

---

## Morphology, Morphoclines and a New Classification of the Pteriomorphia (Mollusca: Bivalvia) [and Discussion]

T. R. Waller and E. L. Yochelson

*Phil. Trans. R. Soc. Lond. B* 1978 **284**, 345-365

doi: 10.1098/rstb.1978.0072

---

### References

Article cited in:

<http://rstb.royalsocietypublishing.org/content/284/1001/345#related-urls>

### Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

---

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

---

## Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia)

BY T. R. WALLER

*Department of Paleobiology, Smithsonian Institution, Washington, D.C. 20560, U.S.A.*

Two morphological paradigms have long been used in comparative anatomical studies of bivalves: (1) the primary ligament is three-layered, with the layers corresponding to three shell layers; and (2) the primary mantle edge is composed of three folds with clearly defined functions. The results of studies of larval development indicate, on the contrary, that the primary ligament is completely organic. Calcified, fibrous ligamental material develops from lamellar material near areas of contact between ligament and shell, and development of the fibrous portions then proceeds toward the mid-line, finally achieving in many lineages a continuous fibrous bridge between valves. Furthermore, these results suggest that the mantle edge in the Bivalvia is primarily twofold and that the only clearly homologous structure between major groups is the periostracal groove itself.

These morphological concepts, with other new and previously published data on shell ultrastructure, ligaments, mantle edges, ctenidia, palps, lips, stomachs, muscles, and photoreceptors, lead to a new picture of the evolution of primitive and derived character states in groups previously included in a subclass Pteriomorphia. Furthermore, a cladistic analysis of these data allows predictions of the morphology of ancestors which can be tested by reference to the preserved morphology and sequence of fossils.

A new phylogenetic classification separates these groups into three superorders within the subclass Autobranchia: Isofilibranchia (mytiloids), Prionodonta (arcoïds), and Pteriomorphia. The most complex radiation has been in the Pteriomorphia. Three orders originated in the early Palaeozoic: Pterioida, Limoida, and Ostreoida. The Pterioida and Ostreoida developed monomyarian, pleurothetic states independently, and each order developed its own mode of shell secretion.

Further differentiation in the order Ostreoida occurred in the mid-Palaeozoic, producing two suborders, the Ostreina and Pectinina, both of which had already developed foliated calcitic ultrastructure from simple prismatic structure. By the early Mesozoic, the Ostreina had given rise to three extant superfamilies – the Ostreacea (true oysters), Dimyacea, and Plicatulacea – through atrophy of the foot, the assumption of a pleurothetic state on either the left or right side, and early obligate cementation. The Pectinina, through retention of the foot and the assumption of a pleurothetic mode of life, had evolved before the late Palaeozoic to the Anomiacea and Pectinacea.

Within the superfamily Pectinacea, four extant families have origins ranging from early Carboniferous to Cretaceous in age: Propeamussiidae, Pectinidae, Syncyclonemidae, and Spondylidae. The new family Syncyclonemidae, which contains a genus long assumed to have become extinct at the end of the Cretaceous, is here recognized in the Recent and late Pleistocene on opposite sides of the Earth.

With regard to extinct groups, many genera previously assigned to the Pteriacean family Malleidae belong in the Ostreacea on the basis of shared derived character states. Incorporation of these taxa as well as the Dimyacea in the Ostreina suggests that oysters have a dimyarian, possibly non-pleurothetic, origin and cannot have evolved from forms like the Pseudomonotids, which retained their foot and became pleurothetic. The new name Buchiacea is introduced for a set of extinct taxa within the suborder Pectinina including the Buchiidae, Monotidae, Oxytomidae, and Pseudomonotidae of previous authors. Derivation of this group is from the common ancestry of the Anomiacea and Pectinacea. The extinct Palaeozoic Aviculopectinidae,

25-2

Pterinopectinidae, Deltopectinidae, and Leiopectinidae are grouped in a superfamily Aviculopectinacea, which also appears to have branched from the early ancestry of the Pectinina.

### INTRODUCTION

New morphological analyses studied in a taxonomic context can lead directly to a new single-character classification, as in the classic study of gill structure of bivalves by Ridewood (1903). Alternatively, they can provide a means whereby previous taxobases are re-examined and re-evaluated, leading to a new multi-character classification which better reflects phylogeny. The latter approach is preferable, because evolution normally involves suites of characters and produces organisms which are mosaics of primitive and more recently evolved characters. It is therefore unlikely that a single taxobasis will be phylogenetically meaningful for many taxa.

In the present study, the multi-character approach is taken in an analysis of phylogenetic relations of arks, mussels, oysters, scallops, and related bivalves which have been variously grouped in recent years in the subclass Pteriomorphia (Newell, in Moore 1969, p. 248), the subclasses Isofilibranchia and Pteriomorphia (Pojeta 1971), or the orders Cyrtodontida and Pectinida within the superorder Autobranchia (Nevesskaya, Scarlato, Starobogatov & Eberzin 1971). The morphology of extant taxa is examined first. Secondly, a phylogeny is inferred from the evolutionary directions suggested by morphoclines, which are primitive-derived transformation series of characters (Maslin 1952). Finally, the phylogeny is tested by reference to the fossil record. The internal logic of such an approach has been aptly described by Schaeffer, Hecht & Eldredge (1972).

Specimens examined are in the U.S. National Museum of Natural History, British Museum (Natural History), and Belgian Royal Institute of Natural Sciences amounting to approximately 300 genera and 1000 species. In addition, approximately 6000 scanning electron micrographs of the ultrastructure and development of shells and ligaments have been examined, and living specimens were observed during field work in Florida, Bermuda, and Belize.

### 2. MORPHOLOGICAL CONCEPTS

Because the 'expectations of theory color perception' (Eldredge & Gould 1972), it is not surprising that certain morphological concepts which have long been accepted by many students of the Bivalvia have influenced morphological observation as well as interpretation. My own interpretations of the development and evolution of ligaments and mantle edges, which differ from the interpretations of others, will be discussed first, because they colour my own perception and analysis and affect terminology in following sections.

FIGURE 1. Grades in the evolution of ligaments in the Isofilibranchia, Prionodonta, and Pteriomorphia. Three diagrams illustrate each ligament type. The bottom diagram represents a cross section through a resilium or the centre of the ligament if a resilium is absent; the middle diagram represents a ventral view of the ligament; and the top diagram represents an anterior-posterior section through the active ligament as well as a planar view of the ligament area resulting from ventral migration of the active ligament. Periostracum and lamellar ligament are shown in solid black, fibrous ligament by vertical lines. Ligament areas are marked by horizontal lines; ligament pits or grooves occupied by inactive lamellar or fibrous ligament are unlined. Overarching (o.l.) of a ligament trace is indicated by horizontal lines extending over the ligament trace.

Examples of each ligament type are as follows: A, late larval *Argopecten*; B, early Palaeozoic cyrtodontids; C, early postlarval *Argopecten*; D, mature pectinids; E, *Lima lima*; F, *Arca*; G, *Plicatula*; H, *Ostrea*; I, *Noetia*; J, *Spondylus*; K, *Glycymeris*; L, *Isognomon*; M, *Mytilus*; and N, *Dimya*. Arrows show the evolution of grades, not the evolution of exemplary taxa.

