Systematics and Phylogeny of Arcoid Bivalves (Arcoida: Pteriomorphia: Bivalvia).

by

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A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree of Doctor of Philosophy,
The City University of New York

2009

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This manuscript has been read and accepted for the
Graduate Faculty in Biology in satisfaction of the
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THE CITY UNIVERSITY OF NEW YORK

ABSTRACT

Systematics and Phylogeny of Arcoid Bivalves (Arcoida: Pteriomorphia: Bivalvia).

by

Louise Crowley

Advisor: Dr. Ward Wheeler

The Arcoida is a large group of mostly marine bivalves, with a global distribution. Familiar taxa in this group include the arks, bittersweets and dog cockles. Relationships among the higher-level taxa of the Arcoida are not well understood and the classification of this group has been the subject of debate and rearrangement. While many views exist as to the evolution of this group, none of them are based explicitly on a phylogenetic analysis. In this study, the phylogenetic relationship of the Arcoida is inferred from a systematic analysis based on both morphological and molecular data. This is the first analysis in which representatives of all seven nominal families are included. 141 morphological characters from the external shell and internal anatomy were coded for 131 taxa. The phylogenetic signal of both these character types was explored. Few non-homoplastic synapomorphies for the group were recovered; shell tubules are confirmed as the sole non-homoplastic synapomorphy for the order. Shell characters failed to

recover the majority of the higher taxonomic ranks that they were initially used to describe. Little coherent signal was received from the analysis of anatomy alone. Four molecular markers, the nuclear 18S rRNA, 28S rRNA, protein coding histone H3 and mitochondrial cytochrome *c* oxidase I, were also investigated using direct optimization as implemented in POY (Varón et al., 2008). These data were analyzed individually as well as simultaneously with the morphological data. A Sensitivity Analysis (Wheeler, 1995) of the molecular data was also performed—this explores the effects of parameter costs (i.e. indels and transition/transversion ratios) on the phylogenetic results. The results of these phylogenetic analyses do not reflect the current classification of the group. In this study, the majority of the higher taxonomic groups of Newell (1969) were not recovered, including the two superfamilies Arcoidea and Limopsoidea, as well as five of the families; only the monophyly of the Glycymerididae and Noetiidae is supported. A major taxonomic review of the order is necessary. This analysis is the largest and most comprehensive phylogenetic analysis of the Arcoida to date.

ACKNOWLEDGMENTS

I would like to thank my committee Robert Anderson, Gonzalo Giribet, Diarmaid O'Foighil and Valerie for the many comments and for making me think more critically about my work. I especially want to thank Ward Wheeler, who took the role of my advisor very seriously and without whom, I am quite sure, I would not have finished this PhD. His constant encouragement and guidance is something for which I will always be grateful.

Funding for this research came from a number of sources, including the Proctor Fund for Malacology, the Libbie Hyman Fund for Marine Research, the AMNH Lerner Gray Grant for Marine Research, Conchologists of America and the CUNY Graduate Program in Biology Dissertation grant. Travel to meetings was supported by the Marie Stopes Award from the Willi Hennig Society and the Sue Rosenberg Zalk Research and Travel Fund. Terrie Gosliner (CAS) and Angel Valdes (LACM) kindly invited me to participate in their NSF sponsored (PEET Informal Science Education supplement) collecting trip to Costa Rica.

This work would not have been possible were it not for the generosity of those working in malacological collections around the globe. For providing me with specimens on loan I would like to thank Ian Loch, Holly Barlow and Alison Miller (AMS); Kathie Way and Amelia MacLellan (BMNH); Terry Gosliner and Christina Piotrowski (CAS); Jochen Gerber (FMNH); Yolanda Camacho-Garcia (InBIO); Angel Valdés (LACM); Philippe Bouchet and Virginie Héros (MNHN); Ellen Strong and Paul Greenhall

(USNM). Gifts of specimens were generously provided by Claudia Arango, Megan Cevasco, Chris Cevasco, Marcos Coltro, Isabella Kappner, Jose Leal, Tripp MacDonald, Claus Nielsen, Cecilia Osorio, Melita Peharda and John Taylor. For assistance in the field, I thank Megan Cevasco, Isabella Kappner, Yvonne Valles, Terry Gosliner, Angel Valdés and Sandra Henry. For all things malacological I thank Ilya Tëmkin, Isabella Kappner, Niko Malchus and Brian Morton. I was very fortunate to share an office with Ilya, where countless discussions of characters and all things morphological took place.

There are many people here at the AMNH that I would like to thank including Rebecca Budinoff, Leo Smith, Taran Grant, Torsten Dikow, Norberto Giannini, Cyrille d'Haese, Ilya Temkin, Joanna Bilz, Ed Gaughan, Christine Johnson, Amy Davidson, Sushma Reddy, Claudia Arango, Kurt Pickett, Sara Bertelli, Nick Lucaroni, Francisca Almeida, Kelly Demeo, Jeni Kuszak and Mohammad Faiz. I have been extremely fortunate in the friendships I have made here at the museum. In one way or another I have learned something from each of these people. It is difficult to think of the words to express my gratitude to Megan Cevasco, Isabella Kappner, Andres Varón and Julián Faivovich: they have helped me in so many ways, technically, intellectually and emotionally. I also thank Ciara Rogers, Hazel O'Sullivan, Terrie Dalgaard, Mags Coughlan, Neil Dalchand, Emil Gernert, Merton Lewis and Sonia Donaldson, whose friendships are especially important to me.

