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Iteration of Ligament Structures in Pteriomorphian Bivalves

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ABSTRACT

Pteriomorpha, the largest subclass of the Bivalvia, includes such highly successful extant groups as the marine mussels, pearl shells, oysters, and scallops. Shells of different groups display surprisingly diverse structural types of ligaments (diagnostic traces of which are recognizable in fossils as old as the Early Cambrian) and the ligaments have figured prominently in pteriomorph classifications.

Within the context of general morphology, seven or eight ligament grades have been used to characterize families of pteriomorphs. But the same, or very similar, ligaments appear repeatedly as evolutionary novelties in separate taxonomic groups without evident phyletic origins or marked adaptive significance. Even their phylogenetic polarity is frequently in doubt.

For example, one complex structure (duplivincular) is replaced geochronologically by a different, and simpler structure (alivincular) in families of the Arcacea, Anomiacea, Aviculopectinacea, and Pteriacea. "Transitional" (new term), multivincular, and duplivincular ligaments all occur in the superfamily Pteriacea. Even where the geological succession of ligaments might be interpreted as indicating an ancestral-descendant relationship, the different grades of ligaments do not form gradational morphoclines.

So this review is intended only to call attention to taxonomic and phylogenetic difficulties in evaluating ligament grades; we are withholding conclusions about classification until later.

INTRODUCTION

The bivalve subclass Pteriomorpha is a major cluster of 46 families, according to the

Treatise on Invertebrate Paleontology (Newell, 1969). Its great diversity may well be an

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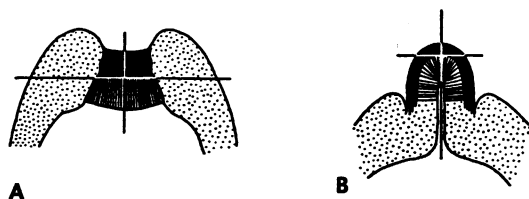


Fig. 1. Cross sections showing the two ligament layers: lamellar (black) and fibrous (ruled). Hinge axis is indicated by cross. Stipple pattern represents shell. A. Primitive; B. parivincular. (From Trueman, 1951)

artifact of its classificatory history. As so defined it spans the entire Phanerozoic and comprises about one-fourth of all the families of bivalve molluscs, including such successful groups as the arks, scallops, pearl shells, oysters, and marine mussels. They include monomyarian, anisomyarian, and isomyarian forms with diverse ligament structures.

Early attempts at classification stressed single anatomical characters, such as gill types, that leave no indication on the shells (e.g., Isofilibranchia), or the reduction or absence of the anterior adductor muscle repeated in separate branches. But these arrangements have fallen into disfavor with increasing knowledge of the fossil record of the Bivalvia (Newell, 1965, 1969).

The shell characters that delimit many of the conventional family groups have been

conservative and stable for tens to hundreds of millions of years, giving credibility to much of the accepted family arrangement. The stratigraphic sequence of fossils, together with development, skeletal morphology, anatomy, and life modes of living representatives, all contribute to ideas about phylogeny and classification. There remain, however, many differences, partly semantic, as to limits and names of higher categories (e.g., compare Newell, 1969, and Waller, 1978). These are being smoothed out with time.

One of the most interesting characteristics of this and some other groups of Bivalvia is a tendency toward evolutionary repetition of shell characters, which is probably attributable to the limited ways in which structural modifications have been genetically constrained. Diverse structural types of the pteriomorph ligament provide examples of parallel repetition of a morphological character in separate taxonomic branches.

As with other bivalves, the ligament consists of two parts. One of these is an upper, elongate, lamellar band usually under tension when the valves are closed. The other is an underlying fibrous layer subject to compression when the valves are closed (fig. 1). The latter is stiffened by microscopic needles of aragonite arranged at right angles to the inner growing surface where both components are secreted by the mantle.

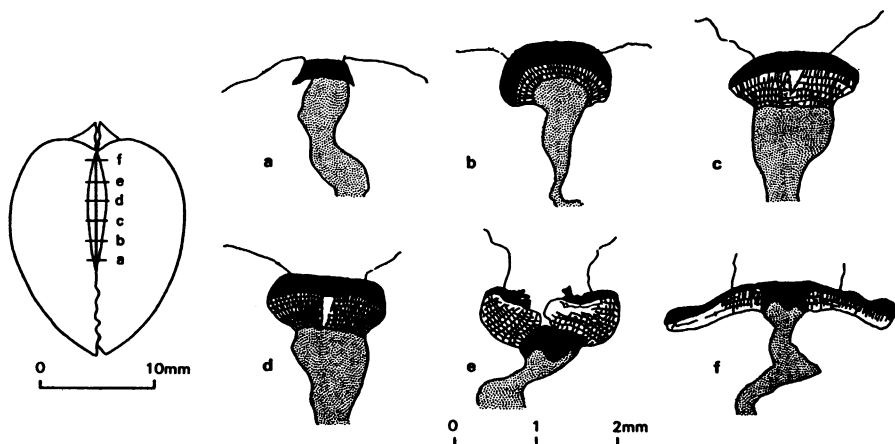


Fig. 2. Transitional ligament illustrated by the arcoid *Lunarca ovalis*. Recent, coastal New Jersey. Serial sections showing median split of fibrous and lamellar layers and added secondary lamellar band below the beaks. Note that the split begins well in front of the posterior end of the hinge. Lamellar layers in black; fibrous layer lined; mantle stippled. Based on several specimens.

