1990). The distribution of calcitic shell layers within the Bivalvia is interesting. Calcitic microstructures have formed continuous layers only in epifaunal taxa (Carter, 1980), and within these, in only four higher taxa, namely the Eupteriomorphs (*sensu* Boss, 1982), the Hippuritoidea (the extinct rudists), and some mytiloids and chamoids (Carter, 1980; Harper, 1998). Within infaunal taxa, calcite is restricted to patches within otherwise aragonitic shells (Carter, 1980; Carter *et al.*, 1998).

With the exception of the Arcoida, the extant Pteriomorphia all develop external calcitic layers. Within this subclass, the Mytiloidea occasionally secrete calcitic fibrous prisms in the outer shell layer, whereas the Eupteriomorphia (*sensu* Boss, 1982) invariably develop calcitic prisms or folia. Other calcitic microstructures, such as chalk or vacuolar microstructures in ostreoids or fibrous prisms in pectinoids and limoids, do not consist of continuous shell layers.

We therefore consider two key events in the evolution of calcitic layers within the Eupteriomorphia: (1) the development of an external layer of prismatic calcite, and (2) the development and extension of foliated layers.

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The most primitive eupteriomorph calcite microstructure is the prismatic, first appearing in the Middle Ordovician Ambonychiidae and Pterineidae (Carter, 1990; Cope, 1996). These prismatic layers are always found on the external surface of the shell, with individual prisms arranged nearly perpendicular to the shell surface and surrounded by organic envelopes (also called organic walls). The prismatic layers thus have a relatively high organic content. Indeed, values reported by Taylor and Layman (1972) and Checa *et al.* (2005) are higher (4%–6% in weight) than for any other molluscan shell microstructure (except for a value of 7% recently recorded for the homogenous layer of the anomalous *Entodesma* [Harper, Checa, and Rodríguez-Navarro, unpubl. data]). The distribution of organic walls provides the prismatic microstructure with a high degree of flexibility.

In Recent eupteriomorphs, foliated shell microstructure often forms a high proportion of the valves. This microstructure comprises parallel and overlapping calcitic flat laths that have typical arrow-pointed endings and are inclined at a small angle (2° – 3°) to the shell surface. The arrangement of the laths can be very variable, and several subtypes of foliated microstructure have been described on the basis of this arrangement (see Taylor *et al.*, 1969; Kennedy *et al.*, 1969; and Carter, 1980, for morphological descriptions; and Checa *et al.*, 2007, for the crystallographic structure of the foliated microstructure). By contrast to prismatic calcite, the foliated microstructure contains very little organic matrix, with measured values ranging from 0.4% to 1.5% weight (Taylor and Layman, 1972; Checa *et al.*, 2005). Foliated layers have been shown to be low density and weak in most mechanical tests, compared to other molluscan microstructures (Taylor and Layman, 1972).

Despite the obvious significance of foliated shell layers to the debate on the development of calcitic shells, there has been little research in this area. We are aware of only two hypotheses to explain the appearance of foliated calcite. The first one, attributable to Taylor (1973, p. 526), suggests that foliated layers are the result of a direct mineralogical transformation from nacre. However, although both structures have a laminar disposition of crystallites, there are no mineralogical, structural, or crystallographic features in common. The second hypothesis is that of Waller (1976) and implies that the foliated microstructure is derived from the calcitic prismatic layer. He based his hypothesis on the facts that (1) both layers share the same mineralogy, and (2) the foliated layer always developed below a prismatic layer (although in many groups the primitive prismatic layer has been secondarily lost). Later, Carter (1990) followed Waller's hypothesis but pointed out that the foliated microstructure could have developed either directly or indirectly through intermediate fibrous prismatic, spherulitic prismatic, or homogeneous grades depending on the groups

(Carter, 1990, p. 256). There is a third possibility—that the foliated layer was initiated *de novo*, thus being unrelated to any other pre-existent shell layer.

Our study examines the relationship between the two main calcitic microstructures of eupteriomorph bivalves (prismatic and foliated) on the basis of their ultrastructural arrangement. In examining the ultrastructure of prisms, we have placed special emphasis on the transition between layers in representative groups of pteriomorph bivalves, as revealed by scanning electron microscopy and diffraction techniques.

Materials and Methods

The eupteriomorph species studied are listed in Table 1. Shell fragments of about 1 cm² from the ventral area of the shell were prepared for scanning electron microscopy (SEM) and mounted on 12.5-mm aluminum stubs oriented so as to allow the study of either both shell surfaces or the fractured edge. Samples were bleached with NaClO (3.5% for 1–10 min) or treated with proteinase K buffer according to the protocol described by Shiao *et al.* (1999) (1 mg/ml, 5–30 min) to remove the organic matter—that is, the organic walls of the prisms. Other samples were slightly etched with HCl (0.5%–1% for 5 s–1 min). Samples were either sputtered with carbon on a Hitachi UHS evaporator for field-emission scanning electron microscopy (FESEM; LEO Gemini-1530) or covered with gold on a Polaron E 5000 for conventional SEM (LEO Gemini 1430VP and FEI Quanta 400).

The three-dimensional orientation of the crystallites (texture) of the prismatic lamella and the underlying layers, either foliated or nacreous, was measured with a Bruker Smart Apex X-ray diffractometer with area detector working in reflection mode with the following parameters: 50 kV, 30 mA, $2\theta = 20^{\circ}$, $\omega = 10^{\circ}$, Mo-K $_{\alpha}$ radiation. Samples were oriented with the growth direction in $\varphi = 0^{\circ}$ and rotated 180° around φ in 3° steps. The resulting collection of frames is a record of the positions of the main reflections of the calcite (Debye rings) for any of the φ -angles considered. The frames were analyzed with specially designed software (XRD2DScan, vers. 2.0, Navarro, 2006.) to determine the position of the main reflections of calcite and aragonite and to represent them as counter plots. Analyses were made on both sides of the prismatic lamella immediately before the transition, and in the underlying layer, either nacreous or foliated, 1 mm after the transition. Texture analyses are represented as 006- and 104-pole figures for calcite reflections in prismatic and foliated layers, and as 002- and 112-pole figures for aragonite in nacre. Since samples were all set with the surface normal to the φ axis of the diffractometer, the center of the pole figures is normal to the growth surface of the shell layers.