Final thanks goes to my family, my sister Veronica and brother Kenneth, but most especially my parents Bill and Betty. I often think that this PhD was as tough on them as it was for me. My mother has been my constant supporter and cheerleader and for this I owe her everything.

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CHAPTER 1

An Introduction to the Arcoida Stoliczka, 1871

(Pteriomorphia: Mollusca).

Mollusks are the second most species rich metazoan group, and are important components of freshwater and marine ecosystems. Bivalvia, second only to Gastropoda in terms of molluscan diversity, with their combination of extant diversity and ancient and relatively continuous fossil record, provide an excellent arena for broad investigations using the more traditionally used anatomical as well as DNA sequence data. Despite the recent flurry of cladistic studies investigating the phylogenetic relationships of Bivalvia (Purchon, 1978; Scarlato and Starobogatov, 1978, 1979; Waller, 1990, 1998; Starobogatov, 1992; Salvini-Plawen and Steiner, 1996; Cope, 1996; Morton, 1996; Steiner and Müller, 1996; Carter, 1990a; Campbell et al., 1998; Waller, 1998; Steiner, 1999; Campbell, 2000; Steiner and Hammer, 2000; Giribet and Wheeler, 2002; Giribet and Distel, 2003) the higher classification of the class is still contested. While there is some degree of consensus at the superfamilial-level, much confusion remains at the subclass and ordinal level (Morton et al., 1998). The higher classification of the Bivalvia used here follows Morton et al. (1998) and is comprised of five subclasses—Protobranchia, Pteriomorphia, Paleoheterodonta, Heterodonta and Anomalodesmata.

The Pteriomorphia is the largest subclass of the Bivalvia with 23 extant families and includes some of the most well-known and economically important bivalves such as mussels (*Mytilus edulis*: Mytiloida), arks and bittersweets (*Arca* and *Glycymeris*: Arcoida), oysters and scallops (*Ostrea edulis* and *Pecten irradians*: Ostreoidea) and pearl oysters (*Pinctada*: Pteriidae). The majority of Pteriomorphia are ecological generalists and occupy a diversity of microhabitats. Most rely on either planktotrophy or lecithotrophy for dispersal (Beesley, 1998). In this subclass, five extant orders are recognized: Mytiloida, Arcoida, Pterioida, Limoida and Ostreoida. There are, as might

be expected given the size of this group, several alternate classifications for these groups. However, the classification system for the Arcoida follows that of Newell (1969) with further adjustments by Morton et al. (1998) and Tevesz (1977).

The Arcoida is a large, extant group of bivalves with an extensive fossil record (Ordovician). Organized into seven nominal families, there are equal numbers of extinct and extant taxa in the group. Although a large volume of work involving studies of these bivalves is available, few have focused on the phylogenetic relationships of the group. Arcoidan studies have concentrated on the taxonomy (Tevesz, 1977; Oliver and von Cosel, 1992a, b; among others), functional anatomy (see the plethora of references in Chapter 2), blood (San George and Nagel, 1985; Terwilliger and Terwilliger, 1985; Suzuki et al., 1992; Piro et al., 1998); morphometrics (Marko and Jackson, 2001), and sperm (Healy et al., 2000; Zhu et al., 2008). This is an interesting group in light of its occupying such a wide range of habitats and global distribution, ostensibly entailing a variety of adaptive traits. For example, some species of the genus *Limopsis* are unusual in that they are among the relatively few suspension-feeding invertebrates that have managed to colonize the deep-sea (Oliver and Allen, 1980b) even though this genus is not represented in shelf faunas. Deep-sea suspension feeding is atypical in that most other bivalves on abyssal plains are deposit-feeders using siphons to feed from sediments.

There are no phylogenetic studies of this group as a whole and the most prominent question regarding the classification of the group, relates to the status of the two superfamilies (Arcoidea and Limopsoidea) and their constituent taxa. This problem is largely addressed in Chapter 2. With the belief that the classification of any group

should reflect its phylogeny, conclusions about the systematics of this group are taken from the total evidence analysis of all the data in Chapter 3.

The principal goal of this research was to clarify the relationships of the Arcoida, with particular focus on the relationships of the higher taxa in the group. Because both morphological and molecular characters are vital to understanding and interpreting relationships among taxa, this research involved a comprehensive phylogenetic analysis incorporating these data types. Chapter 2 is the first cladistic analysis of the Arcoida that includes representatives from all seven families—the majority of analyses in which arcoid taxa have been included, have largely focused on the Arcidae, Noetiidae and Glycymerididae. Traditional descriptions of bivalve characters are often imprecise, bordering on vague, thus a key component of this research was to provide in-depth, unambiguous descriptions of all the characters and character states, with comparisons to those found in outgroup taxa. A large number of these characters and states are presented with associated images. As the classification of the Arcoida and its constituent taxa is largely founded on 'hard' shell characters, one of the goals of this research was to expand upon the number of soft anatomical characters. A detailed historical overview, including historical development of its taxonomy, is also provided in this chapter.