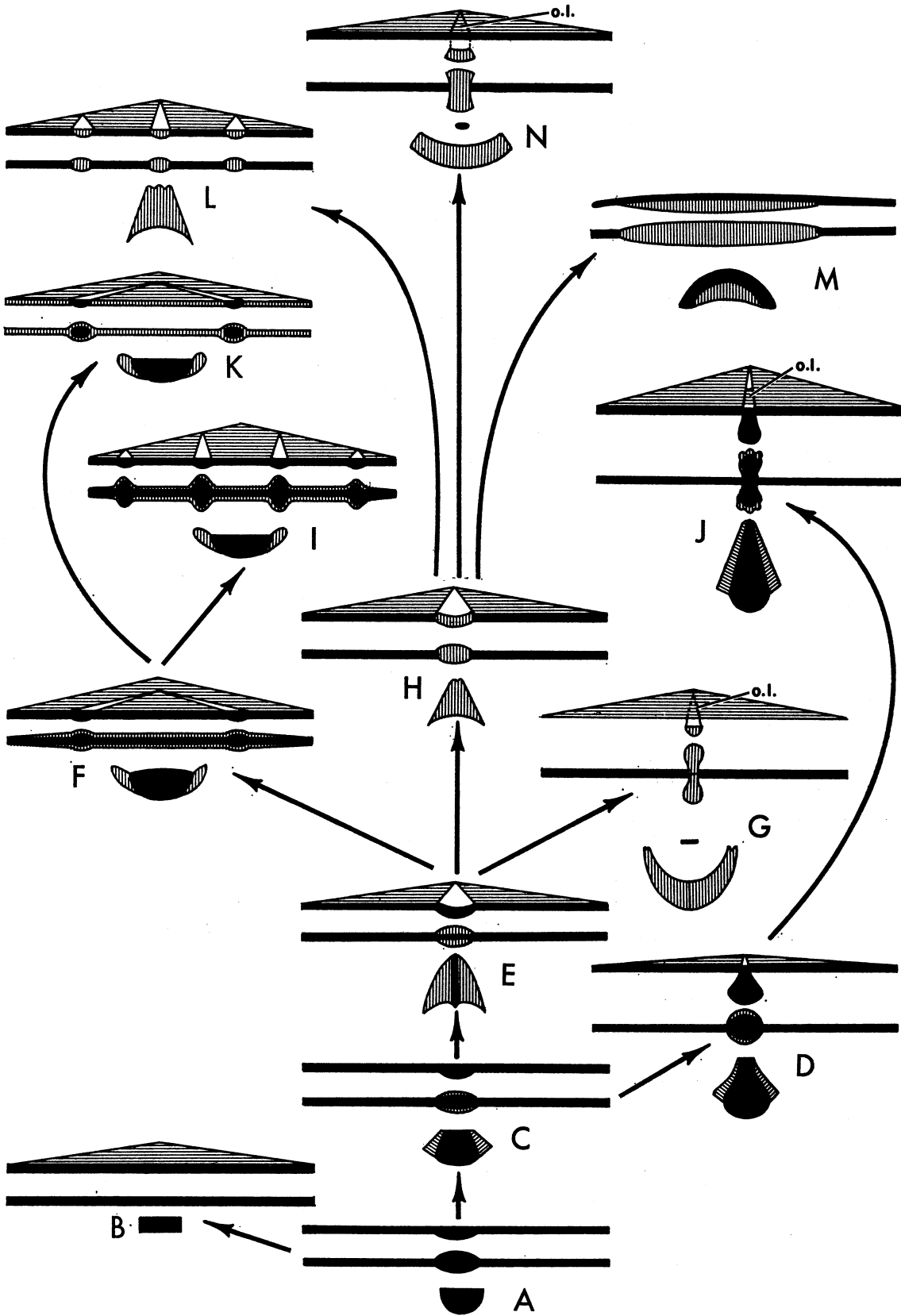


FIGURE 1. For description see opposite.

First, the hypothesis of Owen, Trueman & Yonge (1953) that the bivalve ligament is primarily three-layered (periostracum, lamellar layer, fibrous layer) and that these layers represent modifications of three primary layers in the shell (periostracum and two calcareous layers) is not supported by the following observations: (*a*) the boundaries between the shell layers do not as a rule coincide with boundaries between ligament layers where they meet along the hinge; (*b*) staining with Mallory's triple stain (Trueman 1949), although effective in distinguishing lamellar and fibrous ligament, does not unequivocally demonstrate a difference between periostracum and lamellar ligament (Beedham 1958), particularly in view of the fact that the periostracum is now known to be multilayered; (*c*) studies of the early ontogeny of the ligament (Waller 1976*c*) indicate that the uncalcified, lamellar portion of the ligament represents hypertrophied periostracum and the calcified, fibrous component develops later as a modification of the lamellar component, beginning laterally and extending toward the hinge line until a continuous fibrous bridge between valves is formed. It therefore appears that ligaments in which a wall of lamellar material separates fibrous ligament along the hinge line, as in *Nucula* and *Pecten*, are more primitive than those in which calcification extends across the hinge line, as in most bivalves. These relations are shown diagrammatically in figure 1, which should be compared with figures by Newell (1938, fig. 13) and Trueman (in Moore 1969, fig. 52).

Secondly, the concept that the mantle edges of bivalves characteristically display three folds is weakened by the existence of a fourfold condition in many Veneracea (Oldfield 1955; Ansell 1961; Ockelmann 1964; Hillman & Shuster 1966), Tellinacea (Yonge 1949), and Lucinacea (Allen 1958). Furthermore, the inference that the threefold condition is primary (evolutionarily primitive) ignores the fact that a twofold condition ontogenetically precedes the threefold in larval stages (Ansell 1962; Bayne 1971; Stasek & McWilliams 1973) and that the twofold condition persists even to maturity in some Arcoida (Waller, unpublished data). In *Arca*, the exquisitely developed compound eyespots are developed on the *outer* fold (Rawitz 1890) and receive light through the newly generated periostracum, which lies against the inner surface of the fold. Here the outer fold assumes the secretory, sensory, and water-control functions generally attributed, respectively to the outer, middle, and inner folds.

Terminologically, it would seem reasonable to refer to mantle folds by a system which does not connote homology except for the periostracal groove itself, which indeed appears to be homologous through the Bivalvia. Such a system, whereby mantle folds are numbered consecutively outward and inward from the periostracal groove, is adopted in the following diagnoses and discussion.

Other changes in terminology also follow from the new morphological concepts. The primary secretory discontinuity in the so-called mantle isthmus has been emphasized by referring to ligaments as having fibrous material which is either continuous from one valve to the other, as in *Ostrea* and *Glycymeris*, or discontinuous and separated by a junction of lamellar material, as in *Pecten* and *Arca* (§ 4).

The terminology of shell ultrastructural fabrics follows that of Taylor, Kennedy & Hall (1969), with the exception that the modifiers inner, middle, and outer have been avoided. Calcitic layers are generally outer layers, although they may expand distally from the hinge region over the inner surface of previously formed aragonitic layers. Where both simple prismatic and foliated calcitic structures occur in the same shell, the foliated structure forms on the inner side of the prismatic, which is outermost. Where both calcitic and aragonitic structures are present in the same shell, the aragonitic structures form on the inner side of calcitic

structures. The pallial line may form the boundary between the outer, calcitic and inner, aragonitic structures, but generally it does not. Apparently all myostraca are irregularly prismatic aragonite, and these are excluded from further consideration here. References to shell layers in the diagnoses are to layers secreted by the mantle.

Terms for ligaments follow Moore (1969), with two additional distinctions. *Alivincular* refers to a ligament, the central portion of which occupies a more or less triangular ligament pit. This ligament pit, or resifier, may have an altitude which is perpendicular to the hinge line, as in some Pectinidae, or which may be very oblique, as in some Pteriidae. In contrast, *elongate opisthodetic* ligaments, as in *Mytilus* and *Pinna*, have no distinct resifier throughout most of their post-larval ontogeny.

TABLE 1. CLASSIFICATION

Subclass Autobranchia (in part)† Cam.? – Rec.
Superorder Isofilibranchia† Ord. – Rec.
Order Mytiloida† Ord. – Rec.
Superfamily Mytilacea Ord. – Rec.
Superorder Prionodonta† Ord. – Rec.
Order Arcoida Ord. – Rec.
Superfamily Cyrtodontacea Ord. – Dev.
Superfamily Arcacea Dev. – Rec.
Superfamily Limopsacea Perm. – Rec.
Superorder Pteriomorphia† Ord. – Rec.
Order Pterioida† Ord. – Rec.
Suborder Pteriina† Ord. – Rec.
Superfamily Pteriacea Ord. – Rec.
Suborder Pinnina‡ Dev. – Rec.
Superfamily Pinnacea Dev. – Rec.
Order Limoida‡ Ord.? – Rec.
Superfamily Limacea Ord.? – Rec.
Order Ostreoida‡ Ord.? – Rec.
Suborder Ostreina† Perm.? – Rec.
Superfamily Ostreacea† Perm.? – Rec.
Superfamily Dimyacea‡ Jur. – Rec.
Superfamily Plicatulacea‡ Trias. – Rec.
Suborder Pectinina‡ Ord.? – Rec.
Superfamily Aviculopectinacea‡ Ord.? – Jur.
Superfamily Buchiacea‡ L. Carb. – Cret.
Superfamily Pectinacea† L. Carb. – Rec.
Family Propeamussiidae† L. Carb. – Rec.
Family Pectinidae† Trias. – Rec.
Family Syncyclonemidae‡ Cret. – Rec.
Family Spondylidae Jur. – Rec.
Superfamily Anomiacea Perm. – Rec.
Position uncertain
Superfamily Ambonychiacea Ord. – Jur.?

† Emended with respect to taxonomic content or concept appearing in Newell (in Moore 1969, p. 248) or not appearing in that work. Only the extant families of the Pectinacea are listed.

‡ New taxon.

### 3. DIAGNOSES

Table 1 lists both extant and extinct taxa of pteriomorph bivalves from the level of superorder to that of superfamily. In the case of the extant Pectinacea, reference to the family level is necessitated by significant variation in shell ultrastructure, which is conservative within other superfamilies. The following diagnoses are for extant taxa only; the discussion of extinct taxa (§ 5) follows the discussion of morphoclines. Nomenclatural conventions with regard to priority

and word endings (below the level of superorder) follow those of Moore (1969). Emendation signifies important change in concept or taxonomic content from that in Newell (in Moore 1969, p. 248) and Stenzel (1971).

