

## ***Bivalvia – a look at the Branches***

*Rüdiger Bieler FLS, editor*

# **The Arcoidea (Mollusca: Bivalvia): a review of the current phenetic-based systematics**

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The diversity and adaptive radiations of modern Arcoidea, here considered to contain the families Arcidae, Noetiidae, Cucullaeidae, and Glycymerididae, are reviewed. Most fall into either epibyssate or endobyssate life habits with only the Glycymerididae living as free burrowers. The phenetic characters of the families within the Arcoidea are reviewed and the families are shown to be supported by very few synapomorphic characters. Homoplasy is shown to be widespread and is illustrated in a series of discussions on the ligament, epibyssate–endobyssate radiations, and possible parallelism within genera, and in a review of arcoid anatomical characters. Previously published molecular data are reviewed and these support the inclusion of the Glycymerididae in the Arcoidea. They also indicate, however, that polyphyly is probably widespread at the subfamily level. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, 148, 237–251.

ADDITIONAL KEYWORDS: adaptive radiation – anatomy – shell morphology – taxonomy.

## INTRODUCTION

Recent studies, such as that on the Lucinoidea (Williams, Taylor & Glover, 2004), combining both phenetic and molecular data, have radically altered both family and generic relationships. Attempting to review the superfamily without a major molecular analysis consequently appears rather futile. However, phenetic characters form the basis of the current arcoid classification and remain so for the analysis of the extensive fossil record. The main purpose of this review is therefore to examine the phenetic data and to highlight conflicting or challenging observations that may guide future studies.

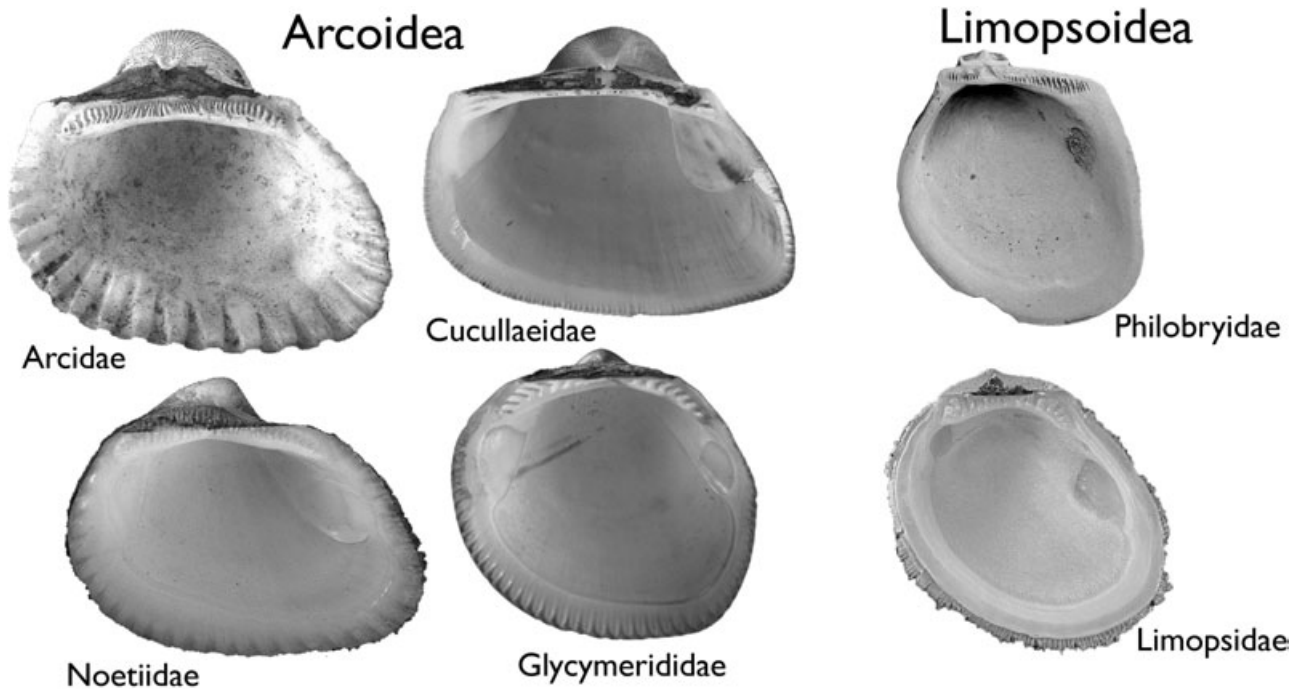
The order Arcoidea encompasses the Recent families Arcidae, Noetiidae, Cucullaeidae, Glycymerididae, Limopsidae, and Philobryidae (Fig. 1). There are, however, a number of conflicting classifications at the superfamily level which mainly centre on the position

of the Glycymerididae. For the purposes of this paper, the superfamily Arcoidea is deemed to include the Arcidae, Noetiidae, Cucullaeidae, and Glycymerididae, and the Limopsidae and Philobryidae alone are retained in the Limopsoidea. The inclusion of the Glycymerididae may be contentious, but the reasons are examined in the ‘Relationships’ section. The diversity of Recent Limopsidae and Philobryidae has been surveyed by Tevesz (1977), Oliver & Allen (1980b), and Oliver (1981).

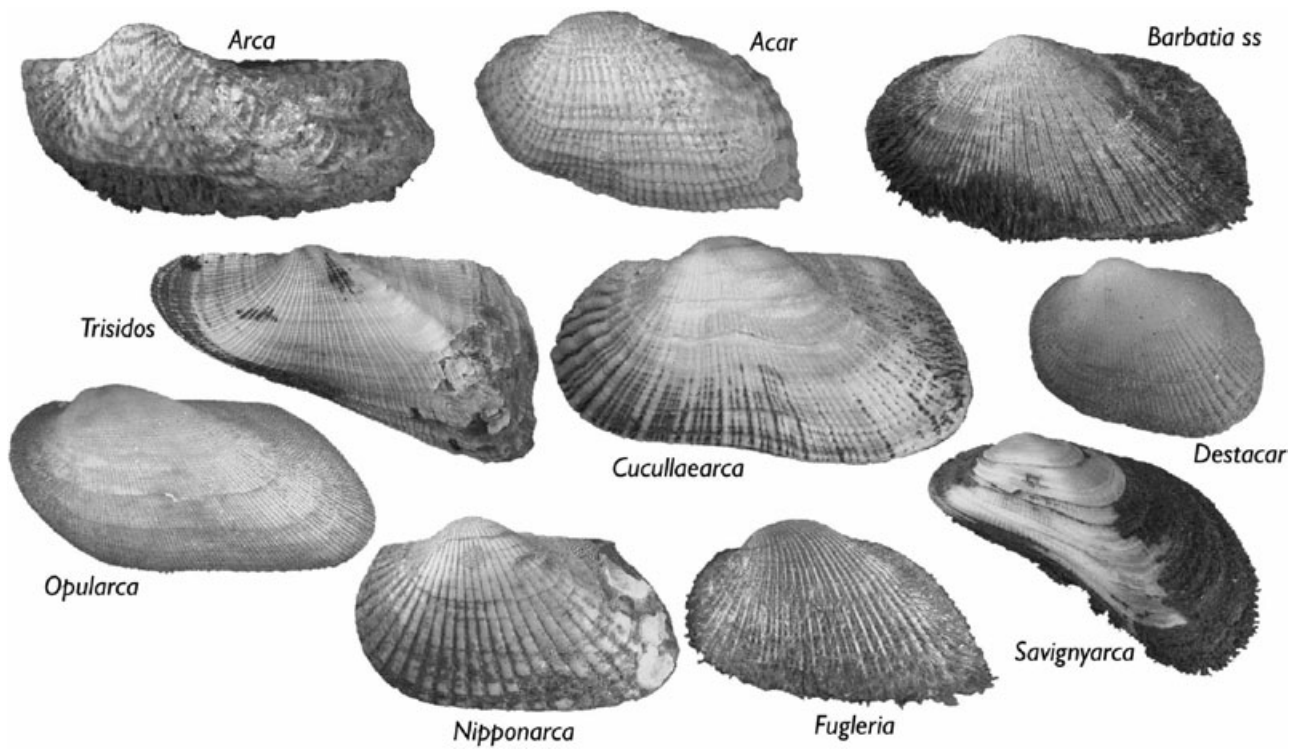
## NUMBER OF TAXA AND DISTRIBUTION

Species of the families Arcidae (Figs 2, 3), Noetiidae (Fig. 4), and Cucullaeidae are collectively known as ark-shells and blood cockles. They are recognized from their trapezoidal ribbed shells with a heavy periostracum and the taxodont hinge. The name blood cockle comes from the presence of haemoglobin in the haemocoel, a feature found in all Arcoidea but not exclusive to them. They are primarily components of tropical shallow waters and warm temperate seas, and have