Chapter 3 presents a total evidence analysis of both morphological and molecular data for the group. To this end, DNA sequence data for four molecular markers (the mitochondrial cytochrome *c* oxidase subunit I, the nuclear ribosomal genes 18S rRNA and 28S rRNA and the nuclear protein-coding histone H3 gene) are included. Cladistic analyses of all the molecular partitions, as well as combinations of all the molecular data ('MOL'), and morphological plus molecular data ('TOTAL') are undertaken. A

Sensitivity Analysis (Wheeler, 1995) of the molecular and 'TOTAL' datasets is performed in order to explore the different parameter costs associated with the different types of transformations (i.e. indels and transition/transversion) and to assess the robustness of the clades under these costs. The inclusion of a large number of carefully chosen outgroups would assess the relationship of these bivalves to other pteriomorphian taxa, which also provided a rigorous test of the monophyly of the group.

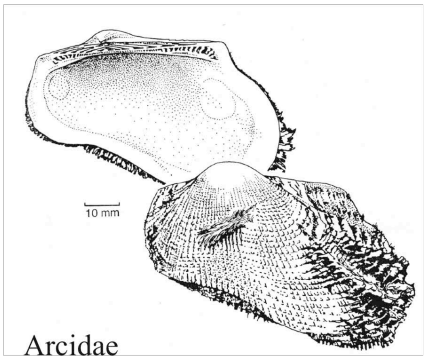
CHAPTER 2

Relationships of the Arcoida (Pteriomorphia: Bivalvia) as inferred from morphological data.

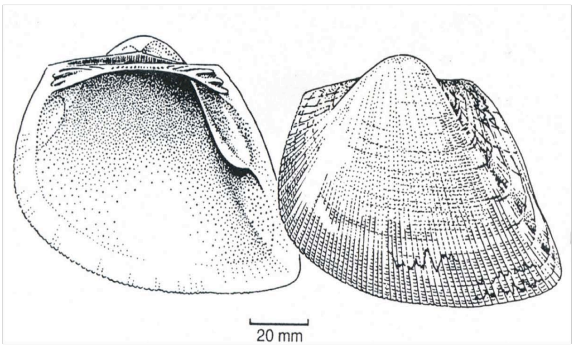
INTRODUCTION

The Arcoida Stoliczka, 1871 is an order of bivalves comprised of seven nominal families: Arcidae Lamarck, 1809; Parallelodontidae Dall, 1898; Cucullaeidae Steward, 1930; Noetiidae Steward, 1930; Glycymerididae Newton, 1922; Limopsidae Dall, 1895; and Philobryidae Bernard, 1897 (Newell, 1969) (Fig. 1). Two superfamilies are generally included in the order, the Arcoidea Lamarck, 1809 and the Limopsoidea, Dall, 1895 (Newell, 1969; Waller, 1978)—with the form of the ligament the defining characteristic for the superfamilies (Waller, 1978). As defined by Newell (1969), this order also included the superfamily Cyrtodontoidea Ulrich, 1894 and the family Manzanellidae Chronic, 1952, which was included in the Limopsoidea (justifications for the removal of these groups from the Arcoida are discussed below). There have been many alternate classifications of this group with conflict generally lying in the placement of the Glycymerididae and with the number of superfamilies in the group (MacNeil, 1938; Vokes, 1967; Newell, 1969; Nevesskaya et al., 1971; Scarlato and Starabogatov, 1979; Carter, 1990a; Amler, 1999; Coan et al., 2000; Giribet and Wheeler, 2002).

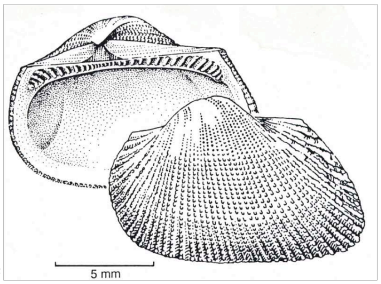
FIGURE 1. Diversity of shell morphology found in the Arcoida: Representatives of the seven families are shown, illustrating the left exterior and right interior valve [all images adapted from Beesley et al., 1998, except that of the Parallelodontidae, which is adapted from Newell, 1969]. →