Neveeskaya *et al.* (1971) have argued that in view of the uniformity of general organization of the Bivalvia, groups should be classified at a level no higher than that of superorder. In contrast, Newell (1965; in Moore 1969 p. 248) and Pojeta (1971) placed many major groups at the level of subclass. At this point I prefer a middle ground and recognize two subclasses in the Bivalvia, the Protobranchia and Autobranchia as delineated by Neveeskaya *et al.* (1971). Their third major group, the Septibranchia, is probably polyphyletic (Bernard 1974; Runnegar 1974), and the taxa composing it may be distributed in the other two subclasses. The superorders treated herein are all within the subclass Autobranchia and share the same basic type of larval development, filamentous gill, and filter-feeding mechanism.

Class Bivalvia Linné, 1758

Subclass Autobranchia Grobben, 1894

Superorder Isofilibranchia Iredale, 1939

Anisomyarian or monomyarian Bivalvia having three folds on the mantle edge, the second inner folds fused at a single point ventral to the dorsal excurrent region, thereby setting off an excurrent aperture or siphon; siphonal mantle septum projecting inward from base of excurrent aperture or siphon. Outer calcitic shell layer, if present, fibrillar in ultrastructure, with each fibril a calcite crystal terminating distally in a pyramid bounded by crystal faces; other shell layers aragonitic, either nacreous, crossed-lamellar, or both. Ligament alivincular or elongate opisthodontic, with fibrous material extending continuously from one valve to the other.

Order Mytiloida Férussac, 1822

Characters of the superorder.

Superfamily Mytilacea Rafinesque, 1815

Characters of the superorder.

Superorder Prionodonta MacNeil, 1937

Isomyarian or anisomyarian Bivalvia having an outer fold and one or two inner folds on the mantle edge, the outer fold muscular and generally bearing eyespots, the inner folds lacking fusion ventral to the excurrent region. Shell completely aragonitic, with outermost layer simple crossed-lamellar and complex-prismatic in structure or only the former; inner layer complex crossed-lamellar. Ligament duplivincular.

Remarks. The presence of complex-prismatic aragonite in the outer shell layer of some arcoids has recently been documented by Kobayashi (1976*a, b*).

Order Arcoida Stoliczka, 1871

Characters of the superorder.

Superfamily Arcacea Lamarck, 1809

Trigonal or anteriorly–posteriorly elongate, transversely inflated Arcoida with fibrous portions of duplivincular ligament interrupted along the hinge line by a medial wall of lamellar material.

## Superfamily Limopsacea Dall, 1895

Circular, ovoid, or subtrigonal Arcoida, not greatly transversely inflated, with fibrous portions of duplivincular ligament extending from one valve to the other without lamellar interruption.

Remarks. The family Manzanellidae was questionably included in the Limopsacea by Keen & Newell (in Moore 1969, p. 269). However, Allen & Sanders (1969) showed that the extant genus *Nucinella* is a protobranch, and Nevesskaya *et al.* (1971) recognized the proto-branchiate nature of the family as a whole. The shell ultrastructure of *Nucinella* (Taylor *et al.* 1969) is in accord with this placement.

Keen (in Moore 1969, p. 269) also included the Philobryidae with a query in the Limopsacea. In spite of their anisomyarian condition and *Mytilus*-like form, there is no question that this group belongs in the Arcoida on the basis of its anatomy and shell ultrastructure.

Superorder Pteriormorphia Beurlen, 1944 [*emend.*]

Anisomyarian or monomyarian Bivalvia with one outer and two inner folds on mantle edge, without mantle fusion ventral to the excurrent region, and without a mantle septum. Outer calcitic shell layers, if present, simple prismatic and/or foliated in ultrastructure; aragonitic shell layers nacreous or crossed-lamellar. Ligament duplivincular (Palaeozoic only), alivincular multivincular, or elongate opisthodetic, with fibrous material either continuous from one valve to the other or interrupted by lamellar material.

Order Pterioida Newell, 1965 [*emend.*]

Anisomyarian or monomyarian Pteriormorphia having a simple-prismatic, calcitic, outer shell layer and a nacreous aragonitic, inner layer on each valve and lacking foliated calcitic or crossed-lamellar aragonitic ultrastructures. Ligament duplivincular (some Palaeozoic groups), alivincular, multivincular, or elongate opisthodetic, with fibrous portions extending without interruption from one valve to the other.

Suborder Pteriina Newell, 1965 [*emend.*]

Anisomyarian or monomyarian, pleurothetic (on right side) or non-pleurothetic Pterioida with calcitic prisms having uneven and generally incomplete optical extinction parallel to long axis of prisms. Ligament duplivincular (some Palaeozoic groups), alivincular or multivincular.

Superfamily Pteriacea Gray, 1847 [*emend.*]

Characters of the suborder.

## Suborder Pinnina, new suborder

Anisomyarian non-pleurothetic Pterioida with simple calcitic prisms having even and complete optical extinction parallel to long axis of prisms. Ligament elongate opisthodetic. Unique pallial organ and triangular shape associated with partial or nearly complete burial in substrate.

## Superfamily Pinnacea Leach, 1819

Characters of the suborder.

## Order Limoida, new order

Monomyarian non-pleurothetic Pteriormorphia having an outer, calcitic fibrous-homogeneous ultrastructure and inner simple crossed-lamellar aragonite. Ligament alivincular,



with fibrous resilium uninterrupted by medial lamellar material or with a very thin, medial lamellar interruption.

Remarks. Scanning electron microscopy of limoid ligaments reveals a narrow, medial wall of lamellar material within the otherwise completely fibrous resilium of *Lima lima*. Other species examined by scanning electron microscopy (*Acesta excavata* (Fabricius), *Lima pellucida* C. B. Adams, *Limatula sulcata* Brown) have completely fibrous resilia.

Superfamily Limacea Rafinesque, 1815

Characters of the order.

Order Ostreoida Férussac, 1822 [*emend.*]

Anisomyarian or monomyarian Pteriomorphia having prominent foliated-calcite shell ultrastructure in some cases overlain by outer, simple-prismatic calcite on one or both valves. Ligament duplivincular (Palaeozoic), alivincular, or multivincular, with fibrous material either continuous from one valve to the other or interrupted by lamellar material.

Suborder Ostreina Férussac, 1822 [*emend.*]

Anisomyarian or monomyarian Ostreoida cemented to substrate at beginning of dissoconch stage or lying free on substrate on either the left or right valve; lacking foot and byssal notch in dissoconch. Shell layers primarily calcitic, with simple-prismatic calcite tending to occur as an outer layer on both valves; foliated calcite prominent; aragonitic layers, if present, crossed-lamellar. Ligament alivincular or irregularly multivincular, with fibrous material in resilium either continuous or discontinuous from one valve to the other.

Superfamily Ostreacea Rafinesque, 1815

Monomyarian, eulamellibranchiate Ostreina cemented by left valve to substrate or lying free on left valve. Inner, crossed-lamellar aragonite absent. Simple prismatic calcite either absent or present as outer layer on one or both valves. Resilium completely fibrous and continuous between valves, without a lamellar junction.

Superfamily Dimyacea P. Fischer, 1886

Anisomyarian, filibranchiate Ostreina cemented by right valve to substrate, with crossed-lamellar aragonite absent, thin, or prominent but rarely extending far outside of pallial line. Simple prismatic calcitic outer layers absent. Inwardly bowed fibrous resilium continuous between valves, overarched dorsally by hinge plate and lamellar ligament.

Remarks. Yonge (1975) considered the resilium of the Dimyidae to resemble that of the Plicatulidae, with a central fibrous portion (the 'inner' ligament) flanked on the right and left, sides by 'outer' (lamellar) ligament, and noted that in both of these groups 'the inner ligament layer is attached to the valves only by way of the combined anterior and posterior outer layers, a unique condition in the author's experience.' However, scanning electron microscopy reveals no compositional boundary within the resilium. The resilium of dimyids, like that of plicatulids (see following remarks), is completely fibrous, the former being continuous between valves the latter discontinuous.

Superfamily Plicatulacea Watson, 1930

Monomyarian, filibranchiate Ostreina cemented by right valve. Crossed-lamellar aragonite prominent, extending outside of the pallial line nearly to margins; simple prismatic outer layers thin or absent. Resilium fibrous, but structurally discontinuous between valves.

Remarks. Yonge (1973) reported that the resilium of *Plicatula* contains outer and inner ligament layers which are 'totally distinct, the former clear and yellowish, the latter silvery and opaque.' Although these distinctions are apparent in reflected light, they disappear in fractured sections viewed with the scanning electron microscope. Mineralized fibres, identical in appearance to the aragonitic fibres typical of fibrous ligament, occur from the central portion of the resilium across those areas interpreted by Yonge as outer (lamellar) ligament. There is no sharp boundary like that between the fibrous and lamellar components in the resilia of spondyliids and pectinids, and it appears that the plicatulid resilium is completely fibrous, with lamellar material restricted to the hinge line. As noted by Yonge (1973), the resilium is split, the two sides being only applied to one another, not structurally united. I have been unable to detect any lamellar material along these opposed surfaces, and in this respect the resilium of *Plicatula* differs from the discontinuous fibrous ligaments of other bivalves (e.g. *Arca*, *Lima lima*, *Pecten*), in which lamellar material forms a connecting link between the fibrous components.