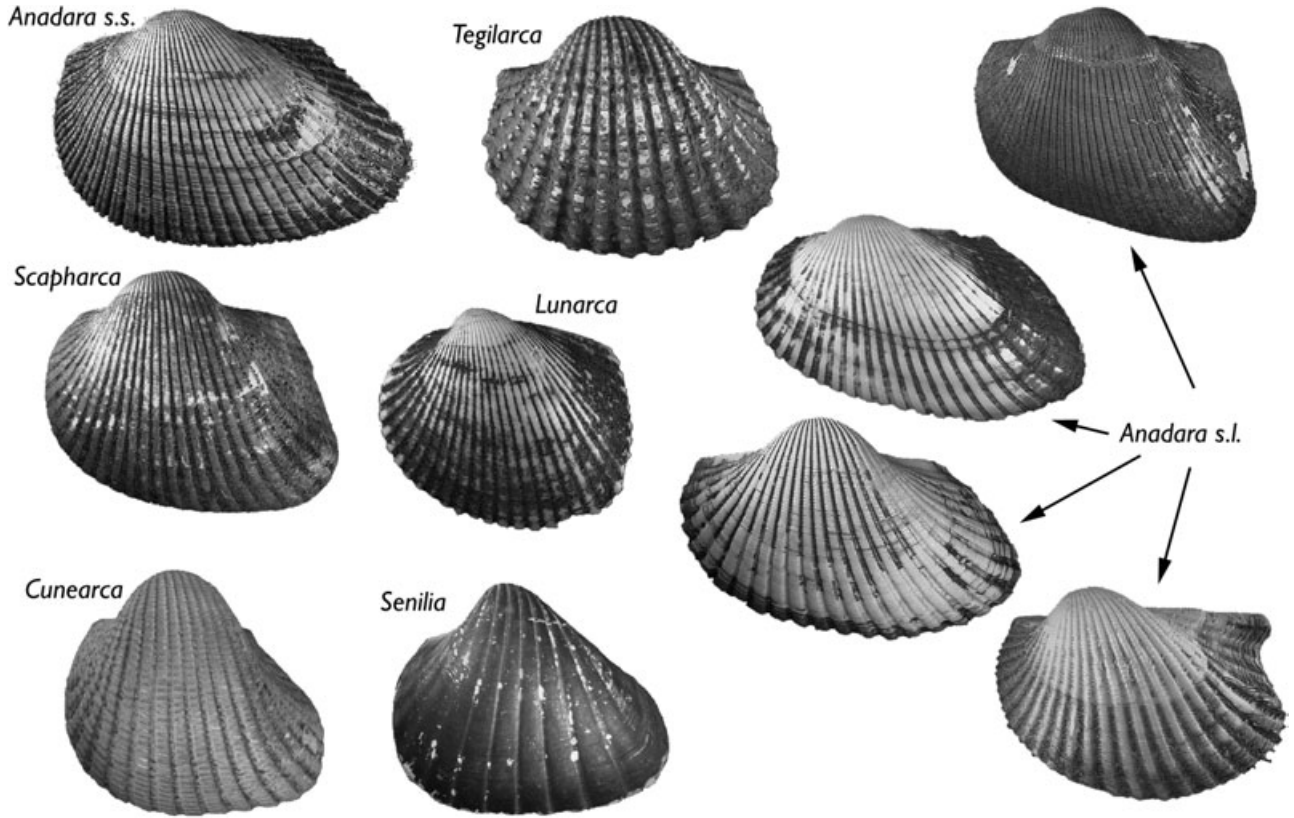
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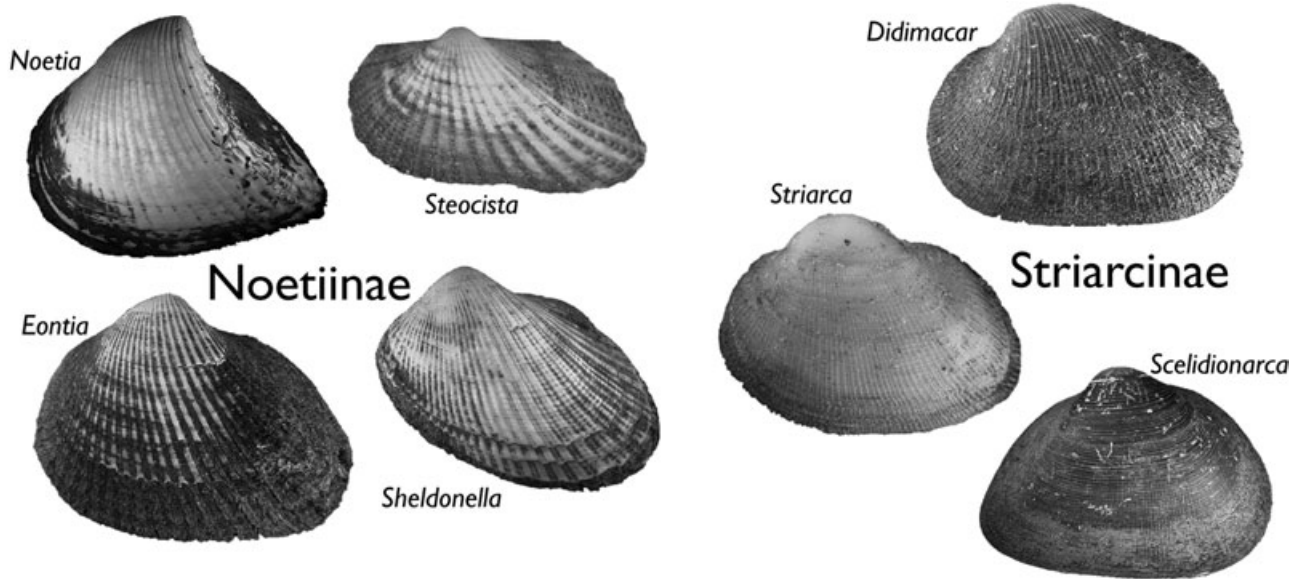
**Figure 1.** Typical representatives of the six Recent families of arcoïd bivalves arranged by the two superfamilies Arcoidea and Limopsoidea.



**Figure 2.** Diversity of form in mostly epibyssate taxa currently assigned to the Arcinae.

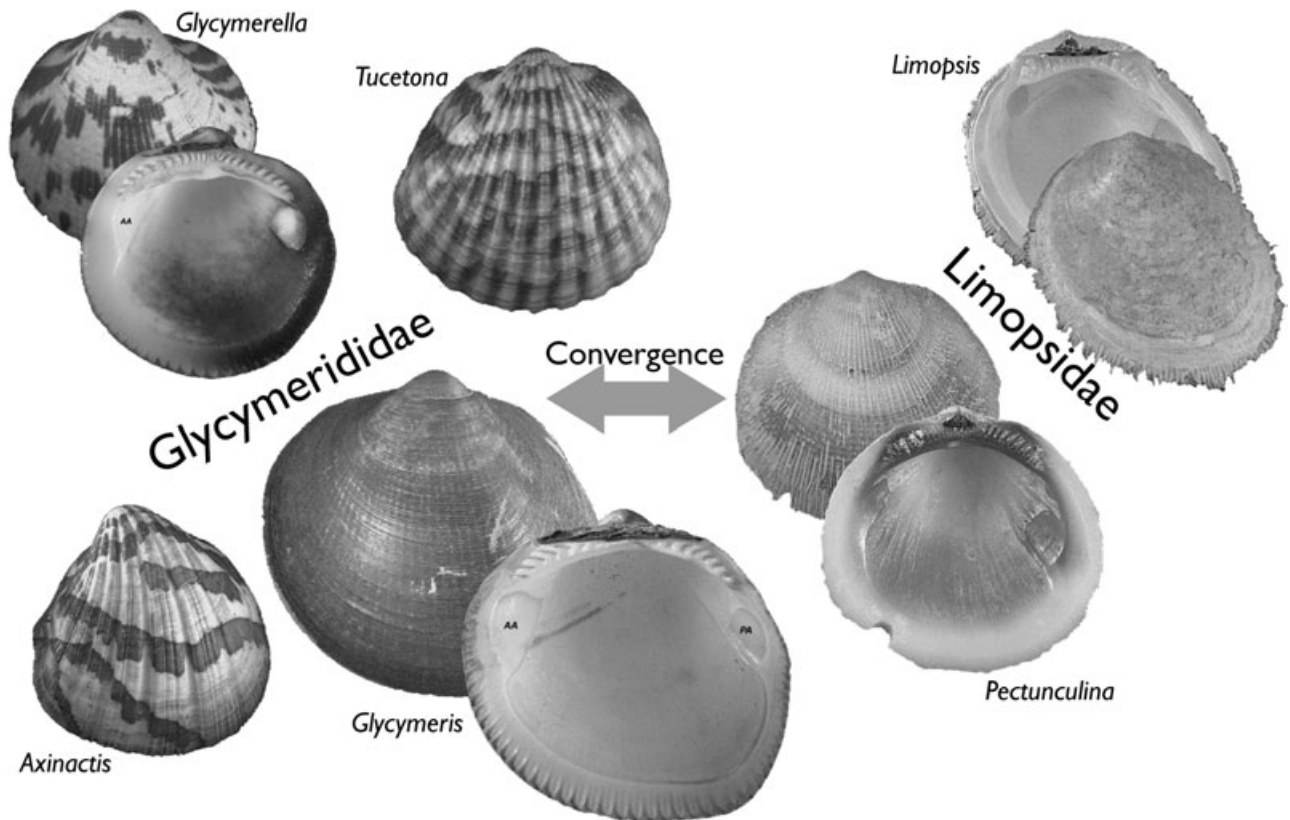


**Figure 3.** Diversity of form in mostly endobryssate taxa currently assigned to the Anadarinae.



**Figure 4.** Diversity of form in the Noetiidae and typical genera arranged in the two subfamilies Noetiinae and Striarcinae.

