

Bivalvia – a look at the Branches

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Morphological perspective on the classification and evolution of Recent Pterioidea (Mollusca: Bivalvia)

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Received February 2005; accepted for publication August 2005

The evolutionary relationships of the Recent Pterioidea are inferred from a phylogenetic analysis of representatives of all pterioidean genera based on original observations of anatomy and shell morphology, and an extensive survey of bivalve literature. The well-resolved cladogram supports monophyly for the superfamily, but renders all but one family (the monotypic Pulvinitidae) polyphyletic. In addition, these results reveal a considerable level of convergence and parallelisms through the Pterioidea. The branching order of pterioidean genera in the morphological analysis is largely corroborated by the sequence of their appearance in the fossil record. The palaeontological evidence provides important information on dating lineage splitting events and transitional taxa. The proposed phylogeny integrates the cladistic analysis of the Recent Pterioidea with the fossil record and suggests that the crown-group pterioideans probably originated in the Triassic from the Bakevelliidae, an extinct paraphyletic stem group from which the Ostreoidea are also ultimately derived. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, 148, 253–312.

ADDITIONAL KEYWORDS: fossil record – Ostreoidea – Pinnoidea – phylogeny – systematics.

INTRODUCTION

The present-day diversity of the superfamily Pterioidea J. E. Gray, 1847 encompasses four families traditionally defined by shell shape and ligament structure: Pteriidae J. E. Gray, 1847, Isognomonidae Woodring, 1925, Malleidae Lamarck, 1819, and Pulvinitidae Stephenson, 1941 (Newell, 1969b; Boss, 1982; Butler, 1998). Despite the fact that some of its members have received much attention as a commercial source of pearls and nacre over the centuries (Donkin, 1998; Landman *et al.*, 2001), and, more recently, as a model system for bone regeneration studies (Lopez, Berland & Le Faou, 1995; Westbroek & Marin, 1998; Mouriès *et al.*, 2002) and invasive species (Carlton, 1996; Borrero & Díaz, 1998), no explicit phylogenetic framework

is available for the group and an understanding of its evolution is in its infancy. Previous works focused either on a few genera containing commercially important species within the family Pteriidae (Jameson, 1901; Ranson, 1961) or were confined to regional revisions of common species and genera (Jameson, 1901; Hynd, 1955; Juan-Juan & Okutani, 2003). Consequently, the diversity of the Pterioidea largely remains unknown, even at the level of families, and comparative anatomical and molecular studies are wanting.

The first Pterioidea (placed in the single family Pterineidae Meek, 1864) appeared in the lower Middle Ordovician (Pojeta & Runnegar, 1985) and are hypothesized to have evolved from the stem group, the family Umburridae Johnston, 1991, based on hinge morphology, shell inequivalvity, muscle scars, and stratigraphic evidence (Johnston, 1991a; Waller, 1998). The Permo-Triassic boundary marks the extinction of

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Pterineidae, the only exclusively Palaeozoic pterioidean family, and the origin and diversification of Pteriidae, Isognomonidae, and Bakevelliidae King, 1950 (the latter becoming extinct in the Eocene; Cox, 1954, 1969a). The two other extant families – Pulvinitidae and Malleidae – evolved, respectively, in the Jurassic (Cox, 1969c) and the Cretaceous (Waller, 1978, 1985). Relationships among the four extant families remain uncertain (Waller, 1998) and ideas range from assumptions of a single origin of the superfamily (Jackson, 1890; Waller, 1998) to polyphyletic theories (Stanley, 1972; reviewed in Carter, 1990).

The shell shape diversity of the Pterioidea is immense and can hardly be circumscribed by the superfamily diagnosis, varying from having a nearly perfectly rounded outline to strongly prosocline alate forms to bizarre irregular shell morphologies. The surface of the outer calcitic prismatic layer varies greatly, being either equipped with periostracal and prismatic scales, overlapping irregular calcitic lamellae, and pronounced ribs (particularly in extinct taxa), or lacking sculpture altogether (with the exception of inconspicuous commarginal growth lines). The inner nacreous layer bears impressions of posterior adductor, pedo-byssal retractor, and pallial muscles, the last two being greatly reduced in some taxa. Examples of shell morphology of the Recent Pterioidea are presented in Figure 1.

The major shell morphological features of Palaeozoic pterioideans – obliquity of the inequivalve shell, extension of the posterior auricle, and shape of the byssal notch – are readily comparable with those of living species, providing grounds for functional interpretations of shell morphology (Kauffman, 1969; Stanley, 1972; Johnston, 1993). However, important differences between Palaeozoic taxa and their descendants were found in the microstructure of the outer shell layer and the morphology of the ligament (reviewed in Carter, 1990). The diversity of ligamental structures within the Pterioidea, which exceeds that of other bivalves, is of paramount importance in the systematics of the group and has been used to infer phylogeny of bivalves at large (Owen, Trueman & Yonge, 1953; Trueman, 1969; Waller, 1978, 1990; Carter, 1990). On the other hand, having functional significance in opening and holding the valves together, the variety of ligaments must be an adaptive feature and could have evolved multiple times (Thomas, 1976; Seilacher, 1984; Newell & Boyd, 1987).

Anatomical studies are few and inadequate to make broad comparisons across the superfamily. The earliest studies are generally restricted to superficial overviews of soft parts (Fischer, 1861; Vaillant, 1868) with the notable exception of an excellent comparison of species of *Pteria* Scopoli, 1777 and *Pinctada* Röding, 1798 by Grobben (1900). An exhaustive and superbly

illustrated analysis of *Pinctada fucata* (Gould, 1850) (as *Margaritifera vulgaris* Schumacher, 1817) by Herdman (1904) remains unparalleled to the present in its detail. Other anatomical works were primarily concerned with the functional morphology of either single species (Reid, 1985; Harper & Morton, 1994; Morton, 1995) or a few species living in similar environments (Kühnelt, 1938; Yonge, 1968; Reid & Porteous, 1980). Many details on the fine anatomy of pterioidean species are scattered in the malacological literature. Several species of *Pinctada* used in the pearl and nacre industries were extensively studied and facts about their anatomy dispersed in the voluminous literature on perliculture.

Especially abundant in the Indo-Pacific, the living Pterioidea occupy tropical and subtropical continental shelf regions around the globe. Pterioideans occur in a remarkable variety of ecological settings, from an endobyssally attached semi-infaunal habit (Yonge, 1968) to byssally attached crevice dwelling (Ubukata, 2003a) to associations with corals (Southwell, 1911; Stanley, 1972; Morton, 1983a, 1988, 1995), algae (Mikkelsen *et al.*, 2004), sponges (Reid & Porteous, 1980; Morton, 1988), and roots of mangroves (Siung, 1980; Morton, 1983b; Harper & Morton, 1994).

The primary objective of the present study was to establish a sound phylogenetic framework for the Pterioidea based on shell morphological and anatomical data. Such a study was not feasible in the past due to a substantial lack of anatomical data for many genera and even families, which are investigated here for the first time. The comparative anatomical analysis across the entire superfamily revealed remarkable diversity in soft anatomy (schematically illustrated in Figure 2) among the major pterioidean lineages, comparable with that of shell morphological data. Therefore, detailed character descriptions supplementing the analysis represent the first anatomy-based definition of the superfamily, as well as all of its families and genera. The phylogeny of the superfamily is discussed in light of palaeontological data, and a new hypothesis of the origin of major pterioidean clades is proposed, revealing problematic aspects of pterioidean history. The results of this work provide the first step towards understanding the evolution of the Pterioidea and indicate the direction of future research. A complementary molecular phylogenetic analysis of the Pterioidea is in preparation.

A BRIEF HISTORY OF PTERIOID SYSTEMATICS

A NOTE ON TAXONOMY

The imminent review of the superfamily Pterioidea must be discussed against the currently accepted

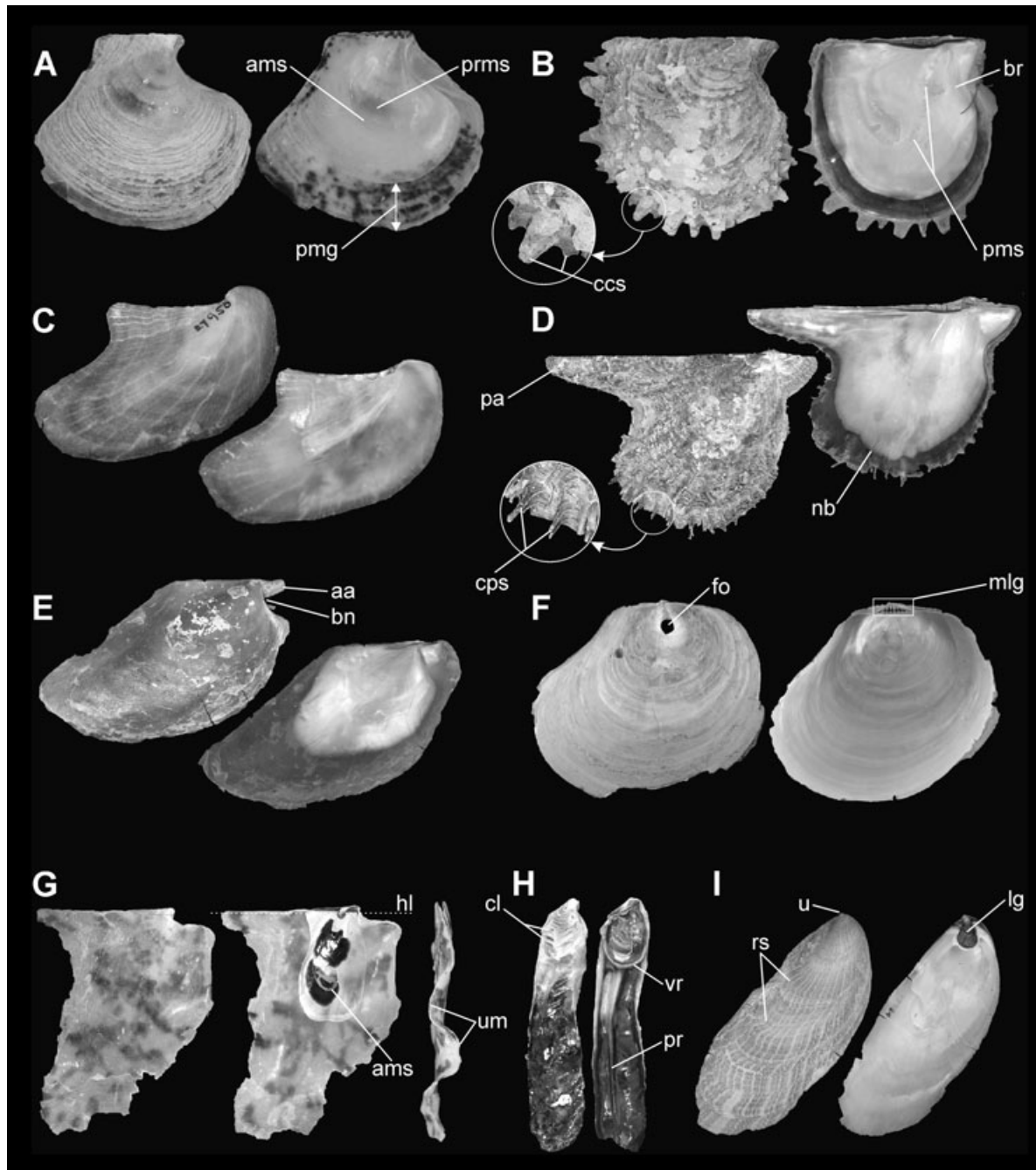


Figure 1. Diversity of shell morphology in the Pterioidea. Major features of the shell, showing the exterior of the right valve and the interior of the left valve [frontal view is shown in (G)]. The shells are arranged with the hinge axis orientated horizontally and anterior to the right. A, *Isognomon alatus* (AMNH 100419, 46.9 mm); B, *Pinctada mazatlanica* (AMNH 311788, 58.6 mm); C, *Crenatula modiolaris* (AMNH 27950, 49.0 mm); D, *Pteria sterna* (AMNH 311789, 58.0 mm); E, *Electroma alacorvi* (USNM 675754, 48.1 mm); F, *Pulvinites exempla* (AMS C.129659, 62.6 mm); G, *Malleus anatinus* (MNHN Expédition Montrouzier September 1993, Stn 1261, 44.38 mm height); H, *Malleus (Malvufundus) candeanus* (MCZ 340681, 69.9 mm height); I, *Vulsella vulsella* (AMNH 27884, 84.2 mm). For clarity, specific structures are labelled only on a single image where best observed. Abbreviations: aa, anterior auricle; ams, posterior adductor muscle scar; bn, byssal notch; br, byssal ridge; ccs, commarginal calcitic scales; cl, calcitic lamellae; cps, commarginal periostracal scales; fo, foramen; hl, hinge line; lg, ligament; mlg, multivincular ligament; nb, border of nacreous layer; pa, posterior auricle; pmg, prismatic margin; pms, pallial muscle scar; pr, pallial ridge; prms, posterior (pedo-byssal) retractor muscle scar; rs, radial stripes; u, umbo; um, undulating shell margins; vr, visceral rim.

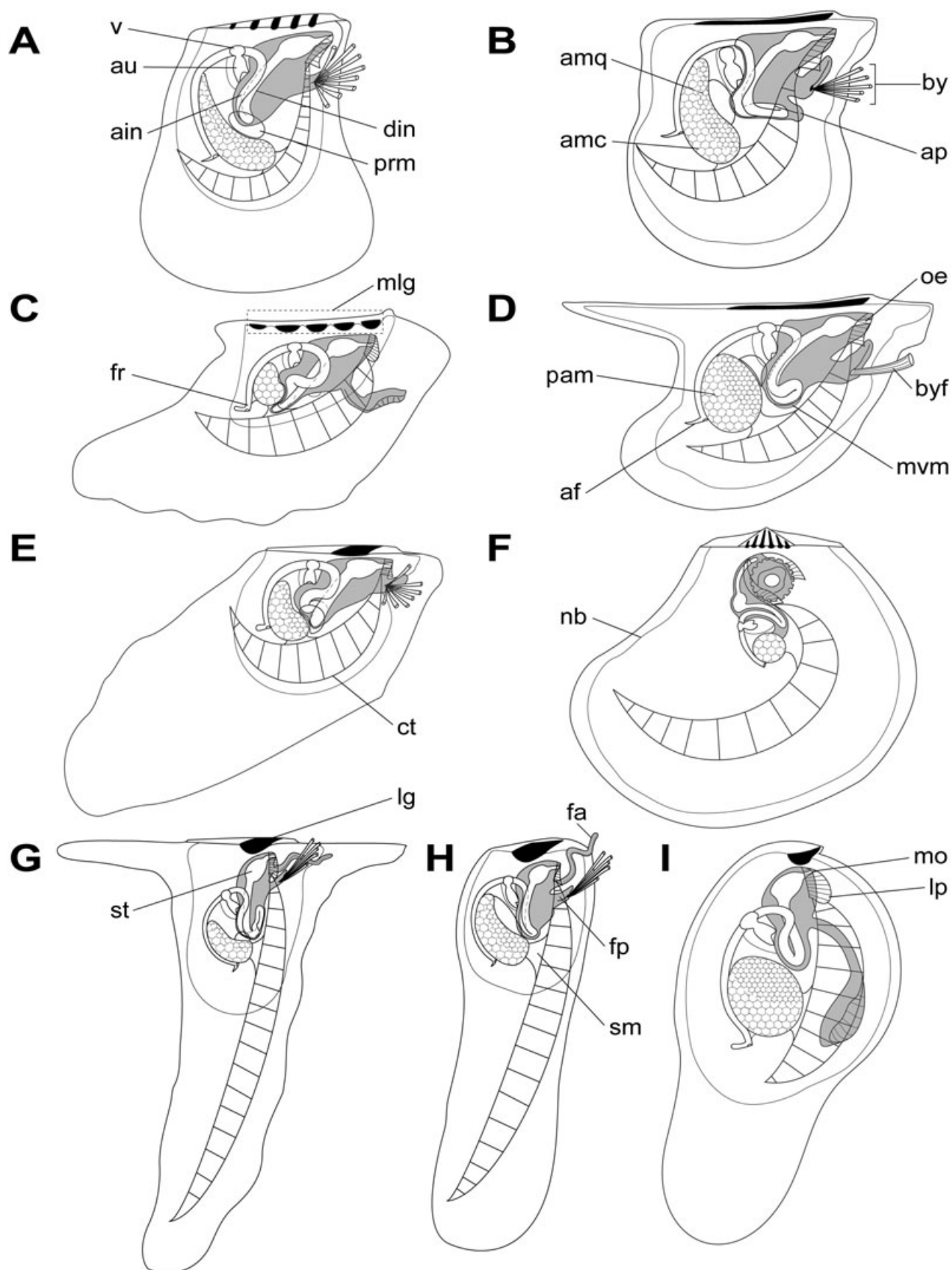


Figure 2. Overview of anatomical diversity of the Pterioidea. Animals are viewed from the right side with the right valve and mantle removed. A, *Isognomon*; B, *Pinctada*; C, *Crenatula*; D, *Pteria*; E, *Electroma*; F, *Pulvinites*; G, *Malleus*; H, *Malleus (Malvufundus)*; I, *Vulsella*. For ease of comparison, animals are arranged with the hinge axis aligned along the horizontal axis with anterior to the right. For clarity, specific structures are labelled only on a single image where best observed. The visceral mass is shaded in grey. Abbreviations: af, anal funnel; ain, ascending intestine; amc, 'catch' component of posterior adductor muscle; amq, 'quick' component posterior adductor muscle; ap, anterior protrusion of visceral mass ventral to foot; au, auricles; by, byssus; byf, byssal thread fusion; ct, ctenidia; din, descending intestine; fa, accessory foot; fp, primary foot; fr, free-hanging rectum; lg, ligament; lp, labial palp; mlg, multivincular ligament; mo, mouth; mvm, midventral membrane of intestinal pouch; nb, border of nacreous layer; oe, oesophagus; pam, posterior adductor muscle; prrm, posterior pedo-byssal retractor muscle; sm, suspensory membrane; st, stomach; v, ventricle.

taxonomic framework (Table 1). The systematics of the Pterioidea has been remarkably consistent with regard to the identity of pterioidean genera over centuries. Despite their ever-changing names, the close affinity of these seemingly clearly delimited taxa – albeit intuitively for the most part – were realized in the mid-19th century and no dramatic taxonomic reassignments have happened since. On the other hand, the suprageneric classification of pterioideans has witnessed virtually every possible arrangement of genera and still remains controversial today. Because old typological and modern phylogenetically informed definitions of genera by and large agree, the following discussion of pterioidean systematics will avoid unnecessary discussion of synonymies and uses presently recognized generic names in referring to early malacological literature. Because of the lack of recent revisions of most genera, in references to species from the literature, the contemporary species or genus name is provided and followed in parenthesis by the name used in the original source on the first mention and thereafter is substituted by the presently accepted name. However, given the present state of pterioidean systematics, the synonymy provided here is by no means definitive. It must also be emphasized that the following review of the group's systematics involves only Recent taxa, and palaeontological sources are referenced only as far as they relate to the living Pterioidea. (The final section, which deals with the evolutionary history of the group, draws much more on palaeontological data.)

One particular pterioidean name deserves a note of caution due to its extremely wide use in the past. The name *Avicula* Bruguière, 1792 was variably used in either a more restrictive sense, corresponding to the contemporary genus *Pteria*, or as a broader category comparable with the presently recognized family Pteriidae. In older palaeontological literature, the term referred to virtually any prosocline species possessing an extensive posterior auricle, thus contributing to the taxonomic chaos surrounding the name. With time, many 'aviculids' were distributed among better-defined taxa (and often quite distantly related pteriomorphian groups), but the name *Avicula* (now a

junior subjective synonym of *Pteria*) is still being sporadically used by some authors and begs taxonomic scrutiny.

PRE-LINNEAN AGE

In the tenth edition of *Systema Naturæ* (Linnaeus, 1758), members of the most speciose and abundant pterioidean genera were already listed, but dispersed among the broadly defined genera *Ostrea* (including species of *Isognomon* Lightfoot, 1786 and *Malleus* Lamarck, 1799), *Mytilus* (including species of pterioid genera *Pteria* and *Pinctada*), and *Mya* (including species of *Vulsella* Röding, 1798). Linnean descriptions were based on works of his predecessors and in many cases reflect previously coined names that later formed the basis for more narrowly defined (and comparable with present-day usage) generic names. Most notable of the Linnean sources is *D'Amboinsche Rareitkamer* by Rumphius (1705) because his 'oysters' (*Ostreum*) included the easily identifiable 'Meshamer' (or hammer oysters of genus *Malleus*) and 'Isognomon', the name with the invention of which he was credited by Martens (1902). Rumphius also used the names 'Vulsella' (a member of his 'Tellinae') and 'Avicula' (placed in 'Mussels' as in the Linnean system), which along with *Malleus* and *Isognomon* were incorporated into *Systema Naturæ* and were later used as generic names by Bruguière (1792) and Lamarck (1819) for various pterioidean taxa. Other chief sources included the classic conchological works of Aldrovandi (1606), Buonanni (1681), Petiver (1713), and Klein (1753). Guillaume Rondeletius' (1554–1555) *Libri de Piscibus Marinis* and an anonymous travel account *Histoire Naturelle des Indes* dated from the early 1590s (Klinkenberg, 1996), contain the earliest recognizable illustrations of pterioidean shells.

EMERGING SYSTEMATICS

Shortly after the publication of the 12th edition of *Systema Naturæ* (Linnaeus, 1767), the Linnean genera were split by his successors, but no agreement was achieved on the arrangement of these genera into

Table 1. Current classification of the Recent Pterioidea in the context of extinct taxa (marked by *). The generic composition of families extending to the Recent is shown with genera of questionable status removed. Taxonomy and stratigraphy are based on Cox *et al.* (1969) with subsequent amendments by Waller (1978, 1985), Carter (1990), Skelton & Benton (1993), Johnston (1995), and Johnston & Collom (1998)

Phylum Mollusca

Class Bivalvia

Order Pterioida Newell, 1965

Suborder Pteriina Newell, 1965

Superfamily Pterioidea J. E. Gray, 1847

Family Pteriidae J. E. Gray, 1847 [1820]

Genus *Electroma* Stoliczka, 1871 (Upper Cretaceous–Recent)

Genus *Pinctada* Röding, 1798 (Miocene–Recent)

Genus *Pteria* Scopoli, 1777 (?Triassic–Recent)

Genus *Arcavicula* Cox, 1964 (Middle Triassic–Upper Triassic)*

Genus *Eopinctada* Tamura, 1961 (Cretaceous)*

Genus *Pteroperna* Morris Lycett, 1853 (Upper Triassic–Jurassic)*

Genus *Pterinella* Toulou, 1882 (Lower Cretaceous)*

Genus *Rhaetavicula* Cox, 1961 (Upper Triassic)*

Genus *Somapteria* Tamura, 1960 (Middle Triassic)*

Family Isognomonidae Woodring, 1925

Genus *Isognomon* Lightfoot, 1786 (Upper Triassic–Recent)

Genus *Crenatula* Lamarck, 1803 (Upper Tertiary–Recent)

Genus *Gervilleioperna* Krumbeck, 1923 (Lower Jurassic)*

Genus *Linsdallia* Cox & Arkell, 1948 (Middle Jurassic)*

Genus *Mulletia* P. Fischer, 1887 (Lower Cretaceous)*

Genus *Pachyperna* Oppenheim, 1900 (Eocene)*

Genus *Waagenoperna* Tokuyama, 1959 (Upper Permian–Upper Triassic)*

Family Pulvinitidae Stephenson, 1941

Genus *Pulvinites* Blainville, 1824 (Middle Jurassic–Recent)

Genus *P. (Hypotrema)* Orbigny, 1853 (Lower Jurassic–Upper Jurassic)*

Family Malleidae Lamarck, 1819

Genus *Malleus* Lamarck, 1799 (Recent)

Genus *M. (Malvufundus)* de Gregorio, 1885 (Recent)

Genus *Vulsella* Röding, 1798 (Upper Palaeocene–Recent)

Genus *Vulsellina* Raincourt, 1876 (Middle Eocene)*

Genus *Stefaniniella* Tavani, 1939 (Upper Cretaceous)*

Genus *Bouleigmus* Basse, 1933 (Upper Cretaceous)*

Family Pterineidae Meek, 1864 (Middle Ordovician–Upper Permian)*

Family Bakevelliidae King, 1850 (Middle Carboniferous–Eocene)*

Family Cassianellidae Ichikawa, 1958 (?Upper Permian–Triassic)*

?Family Lithiotidae Cox, 1971 (Lower Jurassic)*

?Family Dattidae Healey, 1908 (Upper Triassic)*

?Family Posidoniidae Frech, 1909 (Lower Carboniferous–Lower Cretaceous)*

higher taxa. Bruguière (1792) placed *Pinctada*, *Pteria*, and *Malleus* in a single group, as did Röding (1798). Although Röding's *Museum Boltenianum* (1798) does not use a higher-level taxonomic hierarchy other than Bivalvia, *Isognomon* directly follows *Pinctada*, *Pteria*, and *Malleus*, suggesting that the author suspected their affinity. The genus *Vulsella* also appears in his list, but not in the vicinity of other pterioidean genera. Lamarck (1819) subsequently removed *Malleus* into a separate genus under its own name, but placed the two resulting genera into a single family, Malleacea,

together with his recently established genus *Crenatula* Lamarck, 1803. The system of Bruguière and Lamarck widely popularized by the *Encyclopédie Méthodique* (Deshayes, 1830, 1832) became a widely adopted taxonomic framework followed by many successors, including Crouch (1827) and Brown (1833).

Adams & Adams (1858) endorsed the removal of *Vulsella* from their classification, but included pen shells (*Pinna* Linnaeus, 1758) in their assemblage of pterioidean genera. Others included *Vulsella* along with the rest of the pterioidean genera in a category

that entirely corresponds to the currently recognized superfamily Pterioidea: 'Pteriidae' (Gray, 1847; Meek, 1864), 'Malleacea' (Philippi, 1853; Deshayes, 1864), and 'Aviculidae' (Stoliczka, 1871). Meek (1864) subdivided the 'family' into two groups of genera, Pteriinae (or Aviculinae) and Melininae, on the basis of the presence or absence of a multivincular ligament. Stoliczka (1871) further subdivided Meek's Pteriinae into Aviculinae and Vulsellinae. Aviculinae was comprised of a single genus *Avicula* and corresponded to the currently recognized family Pteriidae with all its genera – *Pteria*, *Pinctada*, and *Electroma* Stoliczka, 1871 – recognized at the subgeneric level. Vulsellinae was comprised of the genera *Malleus* and *Vulsella*, thus corresponding to the currently recognized family Malleidae. Fischer (1887) maintained the tripartite division of the Pterioidea, but transferred *Malleus* into Aviculinae and once again included pen shells ('Pinninae') as the fourth group in his version of Aviculidae, which was followed by Dall (1895). The pioneering works on bivalve embryonic shells by Jackson (1890) and Bernard (1898) did not provide explicit classifications, but did emphasize a close kinship of all pterioidean genera, grouped under informal 'Aviculidae and their allies', but with the exclusion of the Pinnidae.

Single-character classifications that emerged at the turn of the 19th century were sharply at odds with the relatively stable Lamarckian tradition. In the gill-based system of Ridewood (1903), the pterioidean genera were split into two families, Melinidae (*Malleus*, *Isognomon*, and presumably *Crenatula* and *Vulsella*) and Aviculidae (*Pteria* and *Pinctada*), placed in different suborders, Mytilacea and Pectinacea, respectively. Pelseneer's system agreed with that of Ridewood in placing pterioidean taxa into two suborders (Pelseneer, 1906). However, he placed *Malleus* back into Aviculidae and placed *Vulsella* in its own family Vulsellidae into the Pectinacea. Pelseneer (1911) changed his outlook later and placed all his pterioidean families (Aviculidae, Pernidae, and Vulsellidae) along with Pinnidae and Ostreidae into a suborder Aviculacea.

The synthesis by Thiele (1934) retained Pelseneer's family Aviculidae (termed Pteriidae), but combined the other two into a single family Vulsellidae. The two pterioidean families together with Pinnidae were placed into stirps Pteriacea, anticipating the removal by Atkins (1938) of Ostreidae based on the discovery of a significant difference in the morphology of latero-frontal cilia between Ostreidae on one hand and Pinnidae/Pterioidea on the other.

Iredale (1939) resurrected the tripartite division of the Pterioidea once proposed by Stoliczka (1871), elevating the three subfamilial divisions to the rank of families, equivalent to the presently used Pteriidae, Malleidae, and Isognomonidae, and placed them in a

new suborder, Aviculiformes. Since that time, the relative ranks of families and genera of the Pterioidea have been maintained (Allan, 1959). Franc (1960), followed by Cotton (1961), reintroduced the Pinnidae into Pteriacea (as well as subsuming malleid genera in the Isognomonidae), but it was subsequently eliminated (and placed in a different order) with the publication of Newell's (1965) classification that formed the taxonomic framework for the influential bivalve section of the monumental *Treatise on invertebrate palaeontology* (Cox *et al.*, 1969). Although the scope of that work aimed at embracing all living and extinct taxa in a single comprehensive classification, it has not resulted in any significant rearrangement of the living pterioidean genera. Nevesskaya *et al.* (1971) maintained the composition of the families and recognized their close relatedness by placing them in the suborder Pteriina, but split the Pterioidea into three superfamilies: Pterioidea (containing the only family Pteriidae), Bakevelloidea (containing Isognomonidae), and Malleoidea (containing Malleidae and Pulvinitidae). The last grouping is unique in suggesting a closer similarity of Malleidae to Pulvinitidae than to any other family, but the reason for this supposition is not explicitly stated. More recently, Hayami (2000) removed *Vulsella* from Malleidae and placed it in a separate family, Vulsellidae, within the Pterioidea.

In summary, the genera of the Pterioidea have been strongly delimited, considered closely related, and generally remained of the same relative rank in most taxonomic treatments, at least since the middle of the 19th century. Despite the general systematic stability of the Pterioidea over the years, two recurrent themes have persisted: (1) the variable position of *Vulsella* with respect to other pterioidean genera and (2) a close association with Pinnidae.