#### Suborder Pectinina, new suborder

Monomyarian Ostreoida, pleurothetic on either right or left valve, cemented, byssate, or lying free on substrate, with byssal notch commonly present on right valve at least in early growth stages but in some cases absent; foot present throughout life. Outer, simple prismatic calcite present on both valves, limited to one valve, or absent altogether; foliated calcite present and commonly dominant; crossed-lamellar aragonite variably developed. Ligament duplivincular or alivincular, with lamellar junction absent, minimal, or hypertrophied.

Remarks. Duplivincular ligaments are absent in extant superfamilies of the Pectinina but present in certain extinct Aviculopectinacea and Anomiacea (§ 5).

#### Superfamily Pectinacea Rafinesque, 1815 [*emend.*]

Byssate, cemented, or free Pectinina with right valve against substrate and with byssal notch generally present at least in early growth stages and commonly throughout life. Simple prismatic calcite limited to right valve or absent altogether; crossed-lamellar aragonite variably developed. Ligament alivincular with hypertrophied lamellar junction extending well below hinge line.

#### Family Propeamussiidae Abbott, 1954

Byssate or free Pectinacea with outer, simple-prismatic calcitic layer on right valve present on main portion of disk throughout ontogeny; crossed-lamellar aragonite extending outside of pallial line, in some cases nearly to distal margins, and commonly covering hinge plate. Byssal notch without ctenolium even in early growth stages. Mantle curtains commonly without guard tentacles.

#### Family Pectinidae Rafinesque, 1815 [*emend.*]

Byssate, cemented, or unattached Pectinacea with outer, simple-prismatic calcitic layer on right valve generally present only in early growth stages, rarely absent altogether; crossed-lamellar aragonite restricted to area inside of pallial line or absent. Byssal notch with ctenolium, at least at early growth stage. Mantle curtains bearing guard tentacles.

#### Family Syncyclonemidae, new family

Byssate or free Pectinacea lacking simple-prismatic calcite; foliated calcite very thin, barely perceptible beneath periostracum, or absent, in which case a thin, homogeneous, possibly

calcitized layer underlies periostracum; crossed-lamellar aragonite dominant, extending well outside of pallial line nearly to distal margins and covering hinge plate, which lacks prominent dysodont teeth. Byssal notch without ctenolium. Morphology of soft parts unknown.

Remarks. The unique combination of characters in this family occurs in the following taxa: (1) *Pectinella sigsbeeii* (Dall 1886), a Recent species known from only seven valves collected at depths from 180 to 270 metres off Cuba and Antigua (Speden 1967); (2) fossil specimens nearly identical to the preceding, but found in the New Hebrides (Waller 1973) in deposits dated as late Pleistocene (Ladd 1975); and (3) *Syncyclonema simplicia* (Conrad 1860) and *Syncyclonema halli* (Gabb 1891) from upper Cretaceous deposits in North America (Speden 1967). Comparison of *P. sigsbeeii* with exquisitely preserved *S. simplicia* (from Coon Creek, Tennessee) by means of the scanning electron microscope revealed a remarkable identity in shell ultrastructure and surface sculpture, and *Pectinella* Verrill, 1897, is clearly a junior synonym of *Syncyclonema* Meek, 1864. The genus *Entolium*, on which the family Entoliidae has been based and in which *Syncyclonema* has been included (Newell, in Moore 1969, p. 346), has a substantially different structure consisting of prominent foliated calcite, crossed-lamellar aragonite which does not closely approach the margins of the disk, and an early prismatic stage on the right valve. These are features of the Pectinidae, in which *Entolium* should be placed. Further discussion of diagnostic features of the new family will appear elsewhere.

#### Family Spondylidae Gray, 1826

Cemented Pectinacea lacking simple, prismatic calcite; crossed-lamellar aragonite prominent, extending well outside pallial line nearly to distal margins and covering hinge plate, which bears prominent dysodont teeth. Byssal notch generally present in early growth stages and lacking a ctenolium. Mantle curtains without guard tentacles.

Remarks. *Corallospondylus gussoni* (Costa 1829) of the eastern Atlantic and Mediterranean lacks the pectiniform early growth stage.

Yonge (1973) interpreted the lateral fibrous portions of the spondylid resilium to be the anterior and posterior outer (lamellar) ligaments which have migrated inward and become transverse (left and right) rather than anterior and posterior as in *Pecten*. The boundary between the anterior and posterior segments of 'outer' ligament on each side of the resilium is indicated in Yonge's fig. 11b by a groove. This interpretation requires calcification of 'outer' ligament and decalcification of 'inner' ligament, which seem unlikely events considering that a more parsimonious interpretation is possible. The early ontogeny of the spondylid ligament is precisely like that of pectinids, with the central, lamellar portion of the resilium being continuous with the anterior and posterior outer ligaments, which continue throughout ontogeny along the straight hinge. The lateral fibrous pads originate as in the Pectinidae. The grooves, which arise late in ontogeny and in many cases become multiple, appear to be nothing more than crenulations of the resilium possibly resulting from confinement to a narrow space.

#### Superfamily Anomiacea Rafinesque, 1815

Strongly byssate Pectinina with lower, right valve conforming to substrate and with early byssal notch becoming a byssal foramen, or without byssus and lying free on substrate on either right or left valve. Simple prismatic calcite occurring as outer layer on right valve or rarely on both valves; foliated calcite on both valves generally prominent but in some cases absent on right valve; crossed-lamellar aragonite absent or forming a thin layer inside of pallial line. Ligament

duplivincular (Palaeozoic) or alivincular, greatly distorted by early coiling of shell and inward migration of resilium; fibrous material in resilium passing without lamellar interruption from one valve to the other.

#### 4. CHARACTER ANALYSIS AND PHYLOGENY

The following analysis seeks to determine the primitive or derived state of each character which has been studied over the range of extant taxa under consideration. For those characters studied by others, this determination is taken whenever possible from the original work. In the case of new characters, and in fact in the work of other authors as well, two kinds of evidence for the state of a character generally have been used: ontogeny and 'immediate outgroup comparison' (Platnick & Gertsch 1976). The use of ontogeny assumes that the state of a character which appears first in ontogeny is more generalized than a state which appears later and is therefore likely to appear first in the evolutionary development of the character. Outgroup comparison assumes that identical character states appearing in some but not all related groups not having an immediate common ancestor are more probably primitive than independently derived. Basically, these are methods of 'phylogenetic systematics' discussed at length by Hennig (1966), summarized by Kavanaugh (1972), and concisely illustrated in a cladistic analysis of spiders by Platnick & Gertsch (1976). Character states are summarized in table 2. Morphoclines inferred for shell ultrastructures and ligaments require further elaboration.

Homologies between ultrastructurally distinct shell layers are difficult to infer because so little is yet known about the ontogeny of the structures and their relations to histologically distinct regions of the mantle. In a study of the larval and early postlarval shell development of *Argopecten* (Waller 1976c and unpublished data), it is shown that both simple prismatic and foliated calcitic ultrastructures appear nearly simultaneously within a thickened periostracum immediately following metamorphosis, the prismatic structure occurring outside and slightly in advance of foliated calcite. Crossed-lamellar aragonite, however, appears to form slightly earlier and is virtually continuous with the inner surface of the prodissoconch, extending distally from that region over the inner surface of the inner calcitic layer. On this basis, it is possible to infer that calcitic and aragonitic structures have different origins. Although there is no unequivocal indication of which may be primitive, the slightly earlier appearance in ontogeny and much broader taxonomic distribution throughout the Bivalvia suggests that aragonitic shell deposition is more primitive than calcitic, a conclusion also reached by Taylor (1973). The narrow taxonomic distribution of foliated calcite in comparison with simple prismatic calcite within the Bivalvia and the direction of ontogenetic change from prismatic to foliated ultrastructure both suggest that foliated calcite is derived from simple prismatic calcite (Waller 1976b).

The nature of the primitive ligament system has already been discussed above in connection with basic morphological concepts (§ 2 and figure 1). No lamellar junctions occur in the fibrous portions of ligaments in the Isofilibranchia, and apparently ligament systems in that group have evolved beyond the lamellar grade. In the Prionodonta, lamellar junctions persist only in Arcacea, the Limopsacea having continuous fibrous connections between valves (Owen 1959, Waller, unpublished data). In both superfamilies, the ligaments are duplivincular, a system which in itself is primitive (Thomas 1976). Although ligaments in some Limopsidae have been called alivincular, in fact even here they are duplivincular, for diverging lamellar bands join the valves within each extremity of the 'resilium'.