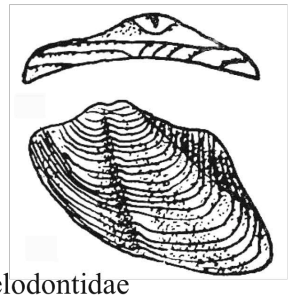
Arcidae



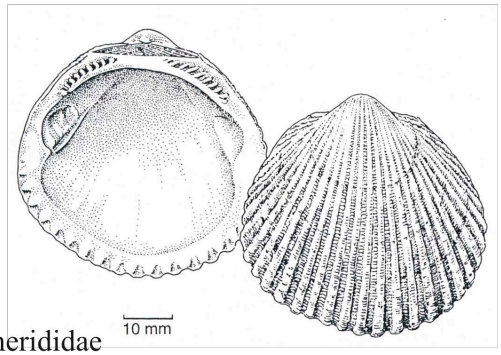
Cucullaeidae



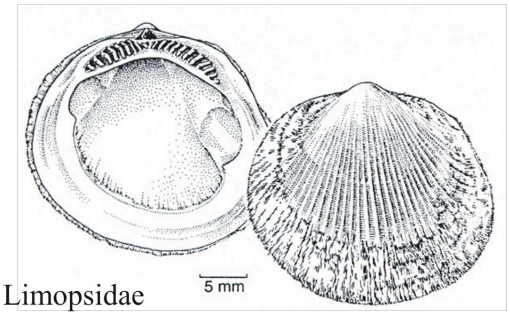
Noetiidae



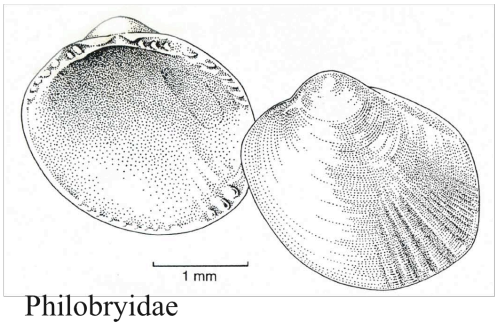
Parallelodontidae



Glycymerididae



Limopsidae



Philobryidae

These bivalves are typically marine, with the exception of the exclusively freshwater taxon *Scaphula*, from India and Burma (Benson, 1856) and a few estuarine taxa e.g. *Senilia senilis* (Linnaeus, 1758). They are especially abundant in tropical and subtropical regions (Lamprell & Healy 1998; OBIS, 2008) reaching their highest diversity in these areas. However, some taxa are found in colder waters (Nicol, 1967; CLEMAM, 2008), with the Philobryidae, various limopsids and the arcids *Bathyarca* and *Bentharca* prevalent in North Atlantic (Oliver and Allen, 1980a; Morton, 1982) and Antarctic waters (Burne, 1920; Knudsen, 1970). They have a vertical range from the littoral (Lamprell and Healy, 1998) to abyssal depths—the arcid taxon *Bentharca asperula* has been recorded at depths of 5300 m (Danish "Galathea" Expedition 1950-52: Knudsen, 1970).

Arcoids occupy a wide range of ecological habitats, suggesting a variety of adaptive features. These life history strategies include epifaunal nestlers assisted by byssal attachment to corals, rocks and stones (typical of the Arcidae), free-living infaunal individuals living in shallow sandy or gravelly regions (common among the Glycymerididae) or in deeper waters (*Cucullaea labiata*) (Boyd, 1998), inhabitants of muddy substrates (*Senilia senilis* and *Anadara trapezia*) (Yoloye, 1975 and Sullivan, 1961 respectively), cave dwellers (found among some arcid and philobryid taxa) (Hayami and Kase, 1993), rock borers (*Litharca lithodomus*) (Frizzell, 1946; Olsson, 1961) and the arcid genus *Anadara* are known to populate mangrove regions (Lim, 1966). The philobryid taxon *Lissarca notorcadensis*, which is endemic to Antarctic waters, has been shown to harbor epizoic bacteria in the foot epithelium (Janssen, 1997). These bacteria are not thought to function in sulphidotrophic or methanotrophic activities, as seen in the

chemoautotrophic bacteria found in other bivalve groups, e.g. Thyasiridae (Dufour, 2005). However, they are believed form a mutualistic relationship with the philobryid by producing mucus-like exudates and exoenzymes that support the degradation of macromolecules and organic matter taken into the mantle cavity by the bivalve.

Estimates of Recent species diversity for this group range from a few hundred to 1300 species for the Arcidae alone (Reinhart, 1935). The greatest diversity lies in this family. Despite the diversity of this group, their familiarity is restricted to species in the families Arcidae and Glycymerididae; these include turkey wings or arks (*Arca*), blood or mangrove cockles (*Anadara* and *Senilia*) and bittersweets or dog cockles (*Glycymeris*).

Many taxa in these genera are important commercial species in the regions of the Indo-West Pacific, Eastern and Western Atlantic. The FAO fishery guide (Poutiers, 1998) lists 20 species that are commonly exploited for artisanal, industrial (lime production) or nutritional purposes in the Indo-West Pacific. Many Arcidae (most notably *Anadara* species) are actively exploited as food sources in the China, Japan, Philippines, Indonesia, Malaysia and Thailand. *Anadara granosa* is one of the most important commercial species in this region in terms of fisheries catch and aquaculture production. The FAO Yearbook of Fisheries statistics reports a yearly capture production, in the region of China, Taiwan and South Korea, ranging from 1415 metric tons in 1995 to 6503 metric tons in 1999. Concurrently, this organization reports a range of yearly aquaculture production from around 252, 233 metric tons in 1995 to 315, 811 metric tons in 1999 in this region also (FAO, 2008).