PREVIOUS PHYLOGENETIC HYPOTHESES

Obviously, the many classifications just reviewed were not built on an explicit phylogenetic framework and, in the most part, reflect pre-Linnean typological approaches to organizing diversity. The first explicit phylogeny pertaining to the Pterioidea is the already mentioned classic work of Jackson (1890) (Fig. 3A). He reconstructed the evolution of the 'Aviculidae and their allies' (an approximate equivalent to the modern concept of the Pteriomorpha less Mytiloidea and Arcoidea) in the paradigm of Haeckeleian 'biogenetic law' (Haeckel, 1866) by comparing larval and adult shell shapes in search of resemblances between geologically older adult forms and features of the larval shells of younger species. He was able, for the first time, to propose a history of the group that included the origin of most pterioidean genera with the excep-

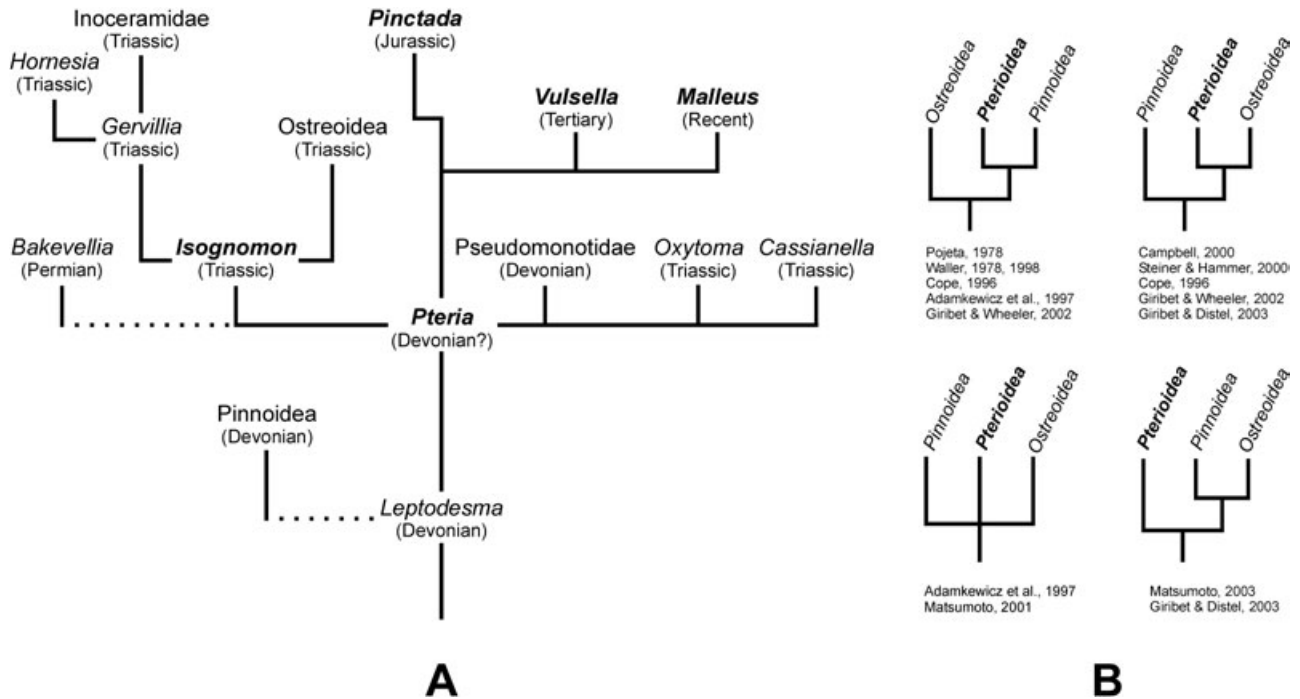


Figure 3. Previous ideas on the phylogeny of the Pterioidea. A, the phylogeny of the 'Aviculidae and their allies' by Jackson (1890: 391) after his genealogical table. Only the relevant part of the tree is shown. For clarity, outdated generic names are replaced with currently accepted names and the genera of Pinnoidea, Pseudomonotidae, Inoceramidae, and Ostreoidea are collapsed without altering the original topology. The Recent pterioidean taxa, the main subject of the present work, are highlighted in bold. The non-pterioidean taxa having their origin in Jackson's *Pteria* have been removed in subsequent revisions, as indicated in Table 1. B, proposed sister groups of the Pterioidea (see text for details).

tion of *Pulvinites* Blainville, 1824 and *Crenatula*. Because Jackson's profound evolutionary insights are considered in the last section of the paper, it will suffice at this point to outline its systematic implications. In Jackson's system, the Recent Pterioidea appear to be closely related and ultimately derived from a *Pteria*-like stem group that gave rise to the Malleidae (*Malleus* and *Vulsella*), *Isognomon*, and Pteriidae (*Pteria* and *Pinctada*). What was really different in Jackson's system was the derivation of the Ostreoidea from the pterioidean genus *Isognomon*. Pinnoidea was the next most closely related living group that shared remote ancestry with the Pterioidea and Ostreoidea through the Palaeozoic genus *Leptodesma* Hall, 1883. Although the association with the Pinnidae was certainly hinted by previous works, the suggested intimate connection of the Pterioidea and the Ostreoidea was certainly novel. Another outstanding work on bivalve classification by Douvillé (1912) based essentially on fossil shell characters also suggested an origin of Ostreidae as well as several other pterioidean taxa from the Pterioidea, albeit not in such detail to allow for extensive comment.

Regrettably, despite intriguing evolutionary trajectories suggested by Jackson's work, no subsequent

analyses focused exclusively on unveiling relationships within the Pterioidea, although several recent higher-level phylogenetic studies have included pterioidean representatives. These studies differ dramatically in sources of data (anatomical, shell morphological, protein, and DNA sequence data), phylogenetic methodologies (phenetic to maximum parsimony to maximum likelihood), and their implementation (either computed-assisted or not). Likewise, sampling varies greatly across studies from as little as a single exemplar for the entire superfamily to multiple taxa representing each major family. Consequently, caution must be taken when interpreting and comparing the results of such disparate studies.

Sister group of the Pterioidea

Palaeontological evidence taken alone (Pojeta, 1978) or integrated with morphological data (Waller, 1978, 1998; Cope, 1996) has suggested a sister relationship of the Pterioidea and Pinnoidea. This result was corroborated by the analysis of morphological data assembled for exclusively Recent taxa (Giribet & Wheeler, 2002).

Molecular analyses aimed at resolving global bivalve phylogeny are divided in favouring either the Pinnidae (Adamkewicz *et al.*, 1997) or Ostreoidea (Campbell, 2000; Steiner & Hammer, 2000; Giribet & Distel, 2003, combined analysis of 18S/28S sequences) as a sister group of Pterioidea. Steiner & Hammer (2000) have also mapped a set of morphological characters on to their maximum likelihood tree (preferred over a maximum parsimony tree because of its better resolution) substantiating their claim of an ostreoid/pteroid sister-group relationship by two features: monomyary and the presence of an anal funnel. The only explicitly combined analysis of morphological and molecular data by Giribet & Wheeler (2002) resolved Pinnoidea basal to the Pterioidea and Ostreoidea. In other studies, the Pinnoidea and Ostreoidea formed a sister group to the Pterioidea [Giribet & Distel, 2003, analyses of cytochrome oxidase I (COI) alone and a combined analysis of an 18S/28S/H3/COI data set; Matsumoto, 2003]. In other studies, the relationships of the three taxa were unresolved (Adamkewicz *et al.*, 1997; Matsumoto, 2001, 2003). Carter's (1990) frequently cited 'phylogenetic diagrams' suggest that the sister of Pterioidea is a clade that includes Pinnoidea, Ostreoidea, and Plicatuloidea. Caution must be taken in interpreting these charts, however, as they do not strictly represent a phylogeny, but depict a synopsis of existing classifications (Carter, 1990) where reticulations indicate conflicting hypotheses rather than polyphyletic or paraphyletic origins.

Relationships within the Pterioidea

Carter's (1990) synthetic phylogeny represents the four pterioidean families as being monophyletic and provides a plethora of their possible relationships, indicated as reticulations. Of the three pteroid families represented in the molecular study of Steiner & Hammer (2000), the Malleidae and Pteriidae were polyphyletic. The status of the pterioid genera *Pteria* (either para- or polyphyletic) and *Pinctada* (either mono- or polyphyletic) was sensitive to optimality criteria. Likewise, Giribet & Distel (2003) failed to recover the monophyly of the two families. The more limited (in sampling of pterioidean taxa) molecular study of Matsumoto (2003) provided support for the monophyly of *Isognomon* and *Pinctada*, but failed to recover the monophyly of the Pteriidae.

In summary, the Pterioidea has invariably appeared to be monophyletic in all studies. The sister group of the Pterioidea – Ostreidae, Pinnidae, or both – remains uncertain. Every possible combination of the three taxa has been proposed (Fig. 3B). Curiously, morphological studies favour a closer affinity of pteroids to pinnids, whereas the majority of molecular studies support a closer relationship of pteroids

and ostreoids. None of the studies had sufficient sampling for all pterioidean families and genera because they were concerned with either uncovering relationships among major bivalve lineages or within the Pteriomorphia and, consequently, provided limited evidence to understanding pterioidean phylogeny.

MATERIAL AND METHODS

TAXONOMIC SAMPLING

The present analysis is the first comprehensive phylogenetic analysis of the Pterioidea to include representatives of all four nominal families and all nine genera included in the superfamily (16 ingroup taxa in total). The only notable exception is a monotypic subgenus *Pterelectroma* Iredale, 1939, of doubtful taxonomic status. Due to the relatively low abundance and/or cryptic life styles characteristic of species of the genera *Electroma*, *Vulsella*, and *Crenatula*, these taxa are represented here by single species. However, previously published anatomical studies of these groups, although fragmentary, suggest anatomical uniformity within each group, and will be discussed accordingly in later sections of this work (see also Appendix 1). The choice of immediate outgroup taxa – a pinnid and an ostreid – was dictated by previously advanced well-grounded phylogenetic hypotheses (see the preceding section). The third outgroup taxon was *Mytilus*, a more basal pteriomorphian, required to polarize characters of the two other outgroup taxa because neither has been unequivocally shown to be an immediate outgroup to the Pterioidea. The species included in the present study are listed in Table 2.

The vast majority of samples came from museum collections worldwide. In a few instances, living animals and empty shells were collected by the author during summer 2003 expeditions to Key Largo [as part of the investigation of marine molluscan biodiversity in peninsular Florida and the Florida Keys, formally initiated by Paula M. Mikkelsen (American Museum of Natural History) and Rüdiger Bieler (Field Museum of Natural History) in 1994] and to Guaymas, Mexico. Animals were collected mainly by hand during snorkelling in shallow water (2 m). Specimens were fixed in 5% formalin, later transferred to 70% ethanol, or fixed directly in 95–100% ethanol for potential molecular investigation. Voucher specimens are deposited in the American Museum of Natural History (AMNH), New York, USA. For sources see Appendix 2.

Other cited repositories include: AMS, Australian Museum, Sydney, Australia; ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; CASIZ, California Academy of Sciences, Invertebrate Zoology, San Francisco, California, USA; FMNH, Field Museum of Natural History, Chicago, USA; MCZ,

Table 2. Taxa used in the analysis (see Appendix 1 for sources)

Family	Genus	Species
Ingroup: Superfamily Pterioidea		
Family Pteriidae	<i>Pinctada</i>	<i>P. imbricata</i> (Röding, 1798) <i>P. fucata</i> (Gould, 1850) <i>P. longisquamosa</i> (Dunker, 1852) <i>P. mazatlanica</i> (Hanley, 1855) <i>P. colymbus</i> (Röding, 1798) <i>P. sterna</i> (Gould, 1851) <i>P. loveni</i> (Dunker, 1872)
	<i>Pteria</i>	<i>E. alacorvi</i> (Dillwyn, 1817) <i>I. alatus</i> (Gmelin, 1791) <i>I. radiatus</i> (Anton, 1839) <i>I. bicolor</i> (C. B. Adams, 1845) <i>C. modiolaris</i> Lamarck, 1819 <i>M. anatinus</i> (Gmelin, 1791) <i>M. (M.) candeanus</i> (Orbigny, 1842) <i>V. vulsella</i> (Linnaeus, 1758) <i>P. exempla</i> (Hedley, 1914)
Family Isognomonidae	<i>Electroma</i> <i>Isognomon</i>	
	<i>Crenatula</i>	
Family Malleidae	<i>Malleus</i> <i>Malleus (Malvufundus)</i> <i>Vulsella</i> <i>Pulvinites</i>	
Family Pulvinitidae		
Outgroup		
Family Pinnidae (Pinnoidea)	<i>Atrina</i>	<i>A. rigida</i> (Lightfoot, 1786)
Family Ostreidae (Ostreioidea)	<i>Crassostrea</i>	<i>C. virginica</i> (Gmelin, 1791)
Family Mytilidae (Mytilioidea)	<i>Mytilus</i>	<i>M. edulis</i> (Linnaeus, 1758)

Museum of Comparative Zoology, Harvard University, Massachusetts, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (= United States National Museum); NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.

MORPHOLOGICAL OBSERVATIONS

Observations on living species were performed on both active and relaxed animals (in either cold water or an isotonic magnesium sulphate solution) on site with the use of a magnifying lens and a compound stereomicroscope. The anatomy of preserved specimens was studied using a combination of histology and gross dissection in various planes. For histology, shells were removed manually from formalin-fixed, ethanol-preserved specimens; tissues were dehydrated through a graded ethanol series, followed by clearing in a xylene substitute, and embedding in paraffin. Complete 5 or 7 µm serial transverse sections were produced for gills and mantle margins and, in a few cases, of entire animals in sagittal plane, and stained with Alcian Blue/Periodic Acid/Schiff's trichrome stain. Dried shells and excised preserved tissues were prepared for scanning electron microscopy by critical-point drying (for tissues only) and gold-palladium sputter coating, and were then viewed on a Zeiss DSM-950 scanning electron microscope at AMNH.

Specimen photography used a variety of equipment and techniques. Laboratory photographs of living animals were taken in aquaria or finger bowls with a Canon G2 4.0 megapixel digital camera or a 35 mm single-lens reflex camera and electronic flashes. Whole-valve and detail light micrography of histological preparations used a Microptics micro/macro imaging system based on a high-resolution Nikon single-lens reflex digital camera or Canon G2 4.0 megapixel digital camera.

Shell measurements (taken with digital callipers or with an ocular micrometer on a stereomicroscope) and meristics were taken from the right valve. The maximum shell height was measured perpendicular to the hinge line to the most distal point of the ventral shell margin; the maximum shell length was taken parallel to the hinge line. Size is expressed as shell length unless otherwise noted.

MORPHOLOGICAL DATA AND CHARACTER DEFINITIONS

Morphological character data were for the most part obtained from original observations and, to some extent, particularly for outgroup taxa, from the literature (refer to Appendix 2 for the list of taxa supplied with the material used and character sources). On a number of occasions, discrepancies were found between previously reported and present observations; these cases are specified in the character definitions (Appendix 1).

The analysis attempted in this work aimed to be an exhaustive morphological survey of all major organ systems within the Pterioidea and included character data for the skeletal (shell and ligament) system, musculature, respiratory–filtrational system (ctenidia and labial palps), alimentary system (stomach and intestinal tract), and partially circulatory (heart) and central nervous systems (major ganglia and sense organs). The lack of fresh material and juvenile stages, plus fragmentary data in the bivalve literature on such important characters as the structure of the provinculum, the development of the postmetamorphic ligament, and sperm ultrastructure, precluded their direct use in the analysis. However, the phylogenetic importance of some of these characters will be discussed in light of the proposed phylogeny.

All characters were formulated in terms of discrete directly observable anatomical structures rather than commonly used character complexes and inferred functional interpretations. Thus, conventional categories, such as stomach, gill, and ligament grades, were dissolved into constituting characters and scored independently. Fully aware of the potentially serious problem of character dependence, each character was carefully examined. In cases where there is no evidence that a change in one character must be accommodated by a compensatory change in another character, or one character is required for the formation of another, the feature was treated as independent. Characters that were considered to be potentially non-independent by these criteria were excluded from the analysis. Examples of such features include the presence of muscle scars (non-independent with respect to the muscles that form the attachments) and the mineralogy of inner shell layers (non-independent from inner shell layer nacreous or foliated microstructures). Likewise, rather than using a functional character definition such as the presence of a promyal chamber, a precise anatomical definition – the fusion of mantle lobe(s) to the sides of the visceral mass and the presence of a supramyal septum – was adopted here because such interpretations can be misleading if based on a wrong or incomplete inference of suspected function. Additionally, in this study the vast majority of observations were made on preserved material and the anatomical observations could not be demonstrably associated with specific functions. Homology, independence, and functional interpretations pertaining to controversial or not previously discussed characters are addressed in Appendix 1. Soft anatomical characters are described in considerably more detail because they have not been extensively used in previous phylogenetic analyses. Where necessary, new terms are introduced and *italicized* where used for the first time. In a few cases where terms for anatomical structures, despite being

extensively discussed in systematic literature, have not been standardized, the most appropriate term (for reasons discussed) was chosen among the synonyms and likewise *italicized*.

Bivalve morphological characters naturally form two categories: shell morphological and soft anatomical. The definition of shell characters was particularly problematic because seemingly obvious descriptive features, such as the outline of the shell margin, obliquity, the extent of the auricles, and various aspects of shell shape and colour, do not constitute discrete, easily diagnosable non-independent characters. A perceived difference in such features was inevitably compromised by intraspecific variation. The Pterioidea are particularly notorious for shell plasticity, which is largely determined by their preference for crevice dwelling, where the direction of shell growth is determined by physical constraints of the environment, despite the fact that its extent is within constraints of predetermined morphogenetic gradients (Ubukata, 2003a). Consequently, to avoid ambiguous formulations leading to unwarranted homology statements, such as ‘predominantly’, ‘variable’, ‘narrow’, and ‘broad’, many characters pertaining to shell shape and colour were excluded from the analysis.

CHARACTER CODING

The data set for 19 terminals was comprised of 134 discrete characters. Of these, 40 (30%) were multi-state, the rest were binary. In total, 103 characters were parsimony informative, the rest were autapomorphic, but were retained for diagnostic and descriptive purposes (the measures of character fit were estimated with and without taking autapomorphic characters into account; see Results). All characters were unweighted. One multistate character was treated as ordered based on ontogenetic criteria: the differentiation of gill filaments (character 17). The current data set did not contain missing data. Character coding was performed strictly on a species level. The use of groundplan coding was rejected because this method assumes the monophyly of supraspecific taxa, which was also being tested by the present analysis. Inapplicable data that essentially resulted from instances of independent losses of several differentiated characters constituted 87 of 2546 total data points (3.4% of entries in the data matrix). All data were entered in the program NDE v.0.5.0 (Page, 2001). For the distribution of character states for all analysed taxa, see Appendix 3. For details of the coding of specific characters, see Appendix 1.

PHYLOGENETIC ANALYSES

The morphological data set was analysed using parsimony as an optimality criterion. Initial heuristic

searches were performed using parsimony ratchet (Nixon, 1999) with 1000 iterations and re-weighting 15% of characters, and holding five trees per iteration. Clade robustness was evaluated using jackknife (Farris *et al.*, 1996) with 5000 replications. Tree searches, consensus construction, support calculations, and character optimization were performed using WinNona (Goloboff, 1999) spawned by WINCLADA v.1.00.08 (Nixon, 1999–2002). The phylogenetic signal was evaluated using the g_i statistic (reviewed in Hillis & Huelsenbeck, 1992) that measures the skewness of the distribution of random trees (50 000 random trees used).

RESULTS

PHYLOGENETIC SIGNAL

The results of the tree length distribution estimation indicated that the data set contained substantial phylogenetic structure. The g_i values (–0.51) were significantly left-skewed at $P < 0.01$.

THE CLADOGRAM STRUCTURE

An analysis of the complete morphological data set recovered a single most-parsimonious tree with a length of 317 (consistency index = 0.54; consistency index excluding uninformative characters = 0.49; retention index = 0.56) represented in Figure 4 (hence the reported character fit values are probably inflated and must be interpreted with caution). Not unexpectedly, given the preceding discussion of bivalve morphology, the relatively low measures of character fit indicated a high level of homoplasy resulting from numerous instances of parallel trends, convergence, and secondary losses. The analysis unequivocally resolved all basal nodes but did not resolve intrageneric relationships. As the goal of this study was the resolution of higher-level relationships among the Pterioidea, no attempt was made to further investigate intrageneric relationships.

The basic structure of the cladogram combines some aspects anticipated from previous phylogenetic studies but contains many novel features. The Pterioidea is monophyletic but none of its constituent families is (with the obvious exception of the monotypic Pulvinidae). Non-monophyly of the Pteriidae and Malleidae has been suggested previously (Steiner & Hammer, 2000; Giribet & Distel, 2003; Matsumoto, 2003), but not of the Isognomonidae. This result is due to the recovery of a previously unrecognized clade comprised of 'smaller' genera representing each family: pterioid *Electroma*, isognomonid *Crenatula*, and malleid *Vulsella*. However, unlike the previous work of Steiner & Hammer (2000), this analysis recovered the mono-

phyly of the pterioid genera *Pteria* and *Pinctada*. The Pterioidea is composed of two major clades. The first one consists of the *Electroma/Vulsella/Crenatula* clade basal to the *Pteria/Pinctada* clade. The second clade consists of the *Malleus* clade basal to *Pulvinites* and *Isognomon*.

The following discussion lists non-homoplastic synapomorphies for each clade, but only those that could be unambiguously optimized on the cladogram (black squares in Fig. 4); to identify homoplastic apomorphies – white squares – refer to Appendix 1. It must be remembered, however, that monophyly is a statement of membership that might not be unambiguously translatable in terms of definitive diagnostic characters due to a possibility of their secondary loss (Sober, 1988). Given the old age of the Pterioidea and a general elevated tendency towards convergence, parallelism, and secondary losses in the Bivalvia (Stanley, 1975, 1977; Newell & Boyd, 1978; Seilacher, 1984), few non-homoplastic synapomorphies might exist at each node, resulting in reduced support.

APOMORPHIES

The outline of non-homoplastic synapomorphies lists characters and character states, defining each node to the level of genus, and is supplemented by corroborating or refuting data from the literature. For character definitions and a more extensive discussion, see Appendix 1; for the entire character matrix, see Appendix 3.

Node 0: Pterioidea/Ostreoidea

1. Tentacles present on middle mantle fold (IF-1) (character 7, state 1). Tentacles on middle fold are absent in the Pinnidae (Grave, 1911; Yonge, 1953a), the immediate outgroup of Pterioidea/Ostreidae. In the latter, simple tentacles appear to be primitive, occurring in oysters (Harry, 1985) and most pterioideans, consistent with previous reports of their occurrence in *I. legumen* (Gmelin, 1791) (Harper & Morton, 1994), *Crenatula modiolaris* Lamarck, 1819 (Reid & Porteous, 1980), *Pinctada imbricata* (Röding, 1798) (Waller, 1976), *V. vulsella* (Linnaeus, 1758) (Reid & Porteous, 1980), and *V. lingulata* Lamarck, 1819 (Vailant, 1868). In *Pulvinites exempla* (Hedley, 1914) (Tëmkin, 2006) and most *Pinctada*, tentacles are branched (character 7, state 2). Branched tentacles have previously been reported in *Pteria brevislata* (Dunker, 1872) (Morton, 1995) and *Pinctada fucata* (Gould, 1850) (Herdman, 1904).

2. Interlamellar junctions form interlamellar septa stretching from ventral to dorsal gill margins (character 15, state 3). This observation is consistent with a previous finding of interlamellar septa in *Ostrea*

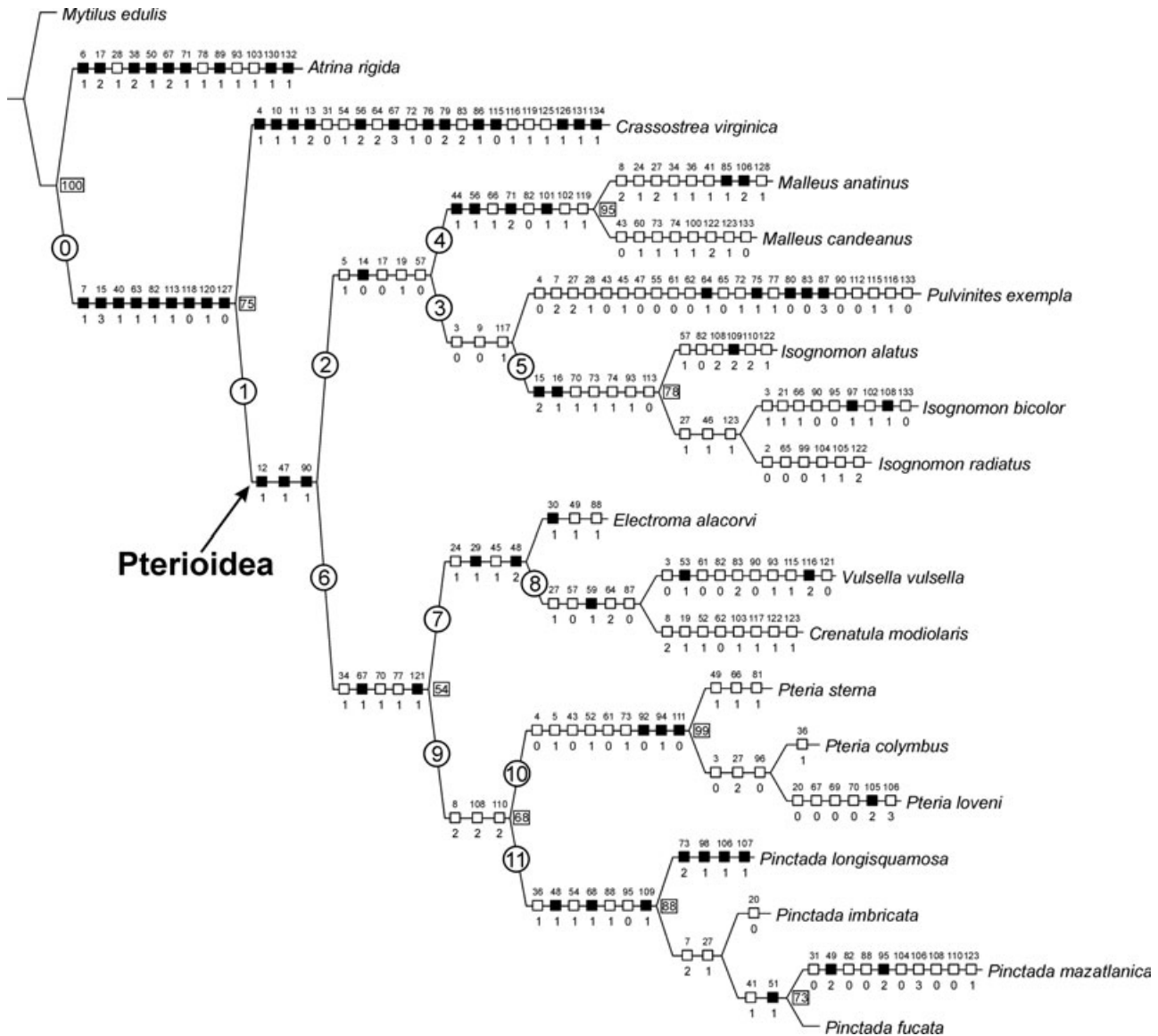


Figure 4. Single most-parsimonious cladogram (length = 317; consistency index = 0.54; retention index = 0.56). Branches are depicted proportional to the branch length. Mapped apomorphies are unambiguously optimized non-homoplastic (black squares) and homoplastic (white squares) character states. The numbers above and below the squares denote characters and corresponding character states, respectively (as numbered and described in Appendix 1). Jackknife values are shown by numbers in rectangles at corresponding nodes. Numbers in circles enumerate nodes discussed in the Results.

edulis Linnaeus, 1758 and *Malleus albus* Lamarck, 1819 by Ridewood (1903), in *Pinctada fucata* by Herdman (1904), and in *Pteria hirundo* (Linnaeus, 1758) by Atkins (1936). Species of the genus *Isognomon* have modified interlamellar septa reduced to the dorsalmost part of the interlamellar space (see below).

3. Descending intestine produced towards posteroventral side of posterior adductor muscle (character

40, state 1) is consistent with all surveyed accounts of pterioidean and ostreoidean anatomy.

4. Loss of anterior adductor muscle (character 63, character 1) is consistent with all surveyed accounts of pterioidean and ostreoidean anatomy. Obviously, this condition is convergent with other monomyarian pteriomorphians, Pectinoidea, Anomioidea, and heterodont Tridacnidae, as reviewed by Yonge (1953b).

5. Left valve more inflated than right valve (character 82, state 1). Inequivalvity of Ostreidae and Pterioidea is well documented and is convergent with other pteriomorphian groups, such as Pectinoidea. Some pterioidean taxa, however, are secondarily nearly equivalve, as are some orthothetic *Pinctada* and crevice-inhabiting *Malleus*.

6. Absence of pseudonymphae (character 118, character 0). The direct interpretation of the cladogram suggests a loss of the pseudonymphae in the Ostreidae/Pterioidean lineage. Although apomorphic in the context of this cladistic analysis based exclusively on Recent taxa and obviously homoplastic with other pterioideans not presently analysed, the phylogenetic interpretation of the cladogram in the context of palaeontological evidence (see Discussion) favours a different interpretation. Pseudonymphae of Mytilidae and Pinnidae are homoplastic autapomorphies because the latter is derived from the extinct Pterineidae that did not possess pseudonymphae (Carter, 1990).

7. Presence of a resilifer throughout ontogeny (character 120, state 1); (8) non-terminal prodissoconch (character 113, state 1); and (9) placement of the posterior adductor muscle entirely within the boundary of the inner shell layer (character 127, state 0) are apomorphic given presently chosen outgroups, but globally represent cases of convergence with other pteriomorphian taxa. The resilia of many pectinoids are situated in the resilifers but are often internalized well ventral to the hinge axis, the condition not found in the extant pterioideans (see Discussion for a detailed argument regarding the evolution of ligamental grades in the Pterioidea).