TABLE 2. MORPHOCLINES USED IN THE CONSTRUCTION OF A CLADOGRAM

(Characters are listed in order of their appearance in the cladogram (figure 2), beginning at the base of the figure and proceeding upward. Lettered derived states are independently derived from the primitive state unless stated otherwise.)

symbol	character	character state	
		primitive	derived
CLP	association of ctenidia and labial palps (Stasek 1963)	ventral tips of anterior filaments of inner demi-branch inserted unfused into distal oral groove (category I of Stasek)	ventral tips of anterior filaments not inserted into distal oral groove (category III of Stasek)
RCP	rejection currents on ventral borders of demibranchs directed toward posterior (Kellogg 1915; Lim 1966; Thomas 1975; Yonge 1973, 1977)	present	absent (with the exception of <i>Plicatula</i> , <i>Spondylus</i> , and certain Anomiacea)
MFF	mantle folds and fusion (Rawitz 1890; Soot-Ryen 1955; Stasek & McWilliams 1973; Waller herein)	mantle edge with 1 or 2 inner folds, the innermost poorly developed if present	(a) two inner folds, the innermost forming a mantle curtain; no ventral fusion (b) two inner folds, the innermost fused at a point ventral to the excurrent opening
PPA	position of posterior adductor relative to pallial line (Waller herein)	posterior and ventral margins of adductor coincident with pallial line	ventral margin of adductor separate from and inside of pallial line or adductor entirely within pallial line
ASU	aragonitic shell ultrastructure (Taylor <i>et al.</i> 1969; Waller herein)	crossed-lamellar and nacreous ultrastructures in the same individual	(a) crossed-lamellar structure present, nacre absent (b) nacre present, crossed-lamellar structure absent
TMM	tentacles on mantle margin (Soot-Ryen 1955; Waller 1976a)	tentacles absent	(a) lobate extensions of mantle edge (b) branching, moderately extensible, generalized tentacles (c) specialized, greatly extensible tentacles of a single type, possibly derived from (b) (d) specialized, greatly extensible tentacles, differentiated in function and position, possibly derived from (c)
CSU	calcitic shell ultrastructure (Taylor <i>et al.</i> 1969; Waller 1976b and herein)	absent	(a) fibrillar structure (b) simple prisms, no foliated structure (c) fibrous-homogeneous structure, no simple prisms; possibly derived from (b) (d) foliated structure
FT	foot (Yonge 1975)	present throughout ontogeny	absent after metamorphosis
BN	byssal notch (Yonge 1953)	absent	present
PRM	photoreceptors on mantle edge (Rawitz 1890; Dakin 1928; Pelseneer 1935; Adal & Morton 1973)	absent	(a) simple and compound eyespots on first outer fold (b) eyes on first inner fold, without lens and with retina not inverted (c) eyes on first inner fold, with lens, cornea, and inverted retina (possibly derived from (b)); secondarily absent in many Propeamussiidae)

## CLASSIFICATION OF THE PTERIOMORPHIA

357

TABLE 2 (*cont.*)

symbol	character	character state	
		primitive	derived
LIG	ligament (Waller herein)	organic, linear ligament, no fibrous material	(a) alivincular, with fibrous lateral regions in resilium separated by a narrow lamellar junction (b) alivincular, with hypertrophied medial lamellar junction in resilium, derived from (a) (c) duplivincular, with continuous lamellar junction, derived from primitive state, (a) or (b) (d) duplivincular, with fibrous material continuous between valves between lamellar secretion areas, derived from (c) (e) alivincular, multivincular, or opisthodontic elongate, with fibrous material continuous between valves, derived from primitive state or (a)
GIL	gills (Ridewood 1903)	eleutherorhabdic	synaptorhabdic
PLC	pleurothetic condition (Yonge 1953; Newell & Boyd 1970)	non-pleurothetic, with plane of commissure perpendicular to substrate	(a) pleurothetic on left side (b) pleurothetic on right side
BF	byssal foramen (Moore 1969)	open byssal notch	byssal notch nearly or completely enclosed to form a foramen, or foramen entirely closed and secondarily absent
MON	monomyarian condition (Yonge 1953)	two adductors	posterior adductor only
LIP	lips (Bernard 1972)	simple	(a) hypertrophied, free or fused, limid type of Bernard (b) hypertrophied, chlamid type of Bernard
STM	stomach (Purchon 1960)	type III of Purchon	type IV of Purchon (could have evolved more than once)
CTN	ctenolium (Waller herein)	absent	present
PC	extent of prismatic calcite (Newell 1938; Taylor <i>et al.</i> 1969; Waller 1972 and herein)	present on both valves of dissoconch throughout ontogeny	(a) present throughout ontogeny on only one valve of dissoconch (b) present in early ontogeny on only one valve, derived from (a) (c) secondarily absent (derived from primitive state, (a) or (b))
CLA	extent of crossed-lamellar aragonite (Waller herein)	well developed, extending outside pallial line	absent outside and present or absent inside pallial line
TMC	tentacles on edge of mantle curtain (Waller 1976a)	absent	present
CRV	obligate cementation by right valve following early byssal attachment (Yonge 1953)	absent	present

In the Pteriomorphia, alivincular systems predominate among extant taxa, but there is an interesting mixture of primitive and derived types. The alivincular systems in the extant Pteriacea, Ostreacea, Dimyacea, and Anomiacea are completely fibrous and in that sense derived. Within the Limoida, *Lima lima* maintains a lamellar wall through the centre of the resilium (see § 3), whereas other species have resilia which are completely fibrous. In the Pectinacea, the lamellar portion of the resilium is hypertrophied and has migrated ventrally into the umbonal cavity so that its active portion is approximately triangular, not crescentic as in other alivincular systems.

Within the remainder of the extant Bivalvia, ligaments which appear to be primitive due to the presence of a lamellar junction separating fibrous portions are found in the subclass Protobranchia, the resilium of *Nucula* being the principal example. The protobranchs have long been viewed as a primitive group on the basis of numerous anatomical features. Significantly, the resilium of *Nucula*, like that of *Pecten*, is hypertrophied, but this was not the case in the Ordovician ancestors of *Nucula*, the ctenodontids. These have no resilifer (Pojeta 1971), and it is possible that their ligaments lacked fibrous components.

The outcome of the character analysis is a cladogram (figure 2) which depicts the derivations of extant character states summarized in table 2. The presence of a particular character state in a stem lineage indicates that this state is present in all subsequent lineages branching from that stem. For example, the character of ctenidium–labial palp association which appears near the base of the cladogram is in a primitive state in all Isofilibranchia and a derived state in all Prionodonta and Pteriomorphia.

The basis for recognition of common ancestry between two or more lineages is the presence of shared derived character states, not shared primitive states. Each group formally recognized in table 1 is strictly monophyletic, meaning that each consists of members descended from a single stem and contains all descendants of this stem (with the exception of extinct taxa, which will be discussed below). An exception is the entire set of taxa under investigation. All possible sister groups, such as Trigoniacea, have not been examined, and hence it cannot be said that all descendants of the stem are represented.

According to Hennig (1966), sister groups (groups which arose from the same immediate stem) must have the same absolute rank in classification. In principle this is undesirable, because it assumes that all branchings are known, and in practice it is seldom feasible because it leads to the creation of new categories and taxa which may tend to obscure phylogenetic relations (Erwin 1970). At the base of the cladogram, the sister group of the Isofilibranchia is unnamed because it is felt that not enough is yet known about shared derived characters to merit the conclusion that the Prionodonta and Pteriomorphia are more closely related to one another than either is to the Isofilibranchia. The same rationale applies to the Limoida and Ostreoida, which split from an unnamed sister group of the Pterioda, and so on.