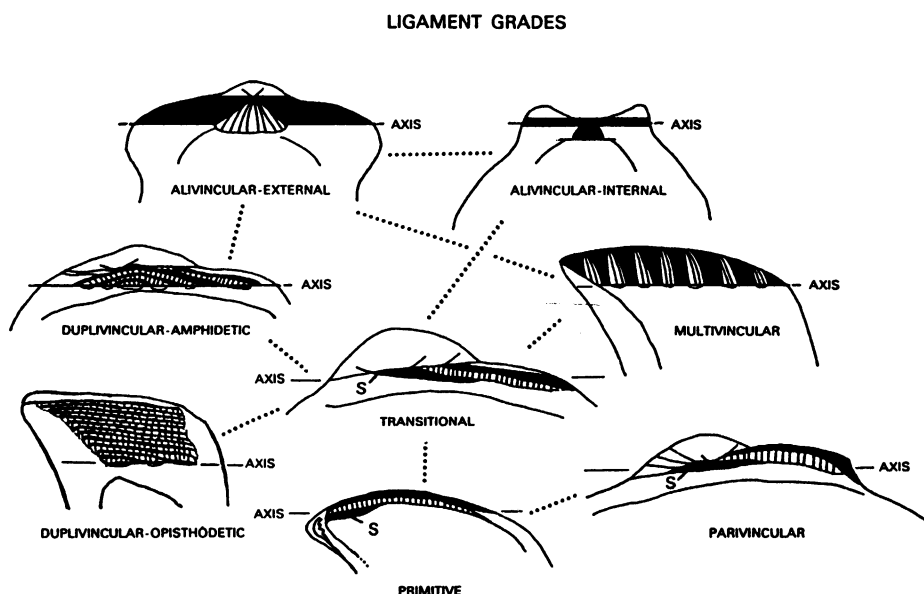


Fig. 3. Ligament grades with possible but uncertain paths of change, some of which could have resulted from neotenus reversal. The phyletic polarity is usually uncertain. S, secondary lamellar band. The alivincular and duplivincular figures at the top are amphidetic; the others are opisthodontic, black, lamellar, ruled, fibrous.

The fibrous layer is weak to tensional stresses and in some forms tends to split as interumbonal growth spreads the two valves apart. Hence, the functional part of the fibrous layer lies below the hinge axis. In this situation expansion carries the obsolete part of the ligament above the hinge axis. In some taxa the fracture is repaired by a secondary plug, or band, of lamellar conchiolin which maintains the juncture of the two valves (fig. 2).

The ligament usually lies behind the beaks, the opisthodontic condition. Or it may extend both in front of, and behind, the beaks where it is said to be amphidetic (fig. 3). It seems that the amphidetic hinge appeared late in bivalve history (mid-Paleozoic) and therefore was probably "derived" from the more ancient and evidently more primitive opisthodontic condition.

A stable trait in some families is the possession of flat or slightly concave cardinal areas (fig. 4B) to which the ligament is attached. These result from the inward and downward migration of the hinge axis as growth expands the valves between the um-

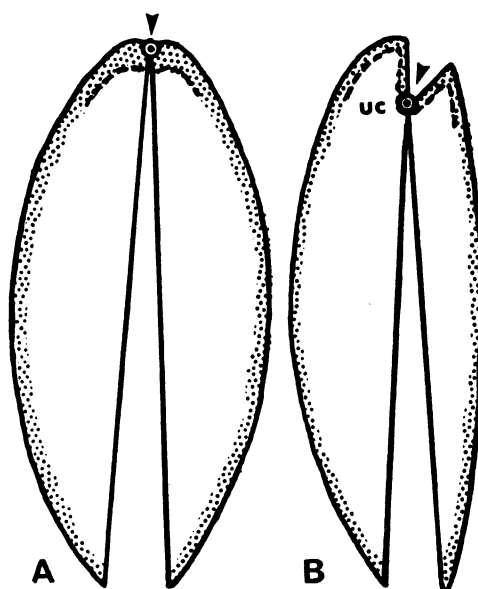


Fig. 4. Hinge axis in relation to internal and external ligament. A. Internal ligament without hinge plates or cardinal areas; B. external ligament with cardinal areas and hinge plate; UC indicates umbonal cavity. Stipple area represents shell; black circle, hinge axis.