Node 1: Pterioidea

1. Ctenidia attached to adductor muscle by suspensory membrane extending from gill axes (character 12, state 1). The presence of the suspensory membrane has been reported from many pterioidean species: in *Isognomon* (as *Isognomum*) *perna* (Linnaeus, 1767) and *I. isognomum* (Linnaeus, 1758) by Pelseeneer (1911); in *Crenatula phasianoptera* Lamarck, 1803 by Vaillant (1868); in *Malleus regula* (Forsskal, 1775) by Yonge (1968); in *Pinctada fucata* by Herdman (1904).

2. Presence of anal funnel (character 47, state 1). The anal funnel is present in many Ostreidae (Harry, 1985) but is absent in most basal ostreoid clades [Gryphaeidae, and basal Ostreidae *Crassostrea* Sacco, 1897; *Striostrea* Vyalov, 1936; *Saccostrea* Dollfus & Dautzenberg, 1920, in the study of Kirkendale *et al.* (2004)]. Therefore, despite the fact that the present analysis agrees with the result of

the molecular analysis of Steiner & Hammer (2000) in supporting the sister-group relationship of the Pterioidea and Ostreidae, it contradicts their conclusion that the presence of an anal funnel is apomorphic to the clade. The present study suggests that the occurrence of the anal funnel is a consequence of parallel evolution, as previously suggested by Waller (1998).

3. Presence of anterior auricle (character 90, state 1). The presence of an anterior auricle is convergent with other pteriomorphian taxa such as Pectinoidea.

Node 2: *Isognomon*/*Pulvinites*/*Malleus*

Absence of food grooves on margins of outer demibranchs only (character 14, state 0). This has been previously reported in *M. regula* (fide Yonge, 1968) and is convergent with Pectinidae and Limidae (Atkins, 1937).

Node 3: *Isognomon*/*Pulvinites*

This clade is not supported by non-homoplastic apomorphic characters.

Node 4: *Malleus*/*M. (Malvufundus)*

1. Dorsal part of descending intestine displaced to left (character 44, state 1).

2. Presence of a differentiated foot (character 56, state 1) and (3) a single large pallial retractor muscle (character 71, state 2) are unique to *Malleus*, as reported for all species of the genus whose soft anatomy has been observed: *M. daemoniacus* Reeve, 1858 (Pelseeneer, 1911), *M. regula* (fide Pelseeneer, 1911; Yonge, 1968), *M. albus* (fide Kühnelt, 1938; Yonge, 1968); *M. malleus* (Linnaeus, 1758) (Yonge, 1968).

4. Pallial ridge (character 101, state 1) also appears apomorphic in *Malleus*, and was reported in *M. regula*, *M. malleus*, *M. albus* (fide Yonge, 1968), *M. (Malvufundus)* [as *M. (Parimalleus)*] *candeanus* (Orbigny, 1842) (Boss & Moore, 1967; Waller & Macintyre, 1982), and *M. (Malvufundus)* *irregularis* (Hayami, 2000).

Node 5: *Isognomon*

Isognomon is diagnosed by unique gill characters of (1) interlamellar dorsal septa (character 15, character 2) and (2) interdemicbranchial buttress (character 16, state 1). Both conditions have previously been reported in *Isognomon* (as *Melina*) *perna* and *I. serratula* (Reeve, 1858) by Ridewood (1903).

Node 6: Pteriidae (Pteria/Pinctada/Electroma) plus Vulsella/Crenatula

This clade is supported by (1) the fusion of anterior pedo-byssal retractor muscles (character 67, state 1) and (2) the widened resilifer, whose width greatly exceeds its height (character 121, character 1). The placement of the fibrous part of the alivincular opisthodontic ligament in the posteriorly expanding, relatively shallow, resilifer is apomorphic to the clade. However, this is not a diagnostic character, due to the presence of the multivincular ligament in *Crenatula* and the uniquely shaped, dorsally expanded ligament in *Vulsella* (the two aberrant groups of sponge-dwelling species). The presence of fused anterior pedo-byssal retractor muscles is likewise not a diagnostic character, because of the absence of the fusion in *Pteria loveni* (Dunker, 1872).

Node 7: Electroma/Vulsella/Crenatula

1. Transverse ridges and grooves on inner surface of lip margins (character 29, character 1) and (2) rounded tip of anal funnel (character 48, character 2) are apomorphic for this group, the latter potentially diagnostic.

Node 8: Vulsella/Crenatula

This clade is diagnosed by the absence of a postlarval byssus (character 59, state 1). However, this condition in *Vulsella* and *Crenatula* is convergent with *Malleus albus*, a species not included in this analysis.

Node 9: Pteria/Pinctada

This clade is not supported by non-homoplastic apomorphic characters.

Node 10: Pteria

Pteria is diagnosed by three shell characters: (1) extension of posterior auricle beyond posteriormost extremity of valves (character 92, state 0); (2) presence of commarginal periostracal scales (character 94, state 1); and (3) configuration of submarginal posterior dentition (ridge in the right valve and a corresponding elongated socket in the left valve; character 111, state 0).

Node 11: Pinctada

1. Lanceolate shape of anal funnel (character 48, state 1); (2) asymmetry of anterior pedo-byssal retractor muscles (character 68, state 1); and (3) anterior subumbonal teeth configuration (a tooth in the right valve and a socket in the left valve; character 109, state 1)

are apomorphic for *Pinctada*. The last is convergent with the condition in some extinct pterioideans, such as Palaeozoic *Leptodesma*, but is unique among Recent Pterioidea.

DISCUSSION

FROM CLADOGRAM TO PHYLOGENY

Before plunging into a discussion of pterioidean evolution, several general statements must be made. An important distinction exists between a cladogram, which is simply a diagram depicting the nesting pattern of synapomorphies, and a phylogeny, which is an explicit statement concerning the history and ancestor–descendant relationships of taxa in question. The two are related through the hierarchy of increasing complexity and explanatory power at the expense of introducing *ad hoc* assumptions (Eldredge, 1979). Thus, phylogenetic reconstruction inevitably incorporates additional data compared with cladogram construction. A single cladogram may correspond to multiple phylogenetic trees, depending upon whether some taxa are considered ancestral to others. The following discussion of phylogeny deals primarily with higher-level taxonomic entities rather than species and avoids postulating specific ancestor taxa, but indicates an ancestral group, such as a genus containing a possible ancestor of a species from another genus, which is appropriate in this case because many genera discussed are probably paraphyletic. The phylogeny proposed here is a combination of the cladogram derived from the analysis of Recent taxa directly calibrated against their known stratigraphic ranges, and combined with the evidence from extinct data not treated cladistically in the present work (Fig. 5). Thus, the cladogram forms the backbone upon which the evolutionary interpretation presented below is built. Deviations from the exact topology of the cladogram stem from recognition of some taxa as possible paraphyletic ancestral groups and acknowledging the fact that a high degree of homoplasy and low branch support for some nodes preclude their unequivocal interpretation. After all, a cladogram is neither true nor false but rather useful or useless in inferring phylogeny (Skála & Zrzavý, 1994).

The completeness of the pterioidean fossil record is unknown, but on the familial and generic levels it appears devoid of major stratigraphic gaps. Given their relatively large size and thickness, there is no reason to suspect that pterioidean shells are more severely affected by taphonomic factors than any other bivalves, for which, by and large, the fossil record gives a reliable indication of their history (Hallam & Miller, 1988). Also, the preference of many pterioideans for crevices and coral reef-associated

The Pterineidae is a heterogeneous assemblage of morphologically and microstructurally diverse genera sharing an inequivalve prosocline shell shape, a duplivincular opisthodontic ligament, an inner nacreous shell layer, and a reduction (sometimes to complete obliteration) of the anterior adductor muscle (Hertlein & Cox, 1969; Carter, 1990). The earliest pterineid, *Denticelox* Pojeta & Gilbert-Tomlinson, 1977, appeared in the lower Middle Ordovician (Pojeta & Gilbert-Tomlinson, 1977; Pojeta & Runnegar, 1985). It is inequivalve, with a slightly deeper left valve, and its hinge is equipped with posterolateral oblique teeth, suggesting a primitive pleurothentic state. Because many pterineid genera were implicated in the evolution of a large number of pteriomorphian higher taxa, the taxonomic status of the family has frequently been questioned. At present, the Pterineidae are regarded as a paraphyletic stem group that ultimately gave rise to many living and extinct pteriomorphian lineages, including the crown groups Pterioidea, Ostreoidea, and Pinnoidea (Waller, 1998; Carter, 2004; Malchus, 2004a).

Jackson (1890) suggested that a Palaeozoic *Pteria*-like ancestor gave rise to the Pterioidea and, through *Isognomon*, the Ostreoidea. The *Pteria*-like ancestor was suggested to derive from the Devonian pterineid genus *Leptodesma* that is similar to *Pteria* in the anteriorly oblique shell, differentiated auricles, orientation of postlarval ligament, and dentition. The differences include the presence of a stronger extent of the posterior wing, a deep subauricular byssal notch in the right valve, and subumbonal teeth in *Pteria* and a reduced anterior adductor muscle in *Leptodesma* (fide Jackson, 1890). This idea was further elaborated by Nakazawa (1959) and Nakazawa & Newell (1968). Independently, Dickinson (1960) proposed that the Pteriidae were derived directly from the Permian species allied to *Leptodesma* (*Leiopteria*) Hall, 1883 and based his claim on the similarity in shell shape, posterior musculature, and dentition, while acknowledging important differences in ligament structure and the presence of an anterior adductor in the postulated ancestor. Like Recent Pterioidea (but unlike the majority of Pterineidae), valves of *Leptodesma* are microstructurally symmetrical, have similar optical properties of the prismatic outer shell layer, and consist of outer calcitic simple prismatic and inner nacreous layers (Carter, 1990). Also, the prismatic layer of *Leptodesma* is expanded, suggesting possible enhancement of the flexibility of shell margins (Carter, 2004) that might function in tight sealing of the shell during closure, as is found in many Recent pterioideans.

According to Jackson (1890), 'Avicula' (now *Pteria*) evolved from the Devonian precursor directly, a view that cannot be accepted without reservations. First,

the question of the taxonomic affinity of extinct 'Avicula'-like forms was raised as early as the hypothesis was proposed, by Jackson himself, who indicated the uncertainty in the age of the group, although suspecting its early appearance during the Devonian or Carboniferous (Jackson, 1890). The uncertainty results from a large number of 'alate' forms ascribed to that genus without any reference to other characters. Consequently, this group probably represents a heterogeneous assemblage of *Pteria*, Bakevelliidae, and possibly *Isognomon*, species. Consequently, it remains to be seen whether the Recent genus *Pteria* had in fact originated in the Triassic (Hertlein & Cox, 1969). Second, the subumbonal teeth of *Leptodesma* have a denticle in the right valve and a corresponding socket in the left valve (Dickinson, 1960; Boyd & Newell, 2001), whereas the opposite configuration is found in all species of *Pteria* and dentate *Isognomon* (Jackson, 1890; Domaneschi & Martins, 2002) [a notable exception is Recent *I. alatus* (Gmelin, 1791), the only species in this group in which both types of subumbonal teeth configuration have been found]. In *Isognomon*, the presence of dentition is an atavistic character and restricted to early ontogeny, as emphasized by Jackson (1890), and, consequently, might be of phylogenetic significance. Third, *Leptodesma* became extinct in the Permian (Newell & LaRocque, 1969), but *Pteria* did not evolve until the Triassic (Hertlein & Cox, 1969) without known members of either genus found on both sides of the Permo-Triassic boundary to substantiate the transition from one group to the other. In fact, the alivincular ligament characteristic of *Pteria* and other Recent Pteriidae is not known from the Palaeozoic rocks (Nakazawa & Newell, 1968). The only exception is a Permian *Ensipteria onukii* Nakazawa & Newell, 1968, that in many respects – extreme posterior elongation, several radiating subumbonal teeth, small internal myophoric buttress – is reminiscent of some Palaeozoic and Mesozoic bakevelliid taxa. Unless the specimens of *Ensipteria onukii* reported by Nakazawa & Newell (1968) are juvenile so that the presence of a single resilifer can be attributed to an early stage of multivincular ligament formation, this condition can be explained by a relatively small size of the specimens and an extensive shortening of the hinge line that does not provide enough space for multiple resilifers. This, in turn, implies a neotenuous retention and utilization of the ontogenetically primary resilifer. Regardless of these facts, Nakazawa & Newell (1968) assigned *Ensipteria* to the family Pteriidae, but suggested its derivation from Monopteriidae Newell, 1969, a pteriomorphian family distantly related to the Pterioidea.

Like the direct derivation of *Pteria* from a *Leptodesma*-like ancestor, the Palaeozoic roots of the Upper Triassic *Isognomon*, the only other archaic

extant branch of the Pterioidea, are suspect. The evidence for the Palaeozoic ancestry of isognomonids rests upon the existence of the isognomonid genus *Waagenoperna* Tokuyama, 1959 that extends to the Upper Permian (Cox, 1969b). This uncharacteristically subequivalve mytiliform genus is based on the Upper Triassic species *W. triangularis* (Kobayashi & Ichikawa, 1952), which strikingly resembles several pterioidean species of an extinct pteroid family Bakevelliidae rather than *Isognomon*, in the strongly prosocline shell shape and progressively broader spacing of resilifers (rather wider than high, unlike in *Isognomon*) towards the posterior end of the hinge (Tokuyama, 1959). The argument for placing *Waagenoperna* in Isognomonidae rests entirely on the arrangement of hinge teeth and on the fact that *Waagenoperna* passes through the 'Pteria-stage' rather than 'Bakevellia-stage' in its ontogeny (Tokuyama, 1959), the latter claim being neither illustrated nor adequately explained. It is noteworthy that the comparison of *W. triangularis* is restricted to bakevelliid taxa and does not include any species of *Isognomon*, a genus to which *W. triangularis* is suggested to be related. Upon a closer look, the morphology of the hinge teeth in *Waagenoperna* does not unequivocally support its relatedness to *Isognomon*. Although *Waagenoperna* and *Isognomon* species share a reduction of posterior submarginal teeth in early ontogeny, the posteriorly orientated subumbonal teeth, as found in juvenile *W. triangularis* (Tokuyama, 1959), do not occur in *Isognomon*, but are characteristic of many species of Mesozoic bakevelliid genera *Gervillella* Waagen, 1907 (Damborenea, 1987; Muster, 1995), *Gervillia* (Gervillia) Defrance, 1820 (Fürsich & Werner, 1988; Muster, 1995), and *Hoernesia* Laube, 1866 (Muster, 1995).

Among actual Permian species, *W. (Permaperna) hayamii* Nakazawa & Newell, 1968, is admittedly *Isognomon*-like in shell outline and the reduction of anterior dentition, but a small number of broad quadrate resilifers suggests relatedness to Bakevelliidae. Poor preservation and the absence of information on muscle scars preclude the exact placement of this species. Another Permian species, *Tambanella gujoensis* Nakazawa & Newell, 1968, was placed in Isognomonidae tentatively because of superficial resemblance (Nakazawa & Newell, 1968), but the presence of robust oblique posterior submarginal and subumbonal teeth, their configuration, and the presence of a continuous pallial line rule out the interpretation of this species (and the genus based on it) as isognomonid.

In summary, there are no unambiguous data for direct Palaeozoic origins of *Pteria* and *Isognomon* lineages. Earlier claims were made primarily on insufficient data and were based on either overall superficial

resemblance or single characters. Consequently, a more conservative view – following Hayami (1957) and Cox (1969b) – is adopted here, that Isognomonidae have evolved from the extinct pterioidean family Bakevelliidae in the Triassic (see below) rather than in the Permian (Nakazawa & Newell, 1968; Stanley, 1972).

POST-PALAEOZOIC HISTORY

Given a doubtful direct ancestry of either *Pteria* or *Isognomon* from the Palaeozoic Pterineidae based on both shell morphological and stratigraphic evidence, the pterioidean family Bakevelliidae is a suitable stem group for these pterioidean taxa. First, the Bakevelliidae is the only well-documented pterioidean group that survived the Permo-Triassic crisis, and its stratigraphic range overlaps with the Palaeozoic and Mesozoic taxa extending from the Carboniferous (Skelton & Benton, 1993). Two of 15 bakevelliid genera originated in the Permian (Muster, 1995): *Bakevellia* (*Bakevellia*) King, 1848 (Permian–Cretaceous) and *Towapteria* Nakazawa & Newell, 1968 (Permian–Middle Jurassic). Their pterineid ancestry (most noticeably from *Leptodesma*) has been expressed in numerous works (Ichikawa, 1958; Nakazawa & Newell, 1968; Stanley, 1972; Carter, 1990) and relies primarily on the following observations: weak development of the subauricular byssal notch and the presence of the anterior adductor, the latter first pointed out in *Bakevellia* by Jackson (1890). Monomyarian *Bakevellia* did not appear before the Middle Triassic (Muster, 1995). Muscle scars in *Towapteria* were not observed, but the presence of a myophoric buttress (Nakazawa & Newell, 1968), reminiscent of a similar structure found in *Leptodesma*, suggests the presence of the anterior adductor muscle. Radial and concentric sculpture in *Towapteria* is similar to that of some pterineid genera. A subumbonal denticle in the right valve and a corresponding socket in the left are reminiscent of *Leptodesma* as well, but nearly horizontal displacement of anterior dentition is typically bakevelliid. Members of these bakevelliid genera are similar to *Isognomon* spp. in having an opisthodetic multivincular ligament (however, generally less regular and more quadrate than found in most isognomonids), a weakly developed anterior auricle, and near equivalvity. They also resemble *Pteria* spp. in having a sinuated, well-demarcated posterior auricle, strongly marked prosoclinity, and the development of a posterior ventral margin resulting in shell length significantly exceeding its height. The shell microstructure of Permian *Bakevellia* and *Towapteria* is unknown, but several species of Mesozoic *Bakevellia*, as well as the majority of species of other bakevelliid genera, display calcitic, regular simple prisms characterized by irregular wavy extinc-

tion symmetrical between valves, as in Pteriidae and a few Pterineidae, including *Leptodesma* (Carter, 1990).

A recent intriguing discovery of bakevelliid larval shells and their close similarity to those of oysters suggested the possibility that the Bakevelliidae is a stem lineage of the Ostreioidea as well as the Pterioidea (Malchus, 2004a). Thus, given the proposed phylogeny, if fossil taxa are extracted and only extant taxa are considered, this would result in the sister-group relationship between the Pterioidea and the Ostreioidea, a result corroborated by the present morphological and prior molecular analyses.

The discussion of the relatedness of the Recent Pterioidea, Bakevelliidae, and Ostreidae, depends on the transition between different ligamental grades. For recent reviews of the vast literature on bivalve and particularly pteriomorphian ligaments, refer to Ubukata (2003b) and Malchus (2004a). The evolution of the multivincular bakevelliid ligament from the pterineid duplivincular ligament must involve reorientation of the ligamental layers with respect to the hinge axis, whereas derivation of the monoresilial alivincular *Pteria*-like ligament from a repetitive duplivincular ligament requires not only a change in the orientation of ligamental layers but also a reduction in their number. In a computer simulation study of ligament morphogenesis, the theoretical morphospace of pteriomorphian ligaments was reconstructed (Ubukata, 2003b). The repetitive ligamental grades cluster at a distance from the alivincular grade with the multivincular region somewhat closer to the alivincular region. This provides grounds to suspect that the transition from duplivincular to multivincular ligaments is potentially easier to achieve than the transition to the alivincular ligament. The distribution of ligamental grades in the theoretical morphospace also suggests that the evolution of the alivincular grade from duplivincular is probable through the multivincular intermediate. The interpretation of the theoretical analyses of ligament pattern formation agrees with the recent detailed empirical analysis of larval and adult ligaments throughout the Pteriomorphia (Malchus, 2004a). The latter study showed that the monoresilial ligaments of the Pterioidea and Ostreioidea are derived by reduction of a multivincular grade, possibly of the stem group Bakevelliidae (Malchus, 2004a). This is further corroborated by the fact that the earliest non-bakevelliid Mesozoic pterioideans were multivincular isognomonids and some extinct Mesozoic ostreioideans likewise had a multivincular ligament (Stenzel, 1971). Interestingly, the multivincular origin of the Ostreioidea had already been proposed by Jackson (1890), who noted similarity between the embryonic shell shape of isognomonids and ostreioideans. He also pointed out their anatomical resemblance, despite an

extremely derived morphology of the latter due to cementation by the left valve. Stoliczka (1871) also pointed out the similarity between the Jurassic genus *Pernostrea* Munier-Chalmas, 1864 and *Isognomon*. It has also been indicated that *Pteria* often has a biresilial ligament (Malchus, 2004a). Because *Pteria* appears to be the oldest non-multivincular pterioidean group, the presence of a biresilial ligament suggests its possible derivation from a multivincular taxon, agreeing with the idea previously advanced by Nakazawa & Newell (1968) that Triassic *Pteria* might have evolved from *Bakevella* by a reduction in the number of resilifers. In addition, such a progressive reduction in resilifer number has been reported for the Cretaceous bakevelliid *Pheloptera* Stephenson, 1952 (Nakazawa & Newell, 1968). Multivincular resilifers are also present in the extant younger genus *Crenatula*, and several irregularly shaped resilifers sometimes occur in species of *Pinctada* (I. Tëmkin, unpubl. observ.).

Taken together, there is strong evidence that the Bakevelliidae is a suitable stem group for both the Pterioidea and the Ostreioidea. The presence of a larval shell septum in some bakevelliids and in Cassianellidae and Lithiotidae (enigmatic small short-lived pterioidean Mesozoic families) provides the basis for their taxonomic placement previously suspected by Ichikawa (1958), Chinzei, Savazzi & Seilacher (1982), Carter (1990), and Waller (1998), providing further evidence that the Bakevelliidae might be a paraphyletic stem group that diversified in the Mesozoic, ultimately giving rise to all other Pterioidea.

A polyphyletic origin of the Pterioidea (Nakazawa & Newell, 1968) is rejected based on the results of the present work and previous molecular, palaeontological, shell embryological, and ligamental data. The supposition that the Pterioidea have evolved from the Bakevelliidae leads to the interpretation of the genus *Isognomon* as a probable precursor to the rest of the pterioideans. It must be noted, however, that *Pteria*'s stratigraphic record possibly (see the discussion earlier in this section) extends to the Triassic, and that the members of the genus share certain aspects of shell morphology with the Bakevelliidae, and some Recent *Pteria* possess an abbreviated multivincular ligament make them a probable candidate as well. It is noteworthy in that regard that the vast majority of *Pteria* species are highly specialized for an attached epizoid life habit on alcyonarians and gorgonians, which evolved much later, in the Jurassic and Cretaceous, respectively (Stanley, 1972). Consequently, possibilities are suggested here for the basal split of the Pterioidean lineage containing Recent taxa: (1) a bifurcating origin of both *Pteria* and *Isognomon* from a single bakevelliid ancestor (Fig. 5) and (2) a stepwise origin of the first *Isognomon* from the bakevelliid lin-

eage, and then of the *Pteria* lineage from the *Isognomon* lineage (Fig. 5, inset).

The results of this work corroborate the previously suggested connection between the Pulvinitidae and *Isognomon* (Cox, 1969c; Palmer, 1984). A close relatedness of *Isognomon* and *Malleus* based on anatomical similarity was indicated by Yonge (1968). This view was corroborated by the results of Stanley's palaeoecological study that implied that *Malleus* retained the endobyssate life habit of isognomonid ancestors (Stanley, 1972). Seilacher (1982) agreed on the close relationship of the two genera, but regarded *Malleus* as a derived group that has invaded soft-bottom habitats secondarily as primarily free-lying epifauna. The presence of the disjunct resilia in *Malleus* [as inferred from the presence of the first two independent resilifers by Bernard (1898) and Malchus (2004a)] corroborates the relatedness of *Malleus* and *Isognomon*. Malchus (2004a) interpreted this as possibly the reduction of a multivincular resilifer, but pointed to Waller's (1990, 1998) suggestion that postlarval resilial discontinuity is probably plesiomorphic in all Pteriomorphia. The present phylogeny differs from the cladogram presented here in placing *Pulvinites* more basally than *Malleus* with respect to *Isognomon*. Its basal placement relative to the *Isognomon*/*Pulvinites* clade is strikingly in disagreement with its late appearance in the fossil record and might be attributed to an elevated rate of evolution, as evidenced by a large number of unique apomorphies in this genus and convergence with other monovincular pterioidean taxa. In addition, the sister-group relationship of *Isognomon* and *Pulvinites* is one of the few poorly supported suprageneric clades lacking diagnostic non-homoplastic characters.

Vulsella and *Crenatula* have been frequently discussed side by side because of their remarkable ecology of living embedded in sponges (Vaillant, 1868; Reid & Porteous, 1980), generally interpreted as convergence. The present study suggests an intimate connection of the two genera, implying a single origin of the colonization of a sponge-dwelling habitat. The sister group to *Vulsella* and *Crenatula* is *Electroma*, a pterioid genus characterized by a reduction of the posterior auricle and expansion of the posterior margin, indicating a tendency towards elongation that to its full extent was exploited by its closest sponge-dwelling neighbours that have subsequently lost the byssus and associated muscles due to the habitat shift. The *Vulsella*/*Crenatula*/*Electroma* clade evolved in the Cretaceous, probably from the *Pteria*-like stem lineage that also gave rise to *Pinctada* in the Miocene. This is largely consistent with the degree of relationships suggested by the cladogram.

PTERIOIDEAN OUTGROUPS

This study provides the first evidence from an analysis of morphological data alone supporting the hypothesis that Pterioidea and Ostreoidea are more closely related to each other than to the Pinnidae (see the review of previous phylogenetic hypotheses discussed earlier). This agrees well with the presence of nacre in the shell of stratigraphically and phylogenetically basal oysters (McRoberts & Carter, 1994; Hautmann, 2001) and is further substantiated by a recent discovery of a duplivincular ligament in the Late Carboniferous pinnid *Pteronites* M'Coy in M'Coy & Griffith, 1844 (Carter, 2004). Based on additional mineralogical and microstructural properties and ligamental structure, it was suggested that *Pteronites* is fundamentally similar to the Devonian pterineids, such as *Leptodesma* (Carter, 2004). The relationship of the Pinnidae with *Leptodesma* was originally proposed by Jackson (1890) based on its overall resemblance to earliest (Devonian) pinnids, despite the presence of unique 'degradational' characters such as the expansion of the prismatic layer accompanied by a reduction in thickness and area of the nacreous layer and a loss of dentition, and hinge prolongation. Extreme modification of the shell, such as the deposition of a continuous prismatic layer across the dorsum (Jackson, 1890; Waller, 1990) and the development of a nacreous sulcus (Chinzei *et al.*, 1982; Waller, 1990), supports the observation of Yonge (1953a) that pinnids rely on muscle contraction rather than on the ligament in opening the valves and suggests a potential cause for the reduction of fibrous sublayers in their ligament (Carter, 2004). In addition to shell features, the secondarily endobyssate habit unique to pen shells has also involved the evolution of a number of distinct soft anatomical characters, as evidenced in extant species (Yonge, 1953a). The Pinnidae also resemble *Leptodesma* in the reduction of the anterior adductor muscle. Despite the strong evidence of this connection, which implies that the symmetry of pinnid valves is a secondary derivation, Newell (1965, 1969a) pointed out that its derivation from an inequivalved ancestor is unlikely and placed the pinnids close to the mytilids. It must be noted, however, that despite the presence of the byssal notch in the right valve in most Pterioidea, some Recent orthothetic *Pinctada* and *Pteria*, as well as Palaeozoic pterineids, are nearly equivalve. Thus, it appears that the same pterineid stem group, namely *Leptodesma*, that ultimately gave rise to the Pterioidea and the Ostreoidea (through a bakevelliid intermediate), had an earlier offshoot in the Lower Carboniferous (Cox & Hertlein, 1969) that marks the appearance of the Pinnidae.

Waller (1998) provided a list of synapomorphies supporting the sister relationship of the Pinnidae and

the Pterioidea, discussed here in turn. (1) The position of the posterior pedal scar relative to the posterior adductor scar. Being inset on the anterior, concave face of a crescent-shaped posterior adductor scar is assumed to be a derived trait restricted to the Pinnidae and all Recent Pterioidea (with the exception of highly derived *Pulvinites*). The position of the pedal retractor on the dorsal side of a rounded adductor is considered plesiomorphic due to its presence in many other living distantly related pteriomorphs and extinct pterioidean bekevelliid and pterineid taxa. First, many Pinnidae, as well as Pterioidea, possess round adductor muscles: oval posterior adductor muscles are characteristic of the pterioidean genera *Pteria* and *Vulsella*, as well as some pinnids such as *Atrina pectinata* (Linnaeus, 1767) (Liang & Morton, 1988). Moreover, in *Isognomon* and many *Pteria* species, the posterior pedo-byssal retractor muscles are not in contact, forming two independent – non-confluent – muscle scars (Pelseneer, 1911; Hayes, 1972; Morton, 1995). In addition, in those taxa where posterior adductor and pedo-byssal retractor scars are coincident, the retractor can be found at the anterodorsal extremity of the adductor (some *Pteria* and *Atrina* species), or the anteroventral extremity of the adductor (even where the adductor is crescent-shaped as in *Electroma* spp.). Both shapes of posterior adductor muscle scar are also present in oysters, as pointed out by Waller (1998), circular in Gryphaeidae and crescent-shaped in the Ostreidae, but due to the lack of posterior retractors associated with early ontogenetic loss of the foot, were not further discussed. However, this condition is directly comparable with that of two pterioidean genera where the byssus is lost despite the retention of the foot. Both genera, *Vulsella* and *Crenatula*, lack posterior pedo-byssal retractor muscles (and, consequently, lack their scars) and display the same variety of adductor muscle shapes as the oysters: subcircular in *Vulsella* and bean-shaped in *Crenatula*. With regard to fossil taxa, it has been indicated that the Pterineidae is an extremely morphologically heterogeneous group. Although certain pterineid taxa do exhibit concentric posterior adductor scars (Bailey, 1983; Johnston, 1993), the genus *Leptodesma*, which has been implicated directly in the evolution of the Pterioidea, has a crescent-shaped posterior adductor (Dickins, 1960). Therefore, the shape of the adductor muscle and its association with the posterior retractor must be taken with great caution in phylogenetic interpretations. (2) A very broad extension of the regular columnar prismatic calcitic outer shell layer. It is noteworthy that in the Pinnidae the most extensive development of the prismatic layer is at the posterior part of the shell, as in some species of *Malleus*, which is, arguably, a consequence of adaptation to an endo-byssate mode of life (Yonge, 1953a, 1968; Stanley,

1972). In similarly extended species of *Isognomon*, which are essentially crevice dwelling, the nacreous layer extends much further. The unequal expansion of the nacreous ventral margins in *Electroma*, *Pteria*, and *Pinctada* primarily serve the function of tight closure. Consequently, although the tendency of prismatic shell margins may be predetermined by common descent, its evolution was probably driven by several different adaptive forces and does not necessarily provide evidence of an immediate close relationship. (3) The discontinuity of the pallial line is characteristic of all Recent Pterioidea, further reduced to a few attachment points in *Malleus*, as noted by Kühnelt (1938) and Yonge (1968), and some *Isognomon* species (present observations). As indicated by Waller (1998), pallial discontinuity was present in the Ambonychioidea, which is noted to be different than that of the Pinnoidea and Pterioidea. The presence of a discontinuous pallial line was also indicated in the more closely related pterineid *Leptodesma* (Dickins, 1960) and is probably plesiomorphic to the Pterioidea and Pinnoidea. Also, pinnid pallial attachments are restricted to a pair of retractor muscle sinuses located dorsally and ventrally to the posterior adductor muscle (Grave, 1911; Yonge, 1953a), a unique situation that is difficult to homologize with the pterioidean pallial line, with the exception of that of *Malleus*, where only one scar is present. However, the scar in *Malleus* is located more anteriorly and represents the attachment of a single long muscle (Pelseneer, 1911; Kühnelt, 1938; Yonge, 1968), whereas in the Pinnidae the attachments are formed by sinuses of multiple merging pallial retractor bundles (Grave, 1911; Yonge, 1953a). Moreover, *Malleus* does not appear as a sister group of the Pinnidae in any phylogenies proposed to date. (4) The presence of alivincular or multivincular ligament grades with resilifers evenly spaced and remaining parallel sided throughout most of the ontogeny.