A cladogram differs from the usual phylogenetic tree in that the horizontal axis does not measure inferred genetic divergence but rather the number of cladistic events based on specified characters. Phylogenetically conservative taxa are, by this measure, those which have undergone few branchings since their inception, in contrast to phylogenetically active taxa, which have undergone many. Thus the order Pterioda is more conservative than the order Ostreoida, but the order Limoida is more conservative than either. Lineages resulting from the split of a stem lineage are shown as diverging equally from the stem, thereby eliminating the need to judge subjectively the primitive or derived state of an entire organism. The cladogram also

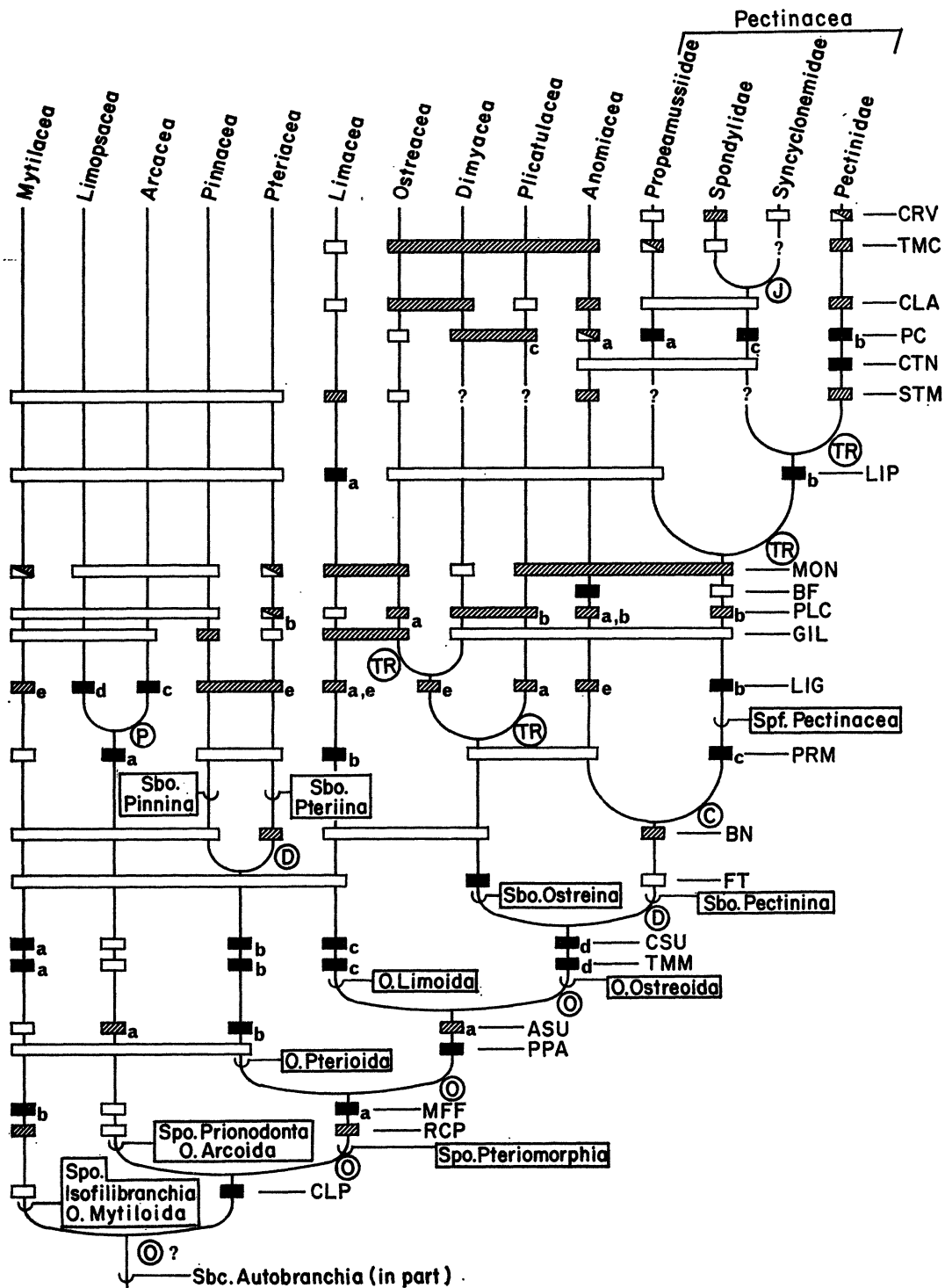


FIGURE 2. Cladogram of the extant superfamilies (and families in the case of the Pectinacea) of the superorders Isofilibranchia, Prionodonta, and Pteriomorphia. Letters on the right refer to characters listed in table 2. Rectangles represent character states: primitive (open), derived (solid), and derived more than once (hatched). Small letters adjacent to rectangles represent different derived character states. Unless specifically stated otherwise in table 2, these states are assumed to be derived independently from the primitive state. The presence of a character in both the primitive and derived states in different taxa within a group is indicated by a rectangle which is half solid (or hatched) and half open. Letters in circles at branching points indicate geological time periods: Ordovician (O), Devonian (D), Carboniferous (C), Permian (P), Triassic (TR), and Jurassic (J). See text for further explanation.



differs from a phylogenetic tree in that the vertical axis is not a proportional measure of time, although the relative positions of branchings reflect what is known about the order of appearance of groups in the fossil record. Lastly, because the character states which led to the inferences of common ancestry in the cladogram are shown, the results are testable and potentially falsifiable. Each of the phylogenetic relations displayed therefore has the status of a scientific theory (Wiley 1975).

The most important phylogenetic conclusions indicated by the cladogram are as follows:

(1) The superorders Isofilibranchia, Prionodonta, and Pteriomorphia have very remote origins but are possibly derived from a common stock.

(2) Both the Isofilibranchia and Prionodonta have been much more conservative than the Pteriomorphia.

(3) Within the Prionodonta, ligament structure suggests that the Limopsacea were derived from the Arcacea.

(4) Within the superorder Pteriomorphia, the order Pterioidea is the most ancient and is a sister group of the stock which produced the orders Limoida and Ostreoida.

(5) The Limoida is a sister group of the stem which gave rise to all of the Ostreoida, including the true oysters, anomiiids, and pectens, and therefore must be more ancient than any of these derived groups.

(6) Phylogenetically, the Ostreoida have been much more active than the Pterioidea and Limoida.

(7) The Ostreina is the most ancient suborder within the Ostreoida and contains both the Plicatulacea and Dimyacea as well as the Ostreacea.

(8) The Anomiacea and Pectinacea have a common ancestry, which means that the Anomiacea are more ancient than any extant subgroups within the Pectinacea.

(9) Within the superfamily Pectinacea, the Propeamussiidae is an ancient group, sister to the stock which produced all other extant Pectinacea. Both the Spondylidae and the new family Syncyclonemidae, like the Propeamussiidae, have many primitive features and may resemble ancient precursors of the Pectinidae more than they resemble extant Pectinidae.

(10) The monomyarian condition has evolved independently in six lineages within the groups under consideration: Mytilacea, Pteriacea, Limacea, Ostreacea, Plicatulacea, and in the ancestral stock of the Anomiacea and Pectinacea.

Certain preservable features of ancestral stocks can also be predicted to occur in the fossil state:

(1) In view of the conservative nature of the Mytiloida, it is likely that ancient mytiloids had the same range of shell ultrastructures as their modern descendants, including the distinctive fibrillar calcitic outer layer.

(2) It is likely that the shells of Prionodonta have always been entirely aragonitic, most likely crossed-lamellar but with nacre possibly occurring in early Palaeozoic representatives.

(3) A primary event in the phylogeny of the Pteriomorphia involved specialization in the mode of secretion of aragonite, nacreous in the Pterioidea and crossed-lamellar in all other groups. The ability to secrete crossed-lamellar aragonite and to exclude nacre was possibly derived independently in different lineages from primitive stocks which were able to secrete both nacreous and crossed-lamellar aragonite in the same shell.

(4) The stem of the order Ostreoida must have been dimyarian, with a shell containing both calcite and aragonite. The calcitic component probably consisted of outermost simple prismatic

calcite on both valves, possibly with a thin foliated calcitic layer underlying the prisms. It is likely that this stem was non-pleurothetic, with the foot and its attendant musculature already reduced. The living habit must have been epifaunal, either reclining on either valve (but not anatomically specialized for life on a particular side) or partially imbedded in a supporting and enveloping organism such as a sponge.

(5) Because all extant Pectinacea have a hypertrophied lamellar junction in the resilium, it is likely that this feature was present in the ancestral stock as well. The fossil resilifer of this stock would therefore have projected well into the umbonal cavity and the cross section of its active, functional portion would have been triangular, not crescentic.

(6) The foliated-calcite ultrastructure in the *Bivalvia* is a primary feature of the *Ostreoida* and is not to be expected in the *Limoida* or *Pterioda* at any point in the fossil record.

#### 5. FOSSIL RECORD

At this point the fossil record will be examined briefly in order to determine whether some of the phylogenetic and morphological predictions of the cladogram (figure 2) are sustained by the sequence and preserved morphology of fossils.

The remote ancestry and phylogenetic conservatism of the *Isofilibranchia* and *Prionodonta* are indeed indicated by fossils. Pojeta (1971) advocated raising the mytiloids to the rank of subclass because of their appearance in the early Ordovician and their lack of a duplivincular ligament, which appears to be present in the early ancestry of other anisomyarians. The diagnostic fibrillar calcitic ultrastructure of the *Isofilibranchia* is observable in Mesozoic mytiloids, and I have detected it by scanning electron microscopy in Mississippian and Pennsylvanian *Lithophaga* and *Vulsellina*. The completely aragonitic, largely crossed-lamellar ultrastructure of the *Prionodonta* is also observable in fossils through the Mesozoic. Upper Palaeozoic arcoids and lower Palaeozoic cyrtodontids, considered by Pojeta (1971) to be ancestral to arcoids, exhibit a mode of preservation which suggests that they were entirely aragonitic.