The bittersweets or dog cockles (e.g. *Glycymeris*) are also exploited locally by coastal fishermen in some regions of Southeast Asia, as well in regions of the western

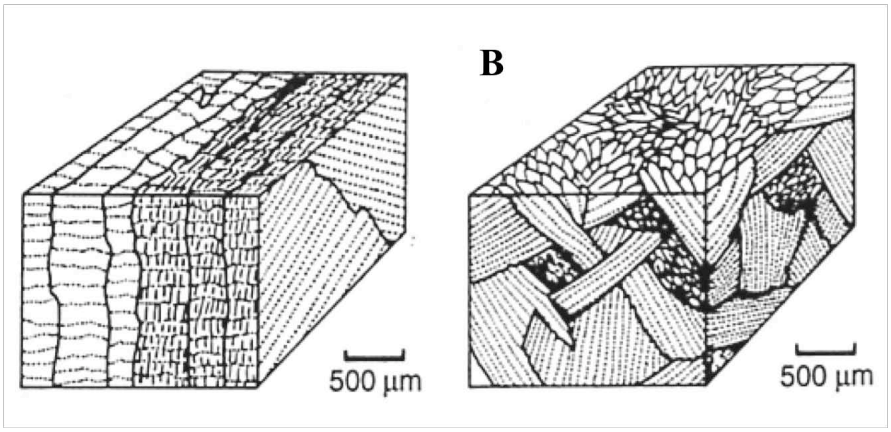
Atlantic near the Strait of Gibraltar, the Atlantic coast of Morocco, Cape Verdes and Senegal. The meat of these species has not been held in high regard because of its tough texture when cooked. However, in France, the collapse of the fisheries for the heterodont clam *Venus verrucosa* resulted in the new exploitation of the bittersweet *Glycymeris glycymeris,* which is an important by-catch of the surf calm *Spisula solida* (Batista et al., 1999). In recent years, advances, specifically directed towards the tenderization of the 'meat' of *Glycymeris glycymeris* (Batista et al., 1999) have vastly increased their consumption in northern European regions such as France and Portugal (Goulletquer and Héral, 1997; Batista et al., 1999). A list of the arcoid taxa that are predominantly harvested in wild catch and aquaculture is provided in Table 1.

TABLE 1. Arcoid bivalves harvested in the global shellfish industry. Common names and regions where they are predominantly collected are provided.

SCIENTIC NAME	VERNACULAR NAME	AREAS of PRODUCTION
Arcidae		
Anadara antiquata	Antique ark	Indonesia, Sri Lanka
Anadara granosa	Granular ark, Blood cockle	China, Malaysia, Thailand
Anadara tuberculosa	Black ark	Korea
Arca pacifica	Chuchoca ark	Mexico
Arca zebra	Turkey wing	Mexico
Arca noae	Noah's ark	Mediterranean
Barbatia fusca	Almond ark	Philippines (food, lime industry)
Scapharca globosa	Globose ark	Venezuela
Scapharca inaequivalvis	Inequivalve ark	Japan, Philippines
Scapharca indica	Rudder ark	Japan, Philippines
Scapharca subcrenata	Half crenate ark	Indonesia
Scapharca pilula	Pill ark	Indonesia, Papua New Guinea
Trisidos semitorta	Half-propellor ark	Thailand (artisanal)
Trisidos tortuosa	Propellor ark	Thailand (artisanal)
Noetiidae		
Striarca olivacea	Olive ark	Philippines (artisanal)
Cucullaeidae		
Cucullaea labiata	Hooked ark	Thailand
Glycymerididae		
Tucetona pectunculus	Comb bittersweet	Philippines
Glycymeris reevei	Reeve's bittersweet	Philippines
Glycymeris bimaculata	Two-spotted bittersweet	Strait of Gibraltar
Glycymeris glycymeris	Dog cockle	Strait of Gibraltar, Morocco
Glycymeris violascens	Purple bittersweet	Strait of Gibraltar, Morocco

