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Nacre in a Carboniferous Pectinoid Mollusc and a New Subfamily Limipectininae

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ABSTRACT

The Carboniferous genus *Limipecten* is an aviculopectinid in most traits except that it possesses nacreous layers unknown, so far, in any other scallop, living or fossil. Nacre is a characteristic of Middle Paleozoic Pterineidae from which the Aviculopectinidae probably were derived. *Limipecten* is regarded here as a member of the Aviculopectinidae rather than the Pterineidae and it is placed in a new subfamily, Limipectininae.

INTRODUCTION

In bivalve molluscs, the individual character traits of simple mosaics often change at different rates in different clades, frequently with homoplastic repetition (e.g., Newell and Boyd, 1975, 1985a, 1985b, 1989). Thus, while patterns of shell microstructure and mineralogy have proved to be of great value in recognition of molluscan taxonomic groups and relationships at the level of families and higher categories (Bøggild, 1930), there are occasional surprises in the bivalves, where these and other traits are at variance with general morphology and anatomy. *Limipecten,* a Carboniferous scallop, provides such a surprise.

The general morphology of *Limipecten* is that of the Aviculopectinidae but it is unique in two respects: it has nacre as a major constituent, and it possesses concave intercostal, pointed scales, rather than hyote spines, as in other aviculopectinids. Consequently we are here proposing a new subfamily for *Limipecten*: Limipectininae.

The special interest of the genus *Limipecten* is that it shares microstructural traits that are supposed to distinguish two orders in the

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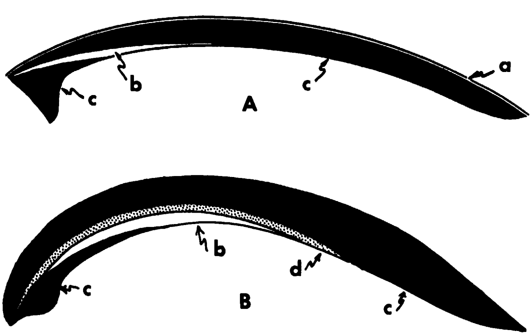

Fig. 1. Generalized shell construction in scallops. **A.** The ordinary structure in upper Paleozoic Aviculopectininae: a, calcite outer layer; b, fibrous adductor pad of aragonite—the myostracum; c, undifferentiated crossed lamellar aragonite. **B.** The ordinary arrangement in post-Paleozoic scallops (Pectinidae). Layer a is lacking in the left valve and obsolete in adult right valves; b, fibrous myostracum of the adductor; c, outer and inner foliate calcite layers separated by d, crossed lamellar aragonite (after Taylor et al., 1969: fig. 57).

Bivalvia (Waller, 1978). As emended by Waller these are the Pterioida (prismatonacreous shells lacking both foliated calcite and crossed lamellar structures) and the Ostreoida (which includes all pteriomorphians lacking nacre). The occurrence of both nacreous and crossed lamellar aragonitic structures in our extraordinarily well-preserved right valve of *Limipecten* indicates a need for reconsideration of these two orders, as we have suggested elsewhere (Newell and Boyd, 1989).

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We benefited from conversations with J. G. Carter, expert on molluscan microstructure, of the University of North Carolina at Chapel Hill. Gillian W. Newell assisted in the preparation of the text.

The following institutions provided specimens and data for our studies (the abbreviations indicate those used in the text): American Museum of Natural History, New York (AMNH); Yale Peabody Museum, New Haven, CT (YPM); U.S. National Museum of Natural History, Washington, D.C. (USNM).

PECTINACEAN SHELL CONSTRUCTION

The shell is secreted by a muscular mantle enclosing the living animal. Peripheral growth of the shell takes place by secretion of calcium carbonate at the free margin of each valve (fig. 1). The resulting increments are visible on the exterior as growth lines. Concentric ornaments (fila) and radial costae, where present, are established in this layer. Ontogenetic increase in thickness of each valve results from secretion at the general surface of the mantle against the inner surface of the valve.

Four basic types of shell microstructure exist: prismatic (including fibrous), nacreous, crossed lamellar, and foliate. These all occur in various combinations and patterns in the many branches of fossil and living scallops.