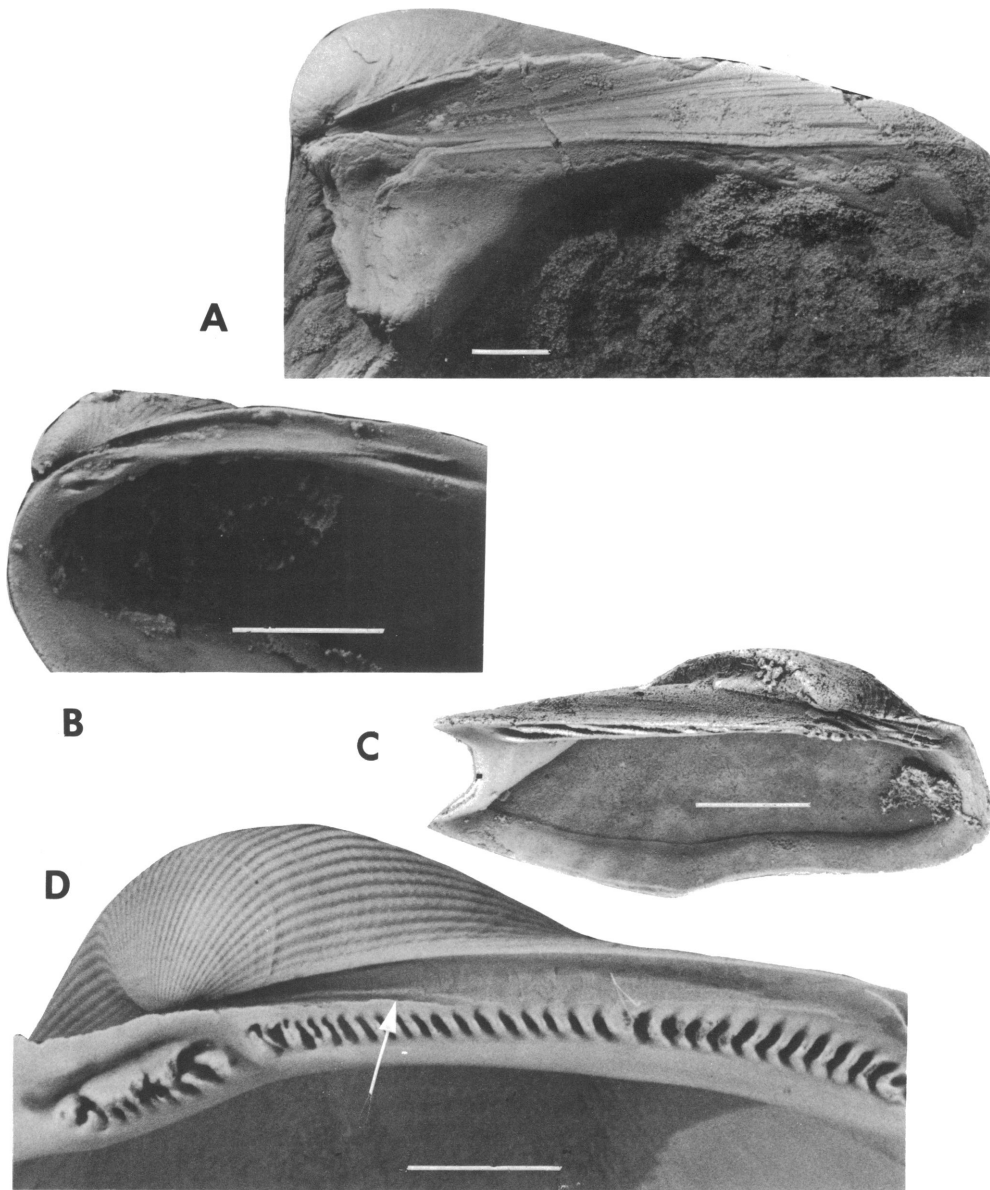


Fig. 5. Growth-line traces of transitional ligament in several families of Pteriomorphia. The scale bars represent 5 mm. **A.** Pteroid (pergamidiid), *Eurydesma playfordi* Dickins. Permian, eastern Australia, Austral. Bur. Mineral. Resources no. 2232. **B.** Cyrtodont, *Cypricardinia* sp., Permian, West Texas, Am. Mus. Nat. Hist. no. 42886. **C.** Parallelodont, probably a n. gen., n. sp. Transitional ligament limited to posterior part of cardinal area, duplivincular on anterior part. Permian, West Texas, Am. Mus. Nat. Hist. no. 42887. **D.** Arcoid, *Lunarca ovalis*. Recent, Georgia. Am. Mus. Nat. Hist. no. M28579. Arrow points to groove of the secondary lamellar band.

bones. The cardinal areas are thus external and they converge downward from the dorsal margins to the hinge line at about 15 up to 45°.

Here we consider eight well-defined types, or grades, of ligaments. They may be designated primitive, transitional, parivincular, opisthodetic-duplivincular, amphidetic-du-

plivincular, external-alivincular, internal-alivincular, and multivincular (fig. 3). In conventional usage many of the pteriomorph families display only one grade of ligament but there are some with more than one ligament type. Ambiguity thus introduced suggests a need to reevaluate the taxonomic significance of the several ligament grades in a general morphological and historical context.