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**Figure 5.** Diversity of form in the Glycymerididae and an illustration of the convergence between the Glycymerididae and Limopsidae.

their maximum species richness in the Indo-West Pacific. The Indo-Pacific Molluscan Database (OBIS, 2005) lists over 180 valid species in over 30 genera for the region. A further 27 are recorded from tropical West Africa (Oliver & von Cosel, 1992a, b), 20 from the west Atlantic (Abbott, 1974; Rios, 1994), and 10 from the north-eastern Atlantic (CLEMAM, 2005). They are, however, not exclusive to warm seas, and a few taxa can be found in polar seas and at abyssal depths, with Oliver & Allen (1980a) recording eight species from the deep Atlantic. A conservative estimate of global species richness is 300 species. The majority of these will belong to the Arcidae, with less than 40 extant species of Noetiidae recorded and only three species of Cucullaeidae known.

At the generic and subgeneric level, Newell (1969) recognized only 24 taxa, but over twice that number of nominal taxa appear in regional faunas and there is little consistency in their use.

The most familiar taxa are those belonging to the genera *Arca*, *Barbatia*, and *Anadara*, but the most important are the blood cockles. *Anadara granosa* is cultured commercially in South-East Asia, species of the subgenus *Scapharca* are exploited in Japan and China, and *Senilia* is gathered in West Africa.

The Glycymerididae (Fig. 5), the 'dog-cockles' or 'bit-tersweets', generally have heavy subcircular shells and probably number less than 100 species. They are inhabitants of shallow waters, but are rarely intertidal and prefer mobile sand and gravel environments. They are found in most oceans, but are absent from polar and deep-sea regions. In Europe and the Mediterranean, *Glycymeris glycymeris* and *Glycymeris violascens* are fished commercially.

#### FOSSIL RECORD

The Arcoidea have a long fossil record, with its origins in the Ordovician (Cope, 1997, 2000) and a major radiation in the Paralleodontidae throughout the Upper Palaeozoic and Mesozoic (Amler, 1989). This radiation mimics that of modern arcs with a variety of trapezoidal, quadrangle, and modioliform shell forms. They are characterized by the subparallel hinge teeth. The Paralleodontidae are probably extinct, although the genus *Porterius* is reported to include a single extant species, *Porterius dalli*, from Japan (Newell, 1969). Other extant species also have subparallel hinge teeth, notably *Bathyarca*, *Bentharca*, *Samacar*, and *Deltaodon*, and these may represent modern parallel-

odonts, or may simply display a secondary appearance of this character due to the thin nature of the hinge plate. Modern Arcidae have their origins in the Jurassic and are believed to have originated from a parallelodont ancestor (Amler, 1989). The Cucullaeidae appear to be contemporary with the Arcidae, but the Noetiidae and Glycymerididae are younger with origins in the Cretaceous.

### ADAPTIVE RADIATION

All of the Arcoidea can be readily recognized by their taxodont hinge and duplivincular ligament. The families Arcidae, Noetiidae, and Cucullaeidae have trapezoidal to quadrate shells and mostly with some radial ribbing. Amongst these families, the morphological and ecological diversity is strongly linked with the major adaptive trends centred on the epibyssate or endobyssate/burrowing life habits.

#### EPIBYSSATE

Epibyssate taxa are generally elongate, with a height to length ratio of less than 1 : 1.35 (Stanley, 1970). They have a byssus in the form of a sheet or plug and, associated with the byssus, are large posterior pedal retractors acting as byssus retractors. The shells are radially ribbed but more weakly than in the endobyssate forms. Living attached to rocks and corals, they are probably less subjected to flooding of the mantle with sediment and, in general, have smaller labial palps. The coiling of the mid gut and hind gut is mostly simple. Many have well-developed mantle 'eyes' and have a rapid response to changes in light intensity (Waller, 1980; Morton, 1987).

Within the epibyssate forms, two major morphologies can be recognized. The boat-shaped taxa are characterized by the wide separation of the umbos and are typified by the genus *Arca* in the Arcidae (Fig. 2) and *Sheldonella* in the Noetiidae (Fig. 4).

Rectangular forms lacking umbonal separation represent the most diverse group of epibyssate arks, and are represented by the genus *Barbatia s.l.* in the Arcidae (Fig. 2) and *Striarca* in the Noetiidae (Fig. 4).

Epibyssate taxa can be found in a wide variety of habitats, with most in semi-cryptic sites in crevices or under rocks and coral debris. Only a few are able to survive in exposed conditions, and these tend to be mytiliform in shape, as represented by the genus *Savignyarca* (Arcidae) (Fig. 2).

Some are intimately linked with living corals, and *Barbatia foliata* and *Arca ventricosa* are commonly found in crypts within massive corals (Zuschin & Oliver, 2003). These habits give a resemblance to a boring habit, and *Litharca* is reported to be the only true arcoid borer, although this has not been

confirmed in this rare genus (Thomas, 1978). In this genus, the umbos are in a posterior position, giving the shell a cylindrical outline and somewhat resembling the lithophagine date mussels.

Small species are truly cryptic and are reported from marine caves (Hayami & Kase, 1993; La Perna, 1998; Oliver & Holmes, 2004). Most of these taxa are like *Acar* in form and are similar to those from deep- or cold-water environments.

*Trisidos* (Fig. 2) is another unusual genus within the Arcidae, in which the shell is twisted around the umbo bringing the posterior margin through 90°. In this orientation, the posterior margin lies in the same plane as the surface of the sediments in which it lives (Morton, 1982a). In this case, the form is epibyssate but the habit is endobyssate. This serves as a caution to the oversimplification of inferred life habits.

Although almost entirely marine, there is a single freshwater taxon, *Scaphula* (Arcidae), that inhabits fully freshwaters in South-East Asia.

#### ENDOBYSSATE/BURROWING

Endobyssate taxa are quadrate and tumid with a height to length ratio of more than 1 : 1.35. Their shells are often heavily ribbed with interlocking marginal crenulations, giving them a strong resemblance to the true cockles, Cardioidea. The majority of species have retained a byssus, but this takes the form of a few threads to a single thread. Consequently, byssus retractors are not developed. In the Arcidae, endobyssate taxa (Fig. 3) are represented by the genera *Anadara*, *Scapharca*, and *Cunearca*, these representing a transition from semi-infaunal to completely infaunal forms. This trend is associated with increasing strength of ribbing, greater frequency of the inequivalve condition, and increasing tumidity. The correlation of shell shape with habitat and grain size has been demonstrated by Alexander (1993), and similar anatomical trends are apparent.

In the Noetiidae, the cockle form (Fig. 4) is represented today by *Noetia* (prosodetic ligament) and *Eontia* (amphidetic ligament), but MacNeil (1938) shows a range of fossil *Eontia* that are more epifaunal in outline. The Noetiidae also have a number of thin-shelled taxa (Fig. 4) that inhabit muddy environments, such as *Noetiella* (Oliver, 1986a, 1987a), *Estellacar* (Oliver, 1986b, 1987b), and *Stenocista* (Oliver & von Cosel, 1992b).

The three species of living Cucullaeidae are identical in form, have a strongly inflated quadrate shell, and are immediately recognizable by the massive myophoric flanges supporting the posterior adductor. These species are shallow burrowers, living with the posterior area flush with the surface or protruding slightly from it (Morton, 1981). Morton (1981)

suggests that the byssus is functional only in juveniles.

#### ABYSSATE

The Glycymerididae (Fig. 5) are more conservative, all having roughly lenticular shells and most with weak ribbing. The Recent species are not subdivided in subfamilies and only four genera are regularly recognized. *Glycymeris* has heavy smooth shells with an amphidetic ligament, and has a cosmopolitan distribution. *Tucetona* has ribbed shells with an amphidetic ligament, is also cosmopolitan, but is confined to subtropical and tropical seas. *Glycymerella* is like *Glycymeris* but the ligament is entirely prosodetic and this genus is restricted to the western Atlantic. *Axinactis* has a dissected ribbed shell with a partly prosodetic ligament and is restricted to the eastern Pacific.

*Glycymeris* species are known to be poor burrowers (Thomas, 1976) and are often found lying on the surface of the seabed. They are protected from wave action and predators by the heavy shell. The foot has a shallow ventral groove suggesting that a byssus gland is present, but an active byssus has not been reported (Heath, 1941).