With regard to the placement of the Ostreioidea relative to the Pterioidea and Pinnoidea, the present findings are in close agreement with previous molecular analyses, but at odds with palaeontological evidence suggesting a much earlier development of the Ostreioidea from the mid-Palaeozoic family Rhombopteriidae, which shares common ancestry with the Pterineidae (Johnston, 1991b, 1992, 1993). It appears, however, that the Ostreioidea did not evolve until the Triassic (Stenzel, 1971) and diagnosable modern ostreoid features, such as the loss of the anterior adductor and the calcitic, foliated shell, did not evolve until after the Carboniferous (reviewed in Carter, 2004). Some Late Triassic Ostreioidea possess anterior retractor muscle scars and nacreous shells (Carter, 1990), consistent with the view that the Ostreioidea probably evolved from Late Palaeozoic pterineids than

from mid-Palaeozoic rhombopteriids (Carter, 2004). However, in the absence of microstructural data on Rhombopteriidae, its relatedness to Ostreidae cannot be ascertained (Waller, 1998). Also, Johnston's (1991) suggestion that the right-sided pleurothetic habit was never part of the evolutionary history of oysters is compromised by the fact that the left abdominal sense organ is less developed in oysters than in the Pterioidea and Pinnoidea (Haszprunar, 1983; present study).

In summary, this review of the Pterioidea is the first detailed morphological study, which provides a comprehensive, synthetic evolutionary framework for the entire superfamily. These findings have major taxonomic implications. However, because of the fact that the phylogenetic analysis did not include the type species of many genera and the taxon sampling was rather limited, any taxonomic revision is premature. Major goals for the future are to increase the taxon sampling for underrepresented genera and to directly incorporate fossil data into a phylogenetic analysis. This work has clearly demonstrated the importance of the fossil record in estimating evolutionary relationships among the living members of the group and called to question the taxonomic status of the earliest representatives of two oldest living genera (*Pteria* and *Isognomon*), suggesting the direction of a future palaeontological investigation. The results of the phylogenetic analysis agree with a complementary molecular study (Tëmkin, 2004a), which will be presented in full elsewhere.

ACKNOWLEDGEMENTS

With gratitude, I extend my thanks to Rüdiger Bieler and Paula M. Mikkelsen for organizing the symposium *Bivalve Systematics – a Look at the Branches* and inviting me to participate. I also express my gratitude to the organizing committee of the World Congress of Malacology (Perth, Western Australia, 11–16 July 2004), which hosted the symposium. I am especially grateful to Paula Mikkelsen for encouragement, advice, and critical comments on the manuscript. I also thank Rüdiger Bieler and two anonymous reviewers for invaluable suggestions for its improvement. For fruitful discussion of anatomical characters I thank Luiz Simone and for general comments on the fossil record I thank Vladimir Blagoderov and Yumiko Iwasaki. Rüdiger Bieler and Isabella Kappner provided great help with the translation of pertinent German texts, and Francisca Almeida assisted with translations from Portuguese. I am indebted to Enrique Arizmendi Castillo (Perlas del Mar de Cortés, Mexico) for providing facilities for collection and study of the pterioidean fauna of Guaymas, Mexico, and donating important specimens during my visit to

Perlas del Mar de Cortés pearl farm in 2003. Osmar Domaneschi and Claudio Mantovani Martins kindly shared with me some critical observations on the anatomy of *Isognomon bicolor* prior to publication. Data gathering from other museum collections was facilitated by Gary Rosenberg and Paul Callomon (ANSP), Adam J. Baldinger (MCZ), Philippe Bouchet (MNHN), Mirosław G. Harasewych (USNM), Elizabeth Kools (CASIZ), Ian Loch (AMS), and Bruce A. Marshall (NMNZ). David Grimaldi and Tam Nguyen (AMNH) assisted with light photography. This research was supported in part by U.S. National Science Foundation (Partnership for Enhancing Expertise in Taxonomy) grant DEB-9978119 to Rüdiger Bieler and Paula M. Mikkelsen, and NSF doctoral dissertation improvement grant DEB-0508311. I dedicate this work to Roman Tëmkin, who passed away just before this manuscript was finished.

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APPENDIX 1

CHARACTER DEFINITIONS

Some of the characters used in this study have previously been used in high-level analyses of the Bivalvia by Salvini-Plawen & Steiner (1996) and Giribet & Wheeler (2002). Therefore, for a discussion of characters not dealt with in depth in the present work, refer to these references. In the following list, the characters are grouped in categories defined by organ system and numbered as they appear in the data matrix and the cladogram (Fig. 4). Discussions pertaining to

several consecutively listed characters generally follow the definition of the last character.

MANTLE

1. Marginal mantle lobe fusion: (0) absent; (1) present. The joining of the mantle margins provides an effective way of separating incurrent and excurrent chambers. The nature of the connection between mantle margins varies from transient ciliary junctions to the formation of siphons involving tissue fusion of all mantle margin folds (for a review, see Yonge, 1957). In the Pterioidea, the mantle margins are generally free, being fused exclusively dorsally along the hinge line, forming a mantle isthmus ventral to the ligament and a hood extended over the lips in the anterior. Nevertheless, the incurrent and excurrent chambers are effectively separated by connections between the inner surfaces of the mantle lobes and the base of the ascending lamella of the outer demibranchs on one hand and the junction between the bases of the ascending lamella of the inner demibranchs on the other. The presence of marginal mantle fusion is restricted to two outgroup taxa, *Mytilus edulis* (Linnaeus, 1758) and *Crassostrea virginica* (Gmelin, 1791), where the inner folds of the mantle lobes are fused posteriorly, forming a branchial septum or membrane.

2. Supramyal septum (Fig. 6): (0) absent; (1) present. The supramyal septum connects the left and right mantle lobes, stretching from the dorsal side of the adductor muscle and mantle isthmus and is penetrated by the intestine. This transverse membrane effectively seals off the supramyal passage. In *Malleus* species, the supramyal septum is absent and the intestine is markedly displaced to the left at the dorsal part of the posterior pedo-byssal retractor muscle and fused to the left mantle lobe. The resulting asymmetry was previously noted by Pelseneer (1911) in *Malleus daemoniacus* Reeve, 1858. Yonge (1968), who found the same condition in *Malleus regula* (Forsskål, 1775), interpreted it as an opening of the supramyal passage ['promyal' passage in Yonge (1968)]. Apparently unaware of the presence of the transverse membrane in other pterioideans, Yonge (1968) ascribed the primacy of the supramyal passage opening to the separation of the posterior adductor from the posteroventral extremity of the visceral mass. The importance of this separation is doubtful because the passage is present in all Pterioidea and its width varies greatly. Consequently, water is free to pass into the dorsal part of the mantle cavity around the pericardium.

3. Pallial fold: (0) absent; (1) present.

The pallial fold is a gutter-like tapering extension of the innermost mantle lobe that meets the tip of the ctenidium. This is a symmetrical structure occurring

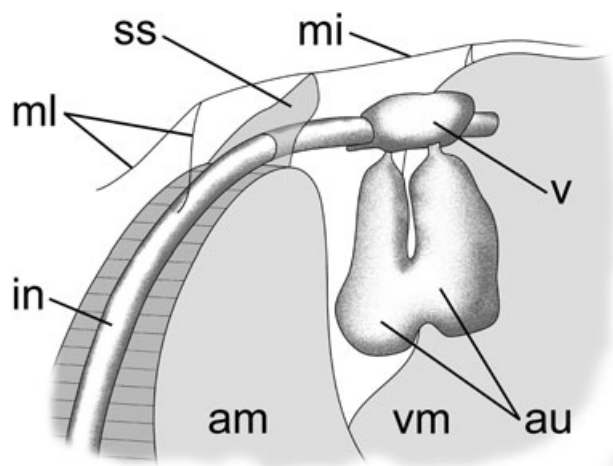


Figure 6. The supramyal septum. Diagrammatic anatomy in posterolateral view. Abbreviations: au, auricles; am, adductor muscle; in, intestine; mi, mantle isthmus; ml, mantle lobes; ss, supramyal septum; v, ventricle; vm, visceral mass.

on opposite sides of the posterior portion of the mantle margins, demarcating the separation of incurrent and excurrent apertures, the former located below and the latter above the pallial fold. The junction between the left and right pallial folds is facilitated by interlocking tentacles of the inner fold that generally reach their greatest size in the vicinity of the pallial fold. The pallial fold was first described in *Pinctada fucata* (Gould, 1850) (as *Margaritifera vulgaris* Schumacher, 1817) by Herdman (1904). It is present in the majority of the Pterioidea, except for *Vulsella*, some *Pteria*, and *Isognomon* species.

4. Fusion of the mantle lobe(s) to the lateral surface of the visceral mass: (0) absent; (1) present on one (left) side only; (2) present on both sides.

In the Pterioidea, the mantle lobes are generally fused to the visceral mass, except notably in the genus *Pteria*, where both lobes are free of lateral fusion (with the exception of the dorsalmost part proximal to the mantle isthmus). In the ostreid outgroup species *Crassostrea virginica* (Gmelin, 1791), the lack of fusion of the right mantle lobe to the visceral mass is associated with the formation of the supramyal chamber, which permits an excurrent flow to proceed dorsal to the posterior adductor muscle in addition to an epibranchial excurrent channel situated ventral to it (Galtsoff, 1964). According to Nelson (1938), water can be actively expelled from the promyal chamber by forceful shell adduction, thus assisting in cleansing the pallial cavity. Great variation on this theme is found in the Ostreioidea and appears to be of systematic importance in this group (Harry, 1985). It is doubtful that this condition in *Pteria* is associated with the promyal chamber, because the

passage dorsal to the posterior adductor muscle is blocked by the presence of the supramyal septum (character 2), but can possibly be related to the epizoic habit of members of the genus, who are subjected to strong currents and having a larger volume of incoming water that might assist in both cleansing and processing a larger quantity of water.

5. Duplicated outer mantle fold, OF-1/OF-2 (Fig. 7): (0) absent; (1) present.

Traditionally, the 'primitive' condition of the bivalve mantle edge was assumed to be comprised of three folds, each associated with a specific function: shell-secreting outer fold, sensory (and often tentaculate and equipped with eyes) middle fold, and muscular inner fold (Yonge, 1957; Taylor, Kennedy & Hall, 1969). Although this condition is common, it varies greatly across the Bivalvia in both the number of folds and their functions, making it difficult to establish their homology across distantly related taxa (Waller, 1978). This led Waller (1978) to adopt a descriptive system of denoting the relative position of mantle folds that is independent of functional interpretations and does not connote homology. In this system, mantle folds are regarded as either 'outer' (OF) or 'inner' (IF) relative to the periostracal groove and consecutively numbered outward. (The lack of a number indicates the presence of a single fold.)

Although assessment of the homology of the mantle folds presents a problem at high-level taxonomic comparisons, the relative uniformity of mantle morphology and the limited number of mantle fold arrangements within the Pterioidea provide grounds for unequivocal assessment of mantle lobe homology.

Two patterns of arrangement of the mantle fold are known in the Pterioidea: three and four folds. The three-fold condition has been reported from *Pinctada martensii* (Dunker, 1872) (Kawakami & Yasuzumi, 1964), *Pinctada fucata* (fide Herdman, 1904), *Pinctada margaritifera* (Linnaeus, 1758) (Jabbour-Zahab *et al.*, 1992), and *V. vulsellata* (Linnaeus, 1758) (Reid & Porteous, 1980). The four-fold condition was found in *I. legumen* (Gmelin, 1791) (Harper & Morton, 1994) and *Pteria breviaulata* (Dunker, 1872) (Morton, 1995). The periostracal groove separates the two inner folds from either one or two outer folds. Thus, the arrangement of mantle folds in *Pinctada* and *Vulsella* is OF/IF-1/IF-2, whereas in *Pteria* and *Isognomon* it is OF-2/OF-1/IF-1/IF-2. In all cases, IF-1 and muscular IF-2 are tentaculate and devoid of pallial ocelli. OF in the three-fold condition and OF-2 in the four-fold condition are morphologically similar, being thin and devoid of tentacles, and presumably shell secreting. OF-1 has a thinner epithelium compared with OF and OF-2 folds and often bears pallial ocelli and other structures associated with photoreception (Morton, 2001).

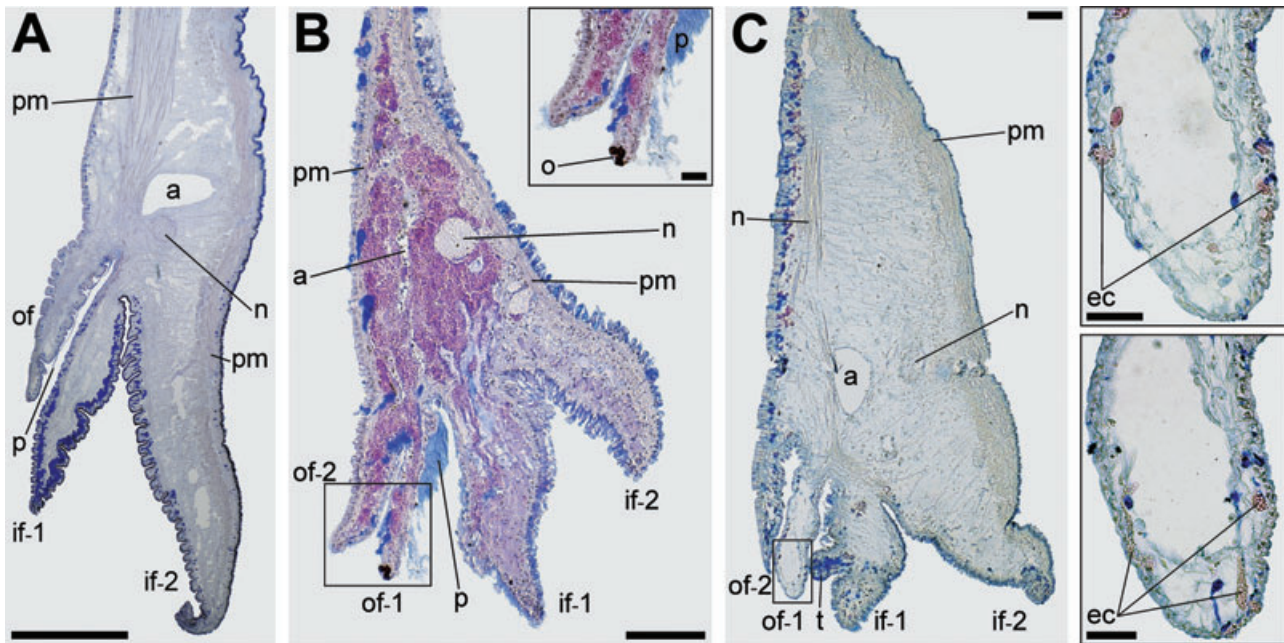


Figure 7. Mantle edge morphology in the Pterioidea. Histological cross-section (5 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain). A, three-fold condition: *Pinctada mazatlanica* (AMNH 311790, 107.6 mm; scale bar = 1 mm); B, four-fold condition: *Isognomon radiatus* (AMNH 298944, 29.3 mm height; scale bar = 0.1 mm); C, *Pteria colymbus* (AMNH 298920, 63.6 mm; scale bar = 0.1 mm). Inset (B), close up of the distal extremity of the OF-1 fold (boxed) showing the ocellus (scale bar = 0.02 mm). The right panel of (C) shows two close ups of the distal extremity of the OF-1 fold (boxed) at different focal planes (scale bar = 0.03 mm). Abbreviations: c, circumpallial artery; ec, eosinophilic cells [putative photoreceptors *sensu* Morton (2001)]; if, inner mantle fold; n, circumpallial pallial nerve; o, ocellus; of, outer fold; p, periostracum; pm, pallial muscle; t, tentacle.

As pointed out by Waller (1978), the two-fold condition ontogenetically precedes the formation of multiple folds. In this early stage of development, the two folds are separated by the periostracal groove, which appears homologous through the Bivalvia (Waller, 1978). Although early ontogeny of mantle formation is not documented in the Pterioidea, a similar condition (two folds with a periostracal groove in between) is present in closely related ostreids (Waller, 1981; Carriker, 1996). Similarly, two folds precede the formation of four folds in the mantle of a venerid *Venus striatula* (Da Costa, 1778) (Ansell, 1962). These observations led to the conclusion that the two-fold condition is primitive in most if not all bivalves and – although retained in some taxa to adult stage (Waller, 1978) – the additional folds emerge by subsequent differentiation of the two primordial ones. Consequently, single folds present on either side of the periostracal groove are directly comparable, such as OFs of *Pinctada* and *Vulsella*. In the case of duplicated folds, it can be postulated that both OF-1 and OF-2 of *Isognomon* and *Pteria* are homologous to the OF of *Pinctada* or *Vulsella*. In effect, OF-1 and OF-2 can be considered paralogues because they probably evolved

through the duplication of OF rather than modification of a pre-existing structure. In a similar manner, Harper & Morton (1994) and Morton (1995) identified the OF-1 and OF-2 in *Isognomon* and *Pteria* as the inner and outer components of a duplicated outer fold.

Equally, the four-fold pattern and the photoreceptive function associated with the OF-1 fold in some arcoids (Waller, 1980) is directly comparable with that of the Pterioidea, but given the distant relatedness of these taxa, the homology assessment requires a comprehensive survey of the mantle morphology of the Pteriomorphia. Outside the Pteriomorphia, the four-fold condition reported in the venerid *Venus striatula* is markedly different, having a single outer fold and three inner folds: OF/IF-1/IF-2/IF-3 (Ansell, 1962). Despite striking differences, the relative position of the folds to the periostracal groove at least suggests a putative homology of outer folds between venerids and pterioideans.

The two-fold condition described in *V. lingulata* Lamarck, 1819 (Vaillant, 1868) was not confirmed; the author probably considered a row of large densely packed tentacles as emerging from the groove between

two folds, rather than arising from the edge of a short and inconspicuous middle fold.

6. Waste canal: (0) absent; (1) present.

The waste canal is a ciliated groove bounded by folds and produced on the inner surface of mantle margins distal to the upper edge of the ascending lamellae of outer demibranchs (Grave, 1911; Yonge, 1953a). Although its presence is only found in the Pinnidae, it might be a highly modified form of a potentially homologous 'ciliated pallial path' found in *Pinctada fucata* that runs along the mantle margins (Herdman, 1904) and possibly performs essentially the same function of posteriorly directed waste removal.

7. Tentacles on middle mantle fold (IF-1): (0) absent; (1) simple; (2) branched.

See character 8.

8. Tentacles on inner mantle fold (IF-2) (Fig. 8): (0) absent; (1) simple; (2) branched.

Waller (1978) distinguished between different kinds of tentacle by their complexity, ability to extend, and position. Judging by the apparent lack of active response to external stimulus, he deduced that tentacles of *Pinctada* and *Pteria* are simple lobate and probably non-specialized extensions of the mantle margins (Waller, 1976). In contrast, the present review of the Pterioidea identified many morphologically diverse kinds of tentacles supplied with muscle fibres and nerve extensions, and differing in their presence and distribution on mantle margins. However, because most of the observations were made on preserved material, the degree of tentacle extension and their behaviour could not be evaluated. Given the discussion regarding the homology of mantle margins (character 5, see above), the distinction is made between tentacles originating on non-homologous

mantle folds [contra Waller (1978) and Giribet & Wheeler (2002)]. Thus, in the present work, tentacles are distinguished by their location on either IF-1 or IF-2 folds, and the presence of lateral branches.

GILLS

The terminology of gill morphology follows Ridewood (1903) and Atkins (1936) unless indicated otherwise.

9. Serial tissue fusion of filaments at the distal (ventralmost) edge of demibranch margins (Fig. 9): (0) absent; (1) present.

Despite limited sampling of Pterioidea, Ridewood (1903) noticed that species of *Pinctada*, *Pteria*, and *Malleus* develop tissue connections between gill filaments where descending filaments turn and begin to ascend, thus providing a continuous stretch of tissue along the demibranch margins, whereas in *Isognomon* spp., filaments are united by ciliary junctions. As a consequence of this ciliary connection, the filaments are easily separable. In *I. bicolor* (C. B. Adams, 1845), tissue connection is present but limited to a very narrow band running medially along the gill margins (Martins, 2000) that provides little to interfilamentar connections because filaments readily separate upon a slight touch of a needle. A similar condition was found in other presently examined *Isognomon* spp.

10. Association of ascending lamellae of inner demibranchs (Fig. 10): (0) absent (ctenidia are not joined); (1) ciliary connection present; (2) tissue connection present.

In the Pterioidea, the upper edges of the inner demibranchs come into contact just posteroventral of the foot, but the nature of this association varies greatly within some genera. Ridewood (1903) reported both ciliary and tissue connections in *Isognomon*. Similarly,

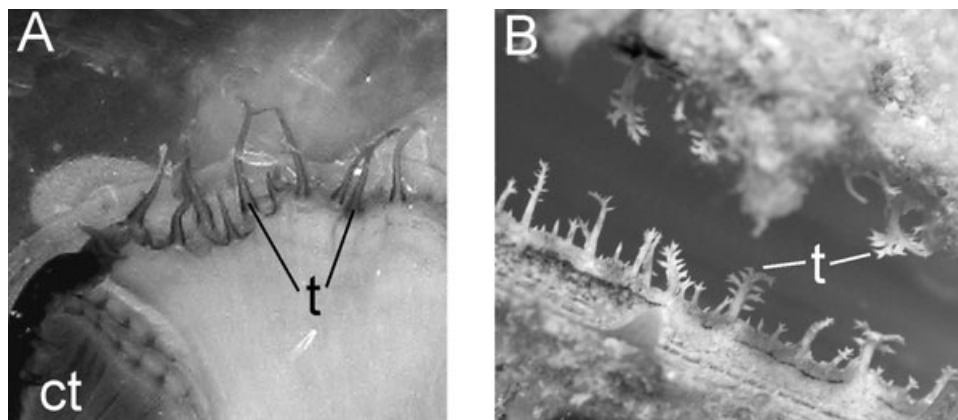


Figure 8. Tentacle morphology. A, simple tentacles on IF-2 at posteroventral part of left mantle lobe, *Isognomon alatus* (AMNH 298023, 43.41 mm); B, branched tentacles on IF-2 along ventral shell margin, *Pinctada imbricata* (FK-689 AMNH). Abbreviations: ct, ctenidium, t, tentacles. (Photograph by R. Bieler.)

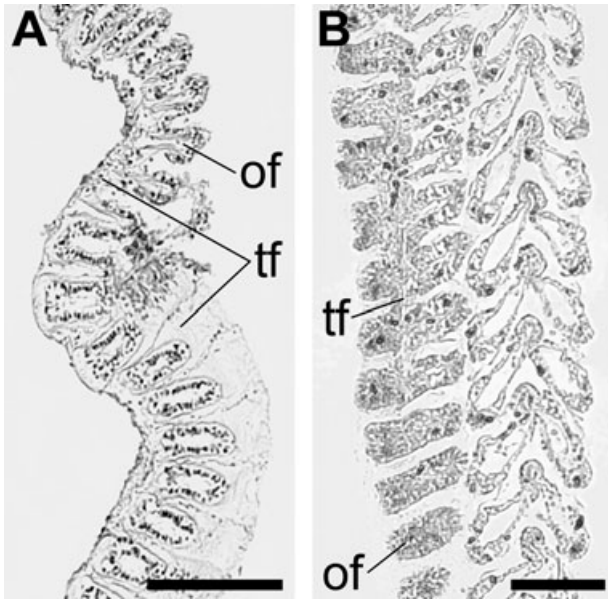


Figure 9. Serial tissue fusion of filaments at ventralmost edge of demibranch margins. Transverse histological section of ctenidia (7 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain). A, extensive interfilamentar serial fusion of gill filaments, *Malleus* (*Malvufundus*) *candeanus* (AMNH 299406, 33.4 mm height); B, interfilamentar serial fusion limited to a transient narrow bridge, *Isognomon alatus* (AMNH 298023, 43.41 mm). Abbreviations: ofg, ordinary gill filaments; tf, tissue fusion. Scale bar = 0.1 mm.

in *Pteria*, Pelseneer (1911) and Morton (1995) found fused ctenidia in *Pteria* (as *Avicula*) *macroptera* (Lamarck, 1819) and *Pteria brevislata*, respectively, whereas Atkins (1936) showed an exclusively ciliary connection in *Pteria hirundo* (Linnaeus, 1758). Both conditions also occur in *Pinctada*. *Pinctada* (as *Meleagrina*) *anomoides* (Reeve, 1857) has fused ctenidia (Ridewood, 1903), whereas in *Pinctada fucata*, the fusion is restricted to the tips of ctenidia (Herdman, 1904). In *Malleus albus* Lamarck, 1819 (Atkins, 1936), *M. regula* (fide Yonge, 1968), *Crenatula phasianoptera* Lamarck, 1804 (Vaillant, 1868), and *Pinna carnea* Gmelin, 1891 (Yonge, 1953a), the interctenidial connections are established by means of interlocking cilia. In some cases, the connection is predominantly ciliary, but definitive, albeit extremely narrow, tissue fusion occurs along the ventral edge of the area connecting the demibranchs, as in *I. alatus* (Gmelin, 1791) (Atkins, 1938) and *I. bicolor* (fide Martins, 2000). Cases in which tissue connections were predominantly ciliary and extremely limited tissue fusion did not prevent ctenidia from being easily separated without damage were coded as ciliary. In addition, such restricted tissue is probably variable within a species, because many specimens of *I. alatus*, *Pinctada fucata*,

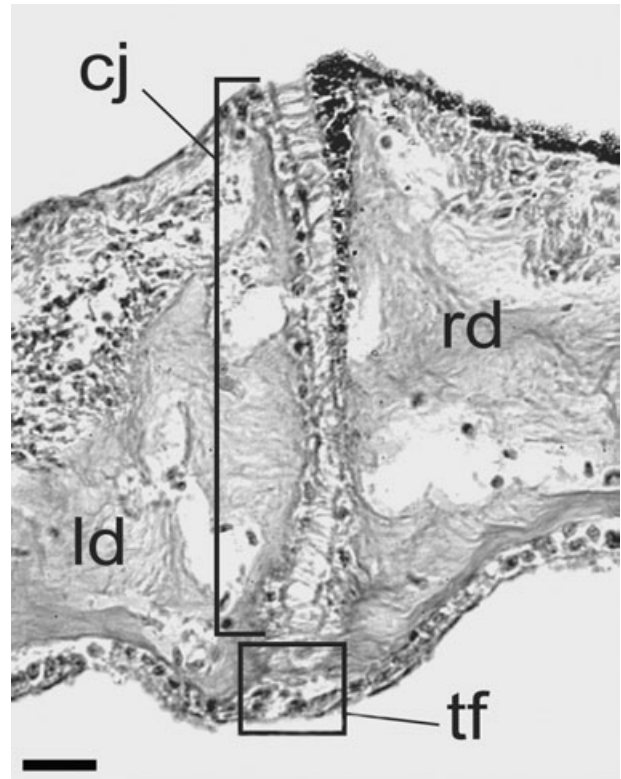


Figure 10. Association of ascending lamellae of inner demibranchs. Frontal histological section of ctenidia (7 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain), *Pinctada longisquamosa* (AMNH 298904, 16.0 mm). Abbreviations: cj, extent of ciliary junction; ld, upper edge of ascending lamella of left demibranch; rd, upper edge of ascending lamella of right demibranch; tf, area of tissue fusion. Scale bar = 0.01 mm.

and *P. longisquamosa* (Dunker, 1852) that display this condition were found with medially separated undamaged ctenidia.

11. Pseudoaxial suspensory septum: (0) absent; (1) present;

The pseudoaxial suspensory membrane (Harry, 1985) is a tissue connection stretching from the interctenidial connection, an area of fusion of upper edges of ascending lamellae of inner demibranchs, to the mid-ventral surface of the visceral mass. This feature is absent in the Pterioidea, but characteristic of many Ostreioidea (Harry, 1985).

12. Suspensory membrane of the posterior adductor muscle (Fig. 2H): (0) absent; (1) present.

In the Pterioidea, ctenidia attach to the anterior or anteroventral region of the posterior adductor muscle by a suspensory membrane extending from the gill axes. The absence of the suspensory membrane is limited to the outgroup taxa.