Table 1

List of species studied in this work

Taxon	Locality
Superfamily Pterioidea, Family Pteriidae	
<i>Pteria hirundo</i> (Linnaeus, 1758)	Fuengirola (Málaga), SE Spain
<i>Pinctada martensii</i> (Dunker, 1872)	Uwajima city, Ehime prefecture (Japan)
Superfamily Pterioidea, Family Malleidae	
<i>Malleus Malleus</i> (Linnaeus, 1758)	Locality unknown
<i>Malleus regulus</i> (Forskål, 1775)	Turkey, locality unknown
Family Isognomonidae	
<i>Isognomon legumen</i> (Gmelin, 1791)	Cape d'Aguilar, Hong Kong
Superfamily Pinnoidea, Family Pinnidae	
<i>Pinna nobilis</i> (Linnaeus, 1758)	Agua Amarga (Almería), SE Spain
<i>Atrina pectinata</i> (Linnaeus, 1758)	Fuengirola (Málaga), SE Spain
<i>Atrina serrata</i> (Sowerby, 1825)	Sarasota, Florida
Superfamily Ostreoidae, Family Ostreidae	
<i>Ostrea edulis</i> Linnaeus, 1758	Mariculture Center PEMARES (Huelva), SE Spain
<i>Ostrea puelchana</i> d'Orbigny, 1842	Southern Atlantic, locality unknown
<i>Crassostrea gigas</i> (Thunberg, 1793)	Lochgilphead, E Scotland
Superfamily Pectinoidea, Family Pectinidae	
<i>Adamussium colbecki</i> (Smith, 1902)	Signy Island, Antarctic Peninsula
Superfamily Pectinoidea, Family Propeamussiidae	
<i>Propeamussium dalli</i> (Smith, 1885)	Maldives Islands
<i>Propeamussium jeffreysii</i> (Smith, 1885)	Josephine Bank, NE Atlantic
<i>Propeamussium sibogai</i> (Dautzenberg & Bavay, 1904)	Philippines, locality unknown
Superfamily Anomioidea, Family Anomiidae	
<i>Anomia ephippium</i> Linnaeus, 1758	Fuengirola (Málaga), SE Spain
<i>Anomia chinensis</i> Philippi, 1849	Cape d'Aguilar, Hong Kong

Results

Prism ultrastructure

In our observations, the ultrastructure of prisms was constant within families but varied among higher taxa. In pinnoids and most of the investigated pterioids (those belonging to the Pteriidae), neither intact nor treated prisms revealed any internal organization or structure (Fig. 1A, B). In such prisms we found only growth lines (Fig. 1B) and, in

some cases, zigzag traces produced by microboring organisms, whereas the growing surface of the prisms is smooth (Fig. 1C). In slightly acid-etched prisms of *Isognomon legumen* (Isognomonidae) there are narrow fissures forming a reticulate engraved over the growing surface of the prisms (Fig. 1D). Such a pattern is identical to the “organic sinuses” described in *Pinctada* by Dauphin (2003), who interpreted them as intraprismatic organic sheets that delineate crystal domains within the prisms.

High magnifications revealed that the growing surface of the prisms is composed of small crystalline units with nanometric size (Fig. 1E). Such nanocrystals have a rhombohedral habit and are disposed with their crystallographic axes and faces oriented in the same direction (*i.e.*, commonly oriented), forming a parallel aggregate (Fig. 1F).

In contrast, prisms in most representative species of the orders Pectinoidea and Ostreoidae (families Propeamussiidae, Pectinidae, Anomiidae, and Ostreidae) show a clear internal structure consisting of a remarkable foliation (Fig. 2C–E). The foliation is nearly perpendicular to the main axis of the prisms in *Propeamussium dalli*, *P. jeffreysii*, *P. sibogai*, and *Adamussium colbecki* (Fig. 2E); while in *Ostrea edulis* (Fig. 2C), *Crassostrea gigas* (Fig. 2D), and *Anomia ephippium*, the foliation is oblique (30°, 30°, and 45°, respectively). In well-preserved specimens, the growing surface of the prisms reveals a substructure formed by slightly inclined small leaves, or laths (Fig. 2F–K). These are chevron-shaped or, less frequently, squared, with straight and well-defined outlines (Fig. 2H, K). Laths are usually juxtaposed side-by-side, forming *folia* that extend laterally all over the prism surface. Laths are all evenly aligned within each prism, although this direction may not be coincident between prisms (Fig. 2I).

The prisms of the two representatives of the pterioid family Malleidae (both of the genus *Malleus*) showed a foliation similar to that of ostreoids and pectinoids. Foliation was visible in both intact and treated samples and is disposed transversal to the prism—that is, subparallel to the growing surface (Fig. 2A). The inner surface of the prisms is composed of micrometer-sized laths (Fig. 2B).

Transition between the prismatic and underlying layers

Transition to the nacreous layer. The transition between the prisms and the underlying nacre of pteriids and pinnids starts with the production of an organic pellicle, which first appears over the interprismatic walls and then extends toward the prism center, until it covers the entire surface (Fig. 3A). Nacre crystals nucleate in the depressed interprismatic walls over the organic pellicles, from where they first invade the prism edges and finally the central area of the prisms until they create a continuous layer (Fig. 3A). In *Malleus regulus*, the organic walls of the prisms vanish abruptly