### REPRODUCTION

All Arcoidea studied to date are dioecious, and the majority produce small eggs and have a planktotrophic development. Small species tend to produce larger eggs and these probably have a lecithotrophic development. Brooding of larvae is suspected in some because of the large size and shape of the prodissoconch (La Perna, 1998; Oliver & Holmes, 2004). Lecithotrophic development is also suggested for the deep-water species (Oliver & Allen, 1980a).

### RELATIONSHIPS

#### SUPERFAMILY LEVEL

The inferred relationships and resulting classifications within the order Arcoidea and the superfamily Arcoidea are primarily based on shell morphology and have a strong palaeontological perspective. The majority adopt two superfamilies with living representatives, the Arcoidea and Limopsoidea, but there is considerable variation concerning the families included in them.

MacNeil (1938) places the Glycymerididae, Limopsoidea, Noetiidae, and Cucullaeidae in the Glycymeracea and retains separate status for the Arcidae as the Arcacea. Vokes (1967), Newell (1969), and OBIS (2005) place the Arcidae, Noetiidae, and Cucullaeidae in the Arcoidea, but place the Glycymerididae in the

Limopsoidea, and it is this classification that is widely accepted. The contentious position of the Glycymerididae is evidenced in Amler (1999), where it is included in the Arcoidea, and in Coan, Scott & Bernard (2000), where it is given superfamily status of its own. Scarlato & Starabogatov (1979) provide the most radical position and give superfamily rank to seven groups: Bathyarcoidea, Cucullaeoidea, Noetioidea, Limopsoidea, Philobryoidea, Arcoidea, and Glycymeridoidea. At first sight, this seems to be little more than elevating families to superfamily level, but some of the family inclusions are surprising. The creation of families for the anadarine genera, *Lunarca* and *Cunearca*, and placing them with the Bathyarcoidea and Cucullaeoidea, respectively, and without explanation, detracts from this study. Consequently, it has largely been ignored, but may yet have some merit (see below).

Table 1 summarizes the shell and anatomical features of the families concerned. From this, it can be seen that the families have few autapomorphic characters, and that the synapomorphies used to define the superfamilies are similarly few and open to interpretation. The diagnosis of the Limopsacea given by Newell (1969), which includes the Glycymerididae, cites the rounded shell form and the weak ornamentation, yet includes two distinctly trapezoidal fossil taxa: *Arcullaea* and *Trigonarca*. The morphological basis to placing the Limopsidae and Glycymerididae in the same superfamily is tenuous. The Glycymerididae have a duplivincular ligament, lack a functional byssus, have a slightly larger anterior adductor muscle, and are generally massive in form, whereas the Limopsidae have an alivincular–multivincular ligament, a functional byssus, a larger posterior adductor muscle, and all are generally small. There are limopsoidea which are convergent in form with small Glycymerididae (e.g. *Pectunculina*) but retain all the limopsoidea characters mentioned (Fig. 5). The shared ovoid form of the shell appears to be the least supportable evidence for assigning relationships.

From the fossil record, the current hypothesis is of a common ancestor to both the modern Arcoidea and Limopsoidea, probably within the early Parallelodontidae (Amler, 1989). Given the age of appearance, those authors that place the Glycymerididae in the Limopsoidea must argue for a reversal in the ligament type from alivincular to duplivincular. If the Glycymerididae are placed in the Arcoidea, no such reversal is required. Newell (1969) linked the extinct subfamily Arcullaeinae with the Cucullaeidae, and this is a possible origin of the Glycymerididae within the Arcoidea. The recent discovery (Stiller & Jinhua, 2004) of a philobryid dating from the Triassic contradicts the accepted Eocene origin of this family and its assumed evolution from the Limopsidae, which is of Cretaceous origin.

**Table 1.** Shell and anatomical character matrix for the extant families of Arcoidea and Limopsoidea. Bold text indicates family level synapomorphies within the Arcoidea

Character	Arcoidea			Limopsoidea		
	Arcidae	Noetiidae	Cucullaeidae	Glycymerididae	Limopsidae	Philobryidae
Shell form	Trapezoidal	Trapezoidal	Trapezoidal	Ovate	Ovate	Ovate/mytiliform
Ligament type	Duplivincular	Duplivincular	Duplivincular	Duplivincular	Alivincular	Alivincular
Ligament orientation	Chevrons	<b>Vertical</b>	Chevrons	Chevrons	Amphidetic	Amphidetic
	Amphidetic	Amphidetic	Amphidetic	Amphidetic	Amphidetic	Amphidetic
	Opisthodetic	Prosodetic	Prosodetic	Prosodetic	Opisthodetic	Opisthodetic
Hinge	Taxodont	Taxodont	Taxodont	Taxodont	Taxodont	Taxodont, reduced
Hinge orientation	Straight	Straight	Weakly arched	<b>Strongly arched</b>	Weakly arched	Weakly arched
	Some weakly arched	Some weakly arched				
Teeth orientation	Vertical	Vertical	<b>Median vertical</b>			
	Distals often oblique	Distals rarely oblique	<b>Distals strongly oblique</b>			
Adductors	Isomyarian	Isomyarian	Heteromyarian	Almost isomyarian	Heteromyarian	Heteromyarian
	Heteromyarian	Heteromyarian	Anterior smaller	<b>Anterior larger</b>	Anterior smaller	Anterior smaller
Myophore	Ridge in a few, posterior	Ridge or shelf in all	<b>Raised flange</b>	Ridge at front of posterior	Absent	Absent
Shell tubules	+	+	+	+	+	+
Shell structure	Aragonite/cross lamellar	Aragonite/cross lamellar	Aragonite/cross lamellar	Aragonite/cross lamellar	Aragonite/cross lamellar	Aragonite/cross lamellar
Adult byssus	+	+	+	+	+	+
Mantle	+	+	+	+	+	+
second outer fold	±	-	-	-	-	-
second inner fold	±	±	±	±	±	±
Compound photoreceptors	+	?±	+	+	-	-
Haemoglobin	+	+	?	+	-	-
Stomach	Purchon type III	Purchon type III	Purchon type III	Purchon type III	Purchon type III	Purchon type III
Gut coiling	Looped/coiled	Looped/coiled	Looped	Looped	Looped	Looped
Labial palps	Small/medium	Small/medium	Small	Small	Small	Small
Ctenidium	Flat, homorhabdic, filibranch	Flat, homorhabdic, filibranch	Flat, homorhabdic, filibranch	Flat, homorhabdic, filibranch	Flat, homorhabdic, filibranch	Flat, homorhabdic, filibranch
Ctenidium/palp junction	Stasek type 3	Stasek type 3	Stasek type 3	Stasek type 3	Stasek type 3	Stasek type 3

*Molecular support at superfamily level*

Monophyly of the Arcoidea as a group within the Pteriomorpha is supported by datasets published by Steiner & Hammer (2000), based on 18S rDNA sequences, and Giribet & Wheeler (2002), based on 18S rDNA, 28S rDNA and cytochrome oxidase I (COI) sequences and morphological data. The taxa used in these studies included representatives of the Arcidae (Arcinae and Anadarinae), Noetiidae (Striarcinae), and Glycymerididae, but the Limopsidae, Philobryidae, and Cucullaeidae have not yet been included. Malchus (2004) alludes to molecular data being available for the Limopsoidea and Philobryidae, and suggests that the Limopsoidea is a sister group to the Arcoidea. In the published molecular studies, in which the superfamily Limopsoidea is used, caution must be taken as this superfamily is represented by the Glycymerididae and not the Limopsidae. The lack of monophyly within the Arcoidea, noted by Giribet & Wheeler (2002), is due to the nesting of the Glycymerididae within arcoidean taxa. If the classification of Amler (1999) had been adopted, monophyly would be preserved because the Glycymerididae would have been included in the Arcoidea. If further data show that limopsoids are sister taxa to all arcoids, Amler's classification would be preferred. The Arcoidea should therefore include the modern families Arcidae, Noetiidae, Cucullaeidae, and Glycymerididae, and it is this concept that is adopted here.

PHENETIC CHALLENGES TO FAMILY, SUBFAMILY, AND  
GENERIC RELATIONSHIPS

*Ligament form and orientation*

The sole synapomorphy (see Table 1) of the Noetiidae is the vertical orientation of the fibrous and lamellar elements of the duplivincular ligament. Within the family, the ligament may be amphidetic, prosodetic, or opisthodetic, and this character has often been used to define genera. The number and size of the lamellar bands also vary (Thomas, 1976): in most, the two elements are of equal size, but, in *Sheldonella*, the lamellar bands are few and relatively large (Oliver & von Cosel, 1992b). Recent studies by Thomas *et al.* (2000) and Ubukata (2003) have shown that the development of the different orientations and patterns displayed by the duplivincular ligament in arcoids can be achieved by a relatively simple developmental switch. This prompted Thomas *et al.* (2000) to state, 'Consequently, the possibility that this evolutionary innovation emerged independently in more than one lineage must be taken seriously'. Given the plasticity seen in pteriomorph ligaments (Malchus, 2004), is it safe to assume that such an alteration in form can have happened only once, and why should this ligament type be recognized phyloge-

netically when the many other variations seen in the Arcidae are not?