Our purpose here is to report some observations and ideas resulting from our continuing studies of bivalves that lived in the seas around the time of the great Late Permian and Early Triassic extinction crisis. It is a cursory review in which we postpone a consideration of pteriomorphian systematics.

We are indebted to E. R. Trueman and Thomas R. Waller for reading our manuscript and making useful suggestions.

THE PRIMITIVE LIGAMENT

The most ancient bivalves, *Fordilla* and *Pojetaia* of the Lower Cambrian, had the simplest ligament remindful of modern *Mytilus* or *Malletia* (Runnegar and Bentley, 1983) (figs. 1A, 3, primitive). The ligament in *Mytilus*, however, is reinforced below by shell "pseudonymphs."

Runnegar and Bentley and some others (e.g., Morris, 1979) referred to this ligament as parivincular (figs. 1B, 3), but we prefer to reserve that term in the conventional sense for the more advanced C-spring ligament of the heterodonts, unionids, and trigoniaceans (fig. 1B). The primitive ligament has also been called primary by Owen et al. (1953).

In the primitive ligament, lamellar and fibrous layers form an elongate ribbon between the dorsal margins of the valves (Trueman, 1950). The lamellar part extends farther toward the rear than the fibrous part in an overlapping relationship that keeps them in contact with the mantle so that both increase in length as the shell grows. As the ligament splits anteriorly the gap in the fibrous part is reinforced by a secondary band of lamellar conchiolin.

THE TRANSITIONAL LIGAMENT

The transitional ligament may be opisthodontic or amphidetic. It occurs in several pteriomorphian groups, e.g., pergamidiids,

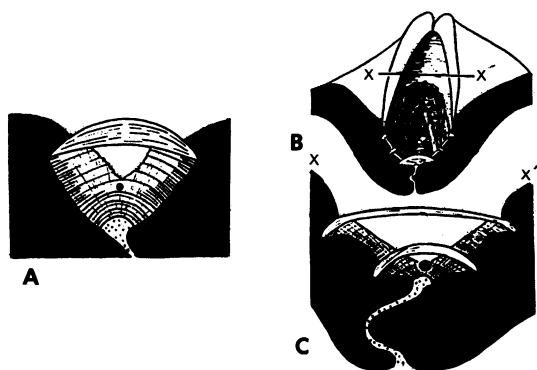


Fig. 6. Sections of modern arcacean ligaments. A. Transitional grade in *Lunarca ovalis* (= *pexata*) Say. Dot indicates location of hinge axis. Fibrous layer (ruptured), below; lamellar above. B, C. Duplivincular ligament of *Scapharca transversa*. Three-dimensional view (above) shows location of section (below). Two bands of lamellar ligament are separated by split and inoperable fibrous layers (after Newell, 1942). Stipple pattern represents mantle; black, the shell.

cyrtodonts, arcids, and parallelodonts (fig. 5). A living example is the arcid genus *Lunarca* in which the structure is that of a juvenile duplivincular ligament possessing a single dorsal band rather than multiple lamellar bands (fig. 5D). It may have been a simpler precursor of the duplivincular ligament (see below), but it could also conceivably be pae-dogenetic, derived from that structure by neoteny. The phyletic polarity is uncertain and we suspect that both conditions may exist.

The transitional ligament is usually attached to the outer areas of hinge plates (figs. 4B, 5, 6A). In addition to the single lamellar band at the dorsal margin of each cardinal area a secondary band is inserted below the beaks near the hinge line where the fibrous layer splits (figs. 2e, f, 5D). This seems to compensate for the loss of function of the split portion of the fibrous band in the inter-umbonal area.

THE DUPLIVINCULAR LIGAMENT

The duplivincular ligament (Newell, 1942, p. 29) is composed of a series of alternating bands of lamellar and fibrous conchiolin extending obliquely along each cardinal area