In bivalves, prismatic and fibrous structures are formed by both aragonite and calcite. Nacreous and crossed lamellar structures are developed *only* in aragonite, and foliated structure is limited to calcite (Carter, 1980). The fine crystals of these structures are embedded in conchiolin, a comparatively impervious protein similar to keratin. In living bivalves this shields relatively soluble calcium carbonate from the aqueous medium. Nacre is the strongest structural type, but crossed lamellar structure is the hardest (Currey, 1976). Whether these differences have any selective significance is not clear.

Many investigators have searched for environmental explanations of the differences in the substance and microstructure of molluscan shells, but with only limited success (Taylor et al., 1969; Currey, 1976). Particular combinations of the constituents generally are characteristic of major clades, and usually more or less independent of habitats. However, it is noteworthy that some Gondwana Permian pectinaceans secreted their shells of foliated calcite while congeneric forms from probably warmer climates, were mainly aragonitic (Newell and Boyd, 1989). The modern family Pectinidae, dating at least from the Triassic, also secretes the shell mainly of foliated calcite (fig. 1B). This has yet to be explained.

AVICULOPECTINID SHELL LAYERS

In a majority of Aviculopectinidae a thin outer layer of calcite covers the exterior of both valves, prismatic in the right and foliated in the left. Before availability of the scanning electron microscope, foliated structure of the left valve outer layer in the aviculopectinids was frequently designated as "homogeneous" (e.g., Newell, 1938). Rarely, the outer layer is prismatic in both valves (for example, "*Aviculopecten*" *mazonensis* Worthen, ibid.), a condition that is true for species of the Pterinopectinidae, and that seems to be the rule for the less specialized pteriaceans.

In some living pteriomorphs the prismatic layer of the right valve extends beyond the free margin of the inner layer as a flexible fringe that seals the closed valves (Newell and Merchant, 1939; Waller, 1972; Carter and Tevesz, 1978). The fringe usually is broken away in fossils so that the right valve presents a false appearance of being appreciably smaller than the left valve.

In general, the Aviculopectinidae possess an inner crossed lamellar aragonite layer that constitutes most of the thickness of the shell (fig. 1A). This layer consists of lamellae a few microns thick lying normal to the shell surface and constructed of thinner second order lamellae. This layer progressively smooths out, or even conceals irregularities and surface ornamentation of the outer layer, except near the free margin, where the outer layer is not deeply blanketed.

Pads of irregular prismatic myostracum (fig. 1) were secreted where pallial, adductor, and other muscles were inserted at the inner surface of the shell. The muscle pads migrated toward the shell margin during growth, leaving localized layers of myostracum surrounded by the inner layer.

Until the present work, nacre was not well documented in the family although its presence in *Limipecten* was mentioned by Newell (1938) and interpreted from an altered structure by Carter and Tevesz (1978: fig. 21C).

SHELL LAYERS IN PECTINIDAE

The outer foliated layer in living Pectinidae dominates the thickness of each valve. Crossed lamellar aragonite, if present, forms only within the pallial line. An inner foliated calcite layer forms the interior of both the umbonal region and the hinge (fig. 1B). An obsolescent film of prismatic calcite may cover the beak of the right valve (Waller, 1972). But a thin outer layer homologous with that of left valves of *Limipecten* and other aviculopectinids apparently has been lost in the Pectinidae, so the outer foliated layer in aviculopectinid left valves (fig. 1A) is not homologous with the outer foliated layer in Pectinidae.

The components of foliated calcite are irregular and variable, usually lying at low angles with respect to the shell surface. They may be tilted in alternating units to produce foliated structure similar to, but less regular and flatter than, an aragonitic crossed lamellar structure.