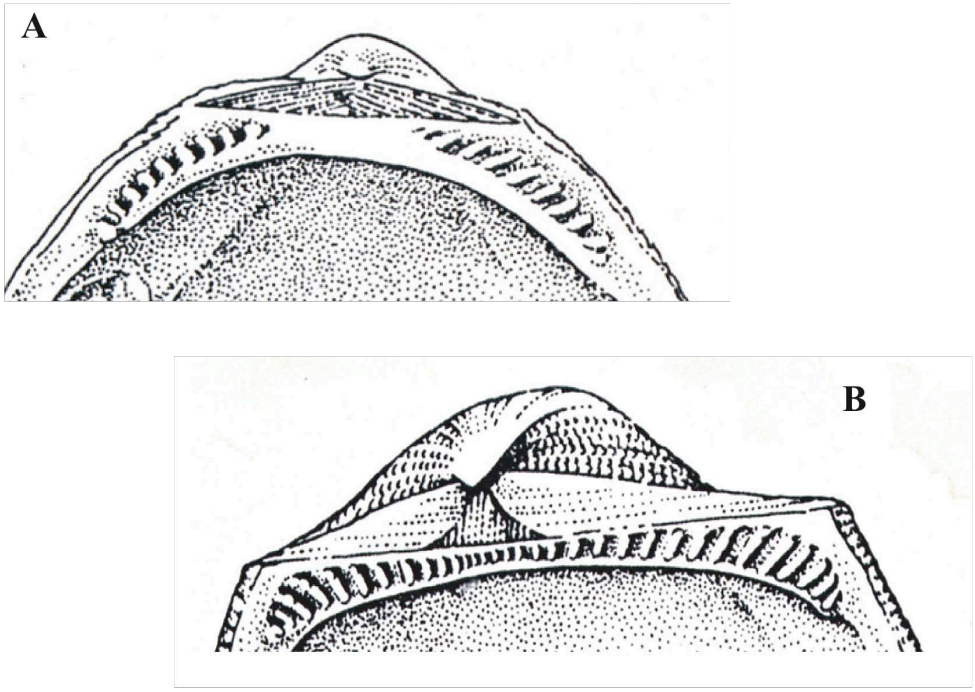
The diversity of shell form is moderately extensive in this group; however, the generalized outline of the shell varies from a somewhat trapezoid form in Arcidae, Parallelodontidae, Noetiidae and Cucullaeidae to orbicular-ovate shells in Glycymerididae, Limopsidae and Philobryidae (Fig. 1). As one might except across a group of this extent, the size of these organisms ranges from ~1.0 mm (e.g. *Cosa* species) to ~15 cm (*Anadara grandis*). Members of the Arcoida are characterized by having an aragonitic shell with an outermost layer of simple crossed-lamellar microstructure and an innermost layer of complex crossed-lamellar microstructure (Fig. 2; see characters 3 and 4 in 'Characters Description'). With the exception of one family (the largely edentulous Philobryidae), they possess a strong, interlocking hinge of taxodont teeth (Fig. 3). The taxodont hinge is comprised of straight or chevron-shaped teeth that are arranged in a row along the hinge plate. It is this feature that separates the arcoids from other pteriomorphs. While this hinge type is also found in the bivalve subclass Protobranchia, it is well established that this characteristic does not reflect a close relationship between these two groups (Cox, 1959; Owen, 1959) as the teeth in the two groups are established in different shell layers and have quite different microstructures.

FIGURE 2. Microstructural arrangement of the arcoid shell: (**A)** Crossed-lamellar structure, comprised on alternating layers composed of similarly aligned aragonitic needles; (**B)** Complex crossed-lamellar structure, wherein lamellae interdigitate at right angles to each other [Image after Beesley et al., 1998].



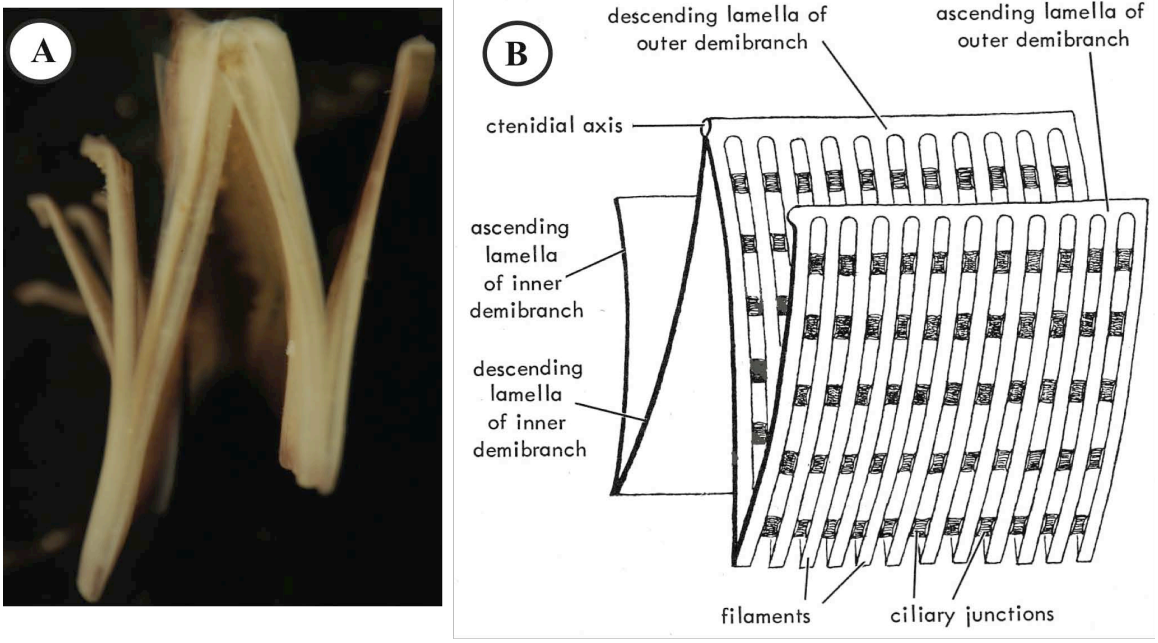
The ligament plays an important role in the abduction of the valves, thus allowing the water to flow in and all concomitant functions to proceed. The ligament in bivalves generally has two components, an internal fibrous and an external non-fibrous or lamellar ligament. All families, except the Limopsidae and the Philobryidae, possess a true duplivincular ligament (Fig. 3; see character 61) that extends across all (Fig. 3A) or part of the cardinal area (Fig. 3B) —this ligament is composed of series of alternating bands of lamellar and fibrous conchiolin extending obliquely along each cardinal area. Each lamellar band is inserted in a narrow groove that extends from below the beaks to the hinge margin (Newell, 1942). The duplivincular ligament is found other pteriomorphs (e.g. Ambonychioidea, *Pterinopecten*), but through parallel trends, some of the families have attained the alivincular (Newell, 1965) (alivincular ligaments are restricted to a hollow resilifer (see character 57).