13. Association between ascending lamellae of outer demibranchs and mantle (Fig. 11): 0 absent; (1) ciliary connection present; (2) tissue connection present.

In a vast majority of the Pterioidea, this union between the inner surface of the mantle lobes and the upper edges of ascending lamellae of the outer demibranchs is achieved by means of interlocking cilia, thereby effectively separating supra- and infrabranchial channels. Grobben (1900) mentioned that ciliary gill–mantle junctions are present in *Isognomon*, *Crenatula*, and *Vulsella*. This has been confirmed by

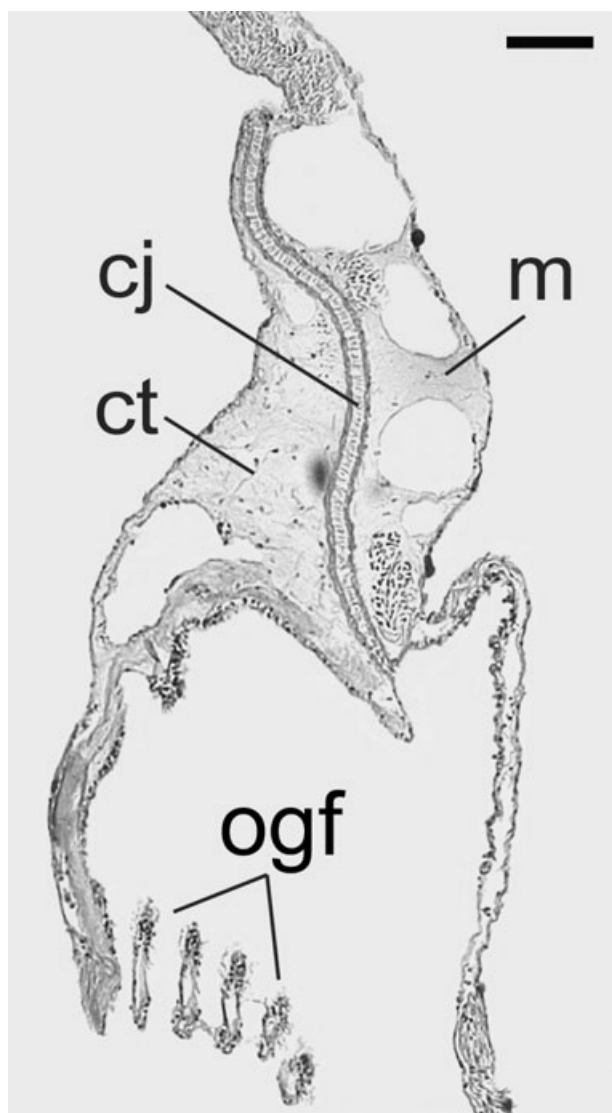


Figure 11. Ctenidia–mantle junction. Frontal histological section (7 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain). *Pinctada longisquamosa* (AMNH 298904, 16.0 mm). Abbreviations: cj, ciliary junction; ct, ctenidium (upper edge of ascending lamella of outer demibranch); m, mantle; ogf, ordinary gill filaments. Scale bar = 0.05 mm.

many other authors in *Isognomon* (as *Isognomum* or *Melina*) *perna* (Linnaeus, 1767) (Ridewood, 1903; Pelseneer, 1911), *I. serratula* (Reeve, 1858) (Ridewood, 1903), *I. bicolor* (fide Martins, 2000), *Pteria hirundo* (Atkins, 1936), *Malleus albus* (fide Kühnelt, 1938), *Crenatula phasianoptera* (fide Vaillant, 1868). The ciliary connection is transient and can easily be re-established upon disruption in a living animal. Although the connection is relatively weak and can easily be disrupted, and in the absence of a gill joined to the mantle in a preserved specimen, it can definitively be established due to the presence of a *ciliary trail* along which the connection is formed. The ciliary trail along which the connection is formed has previously been noted by Grobben (1900) and Herdman (1904). A number of exceptions have been reported, however, for virtually all genera, indicating a complete or large extent of mantle–ctenidia tissue fusion in a number of species: *I. legumen* (fide Harper & Morton, 1994), *I.* (as *Melina*) *linguaeformis* (Reeve, 1858) (Ridewood, 1903), *Pteria brevialata* (fide Morton, 1995), *Pinctada anomioides* (fide Ridewood, 1903). Ridewood's (1903) statement that in various isognomonid species the upper edges of the ascending lamellae are 'free from the mantle/adjacent parts' is ambiguous with regard to differentiating between the complete absence of association on one hand and the presence of a weak ciliary connection on the other. Likewise, Pelseneer's (1892) assertion that Pteriidae (as Aviculidae) is characterized by 'branchies soudées au manteau' fails to explicitly differentiate between ciliary and tissue connection. Moreover, in a number of species, the ctenidia are attached to the mantle along their entire length, with the exception of the tips, where a very narrow but definite organic connection is present: *I. ephippium* (Linnaeus, 1758) (Reid, 1985), *Malleus albus* (fide Ridewood, 1903), *M. regula* (fide Yonge, 1968), *Pinctada anomioides* (fide Ridewood, 1903), *Pteria* (as *Avicula*) *tarentina* (Lamarck, 1819) (Ridewood, 1903). The difficulty in evaluating the state of exclusively terminal fusion comes from the fact that in many taxa the connection between the tips of ctenidia is strengthened by the presence of a pallial fold (character 3) that enlarges the area of ciliary attachment and by preservational artefacts that lead to a strong junction of associated structures, making the separation of ciliary connection difficult without ripping the tissue. Therefore, the terminal ctenidia–mantle fusion was not separated as a character state and the distinction is made between complete or nearly complete ciliary connection (as evidenced by the presence of the ciliary trail), complete or nearly complete fusion, and the absence of any association as evidenced by the lack of the ciliary trail. The absence of any association between ctenidia and mantle is restricted to the mytilid outgroup taxon.

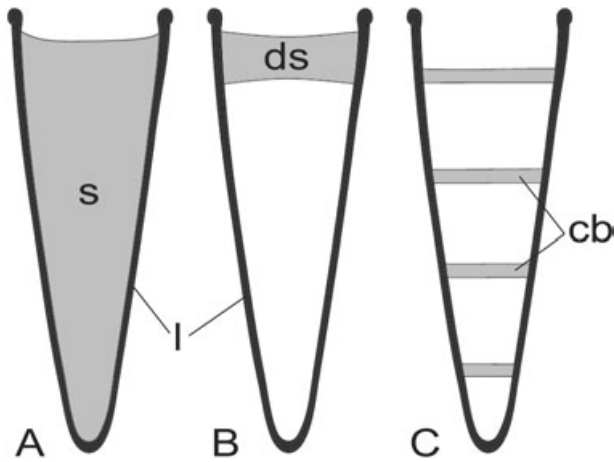


Figure 12. Morphology of interlamellar junctions. Diagrammatic frontal section through demibranch. A, most Pterioidea; B, *Isognomon*; C, Pinnidae and Mytilidae. Abbreviations: cb, cross-bars; s, complete septa; ds, dorsal septa; l, gill lamellae.

14. Food groove on margins of the outer demibranch: (0) absent; (1) present.

Food grooves are absent in the outer demibranchs of all homorhabdic pterioideans presently examined. This confirms Yonge's observation on the gills of *Malleus regula* (fide Yonge, 1968). Atkins (1936), however, indicated the presence of food grooves in *Malleus*, but mentioned that they are not well marked. Only well-defined food grooves defined by characteristic infolding along the ventral edge of the filaments are coded as present.

15. Interlamellar junctions (Figs 12, 13): (0) absent; (1) multiple cross-bars; (2) dorsal septa; (3) complete septa.

In the Pterioidea, the interlamellar junctions are in the form of septa extending from the interlamellar edge all the way to the dorsalmost edge of lamellae (occupying the full height of the interlamellar cavity). Present observations confirm previous accounts of its presence in *Pinctada fucata* (fide Herdman, 1904), *Malleus albus* (fide Ridewood, 1903), and *Pteria hirundo* (fide Atkins, 1936). *Isognomon* is a notable exception, where septa are reduced to the dorsalmost part of the demibranch (Ridewood, 1903). The term adopted here to describe this condition is *dorsal interlamellar septum*, as opposed to interlamellar bar (Ridewood, 1903) to differentiate this state from multiple interlamellar narrow cross-bars characteristic of pinnid and mytilid outgroup taxa. The presence of interlamellar junctions was scored independent of the presence of principal filaments because interlamellar septa develop even in homorhabdic gills, as

indicated by Ridewood (1903) and confirmed in the present work.

16. Interdemibranchial buttresses: (0) absent; (1) present.

The *interdemibranchial buttress* is a membrane connecting the dorsal septa of the demibranch within the ctenidium over a fusion area of descending lamellae. This condition was first described in *I. perna* and *I. serratula* by Ridewood (1903). Ridewood did not give it a specific name, but speculated that the 'continuous membrane or web' might have developed by the fusion of dorsal septa (Ridewood, 1903). The interdemibranchial buttress is present exclusively in species of *Isognomon*.

17. Filament differentiation (Fig. 13): (0) ordinary filaments only; (1) principal filaments present; (2) principal and apical filaments present.

In the Pterioidea, gills are composed of exclusively ordinary filaments (homorhabdic condition) in *Isognomon* [*I. legumen* (fide Harper & Morton, 1994), *I. isognomon* (Linnaeus, 1758) (Yonge, 1968)], *Malleus* (*M. albus* (fide Ridewood, 1903), *M. regula* (fide Yonge, 1968)], and *Pulvinites exempla* (Hedley, 1914) (Tëmkin, 2006). *Pinctada* (Ridewood, 1903) and *Pteria* (Ridewood, 1903; Atkins, 1936) have heterorhabdic gills with principal filaments only. Contrary to the presently collected evidence and previous accounts from the literature, Yonge (1968) mentioned the presence of principal filaments in *Malleus malleus* and *M. albus* without providing any evidence. Ridewood (1903) indicated the presence of apical filaments in *Pinctada margaritifera*, also not illustrating his claim. These two latter observations were not corroborated by the present analysis of other *Malleus* and *Pinctada* species, but until analyses of species on which these claims were made can be performed, the present findings cannot be extrapolated throughout the entire genera. The presence of the apical filaments is restricted to pinnid outgroup taxa (Ridewood, 1903; Grave, 1911).

According to Ridewood (1903), the formation of ordinary filaments ontogenetically precedes the differentiation of principal filaments, providing grounds for polarizing the character. The apical filaments are found only in plicate gills because the formation of apical filaments is dependent upon the prior differentiation of principal filaments. This character is presently treated as ordered (additive).

Another related commonly used character – gill plication – is abandoned in the present study because it described the superficial appearance of gill lamellae that is structurally determined by the presence of principal filaments, an assumption made by Ridewood (1903) and confirmed in the present work. It is noteworthy, however, that plication is independent of

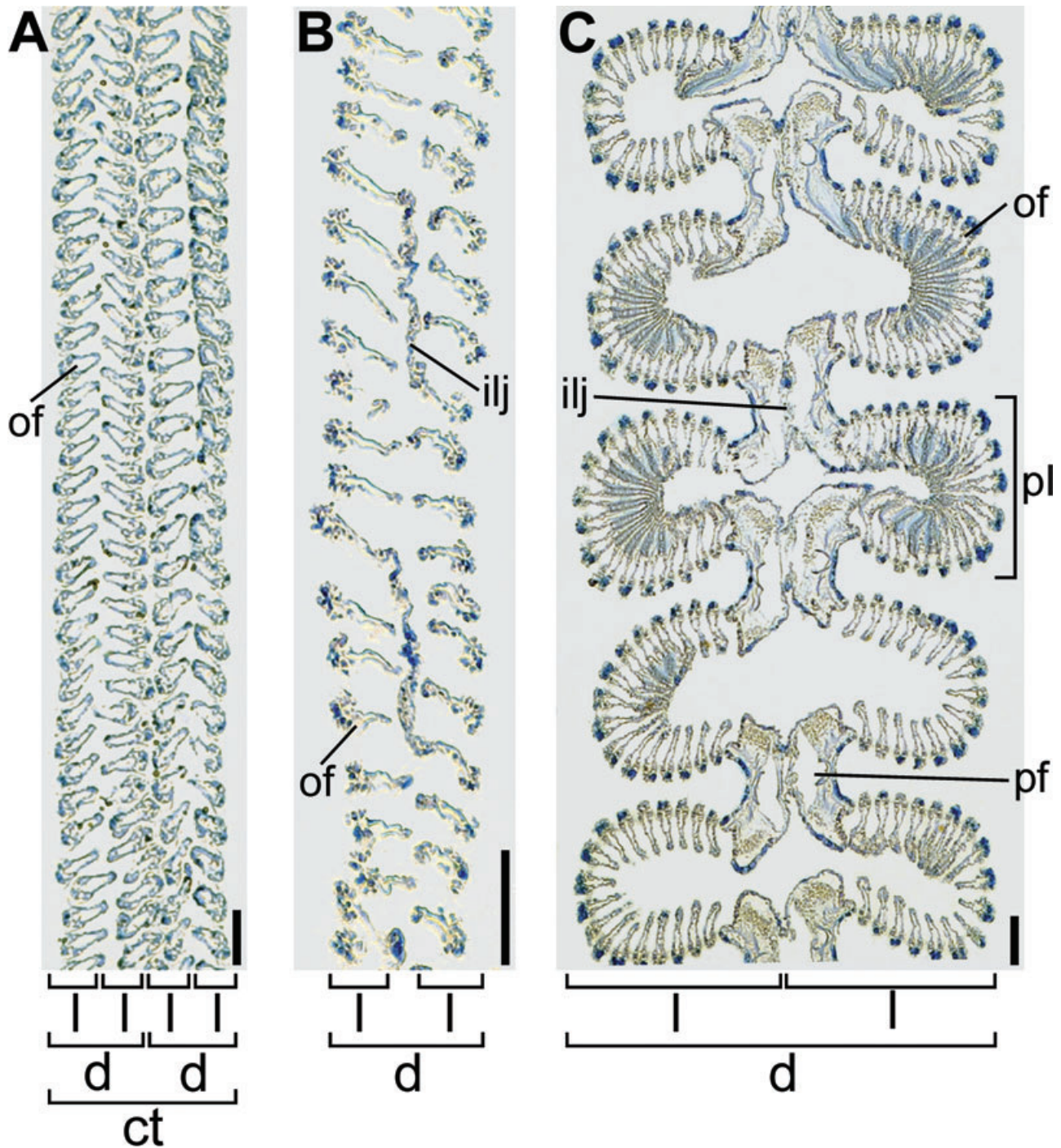


Figure 13. Anatomy of ctenidia in the Pterioidea. Transverse histological section (7 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain). Homorhabdic ctenidia: A, *Isognomon alatus* (AMNH 298023, 43.41 mm); B, *Malleus (Malvufundus) can-deanus* (AMNH 299406, 33.4 mm height); heterorhabdic ctenidia: C, *Pteria sterna* (AMNH 311731, 84.0 mm). Abbreviations: ct, ctenidium; d, demibranch; ilj, interlamellar junction; l, gill lamellae; ogf, ordinary gill filaments; pgf, principal gill filaments; pl, plica. Scale bar = 0.1 mm.

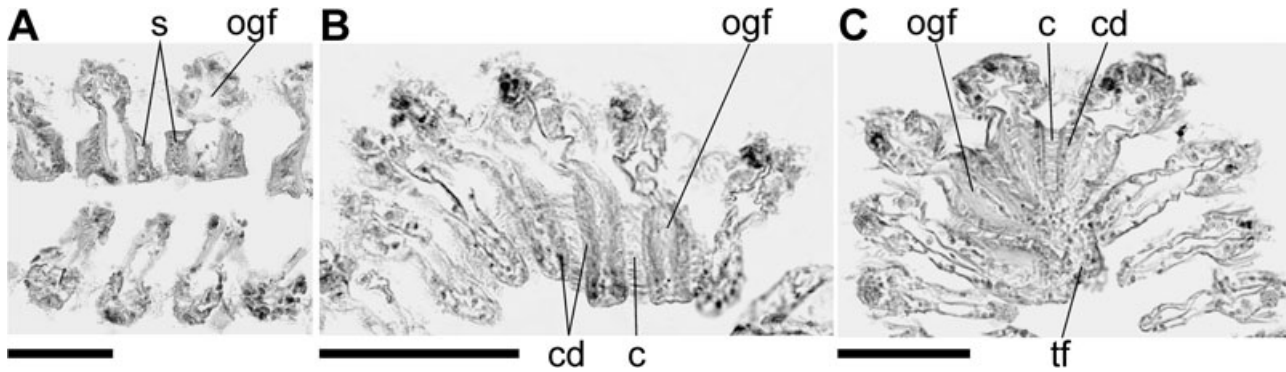


Figure 14. Interfilamental associations in the Pterioidea. Transverse histological section (7 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain). A, connections mediated by ciliated discs projecting from spurs (top lamella), *Isognomon alatus* (AMNH 298023, 43.41 mm); B, connections mediated by ciliated discs projecting from thickened ordinary filaments, *Pteria loveni* (MNHN MD32/Reunion 1982 St. DC85, 29.4 mm); C, connections mediated by both ciliated discs and organic fusion along basal side of filaments, *Pteria colymbus* (AMNH 298920, 63.6 mm). Abbreviations: c, interfilamentar cilia; cd, ciliated disc; tf, tissue fusion; ogf, ordinary filament; s, spur of ciliated disc. Scale bar = 0.05 mm.

the presence of interlamellar junctions, as exemplified by the fact that homorhabdic gills of *Malleus* and *Pulvinites* (fide Tëmkin, 2006) have the same kind of interlamellar septa as the plicate gills of *Pteria* and *Pinctada* but originating from ordinary filaments.

18. Ciliated discs (Fig. 14): (0) absent; (1) present.

Gills of the Pterioidea are of the eleutherorhabdic grade, characterized by filaments connected by means of interlocking cilia projecting from ciliated discs. Ciliated discs do not occur in synaptorhabdic gills of pinnid and ostreid outgroup taxa.

19. Ciliated discs projecting from spurs (Fig. 14): (0) absent; (1) present.

In eleutherorhabdic taxa, the ciliated discs are generally formed by thickening of the basal part of the filament; alternatively, the ciliated discs project considerably upon its lateral outgrowths, so-called spurs (Ridewood, 1903).

20. Interfilamentar tissue junctions (Fig. 14): (0) absent; (1) present.

In the vast majority of the Pterioidea, the neighbouring filaments within a demibranch are joined to each other via ciliated discs, but in many instances discrete tissue processes in the form of horizontal bars are present along with ciliated discs. Herdman (1904, 1905) first described this condition in *Pinctada fucata*. This finding was later confirmed by Atkins (1936), who had also reported the occurrence of similar fusion in *Pteria hirundo* (fide Atkins, 1936) and *Pinctada margaritifera* (Atkins, 1936, 1938). Ridewood (1903) illustrated its presence in *Pteria* (as *Avicula*) *argentea* (Reeve, 1857) and considered this condition as an intermediate between eleutherorhabdic and syn-

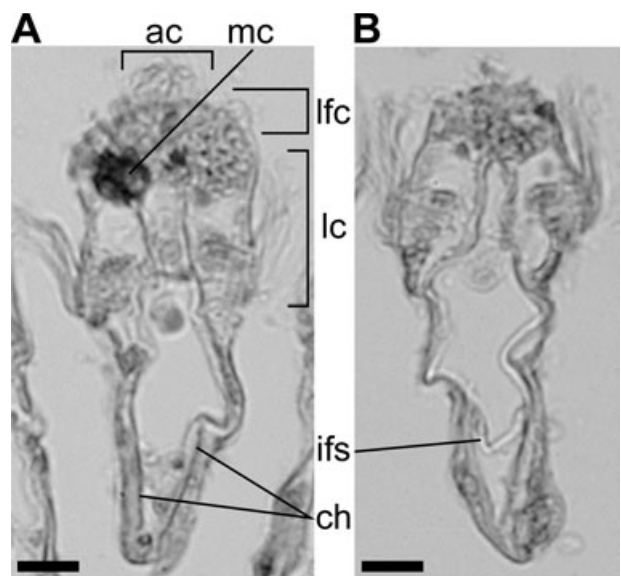


Figure 15. Ordinary filament anatomy. Transverse histological section (7 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain). Filament without (A) and with (B) intrafilamentar septum, *Pteria colymbus* (AMNH 298920, 63.6 mm). Abbreviations: ac, apical cilia; ch, chitinous skeleton; ifs, intrafilamentar septum; lc, lateral cilia; lfc, laterofrontal cirri; mc, mucocyte. Scale bar = 0.01 mm.

torhabdic gill grades. Gills with filaments united exclusively by tissue connections (synaptorhabdic grade) are restricted to ostreid and pinnid outgroup taxa.

21. Intrafilamentar transverse septum (Fig. 15): (0) absent; (1) present.

A distinct transverse intrafilamentar septum, alternatively referred to as a 'muscle fibre' (Galtsoff, 1964), or 'transverse bridge' (Grave, 1911), is absent in most Pterioidea, but was reported from *Pteria hirundo* by Atkins (1936), *I. bicolor* by Martins (2000), and mytilid outgroup taxa by Ridewood (1903). The presence of the intrafilamentar septum has been confirmed by the present work in some but not all species of *Pteria*. Ideas on its function diverged from the potential role in separating afferent and efferent blood channels to mere structural support (reviewed by Grave, 1911).

22. Eulaterofrontal cirri (Fig. 15): (0) absent; (1) present.

Compound eulaterofrontal cirri (Owen, 1978) do not occur in the Pterioidea that have been thought to lack laterofrontal tracts [such as in *Pinctada fucata* by Herdman (1904)]. Atkins (1938), however, discovered in these taxa a single row of small cilia that she termed 'microlaterofrontal cilia'. Atkins (1938) also distinguished so-called anomalous laterofrontal cilia characteristic of Ostreidae on the basis of their smaller size and variation in spacing on different filaments within the same individual. However, it has subsequently been shown that the 'anomalous' laterofrontal cilia of Ostreidae closely correspond to eulaterofrontal cirri (Owen, 1978). The homology between the microlaterofrontal cilia and eulaterofrontal cirri is uncertain, due to obligatory co-occurrence of eulaterofrontal cirri with subsidiary prolaterofrontal cilia, but a general topology of cilia-bearing cells, their arrangement relative to each other, direction of the effective beat, and a similar disposition of their corresponding rhizoplasts (rootlets), and position at rest (Atkins, 1938) permits the provisional acceptance of a deep homology of at least microlaterofrontal and eulaterofrontal ciliary complexes. Consequently, the character denoting the presence of eulaterofrontal cirri does not compromise the notion of the homology of these structures. It is noteworthy that Atkins (1938) herself, while entertaining a wide range of scenarios of evolution of laterofrontal cilia ranging from homology of all their types to independent origin in diverse lineages, favoured the latter explanation based on previously advanced phylogeny based on other characters. It is important to keep in mind that despite the fact that the Pinnidae possess microlaterofrontal cilia, the arrangement of cilia and the number of cilia-bearing cells differ from those of other taxa with microlaterofrontal cilia (Atkins, 1938; Owen, 1978). Due to the lack of fresh material, no attempt was made to distinguish between the two possibilities.

23. Abfrontal cilia: (0) absent; (1) present.

Abfrontal cilia are absent in all taxa surveyed with the exception of the outgroup species *Mytilus edulis* (Field, 1923).

LABIAL PALPS AND LIPS

24. Tips of labial palps (Fig. 2I): (0) angled; (1) rounded.

Thiele (1886) pointed out that the tip of the free edge of the outer labial palp in *Pinctada* (as *Meleagrina*) *margaritifera* (Linnaeus, 1758) is angled, but that of *Malleus* is rounded. The present work identified rounded edges of labial palps in *M. anatinus* (Gmelin, 1791) – but not *M. (Malvufundus) candeanus* (Orbigny, 1842) – and *Electroma*, *Crenatula*, and *Vulsella* species.

25. Fusion of the proximal edges of labial palps to the visceral mass: (0) absent; (1) present.

In the Pterioidea, labial palps are fused along their long proximal edges to the sides of the visceral mass extending ventralward from the lips. In *Mytilus*, the fusion of the palps to the visceral mass is restricted only to a small area immediately proximal to the lips, so that the proximal and distal long edges of the palps are essentially free.

26. Ventral tips of the anterior filaments of the inner demibranchs inserted into the distal oral groove: (0) absent; (1) present.

In all Pterioidea, the ventral tips of the anterior filaments of the inner demibranch are not inserted into the distal oral groove, a condition classified as type III ctenidia–labial palp association by Stasek (1963). Type I, where the tips are inserted but not fused, is restricted to the mytilid outgroup, whereas type II, characterized by the ventral tips of the anterior filaments of the inner demibranch inserted into and fused to the distal oral groove, is not present in any of the taxa.

27. Lip overlap: (0) absent; (1) ventral lip wrapped around the dorsal lip; (2) dorsal lip wrapped around the ventral lip.

The extent of the upper and lower lips differs across the Bivalvia, as demonstrated by the species-poor but taxonomically broad survey of Gilmour (1974). He pointed out that in the pterioidean *Pteria hirundo* and ostreid *Ostrea edulis* Linnaeus, 1758, the upper lip is wrapped around its lower counterpart (Gilmour, 1974). These observations cannot be generalized in light of the data presented in this work. Both conditions were found in *Pteria* and *Malleus* species; the rest of the species have either a more extensive ventral lip or both lips developed to the same extent. It must be noted, however, that in most cases the stronger development of one of the lips is not pronounced, making it a relatively subtle character. Gilmour's observation that the ventral lip of *Pinna nobilis* Linnaeus, 1758 is more extensive is corroborated by the present observation of the same condition in another pinnid, *Atrina rigida* (Lightfoot, 1786).

28. Longitudinal ridges and grooves on the inner lip surface near the oral groove: (0) absent; (1) present. Longitudinal ridges and grooves are reported or depicted as absent in the Pterioidea [*Pteria hirundo* (fide Gilmour, 1974), *V. vulsella*, and *Crenatula modiolaris* Lamarck, 1819 (Reid & Porteous, 1980)]. Their presence is restricted to *Pulvinites exempla*, where this condition appears to be polymorphic, occurring in some but entirely absent in other specimens (Tëmkin, 2006).

29. Transverse ridges and grooves on the inner surface of lip margins: (0) absent; (1) present. Among pterioideans, transverse ridges and grooves were found only in species of *Electroma*, *Crenatula*, and *Vulsella*, supporting previous observations of their presence in species of the last two genera by Reid & Porteous (1980), *V. vulsella* and *Crenatula modiolaris*. This finding agrees with the absence of these structures in *Pteria hirundo*, ostreid, and mytilid species (Gilmour, 1974). Likewise, transverse grooves and ridges were absent in *A. rigida*, unlike in another previously reported pinnid *Pinna nobilis* (Gilmour, 1974).

30. Tentacles on lips: (0) absent; (1) present. Lip tentacles, arborescent processes on the inner surfaces of the lips, were only found in *Electroma alacorvi* (Dillwyn, 1817), confirming previous observations of Pelseneer (1911) of their presence in *Electroma* (as *Avicula*) *alacorvi* and *Electroma meleagridis* (Dunker, 1869).

ALIMENTARY SYSTEM

31. Oesophageal longitudinal grooves and ridges: (0) absent; (1) present.

Several conspicuous ridges originate from the oesophageal orifice immediately posterior to the lips and are produced directly to the opening into the stomach where they terminate. These structures vary in width and are present in most Pterioidea, with the exception of several *Pteria* and *Pinctada* species where the ventral surface of the oesophagus forms inconspicuous irregular folds. A character signifying the presence of oesophageal ridges was used in the high-level analyses of the Bivalvia by Salvini-Plawen & Steiner (1996), but the structure and its variations were neither illustrated nor discussed.

32. Stomach lateral displacement: (0) in the middle of the visceral mass; (1) on the left side of the visceral mass; (2) on the right side of the visceral mass. The stomach is positioned on the left side of the visceral mass in all pterioidean taxa examined in this work [corroborating the previous observation of Pelseneer (1911) in *Pinctada*]. Typically, the stomach directly underlies the epithelium of the left wall of the visceral mass (and is sometimes observable through it), whereas the rest of its surface is densely covered by the digestive gland. The position of the stomach on either the right side or in the middle of the visceral mass is restricted to the outgroup taxa.

33. Fleishy fold (Fig. 16): (0) absent; (1) present. The fleshy fold (Purchon, 1957) is an enlarged posterior wall of the food-sorting (gastric) caecum. This structure divides the stomach into anterior and posterior sections extending from the mid-dorsal part of the stomach roof down along the left wall, and widens at the floor of the stomach. The structure is variously described by other authors as 'the left wall of the caecum' (Graham, 1949), an internally projecting

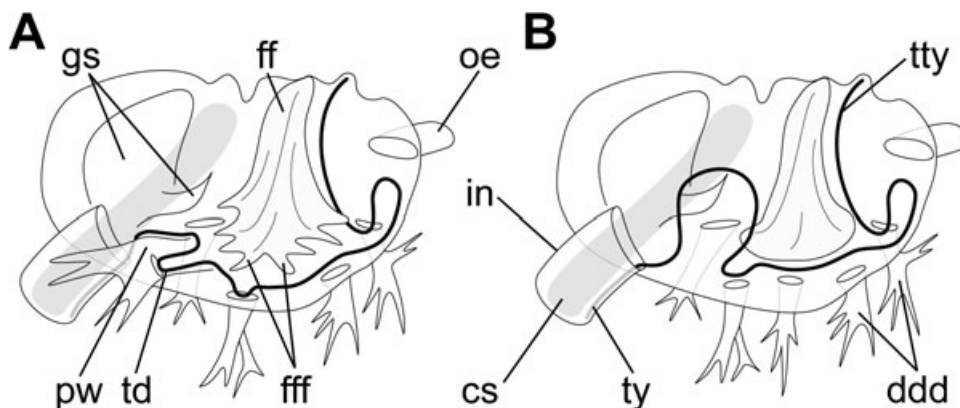


Figure 16. Anatomy of pterioidean stomach. A diagrammatic lateral view through the right stomach wall showing differences in the morphology of the fleshy fold, the course of the tongue of the major typhlosole, and its association with the ducts of digestive diverticula. A, most Pterioidea; B, *Isognomon*, *Pulvinites*, some *Malleus* spp. Abbreviations: cs, crystalline style; ddd, ducts of digestive diverticula; ff, fleshy fold; fff, finger-like processes of fleshy fold; gs, gastric shield; in, intestine (co-joined with style sac); oe, oesophagus; pw, partition wall; td, tongue of major typhlosole diving into digestive diverticula; ty, major typhlosole; tty, tongue of major typhlosole.