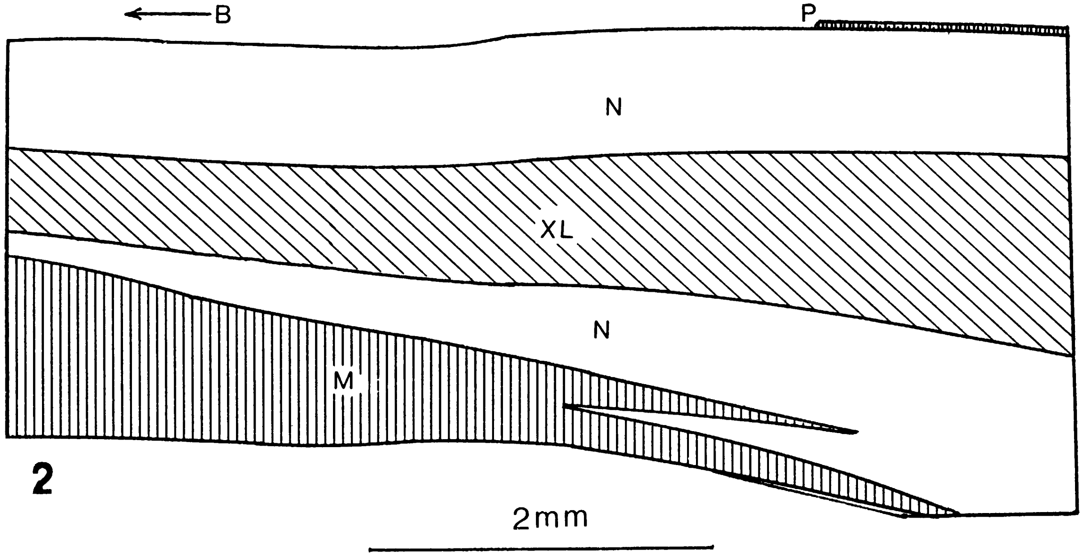
SHELL LAYERS IN *LIMIPECTEN*

In *Limipecten,* as with most other Paleozoic scallops, the outer layer of the right valve, unlike that of the left valve, is composed of vertical prisms of calcite (figs. 2, 3, and 4.2).

Our *Limipecten* material included only a small fragment of the left valve (fig. 4.1). Almost one-half of the thickness of the right valve is imbricate "step" nacre (figs. 4.3, 4.5) similar to that of the modern pearl clam, *Pinctada.* This is interrupted by a thick aragonitic crossed lamellar layer (fig. 4.4) in which components of adjacent first-order lamellae are tilted in opposite directions at about 85–90 degrees.

The adductor myostracum (figs. 4.5, 4.6) is locally thick, almost one-half of the valve thickness, wedging out toward the free margin of the shell. It consists of aragonite fibers of irregular rather than polygonal cross section.

In summary, our *Limipecten* is similar to other aviculopectinids except that the aragonitic inner part of the shell, in addition to the myostracum, consists of two layers of nacre and an intervening crossed lamellar layer. The location and sequence of layers suggest that the aragonitic nacre is homologous with



Figs. 2, 3. *Limipecten morsei* Newell (1938: pl. 10, figs. 5–7). Right valve. YPM no. 8146. Pennsylvanian Kendrick Shale. **2.** Map; **3.** SEM photograph. B, direction of beak; P, prismatic layer; N, outer and inner nacreous layers; XL, crossed lamellar aragonite; M, aragonitic myostracum.

the inner and outer calcite foliate layers of Pectinidae.

A revised taxonomy of *Limipecten* follows:

LIMIPECTININAE NEWELL AND BOYD, NEW SUBFAMILY

DIAGNOSIS: Same as for the genus *Limipecten.*

GENUS *LIMIPECTEN* GIRTY, 1904

TYPE SPECIES: *Limipecten texanus* Girty, 1904; Original designation. Upper Pennsylvanian, Texas; Newell, 1938 (see our fig. 5).