*Epibyssate–endobyssate radiations*

Within the Arcidae, the subfamily split of the Arcinae (Fig. 2) and Anadarinae (Fig. 3) is based on the strength of the byssus corresponding to the attached or free-living modes of life (Newell, 1969). This split corresponds to separate adaptive radiations, one epibyssate and one endobyssate.

The likelihood of these subfamilies being monophyletic is questioned by observations on a single genus: *Bathyarca*. Species within this genus, currently assigned to the Anadarinae, have been shown to display two synapomorphic characters, the mantle flap and mantle flap gland (Oliver & Allen, 1980a), together with a hinge in which the teeth are subparallel. Within the genus, however, there are both endobyssate and epibyssate species (Fig. 6). At the extreme epibyssate end of the spectrum, the byssus forms a single strap and the shells are longer than high; at the endobyssate extreme, the byssus consists of a few weak threads and the shell outline is higher than long. These morphologies correspond to those defining the Arcinae and Anadarinae, respectively.

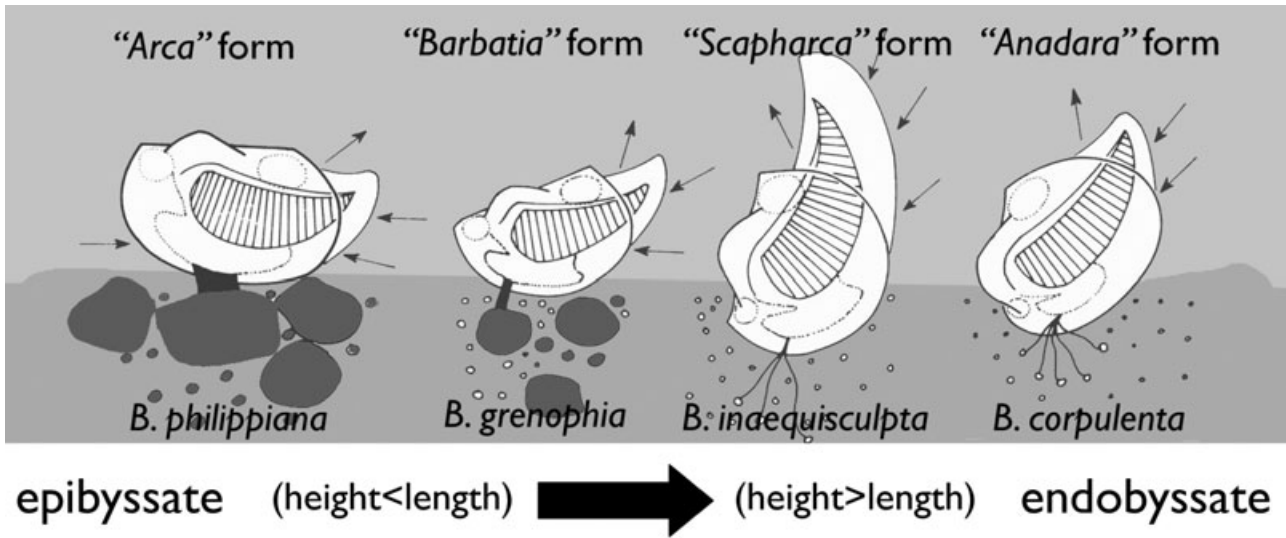
Within the Noetiinae, a similar epibyssate–endobyssate radiation is present, as represented by the genera *Noetia* and *Sheldonella*, and in the Striarcinae, as represented by *Striarca* and *Estellacar*.

One must question, therefore, how many such epibyssate–endobyssate radiations have occurred.

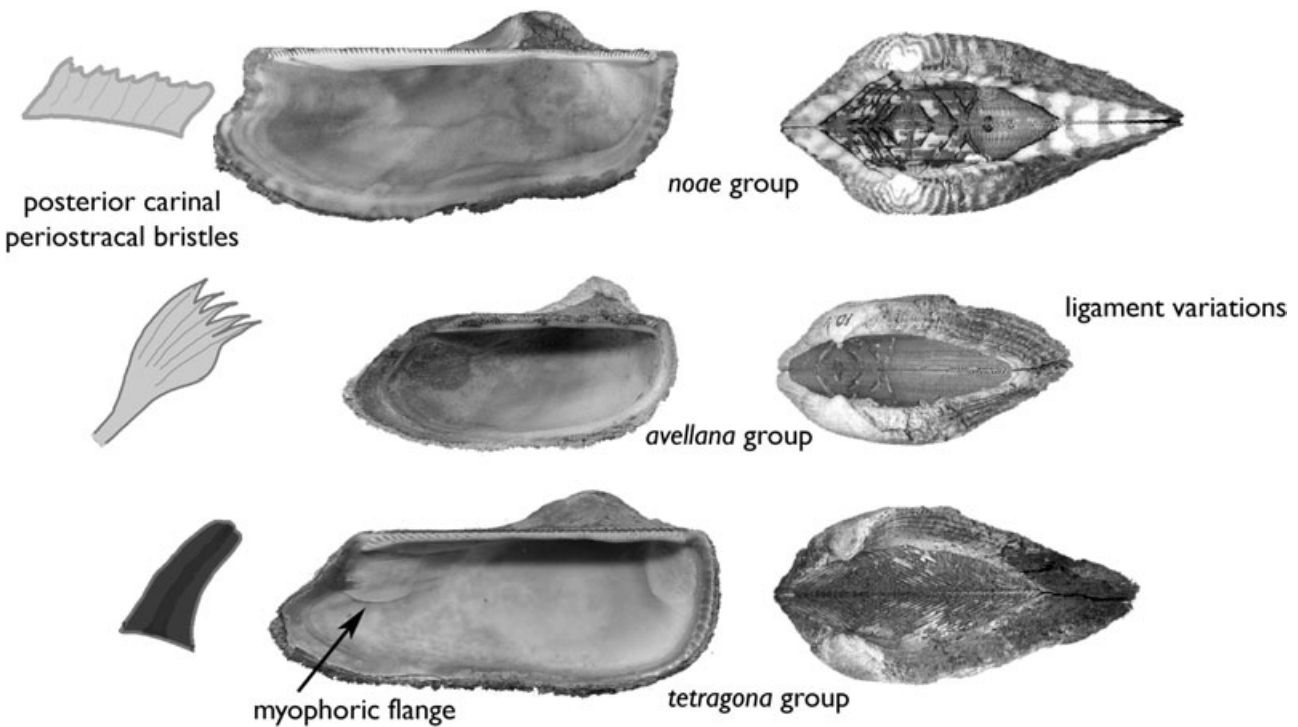
*Generic uncertainties*

In the two preceding sections, potential homoplasy in the family and subfamily taxa was indicated; here, two genera are examined that illustrate similar situations. The genus *Arca*, as currently diagnosed (Newell, 1969), includes all boat-shaped species with a broad flat dorsal area. Furthermore, species in this genus are characterized by having a weak radial sculpture, the ligament covering the entire dorsal area, and being cosmopolitan in warm waters. Despite this overall similarity between species, the genus can be split into at least three groups based on morphology and biogeography (Fig. 7). These groups differ in the form of the ligament, presence or absence of a myophoric flange, structure of periostracal hairs, and orientation of the hinge teeth. They are not all confined to warm waters, with the *Arca tetragona* group being confined to colder temperate waters. Furthermore, some of the diagnostic characters adopted by Newell (1969) do not apply to all species. The ligament does not cover the entire dorsal area in many immature stages and never in *Arca ventricosa*. The sculpture is





**Figure 6.** An illustration of the epibyssate–endobyssate radiation within the genus *Bathyarca* and relating each species to a more typical morphotype within the Arcidae.



**Figure 7.** Three morphotypes within the ‘genus’ *Arca* highlighting overlooked characters and possible homoplasy of the ‘Arca’ morphotype.

not always fine, as evidenced by coarse ribs in *Arca navicularis*. The presence of a myophoric flange is given by Newell (1969) as a defining character of the Noetiidae, yet its presence here in the *Arca tetragona* group has never been given any taxonomic value.

The genus *Barbatia*, unlike *Arca*, has many nominal taxa within it, which are ignored or used inconsis-

tently between authors. The species included can, however, be divided by shell form, and some are illustrated in Figure 2. *Savignyarca* represents a group of mytiliform species found throughout the Indo-Pacific and south-east Atlantic. Given the degree of homoplasy now suggested, can such an ecomorph-based group be assumed to be monophyletic, or can the

mytiliform type have evolved separately on a number of occasions? *Nipponarca* has relatively few wide ribs and has relatively large palps, giving it affinity with the infaunal Anadarinae. However, it has a large stalked byssus and is epibyssate (Oliver & von Cosel, 1992a). Phenetic data alone appear unable to solve relationships at this level.