FIGURE 3. Hinge plates of the Arcoida: (**A)** Glycymerididae hinge plate, illustrating a curved hinge line, above which lie the taxodont teeth. An edentulous space is seen between the anterior and posterior teeth. Above the teeth the chevron duplivincular ligament is found; (**B)** Noetiidae hinge plate, demonstrating the straight hinge line with the central transverse duplivincular [Image after Beesley et al., 1998].



They possess W-shaped filibranchiate gills (Fig. 4; see character 99) and are moderately isomyarian with adductor muscles of approximate equal size (although some philobryids are monomyarian) (see characters 77 and 78). While many of the afore mentioned characteristics are found in various combinations in other pteriomorphian bivalves, the combination of these characters are found in the Arcoida alone.

FIGURE 4. Filibranch ctenidia of the Arcoida: **(A)** Lateral view of the filibranch gills; **(B)** Schematic drawing of ctenidium [adapted from Newell, 1969].

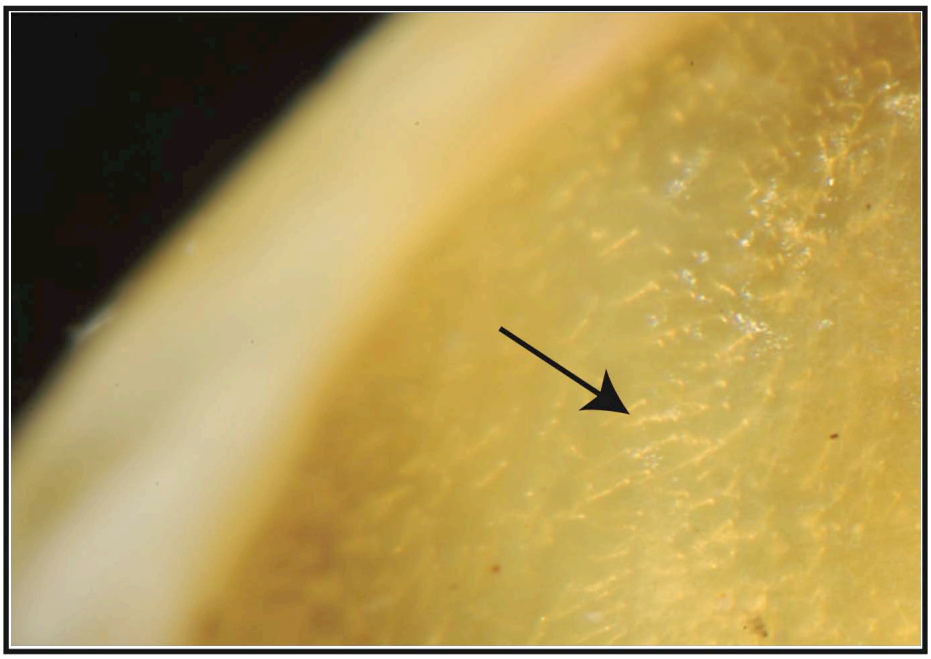


The sole unequivocal synapomorphy for this group appears to be the possession of a dense distribution of shell tubules across the entire area inside the pallial line of the inner shell and they span the entire shell from the inner shell to the periostracum (Fig. 5; see character 5) (Waller, 1980).

The principal goal of this study is to establish a phylogenetic framework for the Arcoida using both shell morphology and soft anatomical data. Previous classifications of this group have been based largely on shell characteristics and have had a strong paleontological perspective. While the soft anatomy of individual species has been studied for some arcoid taxa, these studies have never compared the morphology of the entire group. Traditional descriptions of morphological characters, especially those that

are shell based, are often ambiguous, hence indepth descriptions of all characters and states are provided, including newly described characters. The examination of the morphology and anatomy across all families in this group reveals a far greater morphological diversity than what was previously described. Furthermore, homoplasy is widespread across the group. This study is the first of its kind to include representatives from all extant families.

FIGURE 5. Shell tubules, the sole unequivocal synapomorphy of the Arcoida: shell tubules visible from the internal shell wall of *Neocardia* sp. A. USNM 881111.