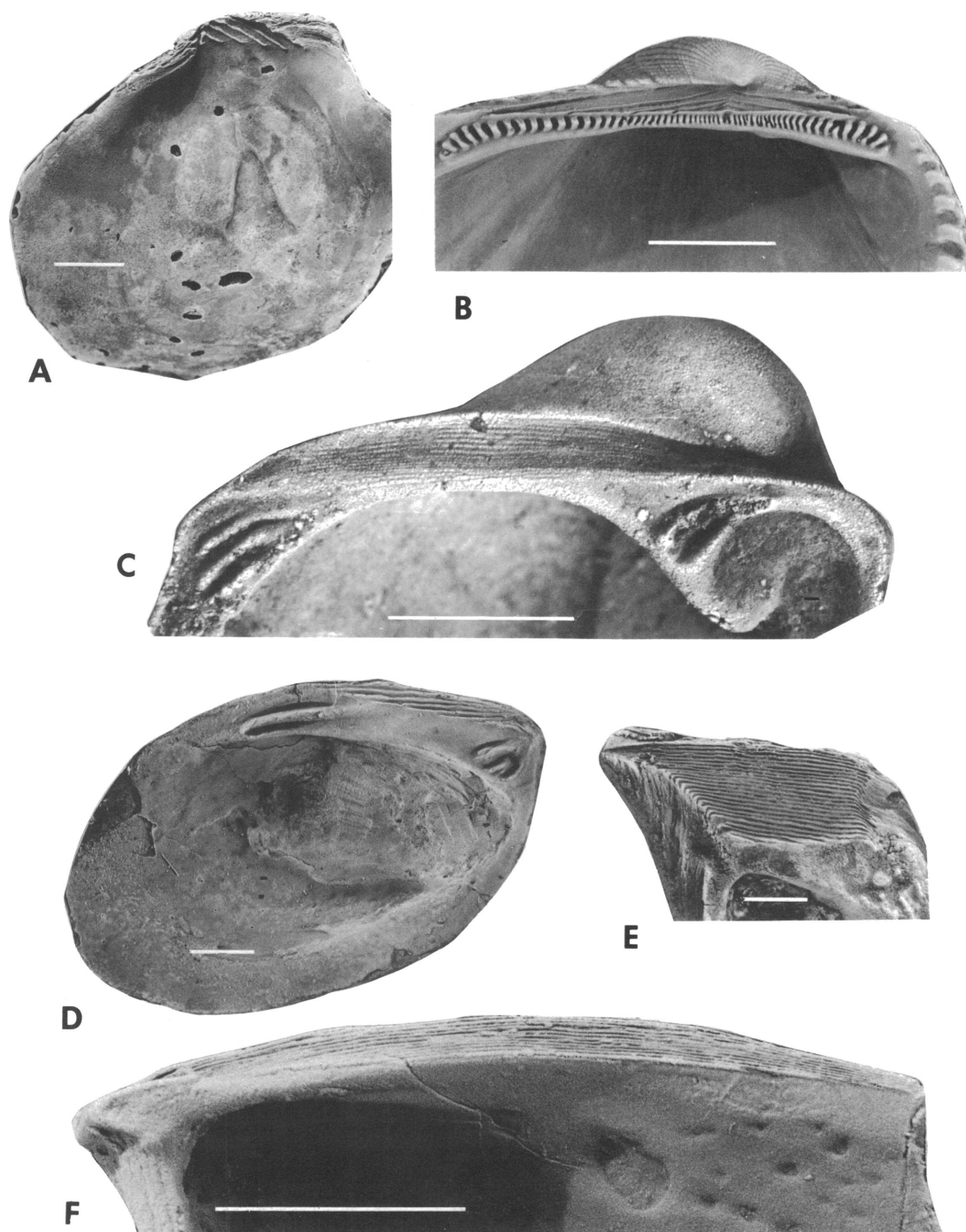


Fig. 7. Duplivincular ligament in diverse pteriomorph families. Scale bars represent 5 mm. A. An Anomiacean, *Permanomia texana* Newell and Boyd, with opisthodetic-duplivincular hinge. Permian, West Texas, Am. Mus. Nat. Hist. no. 28937. B. Arcid, *Scapharca transversa* (Say) with amphidetic-duplivincular ligament area. Recent, Florida, Am. Mus. Nat. Hist. no. M28708. C. Cyrtodont, *Vanuxemia gibbosa* Ulrich, opisthodetic-duplivincular ligament. Middle Ordovician, Tennessee, U.S. Natl. Mus. no. 46942. The very fine ligament grooves simulate growth lines but, unlike growth lines, the last

(figs. 6B, C, 7). Each lamellar band is inserted in a narrow groove that extends from below the beaks to the hinge margin. The bands resemble replications of the dorsal lamellar band of the transitional ligament.

The duplivincular ligament is commonly opisthodontic in juveniles and most adults but also it may be symmetrically amphidetic or become amphidetic during growth, as in *Scapharca transversa* (fig. 7B). The grooves in the amphidetic varieties form an inverted chevron pattern with the apex under the beaks. The duplivincular ligament characterizes several families in the Cyrtodontacea, Pteriacea, Pectinacea, Anomiacea, and Arcaea.

Recognition of the duplivincular condition in extinct taxa poses no problem where the ligament area exhibits coarse grooves that intersect the hinge margin at a high angle (fig. 7A, B, D, and E). At the other end of the duplivincular spectrum, however, the angle of intersection may be so low that all but the one or two last-formed grooves extend all along the length of the hinge and appear to be parallel with its ventral margin (fig. 7C, F). This has led Dickins (1983), to conclude that the relationship of grooves to margin is not significant. We, however, believe that confusion arises only where the grooves are very fine and the preservation of fossils is imperfect.

Discrimination between certain duplivincular, transitional (fig. 5), and elongate alivincular (fig. 8A, B) ligament areas can be difficult. Pojeta (1978, p. 236) encountered a problem in dealing with Ordovician cyrtodontids. Noting that the parallel grooves on his shells apparently did not intersect the hinge margin, he concluded that the ligament was not duplivincular. He also rejected the growth-line explanation because the grooves on the ligament area seemed to lack lateral continuity with growth lines on adjacent parts

of the shell. As an alternative, he suggested that the grooves represent successive insertions of a single, ventrally migrating ligament band. If so, the situation would be unlike any living bivalve known to us.