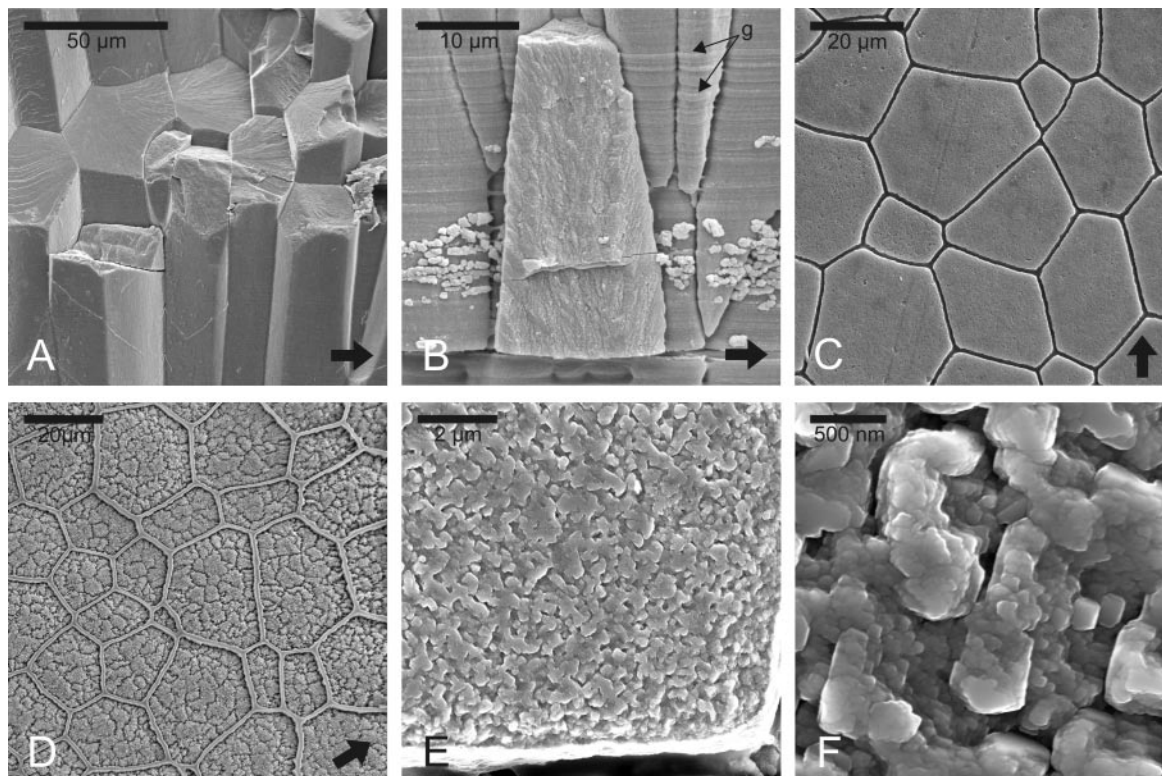


Figure 1. Non-foliated prisms of Pterioida. (A) Fractured prisms of *Atrina serrata* showing the absence of any appreciable internal ultrastructure. (B) Fractured prism of *Isognomon legumen* (center of photograph). Growth lines (g) are evident on the surface of other prisms. (C) Internal (growth) surface of the prismatic layer of *Isognomon legumen*. The surface of prisms appears smooth at this magnification. (D) Internal view of slightly etched prismatic layer of *Isognomon legumen*. Etching reveals narrow fissures that form a reticulate engraved over the growing surface. Sample treated with HCl (0.1%) for 1 min. (E) Inner surface of a prism of *Pinclada martensii* revealing the existence of nano-units. (F) Closeup view of E showing the rhombohedral habit of nano-units. All crystals have their faces and crystallographic axes oriented in the same direction, forming a parallel aggregate. Arrows indicate growth direction.

some distance in front of the boundary with the nacreous layer (where there is no appreciable intermediate organic pellicle) (Fig. 3B); in this way the prismatic layer becomes transformed into a rather continuous calcitic mass.

Transition to the foliated layer. In the pectinoids and ostreids, the transition between the prismatic layers and the foliated layer is marked by the interruption of the organic envelopes at the end of the prisms, but the mineral matter is continuous across layers. This is particularly evident in transverse views (Fig. 3C–E). In surface views the organic envelopes are lost progressively (Fig. 3F, G) and there are loose organic remnants (Fig. 3F, small arrow) as well as fused cells (Fig. 3G, H) within the incipient foliated layer.

The laths in the foliated layer clearly inherit the orientation of the laths inside the prisms. When prisms have their folia evenly oriented, there is a gentle changeover of layers, with the main orientation of laths being continuous into the foliated layer (Fig. 3C, D). When prisms have their folia

differently oriented, the bundles of folia corresponding to the different prisms continue into the foliated layer until the whole becomes evenly oriented deeper within this layer (Fig. 3E).

In *Propeamussium dalli* and *P. jeffreysii* (Fig. 3I) there is an intermediate organic sheet separating both layers, which prevents mineral continuity between layers.

XRD texture analyses

In *Pinna nobilis* (Fig. 4, first row), *Pteria hirundo*, *Mal-leus malleus*, and *M. regulus* (Fig. 4, second row), both surfaces of the prismatic layer display a similar pattern, with the *c*-axis perpendicular to the surface. The 104 poles have a turbostratic distribution indicating that the *a*- and *b*-axes of different prisms are freely rotated around the *c*-axis. This is known as a fiber texture with the *c*-axis as fiber axis.

In *Propeamussium sibogai* (Fig. 4, third row) and *Ostrea puelchana* (Fig. 4, fourth row), the external surface of the