In the *Prionodonta*, the branchings which led to the extant superfamilies appear to have occurred considerably later than the early Palaeozoic origin of the superorder itself. *Limopsacea* are not known below the Lower Permian (Newell, in Moore 1969, p. 264) and thus appear considerably later than the *Arcacea*, from which the character analysis suggests they were derived.

Because of their active phylogenetic history, the major groups of *Pteriormorphia* are much more difficult to follow through the fossil record, and it is convenient to begin with the *Cainozoic* and work downward. In general, the preservable diagnostic features which separate the modern superfamilies within the *Pteriormorphia* can be followed without difficulty through *Cainozoic* and *Mesozoic* fossils. However, one important exception occurs which seems to result from previous misclassification rather than from flaws in the cladogram.

In the *Pteriacean* family *Malleidae* (Hertlein & Cox, in Moore 1969, p. 326), only the extant genera *Malleus* and *Vulsella* and the Eocene genera *Aviculovulsa* and *Vulsellina* are unquestionably members of the order *Pterioda* on the basis of their simple-prismatic calcitic, nacreous aragonitic shells, and the Cretaceous genus *Stefaninella* is probably also a *Pteriodan*. In contrast, it has now been confirmed that other genera placed in the *Malleidae*, including the Tertiary genera *Euphenax*, *Heligma Nayadina* (*Exputens*) and *Ostreinella*, the Mesozoic genera *Chalmasia* and *Eligmus*, and Mesozoic species incorrectly assigned to *Vulsella* (*V. deperdita* Lamarck, *V. crispata*

Fischer, *V. martensii* von Hoen), lack nacre and consist almost entirely of foliated calcite. By inference based on state of preservation and lack of Pteroid features, the Cretaceous–Eocene genus *Pseudoheligmus* and the Cretaceous genera *Bouleigmus*, *Heligmopsis*, and *Nayadina* (*Nayadina*) are also devoid of nacre and possessed foliated calcite. Many of these genera also have an outer layer of simple prismatic calcite on both valves, a condition which in combination with the presence of foliated calcite is today found only in the Ostreacea and in some Anomiacea. Features other than shell ultrastructure, many of which were considered by Stenzel (1971) to be characteristic of the Ostreacea, are also found among these taxa: backward curving umbones, chomata, left-valve cementation, convex right resilifer, branchitellum, myophoric buttress, and lack of a byssal notch. Whether these ‘malleid’ taxa are indeed true Ostreacea or whether some should comprise a new superfamily within the Ostreina is a subject for more detailed study, but they are clearly not Pteriaceans. Incorporation of these taxa as well as the Dimyacea in the Ostreina suggests that oysters have a dimyarian, possibly non-pleurothetic origin and cannot have evolved from forms like the Pseudomontoids, which retained their foot and became pleurothetic, but no satisfactory ancestor has yet been found.

In the Mesozoic, there were two distinct, scallop-like groups within the suborder Pectinina. The first group consists of species that can be diagnosed as Pectinacea on the basis of their triangular ligament pit and shell ultrastructure consisting of a combination of prismatic calcite (right valve only), foliated calcite, and crossed-lamellar aragonite. Representatives of the Syncyclonemidae, Pectinidae, Propeamussiidae, and Spondylidae are all present, and at least the Propeamussiidae can be traced to the Lower Triassic (Nakazawa 1961). Also in this first group are a great many taxa which resemble extant Pectinidae except that they have prominent crossed-lamellar aragonite well outside the pallial line as in the modern Syncyclonemidae, Propeamussiidae, and Spondylidae. Precisely how these taxa should be treated taxonomically at the family level is as yet unresolved, but it is clear that a severe restriction of the ability of the Pectinacea to secrete crossed-lamellar aragonite outside the pallial line occurred at the end of the Mesozoic era.

The second group of Mesozoic Pectinina is one for which I introduce the superfamily name Buchiacea (*ex* Buchiidae Cox 1952). It consists of taxa having shells composed primarily of foliated calcite, with outer simple prismatic calcite commonly on both valves but better developed on the right than on the left. The foliated calcite is generally of the cross-foliated type (MacClintock 1967) outside of the pallial line, like that which occurs near the distal edges of the shells of some modern Pectinidae. Crossed-lamellar and nacreous aragonite are absent. The resilifer is of the ostreid type, which must have borne a largely or entirely fibrous resilium with a crescentic active portion, and the pallial line is disjunct, consisting of a series of pits as in many of the modern Pteriacea, Ostreacea, and Dimyacea. All were pleurothetic on the right valve and have a distinct byssal notch and a slightly to extremely diminutive right anterior auricle. There is no true ctenolium, some taxa such as *Aucellina gryphaeoides* (J. de C. Sowerby) having instead a row of scales on the outer surface of the disk near the byssal notch. The position of the adductor is like that in the Ostreoida, where the ventral margin of the adductor has migrated inward and is not congruent with the pallial line.

In addition to *Buchia*, *Aucellina*, and probably all of the genera included by Cox (in Moore 1969, p. 374) in the family Buchiidae, the superfamily also contains *Monotis* (*Monotis*) and *Monotis* (*Entomonotis*), the genera assigned by Cox & Newell (in Moore 1969, p. 344) to the Oxytomidae, and the Pseudomonotidae of the Palaeozoic as delineated by Newell & Boyd (1970). Also, many

of the Mesozoic genera assigned by Newell, Cox & Hertlein (in Moore 1969, p. 335) to the Aviculopectinidae have Buchiacean features. *Asoella* has the peculiar cross-foliated calcitic ultrastructure, and *Claraia*, *Leptochondria*, *Otapira*, *Oxypteria*, and *Ornithopecten* all have dimittive right anterior auricles. Newell & Boyd (1970) have previously remarked on the resemblance of *Claraia* and *Leptochondria* to the pseudomonotids (see also Ichikawa 1958). The Buchiacea can thus be followed downward from the Mesozoic into the upper Palaeozoic, and on the basis of their morphology it appears that they are branches from the common ancestry of the Anomiacea and Pectinacea.

The Palaeozoic record of early branching in the Pteriomorphia is much more difficult to unravel. In the order Pterioida, the suborder Pinnina can be followed without difficulty downward to the lower Carboniferous, and scanning electron microscopy of *Aviculopinna* has demonstrated that its shell is prismato-nacreous. The Pterineidae, which clearly belong to the subclass Pteriomorphia, were present by the Middle Ordovician (Pojeta 1971) and are generally considered to be ancestral to the Pteriidae. However, differences in shell structure between valves in some taxa, with the outer, calcitic layer of the left valve lacking simple prismatic structure, suggest that this group may be polyphyletic and may contain both ancestral Pterioida and Ostreoida. Other specimens from the Middle(?) Ordovician assembled by Pojeta and not yet referred to in publication are clearly monomyarian, with the adductor well separated from the pallial line and a shell form which suggests lack of a pleurothetic mode of life. These features indicate that these may be ancient limoids. If so, then the three orders of the Pteriomorphia were present by the end of the Ordovician.

The Ambonychiacea, another largely Palaeozoic Pteriomorph group, may also be polyphyletic. Little is yet known about the ultrastructure of Palaeozoic taxa, but specimens which I have examined clearly display simple prismatic structure at least on the right valve and in some cases on both valves (see also Newell 1942). Preserved aragonitic structures have not been found, nor has foliated calcite, and I do not know at this point whether they should be considered ancestral Pterioida or Ostreoida. What is established is that the group as a whole does not belong in the Isofilibranchia.

Microstructural examination of the Palaeozoic Aviculopectinacea, in which I include the Pterinopectinidae, Leliopectinidae, Aviculopectinidae, and Deltopectinidae of Newell (in Moore 1969, p. 332), is in progress. Some taxa have simple prismatic calcite on both valves, a fact noted long ago by Newell (1938), but a non-prismatic structure which was probably originally calcitic is present in others. Extensive crossed-lamellar aragonite outside of the pallial line is also present (Waller 1972), and undoubted foliated calcite has been detected in a Devonian pterinopectinid (Waller, unpublished data). Because early Aviculopectinacea (the Pterinopectinidae) had a duplivincular ligament and later representatives (the Aviculopectinidae) had an alivincular ligament which apparently lacked an hypertrophied lamellar junction, the group must have been derived from the shared ancestry of the superfamilies Anomiacea and Pectinacea at a point very close to that from which the Buchiacea originated.

*Pernopecten*, which lived at the same time as the aviculopectinids, not only had an internal resilium which probably had a hypertrophied lamellar junction, but it also had a shell ultrastructure remarkably like that of the extant Propeamussiidae (Waller 1972). These forms should probably be considered a part of the same lineage.

In summary, the morphology and sequence of fossils are in accord with morphological and phylogenetic conclusions deduced from an analysis of morphoclines of extant character states.