'longitudinal ridge' (Nakazima, 1958), and 'the axial fold' (Dinamani, 1967). Purchon (1985, 1987) later substituted his earlier term 'fleshy fold' for '(fleshy) buttress', which is not adopted in the present work because it implicates structural support that is not associated with this feature. A typical fleshy fold is present in all Pterioidea analysed herein and the ostreid outgroup taxon.

34. Finger-like processes of the fleshy fold (Fig. 16A): (0) absent; (1) present.

In species of most pterioid genera, with the exception of *Pulvinites* (Tëmkin, 2006), *Isognomon*, and *Malleus* (*Malvufundus*), the surface of the widened ventral base of the fleshy fold has conspicuous ridges and grooves ['finger-like processes' in Purchon (1985, 1987)] that spread over the stomach floor. This part of the fleshy fold has been interpreted as a food-sorting area (Purchon, 1957). The finger-like processes of the fleshy fold have been illustrated (but not always explicitly discussed under a specific name) in *Pinctada* (as *Pteria*) *maxima* (Jameson, 1901) (Nakazima, 1958), *Pinctada martensii* (fide Nakazima, 1958; Kuwatani, 1965), *P. fucata* (fide Purchon, 1957), *Pteria breviaata* (fide Morton, 1995), *P. chinensis* (Leach, 1814) (Purchon, 1985), *P. penguin* (Röding, 1798) (Purchon, 1987), *Malleus albus* (fide Purchon, 1957), and *V. vulsellia* (fide Reid & Porteous, 1980).

35. Posterior partition wall of the stomach (Fig. 16A): (0) absent; (1) present.

The posterior partition wall (Kuwatani, 1965) extends into the lumen of the stomach from its posterior wall to the right of the intestinal orifice. In effect, this structure creates a left wall of a posteriorly extending embayment of digestive diverticula on the right posterior side of the stomach. The presence of the posterior partition wall greatly affects the path of the tongue of the major typhlosole in the posterior part of the stomach. Upon emergence from the intestine, the tongue of the major typhlosole climbs up the partition wall (forming a ridge on its dorsal surface), then proceeds to its anteriormost extremity, where it sharply descends ventralward. From there, the tongue of the major typhlosole loops towards the embayment of the digestive diverticula along the right side of the partition wall. The structure has previously been described in the Pterioidea as a 'posteroventral fold' in *Pinctada fucata* by Herdman (1904). Kuwatani's (1965) term is preferable because it avoids the confusion between two distinct structures: Herdman's 'posteroventral fold' and Kuwatani's 'posterior fold' that rounds the posterior stomach wall proximal to the gastric shield. The posterior partition wall was depicted but neither labelled nor discussed in *Pteria penguin* (Purchon, 1987).

36. Tongue of the major typhlosole diving into ducts of the digestive diverticula (Fig. 16A): (0) absent; (1) present.

Never explicitly defined, Purchon's (1957) 'tongue of major typhlosole' apparently refers to the segment of the major typhlosole produced into the interior of the stomach where it is circumnavigated by the intestinal groove on each side. Being a continuation of the typhlosole, it was not recognized as a discrete structure by some other authors (Graham, 1949; Dinamani, 1967) and caution must be taken when interpreting its presence from literature alone. Within the Pterioidea, the tongue of the major typhlosole dives into the ducts of the digestive diverticula in most species of *Pinctada*, and in some species of *Pteria* and *Malleus*. In other taxa, including the non-pterioid outgroup, the tongue winds within close proximity to the ducts. Previously, a close association between the tongue of the major typhlosole and the ducts of the digestive diverticula has been reported from the following pterioidean species: *Pteria breviaata* (fide Morton, 1995), *P. penguin* (fide Purchon, 1987), *Malleus albus* (fide Purchon, 1957, 1987), *Pinctada fucata* (fide Purchon, 1957), and *P. maxima* (fide Nakazima, 1958).

37. Ducts of the digestive diverticula clustered in embayments (Fig. 16): (0) absent; (1) present.

The digestive diverticula open into the stomach via ciliated ducts and function to provide an extensive surface for absorption and intracellular digestion (Yonge, 1926). In the Pterioidea, the ducts of the digestive diverticula open directly into the lumen of the stomach along the right side of the tongue of the major typhlosole (with the exception of the ducts of the left pouch) with few or none forming embayments. The number of ducts varies considerably from species to species. Present observations are corroborated by previously reported numerous ducts opening directly into the stomach in *Malleus albus* (fide Purchon, 1957, 1987), *Pinctada fucata* (fide Purchon, 1957), *P. maxima* (fide Nakazima, 1958), *P. martensii* (fide Nakazima, 1958; Kuwatani, 1965), *P. anomioidea* (fide Dinamani, 1967), *Pteria chinensis* (fide Purchon, 1985), *P. penguin* (fide Purchon, 1987), *V. vulsellia* (fide Reid & Porteous, 1980), and *I. nucleus* (Lamarck, 1819) (Dinamani, 1967). Multiple ducts are also present in the mytilid outgroup *Mytilus edulis* (fide Graham, 1949; Reid, 1965). Ducts are clustered into embayments in the Pinnidae [*A. pectinata* (Linnaeus, 1767) (as *A. japonica* Reeve, 1858) (Nakazima, 1958), *A. vexillum* (Born, 1778), *Pinna bicolor* Gmelin, 1791 (as *Pinna atropurpurea* Sowerby, 1825) (Purchon, 1957), *P. bicolor* (fide Dinamani, 1967)] and some ostreids, including the outgroup species *Crassostrea virginica* (fide Langdon & Newell, 1996).

38. Typhlosole morphology: (0) contains a median shallow groove; (1) complex T-shaped; (2) simple T-shaped.

In most taxa surveyed the typhlosole is a broad ridge widening distally and contains a shallow groove. *Crenatula* and *Electroma* species share a uniquely shaped typhlosole that in cross-section appears as an asymmetrical T-shaped structure with parallel longitudinal grooves. The typhlosole in *Atrina* is also T-shaped in cross-section, but is very different from that of *Crenatula* and *Electroma*, being a thin membranous symmetrical structure equipped with a single median groove.

39. Blind caecum of the descending intestine: (0) absent; (1) present.

The blind caecum of the descending intestine is characteristic of the mytilid outgroup, *Mytilus edulis* (fide Field, 1923) and is absent in the other taxa examined.

40. Descending intestine produced ventrally relative to the posterior adductor muscle (Fig. 2A): (0) absent; (1) present.

In all Pterioidea, the intestine extends towards the protruding posteroventral extremity of the visceral mass (*intestinal pouch*) at the anteroventral side of the posterior adductor muscle.

41. Path of the descending intestine (Fig. 2A): (0) descends straight posteroventrally; (1) curves strongly anteriorly at ventralmost extremity.

See character 43.

42. Extent of the ascending intestine (Fig. 2A): (0) produced anteriorly passed the stomach; (1) not produced anteriorly.

The ascending intestine extends anteriorly passed the stomach only in ostreid and mytilid outgroup taxa.

43. Path of the ascending intestine (Fig. 2A): (0) ascends to the right side of the descending intestine; (1) ascends to the left side of the descending intestine; (2) makes a loop over the descending intestine from left (distally) to right (proximally); (3) makes a loop over the descending intestine from right (distally) to left (proximally).

The course of the intestine is schematically illustrated in Figure 2 for all genera. Present observations closely agree with previous anatomical studies of the Pterioidea that depicted the coiling of the intestine in *Pinctada fucata* (fide Herdman, 1904), *P. margaritifera* (fide Gervis & Sims, 1992), and *Pteria brevislata* (fide Morton, 1995). The topology of the isolated intestine of *I. perna* by Pelseneer (1911) was not confirmed. This overly simplified drawing was probably meant to show the extent of the crystalline style and the penetration of the ventricle by the intestine rather than the topology of intestinal folding.

44. Lateral displacement of the intestine: (0) absent; (1) displaced to the left side.

In the Pterioidea, the external part of the intestine generally leaves the visceral mass at the posterodorsal extremity, extending medially down the posterior surface of the posterior adductor muscle. In *Malleus*, however, the intestine – and, consequently, the heart – is markedly displaced to the left side, with the intestinal sheath fused to the left mantle lobe. This asymmetry was first noticed by Pelseneer (1911) and interpreted by Yonge (1968) as an adaptation for the facilitation of the movement of water through the supramyal opening (see character 2). Although the lateral position of the intestine is probably functionally related to the presence of the supramyal passage, there is no direct link explaining side preference, as evidenced by a similar displacement of the intestine in *Pteria* (as *Avicula*) *coturnix* (Dunker, 1880) and in some ostreids where the intestine is displaced to the right side (Pelseneer, 1911).

45. Free-hanging rectum (Fig. 2C): (0) absent; (1) present.

In most Pterioidea, the intestine passes along the posterior surface of the posterior adductor muscle attached to it for its entire length. In *Crenatula* [including *C. phasianoptera*, previously studied by Vaillant (1868)], *Pulvinites* (fide Tëmkin, 2006), *Electroma*, and *Vulsella*, the tip of the rectum is slightly protruded away from the adductor muscle surface, forming a free-hanging papilla (although attached by a thin membrane). A similar condition was observed in the pinnid outgroup taxon, as well as in *Pinna* sp. by Gray (1857) and *A. pectinata* by Liang & Morton (1988).

46. Intestinal sheath pigmentation: (0) absent; (1) present.

The terminal part of the intestine descends medially along the posterior surface of the posterior adductor muscle and in some pterioideans is conspicuously covered with a sheath of thin epithelium that in some instances is conspicuously pigmented. Pigmentation (noticeable even in preserved specimens) is present in species of *Pinctada*, *Pteria*, *Electroma*, and some *Isognomon*.

47. Anal funnel (Fig. 2D): (0) absent; (1) present.

Anal funnel, the term first used by Herdman (1904), aptly describes a conspicuous funnel- or ear-like membranous structure protruding from the tip of the rectum at an approximate right angle to the posterior adductor and enclosing the anal opening at its base. The structure has variously been referred to as the 'anal process' (Herdman, 1904), 'anal membrane' (Ranson, 1961), 'anal flap' (Hayes, 1972), 'anal flag or ear' (Pelseneer, 1911). It probably functions to direct

faecal pellets outside of the mantle cavity, providing an efficient way of cleansing (Hayes, 1972; Mikkelsen *et al.*, 2004). Herdman (1904) was first to indicate the diagnostic significance of the anal funnel, and subsequently Hynd (1955) and Ranson (1961) used the shape of the funnel to differentiate species of *Pinctada*, whereas Hayes (1972) expressed her doubts regarding the reliability of the character, based on its intraspecific variability. The anal funnel is present in all Pterioidea with the exception of *Pulvinites* (fide Těmkin, 2006). It has rarely been discussed, but often clearly depicted [for example in various species of *Malleus* and *Isognomon* by Yonge (1968)]. The absence of an anal funnel in *Crenatula phasianoptera* reported by Vaillant (1868) (based on a single specimen) was probably a consequence of predation; in several pterioid species observed in the present work, the tip of the intestine was damaged or missing. Given the terminal position of the structure and its proximity to the posterior gape required by its function of waste removal, such instances are expected, perhaps at an even higher rate in *Crenatula* where the rectum is free hanging, extending further outwards compared with other genera.

Outside the Pterioidea, similar structures have been found in some Ostreidae ['anal appendage' in Harry (1985)], where it is similar to the pterioid anal funnel, and in distantly related Arcida (Heath, 1941), where it is significantly less developed and appears as a short triangular fringe surrounding the anus. The presence of structurally similar anal funnels in Ostreidae has been variously interpreted as either convergence (Waller, 1998) or as evidence of common descent (Steiner & Hammer, 2000) (see Results, Node 1).

The term 'anal funnel' is preferable as it avoids confusion with the anal membrane used by some authors

(Field, 1923) to refer to the sheath of the intestine in proximity to the rectum.

48. Anal funnel shape (Fig. 17): (0) triangular; (1) lanceolate; (2) rounded.

Long, narrowing, and essentially triangular anal funnels are characteristic of *Isognomon*, *Pteria*, and *Malleus*. The anal funnels of *Electroma*, *Vulsella*, and *Crenatula*, and some *Pinctada* species (*Pinctada* sp., Herdman, 1904) have a rounded tip. Other *Pinctada* species possess a characteristic lanceolate shape. Some *Pinctada* species have been reported to have palmate anal funnels [*Pinctada* (as *Margaritifera*) *sugillata* (Reeve, 1857) (Southwell, 1911), *P. margaritifera* (fide Herdman, 1904)], but these findings were contradicted by Hynd (1955). In the present analysis, no palmate anal funnels were observed. Possibly, the palmate shape results from marginal folding of the anal funnel in particularly large specimens and due to such transient morphology and the potential effects of preservation can appear as a distinct shape. A larger sampling of pterioid anal funnels will provide an answer. Regrettably, no comparative analyses of anal funnel shapes have been carried out in Ostreidae.

49. Anal funnel pigmentation: (0) absent; (1) present on the entire surface; (2) present as a stripe.

The anal funnel is generally translucent, but in some taxa its dorsal surface is conspicuously coloured (visible in preserved specimens). The pigmentation can be either uniform, covering the entire surface of the organ, or can be present as a dark median stripe. The latter colour pattern was reported in *Pinctada* (as *Margaritifera*) *margaritifera* by Southwell (1911) and was also found in *Pinctada mazatlanica* (Hanley, 1855) in the present study.

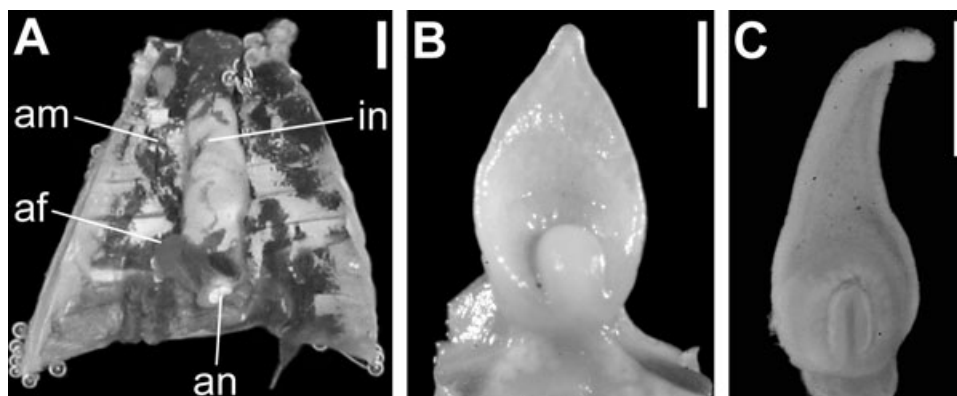


Figure 17. Anal funnel. Ventral view showing different shapes: A, rounded (posterior view of adductor muscle), *Electroma alacorvi* (ANSP 289178, 58.5 mm); B, lanceolate, *Pinctada imbricata* (AMNH 308115, 45.7 mm); C, triangular, *Isognomon alatus* (AMNH 298023, 43.41 mm). Abbreviations: af, anal funnel; an, anus; am, posterior adductor muscle; in, intestine. Scale bar = 1 mm.

OTHER VISCERAL ORGANS

50. Dorsal pallial organ: (0) absent; (1) present.

The dorsal pallial organ, so termed by Yonge (1953a) ['mantle organ/gland' of Grave (1911)], is a conspicuous hydrostatic tube-shaped organ extending posteriorly from the posterodorsal surface of the visceral mass towards the aperture of the posterior gape. The structure is present exclusively in members of the Pinnidae. Its function in chemical defence, and to a lesser degree in physical cleansing of the mantle cavity (Liang & Morton, 1988), appears to be a unique adaptation to the endobyssate ecology of pinnids (Yonge, 1953a; Liang & Morton, 1988). It is present in all surveyed pinnid species: *A. pectinata* (fide Liang & Morton, 1988), *A. rigida* (fide Grave, 1911), and *Pinna carnea* (fide Yonge, 1953a).

51. Anterior protrusion of the visceral mass ventral to the foot (Fig. 2B): (0) absent; (1) present.

A distinct anterior protrusion of the visceral mass is located ventral to the foot in some *Pinctada* spp. and is filled with gonad tissue in mature specimens. This part of the visceral mass has no biological significance in pearl formation, but has been used as a site for pearl nucleation throughout the history of periculture.

52. Midventral membrane of the intestinal pouch (Fig. 2D): (0) absent; (1) present.

A short but conspicuous *midventral membrane* formed by the epithelium of the visceral mass stretches longitudinally along the mid-ventral edge of the visceral mass in species of *Pteria* and *Crenatula*.

CIRCULATORY SYSTEM

53. Paired ventricles: (0) absent; (1) present.

Heart morphology is uniform within the Pterioidea and consists of a single median ventricle situated dorsal to two symmetrical and laterally co-joined auricles (Pelseneer, 1911). An exception was found in *V. rugosa* Lamarck, 1819, where the ventricle is doubled; present observations agreeing with Pelseneer (1911). Vaillant (1868) also reported the presence of a single ventricle in *V. lingulata* Lamarck, 1819.

54. Penetration of the ventricle by the intestine (Figs 2A, 6): (0) present; (1) absent.

The passage of the intestine above rather than through the ventricle is exclusive within the Pterioidea to the genus *Pinctada* [contra Hayami (2000) who diagnosed Pteriidae as having the heart not penetrated by the rectum]. The unique situation of *Pinctada* was first noticed by Grobben (1900) in *Pinctada* (as *Meleagrina*) *margaritifera* [Linnaeus, 1758 var. *cumingii* (Reeve, 1857)] and subsequently in *Pinctada fucata* (fide Herdman, 1904), *P. martensii*

(fide Shiino, 1952), *P. maxima* (fide Takemura & Kafuku, 1957), *P. imbricata* (fide Hayes, 1972; Mikkelsen *et al.*, 2004), and *P. longisquamosa* (fide Mikkelsen *et al.*, 2004). In the Ostreioidea, the intestine penetrates the ventricle in the more basal gryphaeid *Hyotissa hyotis* (Linnaeus, 1758) (Stenzel, 1971; Harry, 1985), but bypasses it in members of the Ostreidae (Harry, 1985), such as *Ostrea edulis* (fide Yonge, 1926) and *Crassostrea virginica* (fide Galtsoff, 1964).

55. Circumpallial artery (Fig. 7): (0) absent; (1) present.

The circumpallial artery is absent only in *Pulvinites* among the Pterioidea (fide Tëmkin, 2006).

FOOT AND BYSSUS

56. Foot (Fig. 2H): (0) present; (1) present and differentiated into two components; (2) absent.

The foot is present in all Pterioidea. In *Malleus*, however, the foot has two parts (Pelseneer, 1911; Kühnelt, 1938; Yonge, 1968). The short distal 'primary' foot is associated with secretion of the byssus, whereas the extensive proximal 'accessory' foot was hypothesized to participate in cleansing the mantle cavity (Yonge, 1968). It is noteworthy that a duplicated foot was occasionally noted in *Pinctada fucata* (Herdman, 1904). Apparently, the aberrant foot in *P. fucata* was not functional (Herdman, 1904), but this observation provides grounds for a possible mechanism of the evolution of the accessory foot in *Malleus*, as a structural duplication followed by functional divergence. In fact, anatomically, the accessory foot is analogous to the primary foot and is distinguished from the latter by its elongated shape, reminiscent of that of *Vulsella* and *Crenatula*, where the foot lacks the byssus and might also be involved in cleansing the mantle cavity. The absence of the foot is restricted to the ostreid outgroup.

57. Surface of the foot covered with pigmented epithelium: (0) absent; (1) present.

The foot, particularly the dorsal surface, is covered with dark brown epithelium (visible in preserved specimens) in all *Pteria*, *Pinctada*, *Electroma*, and some *Isognomon* species. Herdman (1903) noticed that during the formation of byssal threads, individuals of *Pinctada fucata* are particularly sensitive to light and attributed the cause of this 'dermatoptic' sensitivity to the presence of the pigmented epithelia on the foot and other exposed parts of the soft body (Herdman, 1904).

58. Foot curvature: (0) absent; (1) present.

When laterally symmetrical, the foot is produced anteriorly and slightly dorsally with the byssal groove facing ventralward. In most pterioideans, the foot is

contorted to the left to a variable extent so that the byssal groove faces the right valve. This orientation probably facilitates the deposition of byssus through the byssal notch in the right valve. Torsion of the foot, however, is also present in species lacking a byssus. Previously, the left-wise torsion of the foot was noted in *Pinctada* (as *Avicula*) *radiata* (Leach, 1814) (Anthony, 1905), *I. perna* (fide Pelseneer, 1911), and *Pinctada longisquamosa* (fide Mikkelsen *et al.*, 2004). The symmetrical orientation of the foot is limited to pinnid and mytilid outgroup taxa.

59. Postlarval byssus (Fig. 2B): (0) present; (1) absent. Pterioideans typically retain a byssus throughout life, but in a few infaunal (some *Malleus*) and sponge-dwelling (*Crenatula* and *Vulsella*) species it has been lost. The byssus has previously been reported as absent in the following species: *Crenatula phasianoptera* (fide Vaillant, 1868), *C. modiolaris* (fide Reid & Porteous, 1980; Hayami, 2000), *V. lingulata* (fide Pelseneer, 1911), *V. rugosa* (fide Pelseneer, 1911; Hornell, 1922), *V. vulsella* (fide Reid & Porteous, 1980), and *Malleus albus* (fide Kühnelt, 1938; Yonge, 1968). For a summary of the distribution of the byssus in the Bivalvia, including the Pterioidea, see Yonge (1962). The presence of a byssus is treated as inapplicable in the outgroup *Crassostrea virginica* because this species is devoid of the foot that secretes the byssus.

60. Byssal thread fusion (Fig. 2D): (0) byssal threads discrete; (1) byssal threads fused, but the tips of the individual strands are free; (2) byssal threads completely fused.

With the exception of *Pteria*, the byssus of pterioideans is composed of discrete bronze or golden flattened threads terminating as subtriangular flat adhesive fans. In *Pteria*, however, byssal threads fuse (often to their very tips) to produce a single long and flexible stalk. Hayes (1972) attributed the extensive byssal fusion in *Pteria* to the fact that the adhesive material is produced along the entire byssal threads, whereas in *Pinctada* its secretion is restricted to the terminals of the adhesive discs. The suggested difference in chemical composition may account for the brown coloration of the byssus in *Pteria* spp.

MUSCULATURE

61. Posterior adductor muscle shape (Fig. 2D): (0) subcircular; (1) crescent-shaped.

In most pterioideans, the posterior adductor muscle is crescent-shaped in cross-section (approaching a kidney- or bean-like outline in many species). In species of *Pteria*, *Vulsella*, and *Pulvinites*, the posterior adductor muscle is circular or oval in cross-section. The difference has rarely been discussed, but has fre-

quently been depicted for a variety of the pterioidean species, agreeing with present observations without exception.

62. Differentiation of the 'quick' and 'slow' components of the posterior adductor muscle (Fig. 2B): (0) absent; (1) present.

In the vast majority of the Pterioidea, the posterior adductor muscle is composed of two distinct parts, an anterior, semitranslucent 'quick' component composed of finer muscle fibres and a posterior, opaque 'slow' or 'catch' component composed of thicker muscle fibres (Cox, 1969d). The former is responsible for rapid valve closure, whereas the latter sustains prolonged adduction. The differentiation into two separate components is absent in *Pulvinites* (fide Těmkin, 2006) and *Crenatula*. Its absence in *Crenatula* was also implied by Reid & Porteous (1980), who did not depict the separation in *C. modiolaris* but indicated it in *V. vulsella*.

63. Anterior adductor muscle in the adult: (0) present; (1) absent.

All Pterioidea are monomyarian, lacking the anterior adductor muscle in the adult stage. Yonge (1962) attributed the loss of the anterior adductor accompanied by a reduction of the anterior part of the body to neotenous retention of the byssus (essentially a larval attachment structure) in many monomyarian taxa. However, the dimyarian condition precedes the loss of one of the adductors in early development (Jackson, 1890). The dimyarian condition is restricted to mytilid and pinnid outgroup taxa, where the anterior adductor is considerably smaller in size than the posterior adductor (anisomyarian condition). For detailed reviews of the monomyarian condition, see Anthony (1905) and Yonge (1953b).

64. Posterior pedo-byssal retractor muscle(s) (Fig. 2A): (0) paired; (1) reduced to a single muscle attached to one valve only; (2) absent.

Posterior pedo-byssal retractors are lacking in species of *Crenatula*, *Vulsella*, and the outgroup *Crassostrea*. *Pulvinites* has a single posterior retractor muscle attached to the left valve only, a unique condition in the Pterioidea (although convergent with Anomiidae) (Palmer, 1984; Těmkin, 2006).

65. Posterior pedo-byssal retractor muscle(s) shell attachment position relative to the adductor muscle (Fig. 2A): (0) separate from the adductor muscle; (1) adjacent to the adductor muscle.

In the vast majority of the Pterioidea, the posterior pedo-byssal retractor muscles are located adjacent to the posterior adductor muscle and frequently inserted into its concave anterior border. This results in the formation of a single confluent muscle scar. In *Pulvinites*, some *Isognomon* spp. and many *Pteria* spp., the posterior pedo-byssal retractors are removed from the

posterior adductor, resulting in the creation of two independent muscle scars. Non-adjacent muscles have been reported in *Pteria coturnix* (fide Pelseneer, 1911), *P. hirundo* (fide Hayes, 1972), *P. brevia lata* (fide Morton, 1995), and *Pulvinites exempli* (fide Hedley, 1914).

66. Posterior paired pedo-byssal retractor muscle symmetry: (0) subequal; (1) unequal (larger in the left valve).

The cross-sectional areas of left and right posterior pedo-byssal retractor muscles (manifested in the area of corresponding muscle scars) are generally the same, but in some species of *Pteria*, *Malleus*, and *Isognomon* the left muscle is considerably larger, as in *Pteria* (as *Avicula*) *lata* (Gray, 1857) (Pelseneer, 1911).

67. Anterior pedo-byssal retractor muscles (Fig. 18): (0) two pairs; (1) one pair through fusion; (2) one pair through loss; (3) absent.

The musculature of the foot and byssus in the Pterioidea conforms to the basic bivalve body plan in having three pairs of associated muscles (Anthony, 1905; Starobogatov, 1992). One of the pairs – posterior pedo-byssal retractors – is always situated either adjacent or in close proximity to the posterior adductor muscle and does not present a difficulty in identification (Cox, 1969d). The other two pairs form attachments in the anterior part of the shell in the umbonal area. The lack of consistent terminology, varying functional interpretations, and multiple losses in reference to these anterior muscles preclude unequivocal homology assessment. In addition, the lack of consensus on the terminology of pterioidean anterior and umbonal muscle scars led Johnston (1993) to simply refer to them as anterior pedal retractor scars. Another layer of uncertainty comes from the fact that the same pattern of muscle scars can be formed by non-homologous

muscles [which is the case in the extant Pterioidea (see below)].

Much of the confusion in the names of the two pairs of anterior muscles results from their assumed association with either the foot or the byssus, and the direction of their force when contracted. The separation based on associated organs is superficial because the byssus is intimately linked to the foot, so the contraction or relaxation of these muscles affects the position of both structures, admittedly to different extents. In this work, the differentiation between foot- and byssus-associated muscles is disregarded and a more general term ‘pedo-byssal’ is used to denote all three pairs of muscles (one posterior and two anterior) and their corresponding scars. All pedo-byssal muscles are referred to as ‘retractors’ because the term aptly describes the action of the muscles without regard to the direction of their action. Thus, there are three pairs of non-homologous pedo-byssal retractors: a pair of posterior retractors associated with the posterior adductor (character 64) and two pairs of anterior retractors that attach to the shell in the umbonal area. The remaining discussion exclusively addresses the two anterior (near-umbonal) pedo-byssal retractors.

To fully appreciate the level of confusion regarding the identity of anterior pairs of foot- and byssus-associated muscles, the history of their taxonomy in pterioideans is summarized. Fischer (1861) referred to a single pair of anterior muscles in *Isognomon* sp. as ‘protractors’. Grobben (1900) called the more anterior pair ‘anterior pedal retractors’ and the more posterior pair ‘elevators’ in *Pinctada margaritifera*, whereas Herdman (1904) referred to both pairs as (anterior and posterior) ‘levators’ in *Pinctada fucata*. Anthony (1905) defined the two anterior pairs as ‘retractors of the byssus’ and ‘anterior retractors of the foot’,

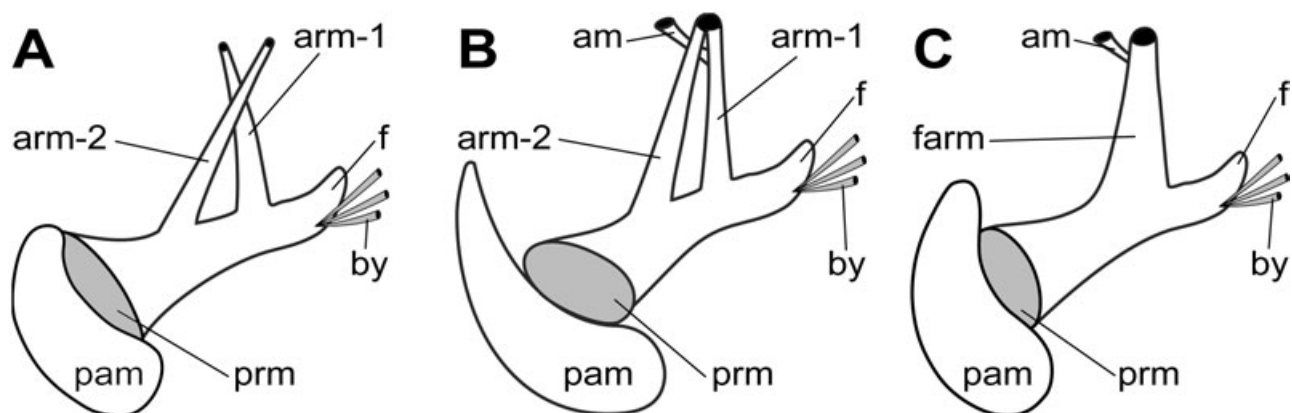


Figure 18. Pedo-byssal musculature in the Pterioidea. Diagrammatic lateral view. A, *Malleus*, some *Pteria*; B, *Isognomon*; C, most Pterioidea. Abbreviations: am, accessory pedo-byssal muscle; arm-1, anterior pair of anterior pedo-byssal retractor muscles; arm-2, posterior pair of anterior pedo-byssal retractor muscles; by, byssus; f, foot; farm, fused anterior pedo-byssal retractor muscles (arm-1/arm-2); pam, posterior adductor muscle; prm, posterior pedo-byssal retractor muscle.

whereas Pelseneer (1911) called both 'anterior retractors'. Cox (1969d) identified these muscles as paired or single 'pedal elevator muscles' that replaced the anterior pedal retractors and pedal protractors in monomyarian taxa. (In the same work, however, Cox illustrated the presence of anterior pedal retractors in *Isognomon*, and both anterior pedal retractors and pedal elevators in *Pinctada*.) Yonge (1968) used the terms 'anterior pedal retractors' and 'anterior byssal retractors' interchangeably in his treatment of the functional morphology of *Malleus* and *Isognomon*.