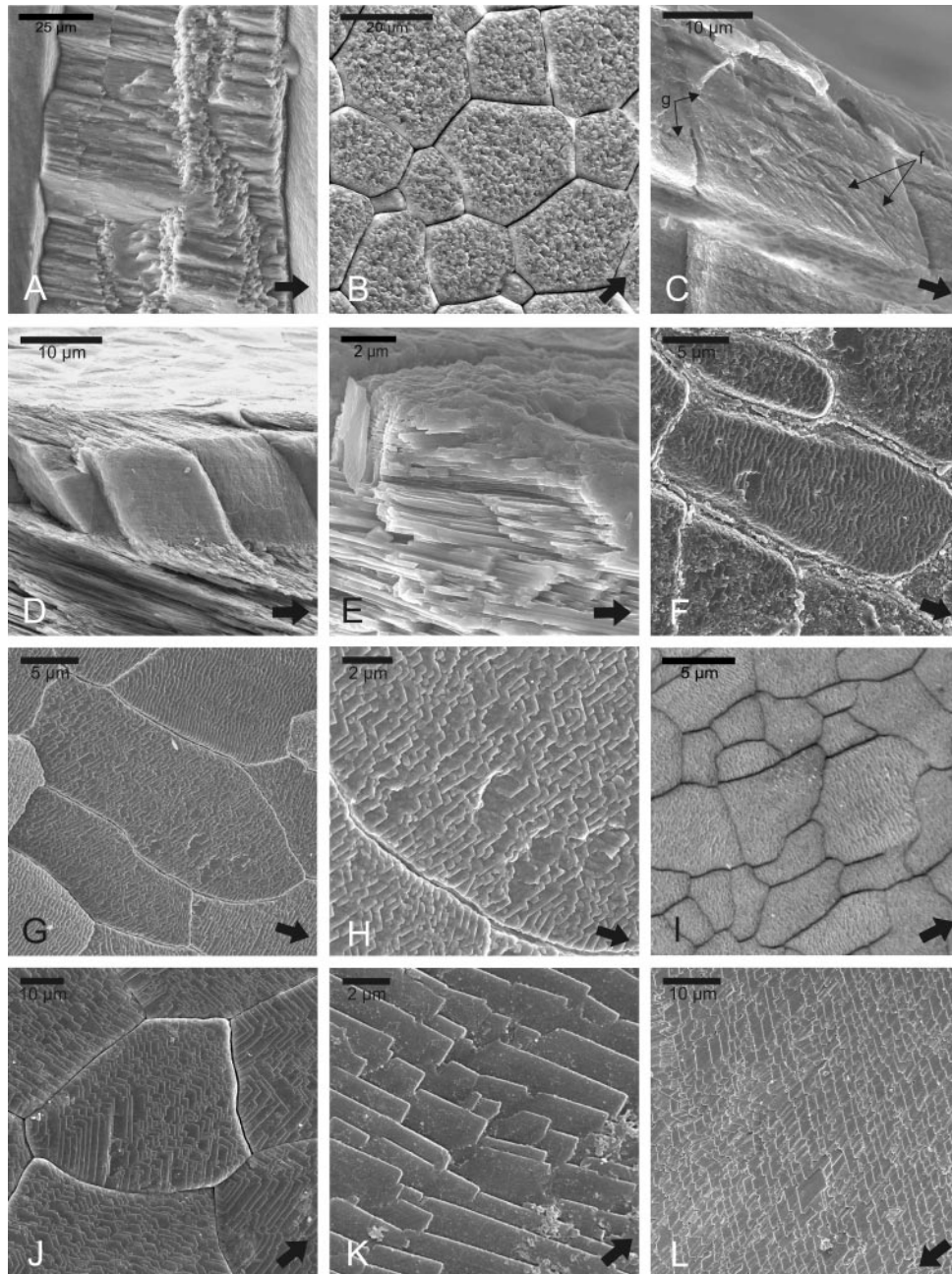


Figure 2. Foliated prisms of Malleidae and Ostreoida. (A) Fractured prism of *Malleus malleus* showing internal foliation. (B) Internal surface of the prismatic layer of *Malleus regulus*. The unevenness is due to the protrusion of lathy units. (C) Cross-sectioned prism of *Ostrea edulis* showing the internal foliation (f) oblique to growth lines (g). Sample slightly etched with HCl (1%, 5 s). (D) Partly fractured prisms of young *Crassostrea gigas*. Foliation is evident in the fractured uppermost part of the prisms. The foliated layer can be seen below. (E) Fractured prism of *Adamussium colbecki*. The internal foliation is similar to that of the underlying foliated layer. (F) Internal surface of the prisms of *Ostrea edulis* showing the folia emerging in parallel to the cross-sectional elongation of the prism. Organic matter partially removed with proteinase K for 10 min. (G) Internal view of the prisms of *Crassostrea gigas* with foliated laths lining the surface. Organic matter was removed by bleaching the sample for 30 min. (H) Detail of G to show the similarity of the surface with that of the foliated layer (compare to L). (I) Inner surface of the prismatic layer of *Anomia ephippium*. The folia have different orientations in each prism. (J) Internal surface of the prisms of *Propeamussium dalli* with particularly well-developed laths. (K) Detail of J. Laths are identical in morphology to those of the foliated layer (compare to L). (L) Surface view of the foliated layer of *Ostrea edulis*. Arrows indicate growth direction.

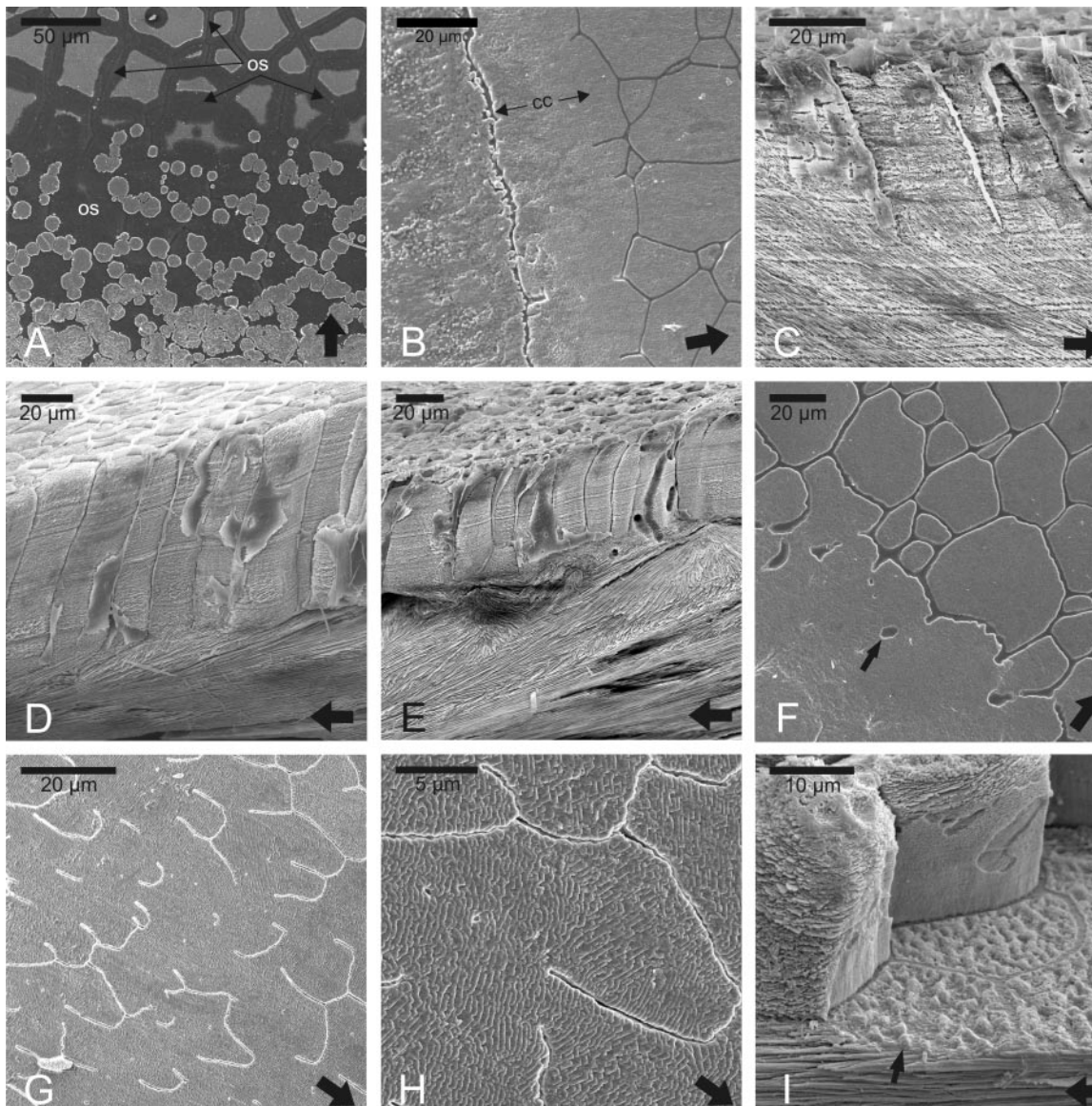


Figure 3. (A) Transition from the prismatic (top) to the nacreous (bottom) layer in *Pinctada martensii*. The transitional organic sheet (os) appears in black. (B) Zone of contact of the prismatic layer (right) and the nacreous layer (left) in the left valve of *Malleus regulus*. Organic envelopes disappear some 20 μm before the nacre, leaving a band of continuous calcite (cc). (C) Polished fracture through the transition from the prismatic to the foliated layer in *Ostrea edulis*. The folia are continuous in morphology and orientation between both layers. Sample slightly etched with HCL (1%, 5 s). (D) Fractured shell of *Crassostrea gigas* showing the continuity between layers. Note homogeneous orientation of laths from the initiation of the foliated layer. Organic envelopes completely removed with NaClO for 3 min and later slightly etched with HCL (1%, 5 s). (E) Fracture through the shell of *C. gigas*. Contrary to D, prisms have their laths mutually disoriented at the transition to the foliated layer, which causes the upper part of the foliated layer to be composed of unevenly aligned laths. A little deeper within the foliated layer, the orientation becomes homogeneous. Same treatment as in D. (F) Surface view of the transition between the prismatic and the foliated layers in *O. edulis*. Small arrow shows an uncovered fragment of the organic walls. (G) Internal surface of the right valve of *C. gigas* at the transition area, showing the progressive blurring of the organic envelopes. Sample bleached for 30 min. (H) Closeup of G. The aspect at the transition is identical to that of the prismatic (compare to Fig. 2F–K) and the foliated (compare to Fig. 2L) layers. (I) Prismatic and underlying foliated layers in the right valve of *Propeamussium jeffreysii*. There is an organic sheet between layers (small arrow). Sample bleached for 5 min and slightly etched with HCL (0.5%, 4 s). Arrows indicate growth direction.