DIAGNOSIS: Robust, subcircular, inequiconvex shells, the left valve being more convex; both valves multicostate; left valve with annular growth lamellae erect over the costae, projecting peripherally in pointed scales;

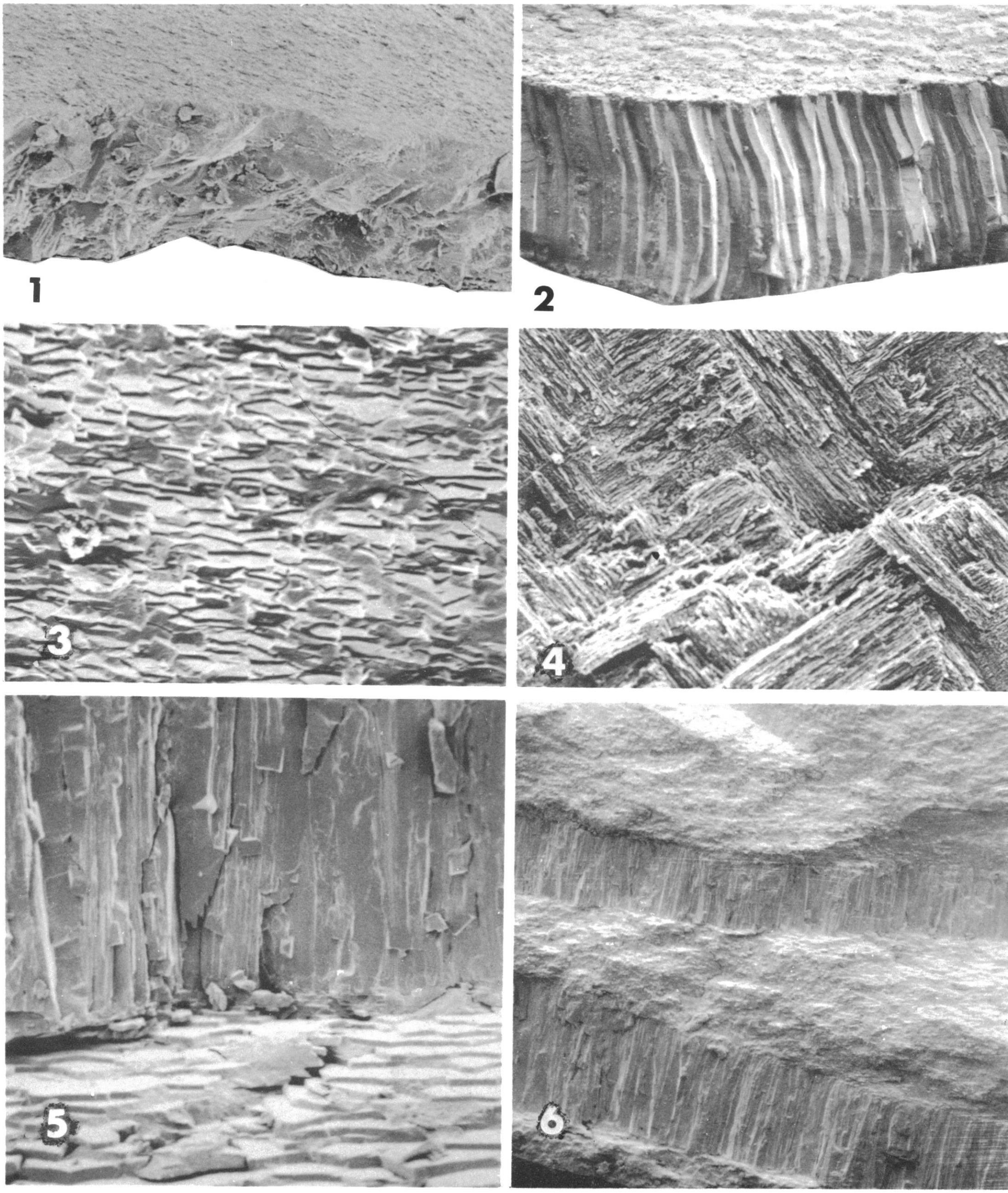


Fig. 4. SEM details of YPM 8146, greatly enlarged, magnifications approximate. **1.** Left valve, outermost layer, irregular foliated calcite, ×250; **2.** right valve, outermost prismatic layer, calcite, ×250; **3.** imbricate nacreous aragonite plates, each about one to three microns thick, ×1000; **4.** aragonitic crossed lamellar layer with second-order lamellae about one to three microns thick, ×250; **5.** aragonitic myostracum and underlying imbricate nacre, ×2000; **6.** aragonitic fibrous myostracum interbedded between nacreous layers, ×105.