This brief review serves to indicate the incomplete phenetic characterization at the genus level, and forces us to consider whether the genus is monophyletic and what level of significance we should place on the differences in shell characters.

#### Anatomical homoplasy

Thomas *et al.* (2000) concluded that 'none of the shell characters by which the family Noetiidae has been distinguished and subdivided is exempt from pervasive homoplasy'. The discussions above indicate that this situation is probably widespread throughout the Arcoidea. In the example of *Bathyarca*, two synapomorphic anatomical characters are noted; does this suggest that anatomical characters in general may show less homoplasy and be more reliable in phyletic analysis?

Anatomical studies of the Arcoidea are relatively few, with that of Heath (1941) being the most wide ranging and including data from 34 species representing all four families: Arcidae, Noetiidae, Cucullaeidae, and Glycymerididae. Some gross anatomical data were presented by Rost (1955) for 13 species of Arcidae and one species of Noetiidae from Pacific America. The mantle of 16 species was studied by Waller (1980); these represented the Arcidae, Noetiidae, and Glycymerididae. Oliver & Allen (1980a) examined the Atlantic deep-sea species of the genera *Bathyarca* and *Bentharca*, and Morton has studied individual species from the following genera: *Trisidos* (Morton, 1982a), *Bathyarca* (Morton, 1982b), *Cucullaea* (Morton, 1981), and *Barbatia* (Morton, 1987). Oliver has studied the comparative anatomy of the noetiid genera *Striarca* (Oliver, 1985), *Didimacar* (Oliver, 1986c), and *Estellacar* (Oliver 1986b, 1987b). Data on the stomach can be found in Purchon (1957) and Dinamani (1967). Data on the ctenidia and labial palps are included in Stasek (1963), and a comparative study of *Anadara* species was made by Lim (1966).

#### Mantle

In the Arcoidea, the mantle edge is entirely free and the inhalant and exhalant apertures are created by the apposition of the mantle folds. Mantle ciliation was first described by Atkins (1936) for *Arca tetragona*, and showed both a primary posterior inhalant current, but also a secondary anterior inhalant cur-

rent. This ciliation pattern applies to all other species of Arcoidea observed, except that the anterior current is not always apparent (Yonge, 1955).

Waller (1980) showed that the typical three-fold structure of many bivalves is not present in the Arcoidea, and there is consistently a second outer fold and inconsistently a second inner fold present. The presence of the second inner fold does not coincide with current family divisions; it may be present or absent within the Arcidae, but absent in the Cucullaeidae and Glycymerididae. Within the Arcidae, it is present in *Barbatia*, *Anadara*, and *Senilia*, but absent in *Arca* and *Litharca*. In *Bathyarca* (Morton, 1982b), it is strongly developed as the mantle flap.

Associated with the mantle edge are both simple and compound photoreceptors, but their presence or absence has no family or subfamily relationship. Rather, as pointed out by Waller (1980), compound receptors are most numerous in exposed epibyssate taxa, such as *Arca*, but decrease in number in cryptic epibyssate species, such as *Barbatia*. In infaunal taxa, both types of photoreceptor are limited to the posterior region and, in species hidden from all light (under boulders), as in *Arcopsis*, they are absent (Waller, 1980). The last statement is not entirely correct: a single anterior pigment spot has been observed in all species of Striarcinae so far examined (Oliver, 1985, 1986a, 1986c; Oliver & Järnegren, 2004), including *Arcopsis adamsi*. Oliver & Allen (1980a) noted pigmentation in the shelf/slope species *Bentharca nodulosa*, but this was absent in the abyssal *Bentharca asperula*. All the observations on mantle pigmentation and photoreceptors indicate strong association with habitat.

#### Foot and pedal musculature

The form of the foot and pedal musculature is linked to the strength of the byssus and the attached or burrowing habits of the taxa concerned. In epibyssate taxa, the foot typically has a well-developed toe and heel and the posterior pedal retractors are greatly enlarged to function as a byssus retractor. In endobyssate burrowing taxa, the toe of the foot is strongly developed, but the heel is diminished, and the posterior pedal retractors are not enlarged. This pattern can be seen within the Arcidae, Noetiinae, and Striarcinae, as well as within the genus *Bathyarca*. These anatomical characters are strongly linked to the shell form.

#### Ctenidia and labial palps

The ctenidia are homorhabdic, non-plicate and filibranch, and there is no deviation of this pattern. The demibranchs are of equal or approximately equal size. The ciliary currents of *Arca tetragona* were described by Atkins (1936), and no significant variation has been

recorded by subsequent studies on other species of Arcoidea. The labial palps are relatively small and the ctenidial–labial palp junction is of category 3 (Stasek, 1963). Although relatively small, there is considerable variation in the size and number of palp ridges present between species. From data presented by Heath (1941), and from comparative studies of infaunal and epifaunal Striarcinae (Oliver, 1985), palp size is related to the mode of life. Infaunal taxa tend to have larger palps than epifaunal taxa. Within the genus *Anadara*, Lim (1966) also linked palp size to habitat, with larger palps present in the most infaunal species and those inhabiting muddy sediments.

#### *Alimentary system*

The gut pattern in the Arcoidea follows a simple format, with a short, straight oesophagus leading to a large stomach from which the cojoined style sac and mid gut exit in a posterior ventral position. The mid gut penetrates ventrally into the visceral mass and loops simply or is weakly coiled before returning dorsally behind the stomach; the hind gut extends posteriorly through the pericardium and over the posterior adductor to form the rectum; the anus is situated ventrally on the posterior adductor.

Heath (1941) reported oesophageal glands but found no true pouches. In one species of *Acar*, he found dense aggregations of glands, but, in other species, the condition was normal.

The stomach is of Purchon type III and, although all Arcoidea studied are of this type, there is considerable variation in the development and size of sorting structures.

The coiling of the mid gut is variable, but, from the data available, it appears that coiling is most developed in burrowing infaunal taxa and least in epifaunal taxa. Considerable variation is also apparent within genera, such as *Barbatia* (Heath, 1941), which suggests that suspension load may be a better correlate than the mode of life.

The anus is always associated with a pair of abdominal sense organs, and the form of these is species specific (Heath, 1941).

#### *Pericardium and renal system*

Heath (1941) paid much attention to the arrangement of the pericardium and the paired heart condition present in *Arca*. He concluded that the degree of development of the paired condition was related to the degree of umbonal separation and development of the byssus retractor muscles.

Heath (1941) also reported little variation in renal organs with little significance to the systematics of the group.

This review of anatomical characters suggests that many structures, as with those of the shell, are linked to the mode of life, and are associated with adaptive radiations rather than having phyletic significance. Those structures related to the endobysate or epibysate modes of life, such as the adductor muscles, pedal retractors and foot, are very likely to show homoplasy. Similarly, palp size and gut coiling are associated with life habits, as is the development of photoreceptors and pigmentation.

Less obviously linked to life habit is the pattern of mantle folds and possibly stomach structure, although both could be linked to the suspension load experienced, which could necessitate mantle cavity protection and particle sorting, respectively.