The two pairs located in the umbonal region are generally discriminated as 'anterior' and 'posterior', based on the place of attachment relative to the hinge axis. In many instances, such a pattern of muscle scars is produced by a different set of muscles, as described below. In the Pterioidea, the anterior pedo-byssal muscles are two pairs of muscle bundles, one pair originating in the area surrounding the foot (anatomically anterior) and the other originating from the posterodorsal surface of the posterior pedo-byssal retractors (anatomically posterior). In cases where both anterior pedo-byssal retractors are present, it is the more anatomically anterior pair that produces the posterior set of scars, whereas the anatomically posterior muscle produces the anterior set of scars on the interior of the shell. Because the place of origin of these muscles is invariable across all taxa observed in the present work, but their attachment sites are not, the terms 'anterior' (ARM-1) and 'posterior' (ARM-2) are used here to denote the origin of the muscles in the viscera along the anteroposterior axis, rather than the order of their attachment to the shell (Fig. 18). This distinction enables unambiguous establishment of the homology of the anterior pedo-byssal retractors.

In all examined species of *Pulvinites* (fide Tëmkin, 2006), *Malleus*, *Isognomon*, and some *Pteria*, there are two distinct pairs of anterior pedo-byssal retractor muscles (Fig. 18A). In *Malleus* and *Pteria*, the posterior retractors form anterior near-umbonal muscle scars extending outside but adjacent to the anterior retractors. The anterior pedo-byssal retractors form posterior attachments near the umbones. In *Pulvinites* (fide Tëmkin, 2006) and *Isognomon* spp., the tips of the anterior and posterior pedo-byssal retractors are fused on each side, forming a single attachment site (and, consequently, a single scar) (character 69; Fig. 18B). Nevertheless, the extremities of these muscles come into contact at different angles, allowing for their straightforward discrimination. The second (posterior) near-umbonal muscle scar in *Isognomon* spp. is formed by the *accessory pedo-byssal muscle* (character 70) that branches off the anterior pedo-byssal retractor muscle at the level of the oesophagus ('posterior levator' *sensu* Herdman, 1904). Obviously, the two

scars formed in *Malleus* and *Isognomon* are not equivalent, but superficially similar.

In all *Pinctada*, *Electroma*, *Vulsella*, *Crenatula*, and most *Pteria* species, only one pair of anterior pedo-byssal retractor muscles (FARM) is present, which results from the fusion of the anteriorly and posteriorly originating muscles, as evidenced by the presence of two discrete muscle bundles orientated at an angle relative to one another at the attachment point as well as in the more proximal part of the muscle (Fig. 18C). As in *Isognomon* spp., the accessory muscle is present in all species (very thin but distinct in *Crenatula* and *Vulsella*).

The major difficulty results in attributing the anterior pedo-byssal muscle scars in fossil taxa. Obviously, neither the number nor the arrangement of muscles can be unequivocally inferred from their scars. Therefore, it is advisable to be aware of possible interpretations and explicitly state the possibilities based upon the closest affinities to living taxa and other available evidence.

In the ostreid outgroup taxon *Crassostrea virginica*, the anterior pedo-byssal retractor muscles are absent altogether, which is probably a consequence of the loss of the foot in the Ostreioidea. The rudimentary Quenstedt muscles of oysters, once thought to be homologous to the anterior pedo-byssal retractors of other pteriomorphs (Stenzel, 1971; Starobogatov, 1992), are presently considered to be the gill retractors or elevators (Boss, 1982; Harry, 1985; Waller, 1991).

68. Anterior paired pedo-byssal retractor muscle symmetry: (0) symmetrical arrangement; (1) asymmetrical arrangement.

In *Pinctada* spp., the left anterior pedo-byssal retractor muscle is noticeably thicker and is placed more anteriorly to the dorsal side of the foot than the right retractor. This asymmetry was previously noticed in *Pinctada fucata* by Herdman (1904) and *Pinctada radiata* by Anthony (1905).

69. Fusion of the distal extremities of the anterior retractor muscles resulting in a single attachment scar: (0) absent; (1) present.

See character 67.

70. Accessory pedo-byssal muscles (Fig. 18B, C): (0) absent; (1) present.

Accessory pedo-byssal muscles are short minor muscles that branch off the anterior pedo-byssal retractor muscle at the level of the oesophagus. These muscles are produced posteriorly through the visceral mass and form posterior attachment scars in the near-umbonal area. Herdman (1904) pointed out that the accessory muscles ('posterior levators') allow for fine attenuation of foot movement (see also character 67).

71. Radial pallial muscle(s): (0) multiple; (1) a pair of anterior and posterior large pallial retractor muscles; (2) a single large anterior pallial retractor muscle. See character 72.

72. Radial pallial muscle(s) attachment (Fig. 1B): (0) attached to the shell interior; (1) not attached to the shell interior.

The mantle in members of Pterioidea can be deeply retracted by multiple radiating pallial retractor muscles. These muscles typically form sinuses at their attachment points, producing a discontinuous pallial line stretching from the anterodorsal part of the posterior adductor to the area slightly posteroventral to the anterior pedo-byssal retractor scars. In *Pulvinites* and the outgroup ostreid taxon, the pallial retractor muscles do not attach to the shell interior. In species of *Malleus*, the pallial retractors are reduced to a single large muscle stretching from the point of its attachment (anterodorsal to the anteriormost extremity of the posterior adductor muscle scar) to the distalmost extremity of the mantle, as previously reported in all anatomical accounts of species of *Malleus* (Pelseneer, 1911; Kühnelt, 1938; Yonge, 1968).

NERVOUS SYSTEM

73. Postlarval ctenidial ocelli: (0) absent; (1) present in both ctenidia; (2) present in one (left) ctenidium only.

Pelseneer (1911) distinguished between two different kinds of eye in the Bivalvia: ctenidial and pallial eyes, both occurring in the Pterioidea. Pallial photoreceptors will be considered in the next section (character 74). For a comprehensive review of bivalve photosensory systems, refer to Morton (2001). Ctenidial eyes consist of a cup of apically ciliated, pigmented cells located on the most anterior filament of the descending lamellae of the inner demibranchs [reviewed by Morton (2001)]. Because of their location at the gill–palp junction, a descriptive term ‘ctenidial’ eyes is adopted in the present work instead of ‘cephalic’, for obvious reasons. The lens is typically absent from pterioid ctenidial ocelli, with the exception of *Malleus* (Pelseneer, 1911) and some *Pteria* spp. (Pelseneer, 1899). Morton (1995) documented the presence of a true optic nerve associated with the eye in *Pteria brevialeta*.

The distribution of ctenidial eyes among pterioids varies from presence on both ctenidia, to presence on one (left) ctenidium, to complete absence. In *Isognomon*, *Malleus*, and most *Pteria* (with the sole described exception *Pteria macroptera*) ctenidial ocelli are present on both sides (Pelseneer, 1911). Stasek (1963) illustrated the presence of an eye at the right gill–palp junction in *I. costellatus* (Conrad, 1837), but given the

fact that in asymmetrical situations eye spots are invariably lacking on the right side, it is probable that the eyes were present on the unillustrated left side as well. In most species of *Pinctada*, ctenidial ocelli are present only on the left side (Pelseneer, 1906, 1911), whereas they are entirely absent in *Vulsella*, *Electroma* (Pelseneer, 1911) and *Crenatula* (Reid & Porteous, 1980). The present study confirms the previously established status of ctenidial ocelli in most pterioidean species, with the following exceptions. Symmetrical eyes were found in *Malleus (Malvufundus) candeanus*, but were lacking in *M. anatinus*. *Pinctada longisquamosa* had a single eye on the left side, as in other *Pinctada* species, as reported by Pelseneer (1911), but *P. mazatlanica* and *P. fucata* did not have any eyes. The latter finding agrees with the statement of Pelseneer (1899) that he was unable to find these structures in *Avicula meleagrinerifera* (= *Pinctada fucata*).

74. Pallial ocelli (Fig. 7B, C): (0) absent; (1) present. Morton (2001) identified two kinds of pallial ‘eyes’ in the Pterioidea. The first and simplest type of photoreceptor consists of large eosinophilic cells located close to the apex of the inner component of a duplicated outer fold (OF-1) and connected to pigmented cells on the inner surface of the fold, as seen in *Pteria brevialeta* (fide Morton, 1995, 2001). Similar structures were found in *Pteria colymbus* (Röding, 1798). However, these large eosinophilic cells, often with extensive outgrowths, were neither restricted to the apices of OF-1 nor always found in the epithelium. Also, their connection with other cells could not be ascertained. Therefore, in the present study, the interpretation of these structures as multicellular ocelli is withheld for a lack of necessary evidence, whereas their potential role as simple photoreceptors is acknowledged. More definitive ocelli were found in *Isognomon*, structurally corresponding to pigmented multicellular innervated cups devoid of a lens.

75. Visceral ganglia position relative to the posterior adductor muscle: (0) adjacent; (1) not adjacent. In the Pterioidea, the pair of visceral ganglia is adjacent to the anteroventral surface of the adductor muscle, with the exception of *Pulvinites exempla*, where the ganglia are suspended in loose connective tissue of the visceral mass close to the adductor muscle (Tëmkin, 2006).

76. Relative position of visceral ganglia: (0) adjacent to each other; (1) widely separated by a commissure. Throughout the Pterioidea, the visceral ganglia are separated by a commissure. The adjacent position of the ganglia is restricted to the ostreid outgroup (Galtsoff, 1964).

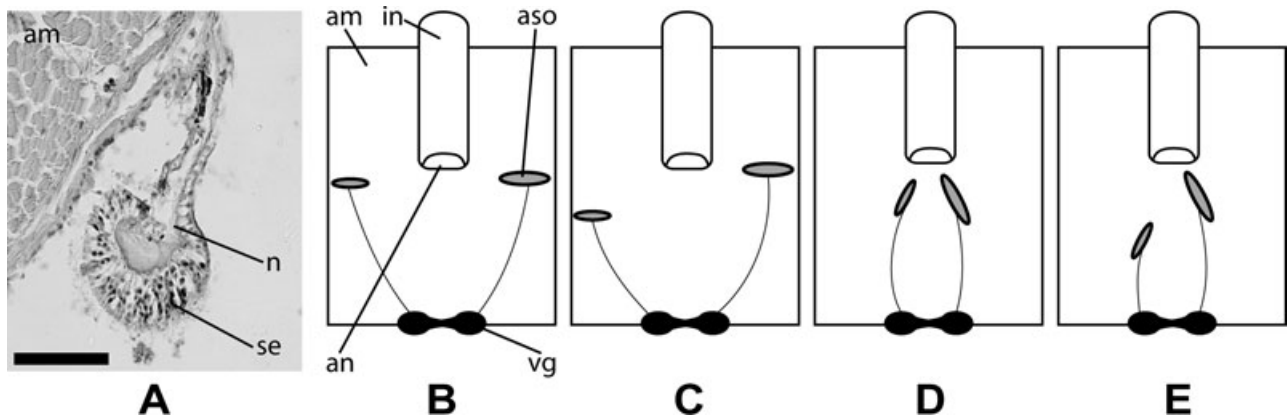


Figure 19. Abdominal sense organ in the Pterioidea. A, histological cross-section of the abdominal sense organ in the sagittal plane (7 μ m, Alcian Blue/Periodic Acid/Schiff's trichrome stain), *Pinctada longisquamosa* (AMNH 298904, 18.1 mm); diagrammatic posterior view of the adductor muscle showing the arrangement of the abdominal sense organs in the Pterioidea: B, *Crenatula*, *Electroma*, *Pinctada*, *Vulsella*; C, most *Pteria*; D, *Malleus*; E, most *Isognomon*. Abbreviations: am (posterior) adductor muscle; an, anus; aso, abdominal sense organ; in, intestine; n, nerve; se, sensory epithelium; vg, visceral ganglia. Scale bar = 0.05 mm.

77. Abdominal sense organ (ASO) position relative to the anus (Fig. 19): (0) far from the anus; (1) clustered close to the anus.

See character 79.

78. Relative position of the left and right ASOs (Fig. 19): (0) right and left ASOs in the same lateral plane; (1) right ASO dorsal to the left ASO.

See character 79.

79. ASO asymmetry (Fig. 19): (0) symmetrical; (1) right ASO larger than the left ASO; (2) left ASO absent. ASOs are paired mechanoreceptors typically found on the posteroventral surface of the posterior adductor muscle and their homology across the Bivalvia is suggested by identical innervation and uniform structure (Haszprunar, 1983, 1985). In the Pterioidea and Pinidae, the right ASO is typically larger than the left ASO, whereas in the Ostreidae the left ASO is absent, confirming the previous observations of Thiele (1889) and Haszprunar (1983). In some species [e.g. *Pinctada longisquamosa*, *Pteria sterna* (Gould, 1851) and *Pteria colymbus*], particularly the ones associated with epizoid habits, the left and right ASOs are nearly the same size. The relative position of the receptors varies greatly laterally as well as dorsoventrally on the surface of the posterior adductor muscle. The ASOs can be as close to each other as in immediate proximity under the anus at the middle of the posterior adductor muscle or as far as the opposing edges of the posterior adductor muscle where the ASOs are partially supported by the inner sides of the mantle lobes (character 77). In addition, one of the ASOs can be positioned dorsally relative to the other (character 78). The lateral displacement of the ASOs is not related to the

separation of incurrent and excurrent channels, as inferred from external vs. internal placement of the receptors relative to the gill axes, as previously suggested by Haszprunar (1983). In all taxa analysed in the present study, with the exception of *Mytilus*, the gill axes are free from the association with the adductor muscle posterior to its ventral surface and instead of running in parallel, they come within close proximity to each other due to the connection between upper edges of inner demibranchs and progressive narrowing of the interlamellar cavities. Thus, upon reaching the posterior region opposing the anus, the gills run along the median line between or at the level of the ASOs. However, regardless of their position relative to the gill axes, the ASOs remain in the excurrent channel separated from the inhalant channel by the outer demibranch–mantle connection on one hand and the interinner demibranch junction on the other.

80. Circumpallial nerve (Fig. 7): (0) absent; (1) present.

The circumpallial nerve is absent in *Pulvinites exempli* (Tëmkin, 2006).

REPRODUCTIVE ORGANS

81. Extension of the gonads into the mantle tissue: (0) absent; (1) present.

The extension of the gonad into the mantle is restricted to the mytilid outgroup (Field, 1923).

GENERAL SHELL MORPHOLOGY

Definitions of various aspects of general shell morphology follow Cox (1969d).

82. Relative valve inflation: (0) equally inflated (equiconvex); (1) left valve more inflated than the right valve.

Inequivalvity in the Pterioidea (as well as in other pteriomorphians) is generally considered to be a consequence of a pleurothetic life position, with byssal attachment mediated through the byssal notch in the right valve (Yonge, 1962). This position has resulted in the flattening of the right valve that faces the substratum, making the opposite left valve more convex. Some orthothetic *Pinctada* (particularly larger species) and *Isognomon*, as well as species of *Malleus* and *Vulsella*, appear to be nearly equiconvex, with the asymmetry reflected in the presence of the byssal notch in one valve (in *Pinctada*, *Isognomon*, and *Malleus*) and a slight elevation of the left umbo over the right one. Outgroup mytilid and pinnid taxa are likewise equiconvex.

83. Valve symmetry: (0) symmetrical (acline); (1) oblique anteriorly (prosocline); (2) oblique posteriorly (opisthocline).

The Pterioidea are typically prosocline with umbones markedly shifted towards the anterior along the hinge axis demarcating the origin of the anterior auricle. Unique coiling in early stages of *Vulsella* results in an opisthocline shell [not to be confused with the opisthogyrous coiling of the prodissoconch (character 114), a situation reminiscent of that of *Crassostrea* (fide Galtsoff, 1964)]. *Pulvinites exempla* is unique, having essentially symmetrical placement of the umbones (acline condition).

84. Ventral flattening: (0) absent; (1) present.

Because of the great diversity in shell shape in the Pterioidea, the position of the maximum shell convexity ['maximum shell width' in Stanley (1970)] was estimated relative to a cross-section perpendicular to the biologically determined normal axis that takes into account the mode of shell growth [defined by Owen (1952)]. Flattening of the valves in the area of their junction along the ventral commissural line occurs as a result of the displacement of the maximum shell convexity (as seen in cross-section) towards the ventral margin (Stanley, 1970). Such a change in cross-sectional shape is attributed to orthothetic epibyssate attachment characteristic of various mytilids (Stanley, 1970). Despite a similar mode of nearly vertical attachment, some nearly equivalent pteriods are not flattened along the commissural line and their maximum shell convexity is somewhat dorsal in cross-section relative to the normal axis.

85. Undulating interlocking shell margin (Fig. 1G): (0) absent; (1) present.

Regularly interlocking shell margins in the Pterioidea are found in some species of *Malleus*. Yonge (1968)

pointed out their presence in *M. albus*; a similar condition was found in *M. anatinus* in the present work. The sinusoid undulation increases the length of the commissure and prevents the shells from gaping widely, maintaining essentially the same width of the gape along the entire length of the valves, permitting sufficient current flow (Seilacher, 1982, 1984).

86. Valve cementation: (0) absent; (1) present.

Cementation is absent in the Pterioidea. Its presence is restricted to the ostreid outgroup taxon *Crassostrea virginica* (fide Galtsoff, 1964).

BYSSUS-ASSOCIATED STRUCTURES AND GAPES

87. Byssal passage (Fig. 1E, F): (0) absent; (1) symmetrical byssal gape; (2) subauricular byssal notch (in right valve); (3) foramen.

A byssal notch in the right valve is present in the vast majority of the Pterioidea, although developed to different degrees, being quite inconspicuous in some *Isognomon* spp. lacking a strongly developed anterior auricle. The byssal notch is absent in sponge-dwelling species of *Vulsella* and *Crenatula*, corroborating previous reports (Gray, 1857; Vaillant, 1868; Reid & Porteous, 1980). In *Pulvinites exempla*, the outer edges of the byssal notch fuse, forming an opening – the foramen – through which the byssus is produced [reviewed by Palmer (1984)].

88. Byssal ridge in the left valve (Fig. 1B): (0) absent; (1) present.

The *byssal ridge* is a thickening on the interior surface of the left valve that proceeds along the curve from the umbo to the ventral edge of the byssal notch, delimiting the anterior auricle. This structure has been described in *Pinctada longisquamosa*, where it is very prominent (Hayes, 1972; Mikkelsen *et al.*, 2004). The ridge probably assists in tight closure of the byssal gape when the valves are adducted. This structure was found in most species of *Pinctada* and *Electroma*.

89. Permanent posterior gape: (0) absent; (1) present. The valves of all pterioidean species adjoin tightly, although in a relaxed state valves slightly gape posteriorly in the area of the excurrent channel. A permanent posterior gape is present in the pinnid outgroup *A. rigida* (fide P. M. Mikkelsen, pers. comm.).

AURICLES

90. Anterior auricle (Fig. 1E): (0) absent; (1) present. The development of the anterior auricle, an anterior elongation of the shell along the hinge line, has occurred in many pteriomorphian lineages. Stanley (1970) suggested that its evolution is an adaptation for shell stabilization in byssally attached pleurothetic

forms, preventing overturning. It is present in most pterioidean taxa, with the exception of *Vulsella* and *Pulvinites*. The absence of the anterior auricles is often claimed to be characteristic of *Isognomon* species. However, small rudimentary auricles are present in many isognomonids as well, often at an angle to the hinge line, resulting in the terminal position of the umbones. The extensive anterior hinge extensions characteristic of *Malleus* s.s., often referred to as 'anterior auricles', are probably not homologous with the true anterior auricles of other pterioideans because they form later in ontogeny and ventral to the byssal notch. The true anterior auricles do, however, exist in these species, but are often greatly reduced, as in many isognomonids.

91. Posterior auricle (Fig. 1D): (0) absent; (1) present. See character 92.

92. Posterior auricle extent: (0) extends beyond posteriormost extremity of valves; (1) does not extend beyond posteriormost extremity of valves.

In addition to the Pterioidea, small posterior auricles, produced by posterior elongation of the hinge line, are found in other pteriomorphians (such as Pectinidae and Myalinidae), but do not reach nearly the same extent as found in some pterioideans. Posterior auricles are extensive and deeply sinuous in epizoic species byssally attached to flexible coral substrata. In these taxa – most *Pteria* and some *Pinctada* – the posterior auricles serve multiple functions in acquisition of the most optimal shell orientation in a water current, facilitating excurrent water flow (Stanley, 1970, 1972), and cleansing the mantle cavity (Johnston, 1993). Considerable expansion of the posterior auricles is also reported in larger species of *Malleus* (*M. albus* and *M. malleus*), interpreted as a mechanism for either anchorage in semi-infaunal endobyssate life position (Yonge, 1968) or stabilization on the surface of soft muddy substrata where there is little support for byssal attachment (Seilacher, 1982).

SCULPTURE

93. Commarginal calcitic scales (Fig. 1B): (0) absent; (1) present.

Commarginal calcitic scales (mostly vertical but sometimes recurved) occur in species of many pterioidean genera, including *Isognomon*, *Pinctada*, *Vulsella*, and some *Pteria*. Usually omitted from discussions of morphology, specific references to the presence of this type of sculpture are found in Jackson (1890; *Pteria sterna*), Herdman (1904; *Pinctada fucata*), Harper & Morton (1994; *I. legumen*), Hayami (2000; *Pinctada martensii*, *P. fucata*, *P. margaritifera*). Scales do not occur in *Malleus*, *Pulvinites*, *Electroma*, and *Crenatula* species.

94. Commarginal periostracal scales (Fig. 1D): (0) absent; (1) present.

Commarginal periostracal scales are characteristic of *Pteria* spp. and in some species (e.g. *Pteria sterna*) can be found together with prismatic scales.

95. Scale shape (Fig. 1B, D): (0) flat; (1) fluted; (2) flat and tubular; (3) tubular.

Scale shapes vary greatly throughout the Pterioidea. Flat and usually broad scales often occur in *Pinctada* and *Isognomon*; fluted scales are characteristic of *Pteria* but also of some *Isognomon* spp. Exclusively tubular scales are found only in pinnid outgroup taxa, but occur in a few *Pinctada* species.

96. Scale tips (Fig. 1B, D): (0) pointed; (1) broadly rounded (blunt); (2) irregular.

The shape of the distal tips of the scales in most *Pinctada* spp. is blunt, whereas in most *Pteria* spp. the tips of the scales are pointed. Both shapes of scale tips, as well as irregularly shaped scale tips, are found in *Isognomon* spp.

97. Relative scale positions: (0) overlapping; (1) irregular.

With the exception of *I. bicolor*, where scales show irregular growth, the commarginal scales in the Pterioidea are overlapping.

98. Interdigitating shell projections: (0) absent; (1) present.

Long lamellae projecting beyond the ventral margin that curve medially interdigitating with those of the other valve are found only in *Pinctada longisquamosa* (fide Mikkelsen *et al.*, 2004).

99. Overlapping calcitic lamellae (Fig. 1H): (0) absent; (1) present.

In *Pulvinites*, some species of *Malleus* and *Isognomon*, the outer shell layer forms commarginal overlapping lamellae. In most species, these lamellae are deposited at low angles to the shell surface and have irregular outlines. In *Malleus (Malvufundus) candeanus*, the lamellae are more regular, much thicker, and are produced almost perpendicularly to the shell surface (Boss & Moore, 1967).

100. Radial costae: (0) absent; (1) present.

Radial costae are generally absent in the Recent Pterioidea and among taxa surveyed herein, but they are present only in *Malleus (Malvufundus) candeanus* (fide Waller & Macintyre, 1982) and *I. radiatus* (Anton, 1839). In addition, radial costae are present in the ostreid and pinnid outgroup taxa.

INTERIOR FEATURES

101. Pallial ridge (Fig. 1H): (0) absent; (1) present.

A single pallial ridge [or 'pallial rib' of Boss & Moore (1967)] is present on the interior of both valves of

many species of *Malleus*, running medially from the distalmost extremity of the ventral margin to either the visceral rim (character 103) in *M. (Malvufundus) candeanus* (fide Boss & Moore, 1967) or to the pallial retractor muscle scar in other species [*M. regula*, *M. malleus*, *M. albus* (see Yonge, 1968)]. The ridge demarcates the line along which ctenidia are fully extended (Boss & Moore, 1967).

102. Visceral rim (Fig. 1H): (0) absent; (1) present.

The *visceral rim* is a slightly elevated ridge on the inner shell surface demarcating the transition between the nacreous and prismatic layers. Where present, the nacreous layer is reduced to a small area surrounding the visceral mass, and upon closure of the valves, the adjoining rims of both valves come in close proximity, possibly enhancing the protection of soft parts against predation. The structure has previously been noted in *I. bicolor* by Domaneschi & Martins (2002).

103. Apical transverse septa: (0) absent; (1) present.

Within the Pterioidea, thin *apical transverse septa* in the umbonal arch occur exclusively in *Crenatula* (present work). The occurrence of such structures in the similarly rounded anterior end of pinnid shells was noticed and illustrated by Turner & Rosewater (1958), who attributed their formation to progressive wear on the shell's anteriormost extremity and the resulting necessity for constant repair to protect the anterior adductor muscle. Seilacher (1984) attributed the regular splitting of pinnid apices to the breakage of the anteriormost part of the ligament that results from the growth of the pinnid ligament. Thus, the septa compensate for the unavoidable predetermined damage. The septa in *Crenatula*, having no anterior adductor, are better explained by the latter hypothesis. Such convergence between *Crenatula* and the Pinnidae is probably related to the environmental constraint for anterior growth in the comparable 'endozoic' crenatulid life habit inside sponges and the endobyssate pinnid ecology in soft muddy substrates. In both cases, the apices are directed into the interior part of the substrata, whereas the excurrent and similarly widened posterior apertures face the outside in the opposite direction. The formation of the septa results in the placement of the umbones on the most anterior septum that is worn off in early juveniles. As pointed out by Bernard (1898), this condition precluded the observation of the prodissoconch of *Crenatula* in his extensive survey of bivalve embryonic shells.

104. Relative width of the prismatic margin (Fig. 1A): (0) equal in both valves; (1) wider in the right valve. Unequal extents of the nacreous layer ventral margins (usually wider in the right valve) result in the greater

flexibility of the right ventral margin. This provides a tightly sealed shell closure by adpression of the flexible ventral edge of the right valve against and fitting within the inner surface of the rigid ventral margin of the left valve. This asymmetry was observed in all *Pteria*, *Electroma*, most *Pinctada*, and some *Isognomon* species in the present study, corroborating previous reports in *I. legumen* (fide Harper & Morton, 1994), *Pteria brevialata* (fide Morton, 1995), and *Pinctada longisquamosa* (fide Mikkelsen *et al.*, 2004).

COLOUR PATTERN

105. Adult radial colour pattern (Fig. 1I): (0) absent; (1) present; (2) irregular.

Radial stripes are the most widespread colour pattern in the Pterioidea, lacking only in *Pulvinites* and *Malleus* (they are present in some *Electroma* species not analysed in the present work). Other genera contain species with and without the radial pattern, which appears to be species specific.

106. Commarginal colour pattern: (0) absent; (1) linear stripe present; (2) zigzag stripe present; (3) blotches.

Commarginal colour patterns are less ubiquitous among pterioideans and were observed only in a few species of *Pinctada*, *Pteria*, and *Malleus*.

107. Divaricate stripe: (0) absent; (1) present.

Divaricate stripes are exclusive to *Pinctada longisquamosa* (Mikkelsen *et al.*, 2004) in the current data set, but they have also been noticed in several species of *Pteria* (I. Tëmkin, pers. observ.). The presence of a divaricate colour pattern has also been reported in *Electroma* (as *Pteria*) *zebra* (Reeve, 1857) by Seilacher (1972) who interpreted the divaricate pattern as mimicry because in life position it closely resembles the branches of the hydrozoan substrate of this characteristically epizoic species.

DENTITION

Teeth are defined by their position relative to the hinge line and umbo. Terms such as 'cardinal', 'lateral', 'taxodont', and other specialized dentition-related terminology are not used in order to avoid denoting unwarranted homology.

108. Subumbonal anterior teeth in the dissoconch; (0) absent; (1) present in juveniles only; (2) present throughout ontogeny.

See character 111.

109. Anterior teeth configuration: (0) right valve socket/left valve tooth; (1) right valve tooth/left valve socket; (2) both occur; (3) multiple interlocking teeth. See character 111.

110. Submarginal posterior teeth in the dissoconch: (0) absent; (1) present in juveniles only; (2) present throughout ontogeny.
See character 111.

111. Posterior teeth configuration: (0) right valve tooth/left valve socket; (1) left valve tooth/right valve socket; (2) both occur.