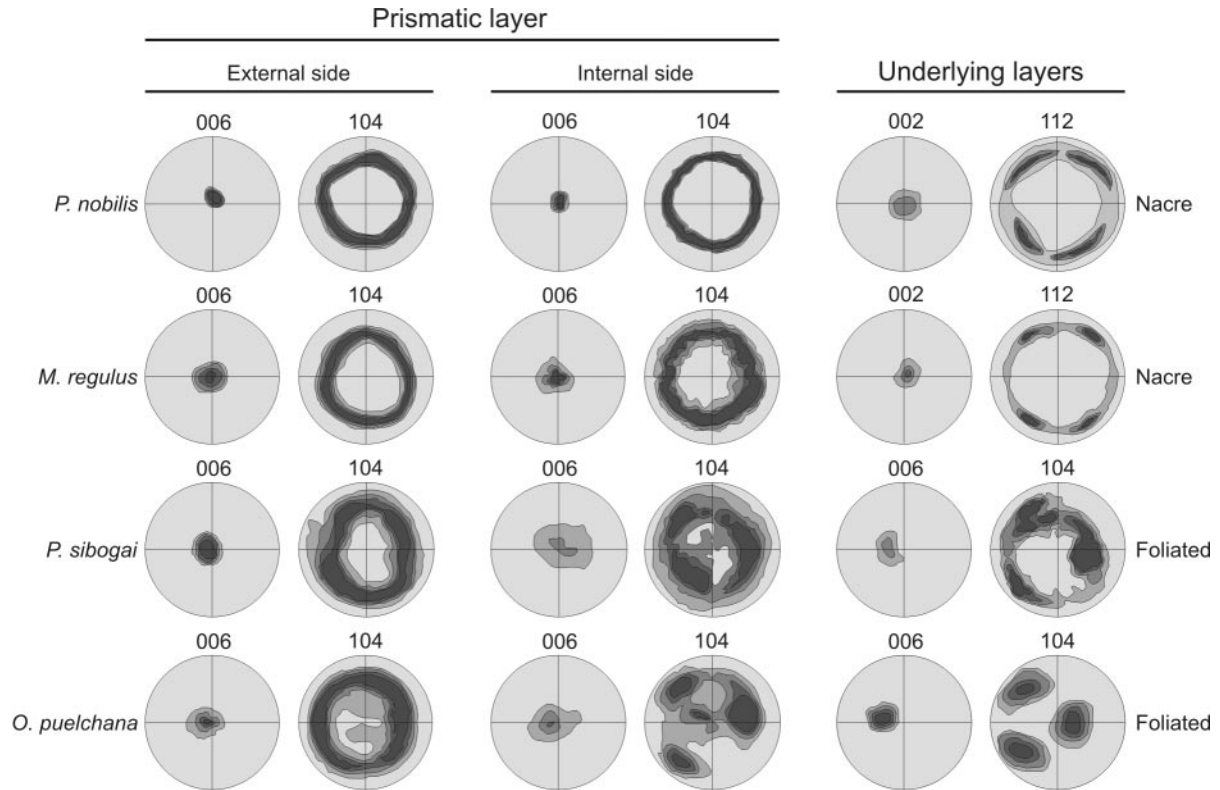


Figure 4. X-ray diffraction texture analyses of the prismatic and underlying nacreous or foliated layers of several pteriomorph species. In all species analyzed, the 006 poles of the prismatic layer indicate that the c -axis of the calcite lies normal to the surface of the prismatic lamella, and hence a - and b -axes are disposed parallel to the surface analyzed. The ring-like disposition of 104 poles of the external surface implies that the a - and b -axes are freely rotated around the c -axis (fiber texture). Texture is also fibrous in the inner surface of *Pinna nobilis* and *Malleus regulus*, which indicates that the crystallographic arrangement of the prismatic layer does not change substantially during its growth. On the other hand, the three discrete 104-pole maxima (sheet texture) found at the inner side of *Propeamussium sibogai* and *Ostrea puelchana* imply that crystals have their a - and b -axes evenly oriented. In the case of these two species, the crystallographic arrangement of the layer changes drastically during growth, with a realignment of the crystallographic axes in the a - b plane. In the nacreous layer of *Malleus regulus*, the 112 poles are distributed in four discrete maxima, which denotes that nacre crystals have a common crystallographic orientation (sheet texture). In *P. sibogai* and *O. puelchana*, the distribution of 104 poles of the foliated layer is indicative of a sheet texture and very similar to that of the inner surface of the corresponding prismatic layer, thus implying crystallographic similarity. The direction of growth is toward the right in all pole figures.

prismatic lamella also has a c -axis fiber texture. In contrast, in the internal surface of both species, close to the transition to the foliated layer, the 104 poles are grouped into three discrete maxima (sheet texture), which implies that prisms in that area have their crystallographic axes commonly oriented. The different width of 104-pole maxima suggests that the a - and b -axes of *P. sibogai* are scattered relative to those of *O. puelchana*.

Texture analyses of the underlying nacreous and foliated layers are also shown in Figure 4. Results from the nacreous layer are similar in all species, and hence we show pole figures only for *Pinna nobilis* and *Malleus regulus*. Disposition of the 002 poles indicates that nacreous tablets have the c -axis lying normal to the surface. The 112 poles are

grouped into four incipient maxima, which indicates that the a - and b -axes of aragonite crystals are well aligned, with the b -axis oriented in the local direction of growth of the shell. The texture of the incipient foliated layer was analyzed in *Propeamussium sibogai* and *Ostrea puelchana* and was found to be typical of this material, with three well-individualized 104-pole maxima (sheet texture), one of them facing the direction of growth, and the 006 poles reclined about 30° opposite to this direction (Checa *et al.*, 2007). In the two species analyzed, the texture of the foliated layer is therefore very similar to that of the prismatic layer previous to the transition, the only difference being the slight shifting of the 006- and 104-pole maxima of the foliated layer opposite to the growth direction (Fig. 4).