THE ALIVINCULAR LIGAMENT

This ligament is characteristically amphidetic, rarely opisthodontic. The compressional part is a more or less triangular pad, the resilium, segregated in a triangular depression, the resilifer, between anterior and posterior areas of lamellar ligament extending along the length of the hinge axis (fig. 8A, B, D, E).

Some have elongated resilifers in which the base of the triangle greatly exceeds its height. Rarely, the resilifer is very broad, asymmetric, and marked with longitudinal grooves that suggest seasonal growth interruptions (fig. 8A).

The alivincular ligament may be attached to the cardinal areas of hinge plates, as with the Aviculopectinidae and Pteriidae. This is called the *external* alivincular ligament (figs. 3, 4B, 8A, B, E).

Or, the alivincular ligament may be essentially internal, in which case true cardinal areas are lacking (figs. 3, 4A, 8D). The internal resilium of the Pectinidae, for example, differs from the external resilium of other Pteriomorpha. The central part of the former lacks aragonite needles (fig. 9B) and the calcified lateral portions are rigid and of uncertain function (Newell, 1937; Trueman, 1953; Waller, 1976). They may be evolutionary relicts of the fibrous resilium.

The curious Upper Paleozoic aviculopectinacean genus *Euchondria* (Euchondriidae) has an external alivincular ligament. The adult hinge retains juvenile pseudotaxodont teeth (fig. 10A) similar to those of many immature pteriomorphs (fig. 10B). Some modern pectinids also retain these neotenous structures

←

formed grooves are progressively shorter and they intersect the hinge margin. D. Cyrtodont with opisthodontic-duplivincular ligament grooves, *Ptychodesma knappianum* Hall and Whitfield. Middle Devonian, New York State, Am. Mus. Nat. Hist. no. 361888. E. Myalinid, *Septimyalina perattenuata* (Meek and Hayden). Ligament opisthodontic-duplivincular. Upper Pennsylvanian, Kansas, Am. Mus. Nat. Hist. no. 42888. F. Myalinid, *Selenimyalina meliniformis* Newell. Ligament opisthodontic-duplivincular. The numerous ligament grooves are comparatively fine. Upper Pennsylvanian, Kansas, Am. Mus. Nat. Hist. no. 42889.