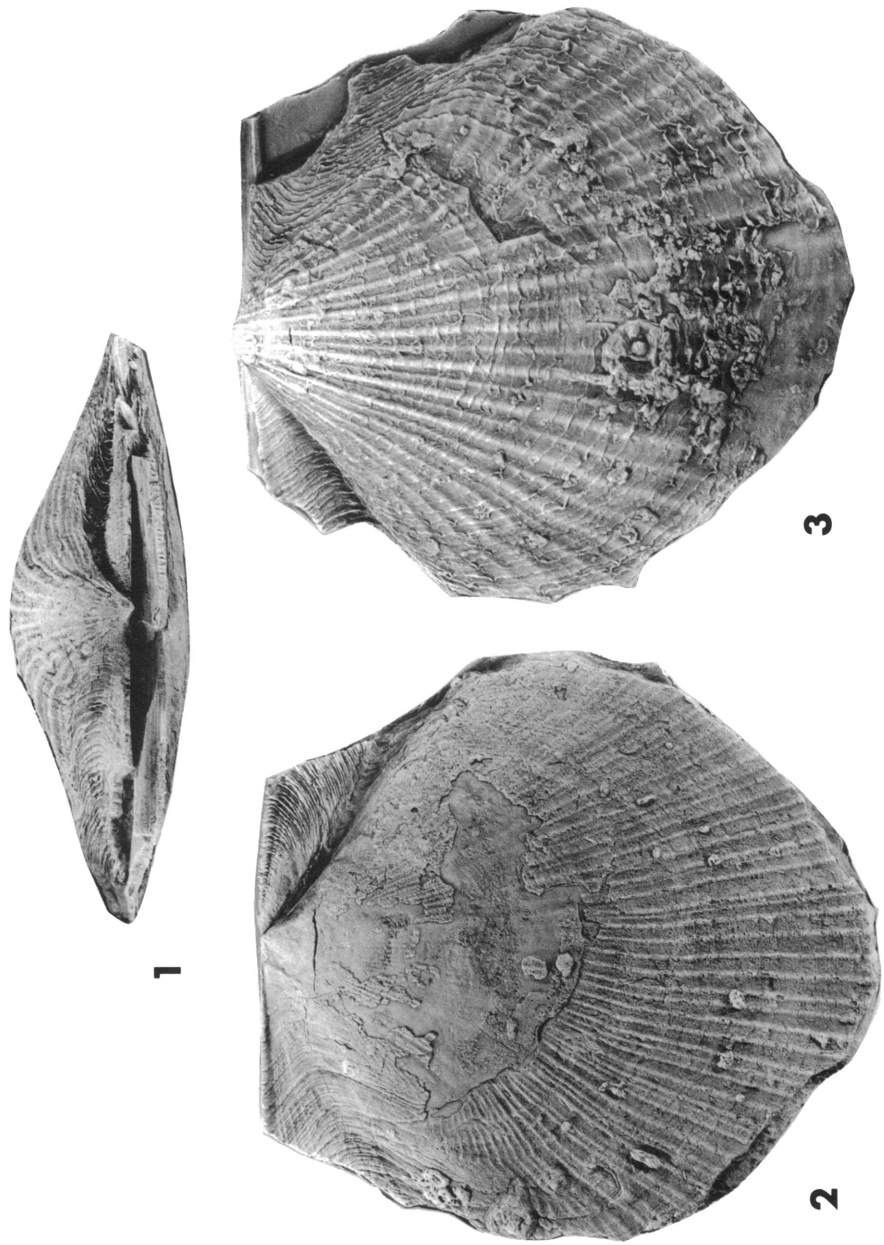


Fig. 5. *Limipecten texanus* Girty; USNM no. 388875, Pennsylvanian Finis Shale, near Jacksboro, Texas, ×1. Type species of *Limipecten.* **1.** Dorsal view, right valve below, showing unequal convexity; **2.** right valve; **3.** left valve.

inner shell consists of an inner and outer layer of nacre separated by a crossed lamellar layer.

RANGE: Carboniferous, Western Europe and North America.

DISCUSSION: Our contribution here is to confirm and describe the nacreous microstructure of the shell, a primitive character that seems to be unique among the aviculopectinaceans.

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