I am grateful to J. Pojeta, Jr, E. G. Kauffman, W. P. Woodring, D. Wilson, H. S. Ladd, N. Morris, A. Dhondt, L. Van de Poel, and M. Glibert for permission to examine collections under their care and for assistance in locating specimens of interest. Dr J. Pojeta, Jr, Dr F. R. Bernard and Professor E. G. Kauffman have kindly read and criticized the manuscript.

## REFERENCES (Waller)

- Adal, M. N. & Morton, B. 1973 *J. Zool. Soc. Lond.* **170**, 533–556.
- Allen, J. A. 1958 *Phil. Trans. R. Soc. Lond. B* **241**, 421–484.
- Allen, J. A. & Sanders, H. L. 1969 *Malacologia* **7**, 381–396.
- Ansell, A. D. 1961 *J. mar. biol. Ass. U.K.* **41**, 489–515.
- Ansell, A. D. 1962 *J. mar. biol. Ass. U.K.* **42**, 419–443.
- Bayne, B. L. 1971 In *4th European Marine Biology Symposium* (ed. D. J. Crisp), pp. 259–280. Cambridge University Press.
- Beedham, G. E. 1958 *Q. Jl microsc. Sci.* **99**, 341–357.
- Bernard, F. R. 1972 *Can. J. Zool.* **50**, 53–57.
- Bernard, F. R. 1974 *Mar. Biol.* **8**, 1–279 (Allan Hancock Monographs).
- Cox, L. R. 1952 *Mem. geol. Surv. India Palaeont. Indica*, (9) **3**, 1–128.
- Dakin, W. J. 1928 *Proc. R. Soc. Lond. B* **103**, 355–365.
- Eldredge, N. & Gould, S. J. 1972 In *Models in paleobiology* (ed. T. J. M. Schopf), pp. 82–115. San Francisco: Freeman, Cooper & Co.
- Erwin, T. L. 1970 *Quaest. entom.* **6**, 4–215.
- Hennig, W. 1966 *Phylogenetic systematics*. Urbana: University of Illinois Press.
- Hillman, R. E. & Schuster, C. N., Jr 1966 *Chesapeake Sci.* **7**, 112–113.
- Ichikawa, K. 1958 *Palaeontographica A* **3**, 131–212.
- Kavanaugh, D. H. 1972 *Biologist* **54**, 115–127.
- Kellogg, J. L. 1915 *J. Morph.* **26**, 625–701.
- Kobayashi, I. 1976a *Jap. J. Malacol. (Venus)* **35**, 63–72.
- Kobayashi, I. 1976b *J. geol. Soc. Jap.* **82**, 446–447.
- Ladd, H. S. 1975 *Veliger* **18**, 134–138.
- Lim, C. F. 1966 *Biol. Bull. mar. biol. Lab. Woods Hole* **130**, 106–117.
- MacClintock, C. 1967 *Peabody Mus. nat. Hist. Yale U. Bull.* **22**, 1–140.
- Mallick, D. I. J. & Greenbaum, D. 1973 *New Hebrid. geol. Surv. A. Rep.* **1973**, 8–12.
- Maslin, T. P. 1952 *Syst. Zool.* **1**, 49–70.
- Moore, R. C. (ed.) 1969 *Treatise on invertebrate paleontology*, part N (1) (Mollusca 6: Bivalvia) (952 pages). Lawrence, Kansas: Geological Society of America and University of Kansas.
- Nakazawa, K. 1961 *Kyoto imp. Univ. Mem. Coll. Sci. B* **27**, 249–291.
- Neveeskaya, L. A., Scarlato, O. A., Starobogatov, Y. I. & Eberzin, A. G. 1971 *Paleont. J.* **1971**, no. 2, 3–20.
- Newell, N. D. 1938 *State geol. Surv. Kansas, Lawrence* **10** (1), 1–23.
- Newell, N. D. 1942 *State geol. Surv. Kansas, Lawrence* **10** (2), 1–115.
- Newell, N. D. 1965 *Am. Mus. Novit.* **2206**, 1–25.
- Newell, N. D. & Boyd, D. W. 1970 *Bull. Am. Mus. nat. Hist.* **143**, 217–281.
- Ockelmann, K. W. 1964 *Ophelia* **1**, 126–146.
- Oldfield, E. 1955 *Proc. malac. Soc. Lond.* **31**, 226–249.
- Owen, G. 1959 *Proc. malac. Soc. Lond.* **33**, 215–223.
- Owen, G., Trueman, E. R. & Yonge, C. M. 1953 *Nature, Lond.* **171**, 73–75.
- Pelseneer, P. 1935 *Essai d'éthologie zoologique d'après l'étude des Mollusques*. Brussels: Palais des Académies.
- Platnick, N. E. & Gertsch, W. J. 1976 *Am. Mus. Novit.* **2607**, 1–15.
- Pojeta, J., Jr 1971 *U.S. geol. Surv. prof. Pap.* **695**, 1–46.
- Purchon, R. D. 1960 *Proc. cent. and bicent. Congr. Biol. Singapore 1958* (ed. R. D. Purchon), pp. 69–82. Singapore: University of Malaya Press.
- Rawitz, B. 1890 *Jena. Z. Naturwiss.* **24**, 1–83.
- Ridewood, W. G. 1903 *Phil. Trans. R. Soc. Lond. B* **195**, 147–284.
- Runnegar, B. 1974 *J. Paleont.* **48**, 904–939.
- Schaeffer, B., Hecht, M. K. & Eldredge, N. 1972 In *Evolutionary biology* (ed. T. Dobzhansky, M. K. Hecht & W. C. Steere), vol. 6, pp. 31–46. New York: Appleton–Century–Crofts.
- Soot-Ryen, T. 1955 *Allan Hancock Pacific Exped. vol.* **20** (1), pp. 1–174.
- Speden, I. G. 1967 *Peabody Mus. nat. Hist. Yale Univ.* **110**, 1–36.
- Stasek, C. R. 1963 *Veliger* **6**, 91–97.
- Stasek, C. R. & McWilliams, W. R. 1973 *Veliger* **16**, 1–19.

- Stenzel, H. B. 1971 *Treatise on invertebrate paleontology* part N (3) (Mollusca 6: oysters). Lawrence, Kansas: Geological Society of America and University of Kansas.
- Taylor, J. D. 1973 *Paleont.* **16**, 519–534.
- Taylor, J. D., Kennedy, W. J. & Hall, A. 1969 *Bull. Brit. Mus. (Nat. Hist.). Zoology*, suppl. **3**, 1–125.
- Thomas, R. D. K. 1975 *Paleontology* **18**, 217–254.
- Thomas, R. D. K. 1976 *Paleobiology* **2**, 64–83.
- Trueman, E. R. 1949 *Proc. zool. Soc. Lond.* **119**, 717–742.
- Waller, T. R. 1972 *24th International Geological Congress*, vol. 7, pp. 48–56.
- Waller, T. R. 1973 In Mallick, D. I. J. & Greenbaum, D. (eds.) 1973, pp. 000–000.
- Waller, T. R. 1976a *Bull. Am. malac. Un.* 1975, 7–13.
- Waller, T. R. 1976b *Bull. Am. malac. Un.* 1975, 57–58.
- Waller, T. R. 1976c *Bull. Am. malac. Un.* 1976, 46.
- Wiley, E. O. 1975 *Syst. Zool.* **24**, 233–243.
- Yonge, C. M. 1949 *Phil. Trans. R. Soc. Lond. B* **234**, 29–76.
- Yonge, C. M. 1953 *Trans. R. Soc. Edinb.* **62**, 443–478.
- Yonge, C. M. 1973 *Phil. Trans. R. Soc. Lond. B* **267**, 173–208.
- Yonge, C. M. 1975 *J. Zool., Lond.* **176**, 545–553.
- Yonge, C. M. 1977 *Phil. Trans. R. Soc. Lond. B* **276**, 453–523.

### Discussion

E. L. YOCHELSON (*Museum of Natural History E-501, Washington, D.C. 20560, U.S.A.*). The interesting cladogram summarizing diversification of the Pteriomorphia through several sequential structural adaptations contains one point which disturbs me. The time scale is badly distorted and does not convey what is known of the radiometric time scale. For a cladogram based only on data from the Recent, the length of bars is hypothetical; in palaeontology one may make the assumption that in a fossil lineage the oldest occurrence of a structure is an approximation of the time of its origin. To use an inaccurate or distorted time scale seems to downgrade the data that are available on the rate of origin of structural features.

T. R. WALLER. The cladogram is a hierarchy of derived character states and, unlike a phylogenetic diagram, is completely devoid of any vertical scale, including a time scale. Absolute length of lines is indeed hypothetical, but relative length is determined by remoteness of ancestry, which in turn is determined from the character analysis. Symbols indicating the times of branching were placed on the diagram merely to show that the order of branching predicted by morphology agrees with the sequence of first occurrences of major groups in the fossil record. This approach provides an independent test of palaeontological data and avoids the circular reasoning which has caused some students of evolution to downgrade palaeontology in the past.