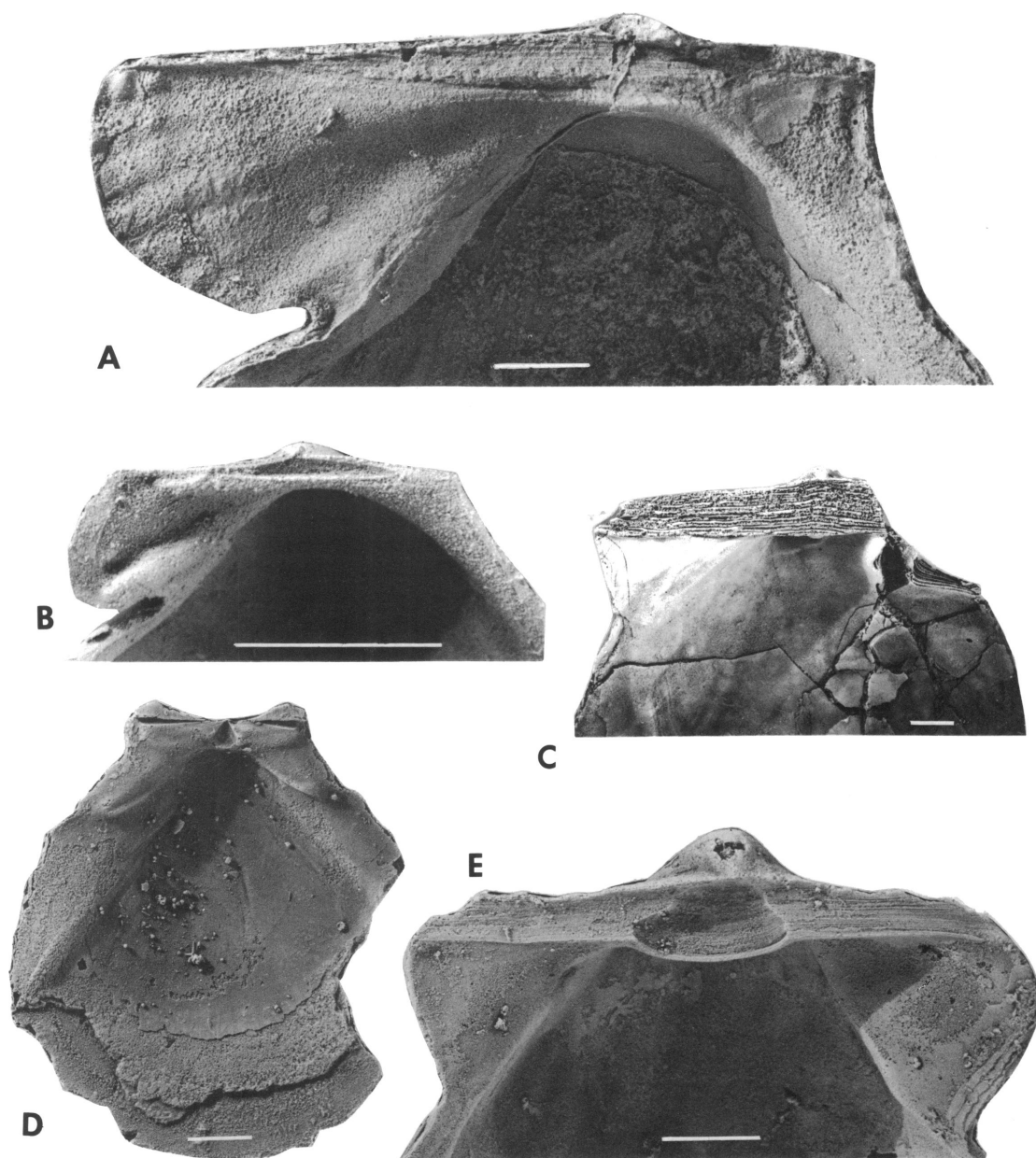


Fig. 8. Diverse pectinoid ligaments. Scale bars represent 5 mm. **A.** Deltoplectinid, *Deltopecten* sp. Interpreted by comparison with B, below, as external-amphidetic. The very elongate resiliifer is marked by regular, probably seasonal, growth lines. Permian, South Kennedy, Queensland, Australia, Am. Mus. Nat. Hist. no. 42890. **B.** Streblopteriid, *Streblopteria* sp., similar to fig. 8A but lacking conspicuous growth lines. Permian, West Texas, Am. Mus. Nat. Hist. no. 42891. **C.** Pterinopectinid with an amphidetic-duplivincular ligament. *Pterinopectinella* sp. Permian, West Texas, U.S. Natl. Mus. no. 388871. **D.** Entoliid, *Entolium* sp. Illustrating internal-alivincular ligament. Permian, Texas, U.S. Natl. Mus. no. 388870. **E.** Aviculopectinid, *Etheripecten vanvleeti* (Beede). External-alivincular ligament. Permian, Texas, Am. Mus. Nat. Hist. no. 42893.

that continue to be functional well into maturity (fig. 10C). In 1937 when Newell dis-

cussed *Euchondria* he mistook the gaps between denticles for multivincular resiliifers.

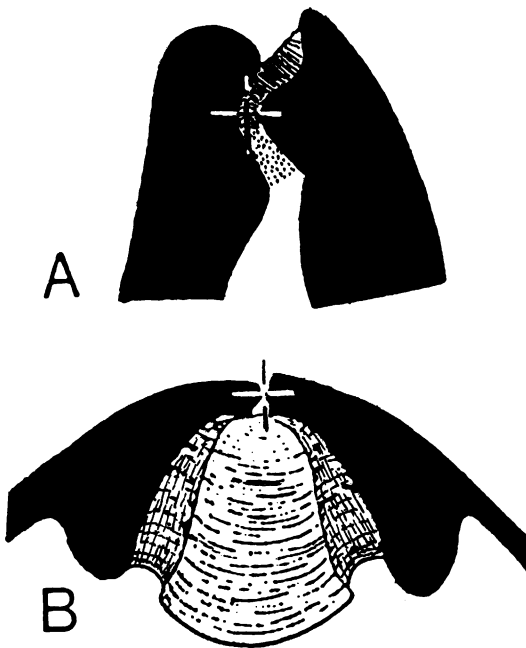


Fig. 9. Internal alivincular ligament of *Chlamys islandica* Müller, modern pectinid. A. Transverse section of lamellar band near posterior end of the hinge (stipple area represents mantle). B. Transverse section at hinge midlength of uncalcified compressional ligament (center), flanked by relict nonfunctional fibrous ligament pads. (Cross represents hinge axis. Black indicates shell. After Newell, 1937.)

THE MULTIVINCULAR LIGAMENT

This ligament possesses multiple resilifers of the external alivincular type and it is usually opisthodontic. Among living bivalves (fig. 3) the multivincular ligament is characteristic of the Isognomonidae (Pteriacea). It is also the mode of several extinct families including the very successful Mesozoic Inoceramidae and some aberrant oysters which have been given the generic name *Pernostrea* (Stenzel, 1971, p. 974). The Noetiidae (Arcacea) possess superficially similar multiple resilia but they are unique in being formed of lamellar rather than fibrous bands.