Discussion

Ultrastructure of prisms and foliated layer

We have showed that the prisms of the eupteriomorph families Pectinidae, Propeamussiidae, Anomiidae, and Ostreidae are constituted internally by laths with arrow-pointed endings, which are morphologically indistinguishable from those of the foliated layer.

Since these laths are invariably present in treated and untreated samples, the observed foliation cannot be an artifact resulting from sample preparation. Preparation artifacts might, however, have been responsible for the sheet-like substructure observed by Suzuki and Uozumi (1981) in etched prisms of *Pinctada fucata martensii*, which we have observed to be homogeneous when untreated.

Our results agree with the observations of Travis and Gonsalves (1969), who found that the decalcified prisms of *Crassostrea virginica* are composed of sheet-like compartments (see their figures 9–11 and 17–19) with a thickness of some 150 nm, and a brick-wall arrangement. Such compartments are in fact the organic pellicles that surround the individual laths, or *folia*, within the prisms. These pellicles had previously been described by Tsuji *et al.* (1958) in the foliated layer of the same species.

X-ray texture analyses confirm that mature foliated prisms have the same texture, or crystallographic arrangement, as the foliated layer. Therefore, taking into account the structural and crystallographic similarities between prisms and foliated layer and the fact that the foliated microstructure is usually developed below a prismatic layer, we support Waller's (1976) hypothesis that the foliated microstructure is derived from the calcitic prismatic. Recent work by Checa *et al.* (2007) stated that the crystallographic arrangement of representatives of five families of bivalves (Ostreidae, Pectinidae, Propeamussiidae, Anomiidae, and Placunidae) is identical, with the main surfaces of the *folia* being coincident with the {108} rhombohedral faces and the *c*-axis inclined opposite to the growth direction. On the basis of Waller's (1976) hypothesis, Carter (1990, p. 256) suggested that the foliated layer could have evolved either directly from calcitic prisms or indirectly through intermediate grades of fibrous prismatic, irregular spherulitic prismatic, homogeneous structure, or a combination of the three. However, our observations indicate that the transition between the prisms and the foliated microstructure is direct, without intermediate grades.

Texture analyses have shown that the crystallographic arrangement of the "non-foliated" and foliated prisms is noticeably different, with the latter developing sheet texture at the inner growth surface of the lamella. The attainment of the sheet texture in the foliated prismatic microstructure is progressive and depends on the thickness reached by the prismatic lamella (unpubl. obs.). This fact accounts for the better definition of the 104-pole maxima in *Ostrea puel-*

chana (prisms length 300 μm) compared to *P. sibogai* (100 μm) (see Fig. 4).

The prismatic and nacreous layers of pterioids are separated by an organic sheet (Fig. 3A), and there is no continuity between layers. Initial nacre tablets grow over the organic sheet, with the *a*- and *b*-axes totally disoriented. It is with the accumulation of successive lamellae that nacre tablets become commonly oriented due to selection by competition (Checa and Rodríguez-Navarro, 2005; Checa *et al.*, 2006). All these facts prevent nacre orientation from being inherited from the prismatic layer. Quite the contrary: in prismato-foliated shells, the foliated layer inherits the structural arrangement attained by mature prisms.

Our observations lead us to conclude that the transition between prisms with foliated structure and foliated microstructure may be achieved simply by the organisms ceasing to secrete the organic envelopes that enclose the foliated prisms.

Phylogeny of the foliated shell microstructure

It is of interest to examine the occurrence of foliated shell microstructures within the Pteriomorphia, in particular to try to establish whether the microstructure is monophyletic within the taxon. The relationships within the Pteriomorphia have been subject to much debate over the last few decades, with hypotheses based solely on morphology failing to reach consensus (see Steiner and Hammer, 2000, fig. 1) and being challenged by the advent of molecular methodologies. Of particular interest to us is the position in such schemes of the superfamilies traditionally included together in the order Ostreoida (*e.g.*, Beesley *et al.*, 1998)—that is, the Ostreoida, Plicatuloidea, Dimyoidea, Pectinoidea, and Anomioidea—because, with the exception of the Dimyoidea, all possess foliated microstructures. Two studies, Campbell (2000) and Steiner and Hammer (2000), based on 18S rRNA analyses have suggested that in fact the Ostreoida is a polyphyletic assemblage. Instead of these taxa being placed together, the Ostreoida have grouped as a sister taxon to the Pterioidea, leaving the Pectinoidea, Plicatuloidea, and Anomioidea in a different clade as a sister taxon of the Arcoidea. Although the bootstrap support for the Ostreoida + Pterioidea clade is not high (50%; Steiner and Hammer, 2000), the basic topology of these trees has been preserved in larger subsequent studies—for example, Giribet and Distel (2003), which investigated 18S rRNA, 28S rRNA, and COI genes (both individually and combined); and Giribet and Wheeler (2002), which analyzed molecular and morphological data. The separation of the ostreoids from the anomioids and pectinoids has also recurred repeatedly in these subsequent analyses, although they provide perhaps stronger evidence for the Pinnoidea being also included with the Ostreoida and Pterioidea (Bremer Support values of 36; Giribet and Wheeler, 2002). In Figure 5,

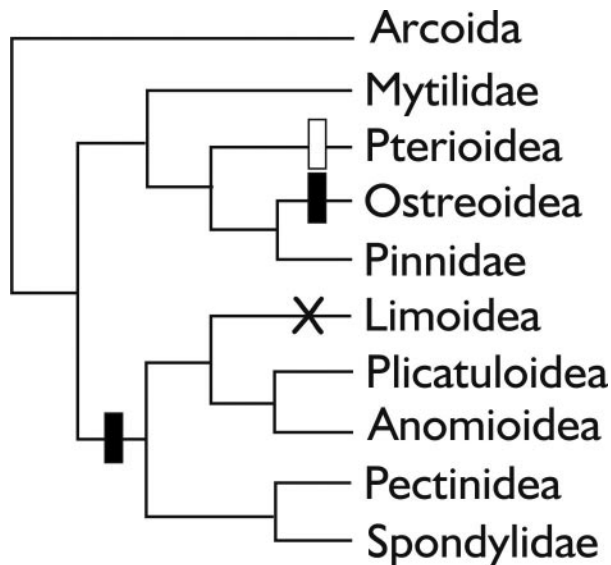


Figure 5. Plot of the occurrence of foliated microstructure onto the tree proposed by Giribet and Distel (2003, fig. 3.6 [with permission of the authors]) on the basis of analysis of the 18S rRNA, 28SrRNA, and CO1 genes. The black bar represents the acquisition of both foliated prism and foliated microstructures, whereas the white bar indicates the occurrence of foliated prisms only in some species. X indicates a reversal in the character.