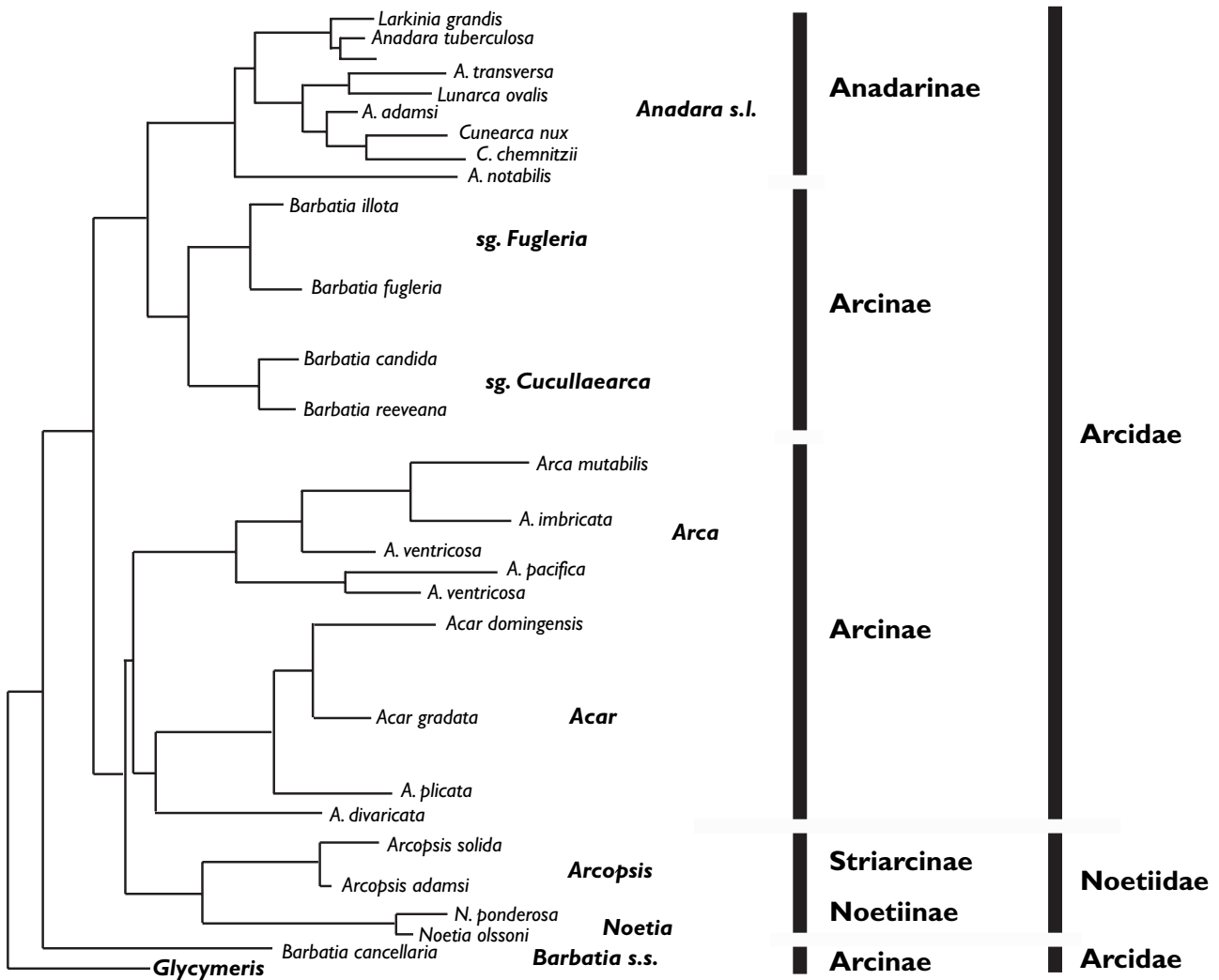
In conclusion, it would appear that much of the anatomy could display homoplasy on a par with the shell!

#### *Molecular support at family, subfamily, and genus levels*

Molecular data from Marko's (2002) paper on geminate species pair divergence in Arcoidea can be used to examine the relationships within the Arcidae in general. Both nuclear (H3) and mitochondrial (COI) genes were used in the analyses, which employed *Glycymeris* as the outgroup to root the phylogenetic tree. His study included mostly species from the Panamic and Caribbean regions, and must be viewed in this limited perspective.

Using Marko's (2002) COI data only, a simplified version of his phylogenetic tree is redrawn here with the current subfamily and family distributions shown (Fig. 8). The Noetiidae forms a single cluster with moderate support, suggesting that this is, indeed, a monophyletic group and that the ligament structure is a synapomorphy for the clade. However, the Noetiidae does not appear as a sister group to the Arcidae, rather as a group within the Arcidae.

Both subfamilies Striarcinae and Noetiinae form their own clades and, at 100%, have strong support. The Arcidae are displayed as polyphyletic due to the Arcinae forming three separate clades. One of these clades, the *Fugleria/Cucullaearca* clade, represents the Arcinae as a sister group to the anadarines, and receives good bootstrap support. The remaining two groups represent *Arca* and *Acar* together as a sister group to the Noetiidae and *Barbatia* (*s.s.*) in a basal position, although neither receives good support, with bootstrap values below 50%. The Anadarinae are grouped together and, at 87%, have very good support, but are not sister taxa to the Arcinae as a whole, and the distribution of genera shows no pattern. This gives support to the argument that the subfamily split of Arcinae and Anadarinae purely by endobysate and epibysate clines is unjust.



**Figure 8.** A phylogenetic tree based on cytochrome oxidase I (COI) sequences of Caribbean and Panamic arcoids, redrawn from Marko (2002), with current subfamily and family distributions attached.

Most of the generic and specific level bootstrap values are good, giving high support for this taxonomic level. The *Anadara* forms a clade with good support, although, within this genus, the support drops to a poor 58% and lower for the majority of the specific clades. The *Fugleria* and *Cucullaearca* form two well-supported clades with the majority of the specific branches receiving 100% bootstrap support, as do *Arcopsis* and *Noetia*. *Acar* is not monophyletic and, at 99%, the major clade is well supported. *Acar divaricata* forms a lone clade with a poor bootstrap value below 50%. Within the Arcinae, *Arca*, *Acar*, and *Barbatia* (s.s.), all of which have poor bootstrap values, should be further examined to shed light on the taxonomic issues within this subfamily, and should be supported by further molecular analyses.

The Anadarinae, Striarcinae, and Noetiinae individually form good tight groups and have high bootstrap support. The Arcinae, however, is spread throughout, suggesting that the current taxonomy should be brought into question and a review of this subfamily is required. Even these preliminary data give great support to the premise that the relationships within the Arcidae are far from clear, and some fundamental alterations might be expected. If we are provided with further molecular data, it may be that some of Scarlato & Starabogotov's (1979) units will have validity and the Bathyarciidae, for example, may be recognized.

## OUTLOOK

At the family level, molecular data are required to resolve the deeper roots of the families.

1. Are the Limosoidea sister taxa to all the Arcoidea (Arcidae, Cucullaeidae, Noetiidae, and Glycymerididae)?
2. What is the relationship of Cucullaeidae to the Arcidae, considering that both appear in the Jurassic? Do they have a common ancestor or are they derived from different parts of the Parallelodontidae radiation?
3. Is the Glycymerididae part of the Arcidae or Cucullaeidae lineages?
4. The Noetiidae appear to be monophyletic; are they, and from which part of the Arcidae lineage are they derived?

A more critical morphological approach is needed to resolve the relationships, especially within the living families Arcidae and Noetiidae. It is evident that many of the characters exhibit homoplasy and that multiple parallel radiations along the epibyssate–endobyssate cline may have evolved. The current subfamily splits, in both the Arcidae and Noetiidae, require evaluation, and it is likely that the relationships are far more complex than outlined by current classifications. More critical appraisal of the characters is required and less emphasis on gross features. Such differences and species groupings need to be catalogued throughout the Arcidae and Noetiidae, and then tested using the molecular approach.

In short:

1. How many epibyssate–endobyssate radiations have there been?
2. Is there a phyletic basis to the morphological groups apparent within the families?

The Arcoidea and Arcoida remain relatively unexplored by taxonomists and phylogeneticists, and there is ample scope for a fundamental re-evaluation of the whole order by both biologists and palaeontologists.

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#### REFERENCES

- Abbott RT. 1974.** *American seashells*, 2nd edn. New York: Van Nostrand Reinhold.
- Alexander RR. 1993.** Correlation of shape and habit with sed-

- iment grain size for selected species of the bivalve *Anadara lethata* **26**: 153–162.
- Amler MRW. 1989.** Die Gattung *Parallelodon* Meek & Worthen (Bivalvia, Arcoida) im mitteleuropäischen Unter-carbon. *Geologica et Palaeontologica* **23**: 53–69.
- Amler MRW. 1999.** Synoptical classification of fossil and Recent Bivalvia. *Geologica et Palaeontologica* **33**: 237–248.
- Atkins D. 1936.** On the ciliary mechanisms and interrelationships of Lamellibranchs. Part I. New observations on sorting mechanisms. *Quarterly Journal of Microscopical Science* **79**: 181–308.
- CLEMAM. 2005.** *Taxonomic database on European marine mollusca*. URL <http://www.somali.asso.fr/clemam/index.php> [accessed April 2005].
- Coan EV, Scott PV, Bernard FR. 2000.** *Bivalve seashells of western North America. Santa Barbara Museum of Natural History Monographs Number 2*. Santa Barbara: Santa Barbara Museum of Natural History.
- Cope JCW. 1997.** The early phylogeny of the class Bivalvia. *Palaeontology* **40**: 713–746.
- Cope JCW. 2000.** A new look at early bivalve phylogeny. In: Harper EM, Taylor JD, Crame JA, eds. *The evolutionary biology of the Bivalvia. Geological Society Special Publications 177*. London: Geological Society, 81–95.
- Dinamani P. 1967.** Variation in the stomach structure of the Bivalvia. *Malacologia* **5**: 225–268.
- Giribet G, Wheeler W. 2002.** On bivalve phylogeny: a high level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebrate Biology* **121**: 271–324.
- Hayami I, Kase T. 1993.** *Submarine cave bivalvia from the Ryukyu Islands*. Tokyo: Tokyo University Press.
- Heath H. 1941.** The anatomy of the pelecypod family Arcidae. *Transactions of the American Philosophical Society* **31**: 287–319.
- La Perna R. 1998.** On *Asperarca* Sacco, 1898 (Bivalvia, Arcidae) and two new Mediterranean species. *Bolletino Malacologico* **33**: 11–18.
- Lim CF. 1966.** A comparative study of the ciliary feeding mechanisms of *Anadara* species from different habitats. *Biology Bulletin* **130**: 105–117.
- MacNeil FS. 1938.** Species and genera of Tertiary Noetinae. *United States Geological Survey Professional Paper* **189-A**: 1–50.
- Malchus N. 2004.** Constraints in the ligament ontogeny and evolution of pteriomorphan Bivalvia. *Palaeontology* **47**: 1539–1574.
- Marko PB. 2002.** Fossil calibration of molecular clocks and the divergence times of geminate species pairs separated by the Isthmus of Panama. *Molecular Biology and Evolution* **19**: 2005–2021.
- Morton B. 1981.** The mode of life and function of the shell buttress in *Cucullaea concamerata* (Martini) (Bivalvia: Arcacea). *Journal of Conchology* **30**: 295–301.
- Morton B. 1982a.** The biology and functional morphology of the Twisted Ark *Trisidos semitorta* (Bivalvia: Arcacea) with a discussion on shell ‘torsion’ in the genus. *Malacologia* **23**: 375–396.