In many Pterioidea (*Electroma*, *Vulsella*, *Crenatula*, *Pulvinites*, and some *Isognomon* species) dentition is entirely absent. When present, the teeth can persist throughout ontogeny (as in most *Pteria*, many *Pinctada*, and a few *Isognomon* species) or be present only in juvenile forms (as in some *Isognomon* and *Malleus* species). The anterior subumbonal and posterior submarginal teeth do not necessarily persist or disappear together. For example, in *Malleus*, anterior teeth are absent, whereas posterior teeth can be retained either in the juvenile only (*M. anatinus*) or in the adult (*M. (Malvufundus) candeanus*) stages. In *I. bicolor*, on the other hand, the subumbonal teeth are present in the juvenile only, but submarginal teeth never develop. The configuration of teeth, however, appears to be a much less variable feature. In all dentate species of *Pinctada*, the subumbonal dentition is characterized by a single denticle in the right valve and a corresponding socket in the left valve; the posterior submarginal dentition is characterized by an elongated oblique ridge-like tooth in the left valve and a corresponding socket in the right valve. The entire configuration of anterior and posterior teeth is reversed in all *Pteria* spp. observed so far. The configuration of the juvenile subumbonal teeth in *I. bicolor* corresponds with that of *Pteria*, whereas the configuration of the posterior subumbonal teeth in *Malleus* is reminiscent of that of *Pinctada*. *I. alatus* displays both configurations in different combinations of anterior and posterior dentition. Among species that have the subumbonal tooth morphology of the 'Pteria'-type (right valve socket/left valve tooth) are *I. ephippium* (fide Jackson, 1890), *I. bicolor* (fide Domaneschi & Martins, 2002), *Pteria sterna* (fide Jackson, 1890), and adults of *Pteria breviaalata* (fide Morton, 2001) and *P. colymbus* (fide Mikkelsen *et al.*, 2004). The subumbonal tooth morphology of 'Pinctada'-type (right valve tooth/left valve socket) has been reported in *Pinctada longisquamosa* and *P. imbricata* by Mikkelsen *et al.* (2004). Opposing submarginal posterior denticles have been noticed in *I. ephippium* by Jackson (1890). Teeth were reported as missing in *Crenatula* (fide Gray, 1857), *Pinctada glabra* (fide Jackson, 1890), *Pulvinites exempla* (fide Palmer, 1984), and *I. legumen* (fide Harper & Morton, 1994).

The presence of multiple interlocking subumbonal teeth is exclusive to the mytilid outgroup *Mytilus edulis*.

LARVAL SHELL

Larval shell terminology is based on Malchus (2004a,b). Unless specified, the term prodissoconch refers to a larval shell passed through two growth phases (P1 + P2).

112. Prodissococonch shape: (0) discoid; (1) subtriangular.

Larval shell shapes and sizes reflect larval ecology. Thus, at least in pteriomorphs, the size of P1 and the P1/P2 ratio in planktotrophic larvae are generally smaller than those in lecithotrophic larvae (Waller, 1981; Malchus, 2004a). In addition, the prodissococonchs of lecithotrophic pteriomorph larvae are discoid in shape, whereas planktotrophic larvae have markedly triangular larval shells. The difference in shape between the two is a consequence of an elevated umbo and a sharp boundary between P1 and P2 growth stages in the latter (Malchus, 2004a). In the Pterioidea, large discoid larval shells are reported only from *Pulvinites exempla* (fide Marshall, 1998).

113. Prodissococonch position relative to the adult hinge line: (0) terminal; (1) non-terminal,

In most Pterioidea, prodissococonchs are located on the anterior part of the hinge line, but are usually non-terminal, being removed from the anteriormost extremity by the presence of the anterior auricle. However, the location of the prodissococonch is not related to the presence of the anterior auricle: in *Isognomon* spp., the auricles are present (although greatly reduced), but their dorsal margin angles ventrally, thus not coinciding with the straight hinge margin. The effect of this is the terminal placement of prodissococonchs (Hayami, 1957). In addition, in *Vulsella* spp. lacking auricles altogether, the prodissococonch is close to the centre of the hinge line, as in *Pulvinites*.

114. Direction of the prodissococonch coiling: (0) anterior (prosgyrous); (1) posterior (opisthogyrous).

In all taxa examined, the prodissococonchs were posteriorly coiled (opisthogyrate), with the exception of *Mytilus* (Jackson, 1890; Carter, 1990; Malchus, 2004a).

POSTLARVAL LIGAMENT

Terminology pertaining to ligamental grades, their position, and support structures follows Waller (1990) and Carter (1990), and includes subsequent amendments reviewed by Malchus (2004a).

115. Initial direction of the adult ligament growth relative to the prodissococonch: (0) ventral; (1) anterior; (2) posterior.

In most pteroids, the ligament is initially directed posteriorly with the exceptions of *Pulvinites*, in which

the ligament grows ventrally, and *Vulsella*, where the ligament is initially directed anteriorly.

116. Growth trajectory of the resilium relative to the adult shell umbo: (0) posterior; (1) both posterior and anterior; (2) anterior.

The resilium extends posteriorly relative to the adult shell umbo in all pterioidean taxa surveyed herein. The exceptions are *Vulsella*, where the resilium extends anteriorly, and *Pulvinites*, where individual resilia are deposited anterior and posterior to the umbo (Malchus, 2004a; Tëmkin, 2006).

117. Serial repetition of ligamental layers (Fig. 1F): (0) absent; (1) present.

Ligaments characterized by alternation of fibrous and lamellar sublayers are characteristic of all species of the genera *Isognomon*, *Crenatula*, and *Pulvinites*. In such ligaments, a serially repeated fibrous component is deposited into recessed pits (resilifers) along the length of the hinge plate and is connected by a lamellar component secreted between the resilia. In Recent Bivalvia, this type of repetitive ligament – called multivincular – is unique to the Pterioidea and distinct from the repetitive duplivincular ligament of arcoids, where alternating broad lamellar and narrow fibrous ligamental sublayers form a series of parallel bands unsupported by specialized resilifers.

LIGAMENT SUPPORT AND HINGE STRUCTURES

The definition of ligament supports follows Waller (1990) and Carter (1990). The terminology for a resilifer (a recessed, generally subtriangular, groove on the surface of the cardinal area housing the fibrous portion of the ligament), resilifer shape, and associated features of the hinge plate is based on Crampton (1988).

118. Pseudonymphae: (0) absent; (1) present.

Pseudonymphae are microstructurally distinct ridges providing a site for ligament attachment just below the hinge line margin (Waller, 1990). The presence of these structures is restricted to mytilid and pinnid outgroup taxa. Morton (1995) claimed the presence of a pseudonymph and ligamental fossette in *Pteria brevialata*, but these findings were not confirmed by the present study. The ligamental fossette is defined as a transitional area between the end of the nymph and the posterior edge of the ligamental groove (Runnegar, 1968). Because ligaments equipped with nymphae (parivincular) are absent in the Pteriomorphia (Waller, 1990), the fossette-like structure in *Pteria brevialata* must have resulted from damage, with subsequent filling of the gap with ligamental tissue, as previously reported in the case of *Pteria colymbus* (fide Tëmkin, 2004b).

119. Expansion of the cardinal area: (0) absent; (1) present.

Pterioidea have a fairly narrow cardinal (ligament) area slightly elevating along the hinge line, with its length exceeding its height. In *Vulsella*, in addition to an extremely ventrally expanded ventral margin, the cardinal area is likewise extended to a height that exceeds its length along a relatively short hinge line.

120. Resilifer(s): (0) present in early ontogeny only; (1) persist throughout ontogeny.

In the Pterioidea, resilifers persist throughout development, whereas in mytilid and pinnid outgroup taxa, resilifers are present in early ontogeny.

121. Resilifer wider than high: (0) absent; (1) present. Species of *Isognomon*, *Malleus*, and *Vulsella* are characterized by having narrow resilifers stretching perpendicular to the hinge line so that their height exceeds their width. It must be noted that the total extent of the resilifer is taken into account, not just the portion occupied by an active resilium.

122. Resilifer shape: (0) (sub)triangular; (1) rectangular; (2) subtriangular/rectangular.

In most pterioideans, resilifers are subtriangular in lateral view. This outline results from continuous widening of the resilifer(s) during growth. In *Crenatula* and some *Isognomon* species, resilifers develop in a similar manner in early stages but then proceed to grow ventrally without further widening, producing predominantly rectangular or quadrate resilifers. Individuals of some species of *Isognomon* and *Malleus* have either kind of resilifer.

123. Resilifer crenulation at the ventral margin of the hinge plate: (0) absent (breached); (1) present (crenulated).

The ventral margin of the resilifers is crenulated in *Crenatula*, some *Isognomon*, *Pinctada*, and *Malleus* species.

124. Hinge area bordering the resilial groove: (0) flat; (1) rounded.

In the Pterioidea, a resilifer forms a depression on an otherwise flat hinge plate. In *Crassostrea*, the area bordering the resilifer forms convex ridges, or bourrelets (Stenzel, 1971).

125. Hinge line (Fig. 1G): (0) straight extended; (1) curved abbreviated; (2) irregular.

The hinge line in the Pterioidea is typically straight and continuous with the anterior and posterior auricles. In *Vulsella*, as well as in the ostreid outgroup, the hinge line is markedly shortened, being restricted just to the area immediately anterior and posterior to the ligament, and somewhat curved (forming an arch in side view of the shell interior). In *Crenatula*, the hinge line can be straight, but often displays irregular cur-

vature, being either concave or laterally bent. Such plasticity, often resulting in bizarre shapes in this genus, is probably an adaptation for accommodating the direction of growth of *Crenatula*'s sponge host.

126. Cardinal area symmetry between valves: (0) present (symmetrical); (1) absent (asymmetrical). Despite sharing the pleurothetic habit, the cardinal area and the ligament in the Pterioidea are symmetrical in the right and left valves, unlike in many ostreids, including the outgroup taxon *Crassostrea virginica*. In this species, the left valve possesses extensive dorsal expansion of the cardinal area (forming bourrelets separated by a subtriangular resilifer), whereas the considerably shorter hinge plate of the right valve bears the buttress supporting the ventral side of the resilium (Stenzel, 1971).

MUSCLE SCARS

Only those features of muscle attachments that are independent from the analysis of soft parts are considered in this section.

127. Posterior adductor muscle placed outside or coincident with the border of the inner shell layer: (0) absent; (1) present.

With the exception of pinnid and mytilid outgroup taxa, the other species analysed in this work have the posterior adductor entirely enclosed within the border of the inner shell layer (aragonitic in the Pterioidea and calcitic in the ostreid outgroup taxon).

128. Posterior adductor muscle scar distinctive in colour (Fig. 1G): (0) absent; (1) present.

The absence of distinctive contrasting dark coloration of the adductor muscle scar distinguishes the Pterioidea from its ostreid and mytilid outgroup taxa. The only notable pterioidean exception is *Malleus anatinus* (present work) and *M. albus* Lamarck, 1819 (I. Tëmkin, pers. observ.). The nature of the darkened appearance is not known.

MINERALOGY AND SHELL MICROSTRUCTURE

Shell microstructure terminology follows Carter (1980a, b).

129. Outer layer microstructure: (0) simple prismatic; (1) fibrous.

Fibrous outer calcitic prisms are characteristic of the mytilid outgroup taxon (Carter, 1990).

130. Continuous prismatic layer across the dorsum: (0) absent; (1) present.

A continuous prismatic layer across the dorsal surface of the hinge is seen in *Atrina*, a pinnid outgroup taxon. A similar condition was reported from another pinnid, *Streptopinna sulcata*, by Waller (1990).

131. Inner layer microstructure: (0) nacreous; (1) foliated.

The foliated inner layer of the ostreid outgroup distinguishes it from the rest of the taxa presently analysed, the latter characterized by a nacreous inner layer microstructure. The mineralogy of the inner layer was not scored because each variety of the laminar microstructural group is invariably associated with a particular form of calcium carbonate: aragonite in the case of nacre and calcite in the case of a foliated structure (Carter, 1980a, b).

132. Nacre variety: (0) sheet nacreous; (1) row stack nacreous.

In the Pterioidea, the inner shell layer is comprised of sheet nacre, characterized by an irregular, stair-step, stacking mode in vertical sections (Carter, 1990). Row stack nacre (defined by a vertical column-wise stacking mode of nacreous tablets in vertical sections) was not found in the Pterioidea and appears to be restricted to the Pinnidae (Carter, 1990).

133. Growth pattern of aragonite tablets: (0) homogeneous; (1) spiral.

Growth of nacreous crystals can occur in three ways: (1) by growth with subsequent coalescence, (2) by rising of the crystals forming inclined steps, and (3) by spiral growth (Wada, 1972; Wilbur, 1972). The first two modes of growth produce a homogeneous appearance of the nacre, whereas the third results in a spiral arrangement of aragonitic crystals. The last was found to be predominant in the Pterioidea and has previously been illustrated in *Pinctada martensii* (fide Wada, 1958, 1968), *I. ephippium* (fide Taylor *et al.*, 1969), and *Pteria sterna* (fide Kiefert *et al.*, 2004). In *Pulvinites exempla*, *I. bicolor*, and *Malleus (Malvufundus) candeanus*, nacre appeared homogeneous. Spiral growth was also detected in *A. rigida*, a pinnid outgroup, corroborating the previous observation of spiral crystal growth in *Pinna bicolor* Gmelin, 1791 [as *P. attenuata* (Reeve, 1858)] by Wada (1972) and Wilbur (1972).

134. Chalky deposits: (0) absent; (1) present.

Chalky deposits, irregularly distributed white patches of porous ostracum exposed to the inner shell surface, are characteristic of ostreoids, including the ostreid outgroup, *Crassostrea virginica* (fide Stenzel, 1971).

APPENDIX 2

SPECIMENS AND PRINCIPAL SOURCES USED FOR CHARACTER CODING

PINCTADA IMBRICATA (RÖDING, 1798)

West Atlantic, FK-239, south-east of Lignum Vitae Key, Florida Keys, Florida, USA, 24°53'45"N, 80°41'10"W, snorkelling on *Thalassia* seagrass,

wooden stakes, 0.3–0.8 m (two pairs with tissue; AMNH 298894); West Atlantic, wreck of THUNDER-BOLT, c. 6 nmi east of Marathon, Monroe County, Florida Keys, Florida, USA, 24°39.68'N, 80°57.82'W, steel wreck with fouling organisms, orange/red sponge overcoating most specimens, scuba, 34.1 m (one pair with tissue; AMNH 308926); West Atlantic, FK-287, 'The Horseshoe' site, bay side of West Summerland Key (Spanish Harbor Keys), inside of west arm, MM 35, Monroe County, Florida Keys, Florida, USA, 24°39.35'N, 81°18.22'W, shallow subtidal, by hand, snorkelling (two pairs with tissue; AMNH 308114); West Atlantic, FK-689, north-east of Dove Key, ocean side of Key Largo, Monroe County, Florida Keys, Florida, USA, 25°03.055'N, 80°28.220'W, hard bottom with silty sand, sponges, gorgonians, 0.5–1.0 m, snorkelling (one pair with tissue, AMNH); West Atlantic, Bear Cut, Biscayne Bay, Miami, Florida, Dade County, USA (two pairs; AMNH 172356); as previous, exposed in sand after low tide (five pairs; AMNH 99957); West Atlantic, Bahia Honda Key, Florida, USA, on beach, alive, after storm (five pairs; AMNH 210234); West Atlantic, Bailey's Bay, Hamilton Island, Bermuda, USA (five pairs; FMNH 29826).

Principal reference: Hayes (1972) (gross anatomy).

PINCTADA FUCATA (GOULD, 1850)

Tatakua-Jima, Mijie Prefecture, Japan (four pairs with tissue; AMNH 179633); West Indian Ocean, station H35, 3 mi north-north-east of Nossi Fali, east of Nossi Bé, north-west Madagascar, 16.5 m, mud, sand, broken shells (26 pairs; AMNH 97134); West Pacific, Nada, Wakayama Prefecture, Japan, collected in net for spiny lobster at 5–18.2 m on rocky bottom (three pairs; AMNH 307417); West Pacific, Padada Beach, Gulf of Davao, Celebes Sea, Philippines (approximately 40 valves; AMNH 181309).

Principal references: Herdman (1904) (detailed anatomy); Shiino (1952) (detailed anatomy).

PINCTADA LONGISQUAMOSA (DUNKER, 1852)

West Atlantic, FK-165, off west shore of Pigeon Key (bay side of Tavernier), 25°03.33'N, 80°30.78'W, Florida Keys, Monroe County, Florida, USA, *Thalassia* seagrass, scuba, by hand, 1.4 m (32 pairs with tissue plus two valves; AMNH 298904); FK-174, same as FK-165 (12 pairs with tissue; AMNH 298902).

Principal reference: Mikkelsen *et al.* (2004) (detailed anatomy).

PINCTADA MAZATLANICA (HANLEY, 1855)

East Pacific, Gulf of California, Mexico, Guaymas, Sonora, Bahia de Bacoichampo, 2 m (three pairs with tissue, AMNH 311788); same as previous (one pair

with tissue, AMNH 311790); East Pacific, Colorado Point, Guaymas, Mexico (one pair; AMNH 249645); East Pacific, Port Guatulco, Mexico (two pairs plus one valve; AMNH 78113); East Pacific, Bay of La Paz, Baja California, Mexico (one pair; AMNH 266407); East Pacific, Iagoon, Puerto Escondido, Baja California (one pair; AMNH 136; 76399).

PTERIA COLYMBUS (RÖDING, 1798)

West Atlantic, FK-048, American Shoals, ocean side, Monroe County, Florida Keys, Florida, USA, 24°31.43'N, 81°31.26'W, scuba, 4.6 m, reef (four pairs with tissue; AMNH 298921); West Atlantic, FK-237, East Turtle Shoal, ocean side off Grassy Key, Monroe County, Florida Keys, Florida, USA, 24°43'15'N, 80°55'42'W, scuba, maximum 4.3 m, patch reef with gorgonians, on sand patches (two pairs with tissue, AMNH 298920); West Atlantic, Gulf beach, at Lighthouse, Sanibel Island, Florida, USA (six pairs; AMNH 210230); West Atlantic, Gulf of Mexico, off Port Isabel, Texas, USA, 32.9 m (ten pairs; AMNH 144391); West Atlantic, Lemon Bay, Florida, USA (five pairs; FMNH 167474); West Atlantic, Swanesborough, North Carolina, USA (one pair; FMNH 184280); West Atlantic, Marco Island, Collier County, Florida, USA (three pairs; FMNH 166368).

Principal reference: Hayes (1972) (gross anatomy).

PTERIA STERNA (GOULD, 1851)

East Pacific, Gulf of California, Mexico, Guaymas, Sonora, Bahia de Bacoichampo (one pair with tissue, AMNH 311731); same as previous (one pair with tissue, AMNH 311789); East Pacific, San Diego, California, on rocks, just below low tide (one pair; AMNH 206564); East Pacific, Veracruz, Vacamonte, Panama (seven pairs; AMNH 156682); East Pacific, Topolobampo, Mexico (approximately 40 pairs; AMNH 262822); East Pacific, Puerto Penasco, Mexico (two pairs; FMNH 171811).

Principal reference: Kiefert *et al.* (2004) (shell microstructure).

PTERIA LOVENI (DUNKER, 1872)

West Pacific, New Caledonia, 58–70 m, 21°00'S, 55°15'E [five pairs with tissue, MNHN MD32/REUNION (1982), St DC85]; West Pacific, Kusui, Nada-Cho, Wakayama Prefecture, Japan, 9.1–18.2 m (four pairs; AMNH 241717), West Pacific, Kii, Japan, 9.1 m (two pairs; AMNH 126247).

ELECTROMA ALACORVI (DILLWYN, 1817)

Samoa Islands, Asau harbour, north coast, in-shore edge of reef, 6 ft (four pairs with tissue, USNM

675754); Indian Ocean, Cocos Keeling, 4.8 km south-west of Home Island, 0.9–1.8 m, staghorn, sand, heads, near deep holes, station B20 (21 pairs with tissue, ANSP 289178); same as previous (six pairs with tissue; AMNH 292446); same as previous (nine pairs; AMNH 112530).

Principal reference: Pelseneer (1911) (gross anatomy).

ISOGNOMON ALATUS (GMELIN, 1791)

West Atlantic, FK-259, Ramrod Key, at dock, ocean side, Monroe County, Florida Keys, Florida, USA, 24°39.72'N, 81°24.41'W, intertidal, rocks, by hand (seven pairs with tissue, AMNH 298023); West Atlantic, west side of Maguëyes Island, Puerto Rico (13 pairs, AMNH 100419); West Atlantic, bay side, Grassy Key, Florida Straits, Florida, USA (35 pairs; AMNH 247493).

Principal reference: Siung (1980) (gross anatomy; embryonic shell).

ISOGNOMON RADIATUS (ANTON, 1839)

West Atlantic, FK-351, Looe Key back reef, Monroe County, Florida Keys, 24°32.87'N, 81°24.41'W, 0.9–2.1 m, snorkelling, rubble (one pair with tissue, AMNH 298944); West Atlantic, Kingston, Jamaica, West Indies (one pair with tissue; AMNH 141889); West Atlantic, St. Thomas, Virgin Islands (five pairs; AMNH 158229), West Atlantic, north end, Lake Worth, Florida (two pairs; AMNH 293729), West Atlantic, south-west side of Grand Banc, Port-au-Prince, Haiti, on underside of slabs of dead coral or rocks, 0.6–1.5 m depth (two pairs; AMNH 177666); West Atlantic, Honeymoon Beach, East End, Water Isle, St. Thomas Bay, Caribbean Sea, under rocks, 0–0.3 m (approximately 60 valves; AMNH 292524).

ISOGNOMON BICOLOR (C. B. ADAMS, 1845)

West Atlantic, Honeymoon Beach, East End, Water Isle, St. Thomas Bay, Caribbean Sea, under rocks, 0–0.3 m (two pairs; AMNH 292524); West Atlantic, Magens Bay, St. Thomas, Virgin Islands (approximately 50 pairs with tissue; AMNH 141725).

Principal references: Martins (2000) (detailed anatomy); Domaneschi & Martins (2002) (detailed shell morphology).

CRENATULA MODIOLARIS LAMARCK, 1819

West Pacific, New Caledonia, Secteur de Koumac, Anse de Koumac (= Baie de Ouanap), 20°34'S, 164°16'E, 0–2 m, fonds meubles, herbiers (two pairs with tissue; MNHN Expédition Montrouzier October

1993, station 1277); Constable Coll. (three pairs, AMNH 27950); Caroline Islands, Tomil Harbour, Yap, growing at tips of sponges on tidal flats (four pairs; USNM 634507); Pacific, New Caledonia, south-east of Ile Ouere, near Noumea, 8 m, dredged (two pairs with tissue; USNM 795306).

Principal reference: Reid & Porteous (1980) (gross anatomy).

MALLEUS ANATINUS (GMELIN, 1791)

West Pacific, New Caledonia, Secteur de Touho, Chenal de Touho, 20°46'–20°47'S, 165°15'–165°16.5'E, 45–56 m, sable détritique (two pairs with tissue, MNHN Expédition Montrouzier September 1993, station 1261); West Pacific, New Caledonia, 19°08'S, 163°29'E, 54–120 m (one pair with tissue; MNHN N.O. 'Vauban', Musorstom 4, St. DW 187).

MALLEUS (MALVUFUNDUS) CANDEANUS
(ORBIGNY, 1842)

West Atlantic, FK-302, Sand Key transect, Monroe County, Florida Keys, Florida, USA, 24°26.30'N, 81°53.32'W, 20 m, scuba, rubble (two pairs with tissue, AMNH 299406); West Atlantic, FK-260, Looe Key coral reef, just east of channel marker 24, ocean side of Ramrod Key, Monroe County, Florida Keys, Florida, USA, 24°32.80'N, 81°24.80'W, scuba, spur and groove reef, maximum 7.3–7.6 m (one pair with tissue; AMNH 298194); West Atlantic, Bermuda, Harrington Sound, in old 'Lithophaga' holes (three pairs with tissue, MCZ 340681); West Atlantic, Bermuda, Harrington Sound (one pair; AMNH 247234).

Principal references: Boss & Moore (1967) (shell morphology); Waller & Macintyre (1982) (shell morphology and prodissococonch).

VULSELLA VULSELLA LAMARCK, 1819

Thailand, Gulf of Thailand, Ko-Sichang, 21.9–23.8 m (one pair plus one valve with tissue; CASIZ 159752).

Principal reference: Reid & Porteous (1980) (gross anatomy).

PULVINITES EXEMPLA (HEDLEY, 1914)

West Pacific, Australia, New South Wales, north-north-east of Sydney, 33°42.000'S, 151°53.000'E–152°0.000'E, 406 m, on junked aeroplane, trawled (four pairs with tissue, AMS C.129659); Pacific, New Zealand, South Island, off point east of Joseph Point, Doubtful Sound, Fiordland, 45°18.93'S, 166°58.36'E, 340 m (one pair; NMNZ M.153627).

Principal references: Marshall (1998) (prodissococonch); Tëmkin (2006) (detailed anatomy, shell morphology, and microstructure).

ATRINA RIGIDA (LIGHTFOOT, 1786)

West Atlantic, St. Andrews Bay, Gulf of Mexico, Franklin County, Florida, USA (two pairs with tissue; AMNH266904); West Atlantic, west of Anclate Keys, Gulf of Mexico, Florida, USA (one pair; AMNH 262834).

Principal reference: Grave (1911) (detailed anatomy).

CRASSOSTREA VIRGINICA (GMELIN, 1791)

West Atlantic, Jones Beach (bay side), Nassau County, New York, USA (one pair with tissue; AMNH 269842); West Atlantic, North Beach, St. Catherine's Island, Liberty County, Georgia, USA, in dead fallen trees (four pairs; AMNH 178487); West Atlantic, San Carlos

Bay, Sanibel Island, Florida, USA (approximately 40 valves; AMNH 103345).

Principal references: Galtsoff (1964) (detailed anatomy and shell morphology); Kennedy, Newell & Eble (1996) (detailed anatomy, adult and embryonic shell morphology, shell microstructure).

MYLILUS EDULIS (LINNAEUS, 1758)

West Atlantic, Eastern Point, Nahant, Essex County, Massachusetts, USA, in pool tides, in rocks at low tide (approximately 30 pairs with tissue; AMNH 3399-A); East Atlantic, near Tarbet Ness, Rossshire, Scotland, on rocks in tidal pools, 0.1 m (three pairs with tissue; AMNH 179590).

Principal references: Purdie (1887) (gross anatomy); Field (1923) (detailed anatomy and shell morphology).

APPENDIX 3

DATA MATRIX

<i>Mytilus edulis</i>	10-2000202	0031100100	1110010000	120-000010	0030000-0	0000001000	0100100000	0010010001	1011001000	0-00-000	0000000230	-000200100	---001110	0000
<i>Atrina rigida</i>	01012010110	00011020-1	000010101100	1210001200	0120000-1	0000101000	1100102000	1000011111	0010001010	0-10310001	00100000-0	-101200100	---001001	0110
<i>Crassostrea virginica</i>	10-1001011	10213010-1	010010101000	00100001001	0030000-0	0000112-000	0112-30-0	0100001-21	01200010000	0-00-011	000010000-0	-111010011	0001110100	1-1
<i>Isoognomon alatus</i>	01012010	01010100	000000100000	11100000001	0030000-0	000000101100	1110100011	0011011111	00100002001	1110110010	0000000222	2101201001	01000000000	0010
<i>Isoognomon bicolor</i>	000101210	0001010100	00000010000	11100000001	0001002010	000000001000	1110110011	0011011011	01100002000	0-0002010	0100000100	-101201001	00100000000	0000
<i>Isoognomon radiatus</i>	00002010	01002010110	000000101000	11100000001	000000001000	000000001000	1110000011	0011011111	01100002001	111011000000	000110000-0	-101201001	02100000000	0010
<i>Pulvinites eximpta</i>	0100102100	01003000110	000000102100	11100000001	000100-0	0000000100	00110-010	0100110010	01000003000	0-00-010	000000000-0	-011111001	00000000000	0000
<i>Pteria colymbus</i>	0100101210	0101301101	1000102000	01111100001	0100011000	0100101102	0110101011	0010010011	01100002001	1001100000	0001100202	0111200001	10000000000	0010
<i>Pteria sterna</i>	01010101210	0101301101	1000101000	01111100001	0100010010	0100101101	0110111011	0010010111	11100002001	10111110000	0001100202	0111200001	10000000000	0010
<i>Pteria loveni</i>	0100101210	0101301100	0000102000	11111100001	0100011000	0100101102	0110100000	0010010111	01100002001	1001100000	0001230202	0111200001	10000000000	0010
<i>Malleus anatinus</i>	0100101210	0100300100	0000101000	11111100001	0100011000	0100101101	1110111011	0000011011	001010102001	1100-000	110002000-1	1111200011	00000000100	0010
<i>Malleus candeanus</i>	0101012100	0100300100	00000010000	11101000001	0100010010	0101101000	1110110000	2000011011	001010102001	1100-000	110000000-2	1111200011	02100000000	0000
<i>Pinctada imbricata</i>	0100101210	0100300100	00000010000	11101000001	0100010010	0101101000	1110101011	0000000000	01100002101	11100010000	0001100212	11112000001	10000000000	0010
<i>Pinctada longisquamosa</i>	0100101210	0100300100	00000010000	11101000001	0100010010	0101101000	1110101011	0000000000	01100002101	11100010100	000110101212	11112000001	10000000000	0010
<i>Pinctada mazatlanica</i>	0100101210	0100300100	00000010000	11101000001	0100010010	0101101000	1110101011	0000000000	10100002100	11102100000	00013001000	11112000001	10100000000	0010
<i>Pinctada fucata</i>	0100101210	0100300100	00000010000	11101000001	0100010010	0101101000	1110101011	0000000000	10100002100	11102100000	00013001000	11112000001	10100000000	0010
<i>Vulsella vulsellia</i>	0100101210	0100300100	00000010000	11101000001	0100010010	0101101000	1110101011	0000000000	10100002100	11102100000	00013001000	11112000001	10100000000	0010
<i>Crenatula modiolaris</i>	0100101210	0100300100	00000010000	11101000001	0100010010	0101101000	1110101011	0000000000	10100002100	11102100000	00013001000	11112000001	10100000000	0010
<i>Electroma alacorum</i>	0100101210	0100300100	00000010000	11101000001	0100010010	0101101000	1110101011	0000000000	10100002100	11102100000	00013001000	11112000001	10100000000	0010