the occurrence of foliated shell microstructure is plotted on a tree constructed in accordance with the hypothesis proposed by Giribet and Distel (2003), the most recently published and most densely sampled study of pteriomorph bivalves, which suggests that the character is at least diphyletic and constitutes a synapomorphy for a clade consisting of ([Plicatuloidea + Anomioidea] + [Limoidea + Pectinoidea]) and another clade for the Ostreoidea. Our observations on *Malleus* suggest that there may also be a third small clade, of taxa that secrete only the foliated prisms, within the pterioidea. All other pterioidea studied possess simple calcite prisms. The current understanding of the “Malleidae” is, however, incomplete. The two malleid species (unfortunately none of the genus *Malleus*) included by Steiner and Hammer (2000) in their molecular analysis were found to be non-monophyletic, yet securely within the Pterioidea; Tëmkin (2006), who used 103 informative morphological characters in a cladistic analysis of 19 pterioidea taxa, reached the same conclusion. It is worth noting that Hertlein and Cox (1969, p. N326) included a number of extinct genera with extensive foliated layers (*e.g.*, *Euphemax*, *Heligmina*, *Nayadina*, *Ostreinnella*, *Chalmasia*, *Eligmus*) within the Malleidae. However, these genera were subsequently transferred to the Ostreidae by Waller (1978, 1985) on the basis of their lack of nacre, possession of foliated layers, and other characteristic features such as chomata, lack of byssal notch, and pleurothetic life habit over the left valve.

Development of foliated shell layers over geological time

To investigate further the development of the foliated shell layers over time, we have analyzed information on the microstructure of a wide range of fossil pteriomorph taxa. The shell structure of fossil pteriomorphs is relatively well known, not least because the diagenetic stability of calcite allows good preservation of these layers. We have used published sources, of which the works of Carter (1990) and Hautmann (2001, 2006) have been key, and our own observations to compile data for the first appearance of various calcitic microstructures and their arrangement within the shells of particular taxa.

The fossil record indicates that calcite prisms first appeared in the external layers of the Middle Ordovician ambonychiids and pterineids (Pterioidea) Carter, 1990), but the first foliated shell structures were recorded in the Upper Devonian Saharopteriidae (Pareyn *et al.*, 1971), some 100 million years later. Shells comprising extensive foliated layers remained uncommon during the Paleozoic, being present only in the Saharopteriidae (Upper Devonian—Carboniferous) and Deltopectinidae (Upper Carboniferous—Lower Permian) (Carter, 1990). During the post-Paleozoic there was a marked increase in the prevalence and importance of foliated shells. An interesting aspect of the record of the evolution of foliated shell microstructures is the expansion of foliated calcite into the middle and inner shell layers within several pectinoid families, the Ostreidae and the Gryphaeidae; this expansion occurred in parallel in both of the clades we identify in Figure 5. The most primitive internal layer in pteriomorph bivalves is nacre (Taylor, 1973; Carter, 1990; Carter *et al.*, 2006), which appears in all pterioidea (Carter, 1990), in some Paleozoic pectinoids (*e.g.*, Pterinopectinidae), and in early oysters. In pectinoids, nacre was replaced by crossed-lamellar microstructure, but it is completely absent in all post-Paleozoic members of the order (Carter, 1990). The crossed-lamellar microstructure constitutes the middle and inner shell layers of limoidea, plicatulids, propeamussids, and spondylids, but is absent in oysters (Carter, 1990). In some groups (*e.g.*, anomioidea) the crossed-lamellar microstructure coexists with the foliated microstructure, but in others (*e.g.*, pectinoids) the latter occupies almost all middle and inner layers (Carter, 1990). Oysters followed a seemingly different route because they replaced the primitive nacre by foliated shell directly, without the intermediate production of crossed-lamellar layers (Carter, 1990; McRoberts and Carter, 1994; Hautmann, 2001). There are different opinions as to when the expansion of foliated layers to the shell interior occurred. Carter *et al.* (1998) suggested that it took place during the latest Paleozoic and early Triassic in many taxa, but Hautmann (2006) thought that it was actually rather later, in the late Triassic and Jurassic. At the same time, other pteriomorphs (namely pterioidea, limoidea, and some pectinoidea), re-

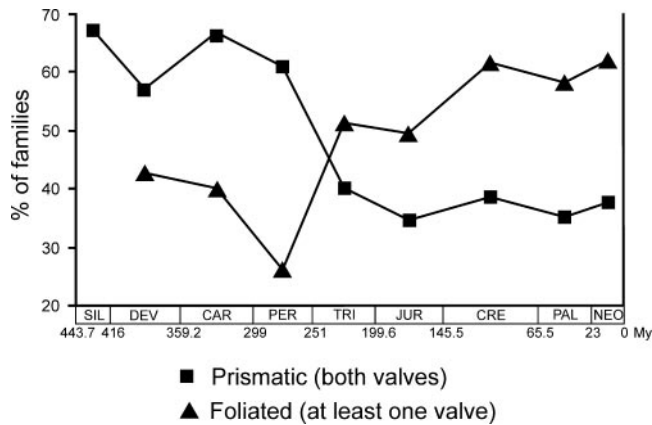


Figure 6. Relative diversities through time of euperiomorph families that possess external prismatic layers in both valves (squares), and of those that have replaced the prismatic layer by foliated layer at least in one valve (triangles).

tained internal aragonitic (nacreous and crossed-lamellar) layers.

Over the same time scale that the extent of the foliated microstructure in the inner shell layers was increasing within some pteriomorph groups, the number of taxa showing well-developed prismatic outer shell layers was decreasing (Fig. 6), although in some groups there was a trend toward increasing the dominance of the prismatic layer. For example, Taylor *et al.* (1969) observed that of the three extant genera of Pinnoidea, the surface area of the inner nacreous layer is markedly smaller in successively younger taxa.

Possible adaptive significance of foliated calcite in pteriomorph shells

It is tempting to put forward hypotheses that might suggest the selection pressures that favor both the evolution of foliated microstructure and its expansion into a large volume of the shell, apparently achieved over similar time-scales in two major clades of pteriomorphs. Because there is a significant time lag, of about 250 million years, between

the first appearance of calcite (in the form of external prisms) in the shells of pteriomorphs and the expansion of foliated calcite to occupy large volumes of the shell, the selection pressures involved in the acquisition of foliae are likely to be different from those that have been discussed for the evolution of calcite in the outer layer (see Taylor and Reid, 1990; Harper *et al.*, 1997; Carter *et al.*, 1998; Harper, 2000).