- Morton B. 1982b.** Functional morphology of *Batharca pectunculoides* (Bivalvia: Arcacea) from a deep Norwegian fjord with a discussion of the mantle margin in the Arcoidea. *Sarsia* **67**: 269–282.
- Morton B. 1987.** The pallial photophores of *Barbatia virescens* (Bivalvia: Arcacea). *Journal of Molluscan Studies* **53**: 241–243.
- Newell ND. 1969.** Order Arcoidea Stoliczka, 1871. In: Moore R, ed. *Treatise on invertebrate paleontology, Part N, Mollusca*, Vol. 1. *Bivalvia*. Boulder, CO: Geological Society of America & University of Kansas, N248–N270.
- OBIS. 2005.** *Indo-Pacific molluscan database*. URL [http://data.acnatsci.org/obis/find\\_mollusk.html](http://data.acnatsci.org/obis/find_mollusk.html) [accessed April 2005].
- Oliver PG. 1981.** The functional morphology and evolution of Recent Limopsidae (Bivalvia: Arcoidea). *Malacologia* **21**: 61–93.
- Oliver PG. 1985.** A comparative study of two species of Striarcinæ from Hong Kong with comments on specific and generic systematics. In: Morton B, Dudgeon D, eds. *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China*. Hong Kong: Hong Kong University Press, 283–310.
- Oliver PG. 1986a.** A new species of *Noetiella* (Bivalvia: Arcacea) from Hong Kong. In: Morton B, ed. *Proceedings of the Second International Marine Biological Workshop: the Marine Fauna and Flora of Hong Kong and Southern China*. Hong Kong: Hong Kong University Press, 413–417.
- Oliver PG. 1986b.** Observations on the life habits of *Estellacar galactodes* Benson (Bivalvia: Arcacea) in Hong Kong. In: Morton B, ed. *Proceedings of the Second International Marine Biological Workshop: the Marine Fauna and Flora of Hong Kong and Southern China*. Hong Kong: Hong Kong University Press, 1015–1021.
- Oliver PG. 1986c.** Functional morphology and systematics of the genus *Didimacar* (Bivalvia: Arcacea: Noetiidae). In: Morton B, ed. *Proceedings of the Second International Marine Biological Workshop: the Marine Fauna and Flora of Hong Kong and Southern China*. Hong Kong: Hong Kong University Press, 1075–1094.
- Oliver PG. 1987a.** The Tertiary-Recent bivalve *Noetiella* (Arcacea) and its evolutionary relationships. *Journal of Conchology* **32**: 263–278.
- Oliver PG. 1987b.** *Estellacar* Iredale, *Rectangularca* Eames and the systematic position of *Barbatia pectunculiformis* Dunker (Bivalvia, Arcoidea, Noetiidae). *Journal of Conchology* **32**: 279–288.
- Oliver G, Allen JA. 1980a.** The functional and adaptive morphology of the deep-sea species of the Arcacea (Mollusca: Bivalvia) from the Atlantic. *Philosophical Transactions of the Royal Society of London, Series B* **291**: 45–76.
- Oliver G, Allen JA. 1980b.** The functional and adaptive morphology of the deep-sea species of the Limopsidae (Mollusca: Bivalvia) from the Atlantic. *Philosophical Transactions of the Royal Society of London, Series B* **291**: 77–125.
- Oliver PG, Holmes AM. 2004.** Cryptic bivalves with descriptions of new species from the Rodrigues lagoon. In: Oliver PG, Holmes AM, eds. *The marine biodiversity of Rodrigues (Indian Ocean). Proceedings of the First International Biodiversity Workshop for Rodrigues, 10 September–5 October 2001. Journal of Natural History* **38**: 2927–3344.
- Oliver PG, Järnegren J. 2004.** How reliable is morphology based species taxonomy in the Bivalvia? A case study on *Arcopsis adamsi* (Bivalvia: Arcoidea) from the Florida Keys. In: Bieler R, Mikkelsen PM, eds. *Bivalve studies in the Florida Keys. Proceedings of the International Marine Bivalve Workshop 2002. Malacologia* **46**: 327–338.
- Oliver PG, von Cosel R. 1992a.** Taxonomy of tropical West African Bivalves IV. Arcidae. *Bulletin du Museum National d'Histoire Naturelle, Paris* **14**: 293–381.
- Oliver PG, von Cosel R. 1992b.** Taxonomy of tropical West African Bivalves V. Noetiidae. *Bulletin du Museum National d'Histoire Naturelle, Paris* **14**: 655–691.
- Purchon RD. 1957.** The stomach in the Filibranchia and Pseudolamellibranchia. *Proceedings of the Zoological Society of London* **129**: 27–60.
- Rios EC. 1994.** *Seashells of Brazil*, 2nd edn. Rio Grande: Fundação Universidade do Rio Grande.
- Rost H. 1955.** A report on the family Arcidae. *Allan Hancock Pacific Expeditions* **20**: 177–236.
- Scarlato OA, Starabogatov YI. 1979.** General evolutionary patterns and the system of the class Bivalvia. *Transactions of the Zoological Institute and Academy of Science, USSR* **80**: 5–38.
- Stanley SM. 1970.** Relation of shell form to life habits in the Bivalvia (Mollusca). *Memoirs of the Geological Society of America* **125**: 1–296.
- Stasek CR. 1963.** Synopsis and discussion of the association of ctenidia and labial palps in the bivalve molluscs. *Veliger* **6**: 91–97.
- Steiner G, Hammer S. 2000.** Molecular phylogeny of the Bivalvia inferred from 18S rDNA sequences with particular reference to the Pteriomorpha. In: Harper EM, Taylor JD, Crame JA, eds. *The evolutionary biology of the Bivalvia. Geological Society Special Publications 177*. London: Geological Society, 11–29.
- Stiller F, Jinhua C. 2004.** *Eophilobryoidella sinoanisica* new genus and species, an early philobryid bivalve from the Upper Anisian (Middle Triassic) of Qingyan, Southwestern China. *Journal of Paleontology* **78**: 414–419.
- Tevesz MJS. 1977.** Taxonomy and ecology of the Philobryidae and Limopsidae (Mollusca: Pelecypoda). *Postilla* **177**: 1–64.
- Thomas RDK. 1976.** Constraints of ligament growth, form and function on evolution in the Arcoidea (Mollusca: Bivalvia). *Paleobiology* **2**: 64–83.
- Thomas RDK. 1978.** Shell form and the ecological range of living and extinct Arcoidea. *Paleobiology* **4**: 181–194.
- Thomas RDK, Madzvamuse A, Maini PK, Wathen AJ. 2000.** Growth patterns of noetiid ligaments: implications of developmental models for the origin of an evolutionary novelty among arcoid bivalves. In: Harper EM, Taylor JD, Crame JA, eds. *The evolutionary biology of the Bivalvia. Geological Society Special Publications 177*. London: Geological Society, 279–289.

- Ubukata T. 2003.** A theoretical morphologic analysis of bivalve ligaments. *Paleobiology* **29**: 369–380.
- Vokes HE. 1967.** *Genera of the Bivalvia: a systematic and bibliographic catalogue*. *Bulletins of American Palaeontology* **51**, No. 232. Ithaca, NY: Paleontological Research Institution.
- Waller TR. 1980.** Scanning electron microscopy of shell and mantle in the order Arcoida (Mollusca: Bivalvia). *Smithsonian Contributions to Zoology* **313**: 1–58.
- Williams ST, Taylor JD, Glover EA. 2004.** Molecular phylogeny of the Lucinoidea (Bivalvia): non-monophyly and separate acquisition of bacterial symbiosis. *Journal of Molluscan Studies* **70**: 187–202.
- Yonge CM. 1955.** A note on *Arca* (*Senilia*) *senilis* Lamarck. *Proceedings of the Malacological Society of London* **31**: 202.
- Zuschin M, Oliver PG. 2003.** *Bivalves and bivalve habitats in the northern Red Sea. The Northern Bay of Safaga (Red Sea, Egypt): an actuopalaeontological approach. VI. Bivalvia*. Vienna: Der Verlag des Naturhistorischen Museums.