Sequential development of the multivincular ligament in an individual suggests that it could have been derived phyletically from the external-alivincular ligament by serial repetition. However, as well as we can now ascertain the stratigraphic succession does not

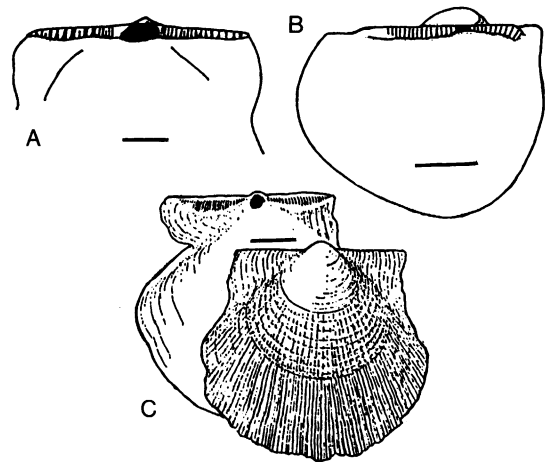


Fig. 10. Pseudotoxodont hinges characteristic of the early development of some pteriomorphians. Scale bars represent 0.5 mm. A. Neotenus hinge in *Euchondria levicula* Newell, a small adult aviculopectinacean with an external ligament. Middle Pennsylvanian near St. Louis, Mo., Univ. Kansas no. 58805; B. external ligament in juvenile *Pteria staminensis*, Recent, after Bernard (1896); C. internal ligament of *Pecten magellanicus*, Recent, after Jackson (1890).

support this hypothesis. Morris (1979, fig. 8) thought that the multivincular ligament might be derived from the duplivincular structure but we do not know of any evidence for this.

In the Permian Period the multivincular ligament suddenly appeared in a population of the Australian ambonychiid genus *Atomodesma* (*Aphanaia*) which had a very different (transitional) ligament (Browne and Newell, 1966; Kauffman and Runnegar, 1975; Newell and Boyd, 1978; Dickins, 1983). The Permian multivincular variety was given the generic name *Permoceramus* by Waterhouse (1970). Later Muromtseva (1979) found the same association of *Permoceramus* and *Atomodesma* in northeastern Siberia. Except for the ligament, the shells of the two genera are virtually identical and they are very like the Mesozoic Inoceramidae.

Everyone who has studied the geological occurrences of *Permoceramus* has regarded it as marking the intrapopulation origin of the multivincular pteriacean family Inoceramidae which otherwise is not known prior to the Jurassic a hundred million years later.

Why was *Permoceramus* so short-lived as compared with the later inoceramids?

Because of this exceptional Permian occurrence Kauffman and Runnegar (1975) have suggested that the multivincular family Inoceramidae may logically be extended to include not only *Permoceramus*, but also the associated *Atomodesma* with its transitional ligament.

Could *Permoceramus* simply be an unsuccessful variant that was repeated again in the Jurassic as *Inoceramus*? If they are not closely related this would be a most remarkable example of nearly identical iteration because *Permoceramus* is morphologically an inoceramid in all known details. Or did *Permoceramus* retire to an unknown haven during the Permo-Triassic environmental crisis until its chance to spread throughout the world as *Inoceramus* in the later Mesozoic?

ADAPTIVE SIGNIFICANCE OF LIGAMENT PATTERNS

The adaptive significance of ligament type is not clear. In a series of experiments in 1950–1969, Trueman studied the relative efficiency of several kinds of ligaments in living bivalves. This was done by measuring stress differences between opening and closing moments of the valves as follows (Trueman, 1964).

Ratio of Ligament Resistance to Muscle Adduction (in Grams)

Arcacea (duplivincular)	83/105, 79%
Mytilacea (primitive)	660/780, 84%
Ostreacea (alivincular-external)	370/425, 87%
Pectinacea (alivincular-internal)	160/167, 96%

Evidently there is some relationship between ligamental resistance and mode of life of the various species, but it is not marked. Shallow burrowers among living pteriomorphs (e.g., arcoids, fig. 2) have relatively weak ligaments which are aided in opening the valves by a strong foot (Thomas, 1978), while swimmers have relatively stronger and more efficient ligaments. Among these, the Pectinidae have internal alivincular ligaments but the Limidae, with external alivincular ligaments, are also swimmers.

Contrasted with the more convex arcaceans, the Paleozoic Pterinopectinidae, with

duplivincular ligaments and probably a small, weak foot, had thin, flattened shells shaped very much like living scallops. By analogy they were probably active members of the epifauna.

The Mytilidae, Ambonychiidae, Myaliniidae, and Inoceramidae probably were all adapted to similar modes of life—i.e., sedentary and byssate. Apart from the fact that they were all opisthodontic, they had different ligament styles—what we are calling primitive, transitional, duplivincular, and multivincular, respectively. There is little, if any, correlation in these families between shell form and ligamental grade. The ligaments alone do not tell us about life modes.

CONCLUSION

Although the several distinctive kinds of pteriomorphian ligament patterns have been given high priority in taxonomic discrimination and some appear to have been stable for long geological intervals, they are not themselves reliable guides to relationships at high taxonomic levels. The various ligament grades are basically the same in construction and function but they differ in patterns that have uncertain interrelationships. The high frequency of convergence of ligament grades in separate taxonomic categories indicates a need for a thorough revision of morphology and taxonomy of the subclass beginning preferably at low taxonomic levels.

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