The evolution and spread of the apparently weak foliated structure into considerable thicknesses of shells seems counterintuitive. In a study of the mechanical properties of bivalve shell microstructures, Taylor and Layman (1972) discovered that the foliated layers of an ostreid (*Crassostrea gigas*) and a pectinid (*Pecten maximus*) performed poorly in a range of tests that examined their ability to withstand compression, bending, and loading, when compared to the full range of bivalve microstructures, and specifically much worse than the prismatic calcite layer of the pteriids (*Pinctada maxima*), which were more flexible (see Table 2 for summary). In fact, their prismatic samples were dry at the time of testing, and it seems that wet samples are actually even more flexible and resistant to breakage during bending (Zhou and Checa, unpubl. data). Taylor and Layman did, however, note that, although the rigid foliae of the oyster were the weakest microstructure they tested, cracks did not propagate readily within it and damage was restricted to the site of impact. Comparisons of other characteristics of different bivalve microstructures have shown that foliated microstructure has a low organic content and density compared with others (Taylor and Layman, 1972; Harper, 2000). It has also been shown that the structure is more susceptible than others to attack by both the chemicals released by drilling gastropods and corrosive seawaters (Gabriel, 1981; Harper, 2000).

Despite these apparent disadvantages, there are, as noted by others (*e.g.*, Carter *et al.*, 1998), a number of possible advantages to the foliated microstructure—for example, allowing reduced shell density for swimming and soft-bottom reclining species, and fracture localization. The suggestion (following the work of Palmer [1992]) that, owing to its low

Table 2

Summary of mechanical performance and physical properties for prismatic and foliated calcitic and nacreous microstructures

	Calcite prisms of <i>Pinctada maxima</i>	Calcite foliae of <i>Pecten maximus</i>	Calcite foliae of <i>Crassostrea gigas</i>	Aragonite nacre of <i>Pinctada maxima</i>
Compression stress at fracture ($\text{kg}\cdot\text{mm}^{-2}$)	23.6	10.2	0.64	38.2
Bending fracture stress ($\text{kg}\cdot\text{mm}^{-2}$)	9.94	ND	0.41	36.1
Impact strength (number of impacts to fracture)	24	ND	6	69
Density (Relative)	2.56	2.67	2.52	2.74
Organic content (Weight %)	4.8	ND	0.4	2.3

Data from from Taylor and Layman (1972). ND, not determined.

organic content, foliated shell might be relatively cheap to secrete could mean that many of the perceived weaknesses might be overcome by the ability to create a thicker shell. We suggest a further advantage that may have had far-reaching implications for the ability of eupteriomorphs to produce a wide range of new shell morphologies and made the evolution of foliated microstructures a key innovation in the adaptive radiation of the pteriomorphs.

New hypothesis: rigidification of valve margins. The mechanical behavior of the valve margins of bivalve molluscs is critically determined by the nature of the outer shell layers. Extensive and well-developed layers of calcite prisms, which extend ventrally beyond the more internal shell layers, have allowed pterioids to possess flexible flange-like margins. The Malleidae seem exceptional in this respect, because the prismatic layer may achieve a thickness of up to 1 cm, with prisms up to 100 μm in diameter, and it usually represents a much higher volume than the inner nacreous layer (Yonge, 1968). There appear to be definite advantages to possessing the kind of broad flexible flange of prismatic shell microstructure around the valves that is seen in pterioids. In particular, this arrangement allows tight sealing from changes in ambient water conditions, minimizes damage from unsuccessful predation (*e.g.*, by crushing decapods or fishes; Vermeij, 1983, 1987; Dietl and Alexander, 2005), and makes it difficult for predators (*e.g.*, extra-oral feeding asteroids) to prise apart the valves (Harper and Morton, 1994). However, there are also some limitations of this arrangement. For example, it necessitates the valve margins to be almost parallel and flat, which prevents the development of voluminous shells. All bivalves with this arrangement are essentially flat, with a low width between the valves. We suggest that those clades able to produce foliated layers and reduce or eliminate the prismatic outer shell layer have been able to make their shell margins more rigid and to build markedly convex valves with greater volume available for the soft parts. This has not only provided the opportunity to produce strikingly biconvex valves (and introduced the possibility of gross inequivalvy, as in oysters and scallops), but it has also permitted a wider repertoire of valve ornament. Flexible margins are unsuited for the development of radial folds, ridges, and other more extravagant ornamental features such as spines or tubercles that tend to rigidify the margins (Waller, 1972; see also the discussion in Carter, 1990, p. 234).

It seems to us that the evolution of the ability to form foliated shell microstructures in some clades but not in others has opened up different pathways for the evolution of shell form within the eupteriomorphs and proved to be a key innovation. We note that the expansion of foliated microstructure within the shells of the ostreoid and pectinoid clades is coincident with the post-Paleozoic adaptive radiation experienced by the pteriomorphs. In an analysis of this

adaptive radiation, Skelton *et al.* (1990) saw a post-Paleozoic burst in taxonomic diversity in concert with a marked increase in the adaptive repertoire of the group: the primitively epi- and endo-byssate life habits diminished in importance and more derived lifestyles such as cementing, swimming, or free-reclining were repeatedly evolved. The groups that have retained flexible prismatic layers in both valves (*e.g.*, the pterioids and pinnoids) are still restricted to the primitive epi- and endo-byssate habits, and although they have long evolutionary histories and persist into the Recent, they are today relatively genus-poor families with a restricted, mostly tropical/subtropical, distribution. By contrast, the clades that have developed shells of foliated calcite are widespread, have high generic diversities, and have repeatedly evolved more derived life-habits. Interestingly, groups such as propeamussids, anomiid, and ostreids, which secrete either only foliated calcite or a very reduced prismatic layer in one valve, have retained a functional prismatic outer layer in the other. In these animals with "flexible-rigid margins," effective sealing is still possible, as evidenced by oysters, which have just one flexible right flat valve adpressed against the opposite, rigid convex, valve.

Conclusions

The study of the internal structure of the calcitic prisms of some representatives of the subclass Pteriomorphia (Bivalvia) has revealed noticeable differences between the main groups. The studied members of the order Pterioida did not show any appreciable ultrastructure in their prisms except for small nanometric units with a common orientation. The only exception was found in Malleidae, where prisms had internal lathy crystals. On the other hand, the prisms of Pectinidae, Anomiidae, Propeamussiidae, and Ostreidae showed an internal structure made with calcitic laths identical to those of the foliated layer. This implies that the difference between the prismatic and the foliated microstructures in these groups is due to the presence (prismatic layer) or absence (foliated layer) of interprismatic organic envelopes. The similar constitution of both layers allows us to confirm that the foliated microstructure is derived from calcitic prisms, as previously assumed by Waller (1976) and Carter (1990). The foliated microstructure appeared internally to calcitic prisms. On the basis of current understanding of the phylogeny of pteriomorphs, we propose that this transition must have occurred in two clades and was accompanied, in both, by a parallel trend of expansion into the inner shell layers. This appearance was a key event in the evolution of eupteriomorph bivalves because it allowed the replacement of primitive flexible prismatic shell margins by rigid foliated margins and the production of largely calcitic shells. This event has no doubt contributed to the evolutionary success of the group, since those groups that carried out this replacement have undergone a pronounced diversifica-

tion over time, whereas those that retained the prismatic layers in both valves are clearly less diversified.

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