PREVIOUS MORPHOLOGICAL STUDIES

Descriptions of the shell morphology of this group are numerous (Lamy, 1907; Reinhart, 1935; Iredale, 1939; Tevesz, 1977; Kilburn, 1983; Dell, 1990; Oliver and von Cosel, 1992a, b; Tschudin, 2001, among many others) and yet anatomical studies of this group are few, considering the size of the group. The majority of these studies have documented, often in great detail, the functional morphology of a single species (Yonge, 1955; Olsson, 1961; Sullivan, 1961; Oliver and Allen, 1980a, b; Morton, 1978, 1981, 1982, 1983; Morton and Peharda, 2007) (see Appendix 1 for additional literature sources). More comprehensive investigations comparing the functional morphology of a number of taxa are less common. These studies include Pelseneer's (1911) excellently illustrated study of the soft anatomy of 14 arcoid taxa from four families. Despite his mistaken view that the philobryid *Adacnarca nitens* had an anterior adductor (this species is in fact monomyarian; see character 76), this study was the first comprehensive anatomical examination of this group that was clearly illustrated. Burne (1920) documented the internal morphology of five arcoid taxa from Antarctic waters. What Burne lacked in illustrative abilities, he made up for in amply detailing all the major organ systems. In 1941, Heath undertook the largest study of the anatomy of the group—a total of 34 species representing four families, Arcidae, Cucullaeidae, Noetiidae and Glycymerididae, were examined and illustrated. There is no doubting the depth of Heath's examination of the internal morphology of the group, however, it suffered *greatly* from the lack of annotation on illustrations. Rost (1955) concentrated her attention on the Arcidae and Noetiidae, focusing mainly on the eyes and mantle margins

of the 23 arcid and two noetiid taxa. Other comparative studies of the functional morphology have been published, but these have been more limited in their taxonomic scope (Lim, 1966; Oliver, 1981, 1985, 1987; Oliver and Allen, 1980a, b; Oliver and von Cosel, 1992a, b; Simone and Chichvarkhin, 2004). Undoubtedly, the greatest volume of morphological studies has been directed towards the Arcidae, while studies of the Glycymerididae have been restricted largely to shell morphology. Only three studies being directed towards their anatomy (Pelseneer, 1911; Heath, 1941; Thomas, 1975—although this last study only mentions the general characteristics of their soft anatomy).

Much focus has been placed on studying both the shell form (Stanley, 1975; Thomas, 1978; Alexander, 1993) and ligament (Thomas, 1976; Thomas et al., 2000; Ubukata, 2003; Malchus, 2004a) of this group. In addition to these studies, the Arcoida have been chosen as exemplars in more focused studies of anatomical features of bivalves, including mantle structure (Waller, 1980), ctenidia and palps (Stasek, 1963), eyes (Morton, 1987, 2001; Nilsson, 1994; Schulz, 1932; Levi and Levi, 1971), abdominal sense organs (Thiele, 1889; Haszprunar, 1983, 1985), osphradia (Haszprunar, 1987), lips (Gilmour, 1974), stomach (Purchon, 1957, 1983) and pericardial cavity (White, 1942).

FOSSIL RECORD

The Arcoida is an extant group of bivalves with a geological history extending back to the Paleozoic. The earliest record for this group dates to the Lower Ordovician (Tremadocian) (Newell, 1969; Cope, 1997, 2000). The arcoid family Parallelodontidae, an extinct taxon save for a single extant species *Porterius dalli,* has the oldest fossil

record, appearing in the Lower Ordovician. The record of the Arcoida indicates that there was a major diversification during the Mesozoic with the appearance of most of the modern families in the Jurassic (Arcidae, Cucullaeidae, Limopsidae) and the Cretaceous (Noetiidae, Glycymerididae). The Philobryidae was long thought to have appeared in the Lower Cenozoic, in the Eocene, until recently when a philobryid *Eophilobryoidella sinoanisica* was discovered in the Middle Triassic of Southwestern China (Stiller & Jinhua, 2004). This discovery was believed to contradict the long-held belief by many (Carter, 1990b; Tevesz, 1977) that the Philobryidae evolved from the Limopsidae, which is of Cretaceous origin (Oliver and Holmes, 2004) (see discussion of polarity below). However, stratigraphic evidence should be viewed with caution, as many phylogenetic studies show that this line of evidence can be misleading.

Newell (1969) included the superfamily Cyrtodontoidea in the Arcoida on the basis of hinge dentition and ligament. This group has since been considered an order (Cyrtodontoida) (Cope, 1996; Malchus, 2004a). This extinct taxon is thought to be the earliest of the pteriomorphs (Newell, 1969; Cope, 1996) originating in the Early Ordovician. The shell form of the cyrtodontids, together with paleoecological data, suggests that these organisms were either endobyssate or shallow burrowers in unstable substrates (Pojeta, 1971; Stanley, 1972). While some cyrtodontids may have had a weak byssus, they were almost certainly burrowers, being suborbicular or posteriorly extended in shape and their shells lack features associated with byssal attachment (Stanley, 1972). These characteristics are common in many living arcoids.

The fossil record of the outgroup taxa currently indicates a much younger geologic history as that seen in the Arcoida. The mytilid, pinnid, limid and isognomonid

taxa included in this study date back to the Permian and Carboniferous. The other outgroup taxa are purportedly Mesozoic, with Malleidae and Pteriidae dating to the Triassic and Upper Cretaceous and the ostreioids being recorded from the Upper Triassic and the Jurassic.

A HISTORY OF ARCOID SYSTEMATICS

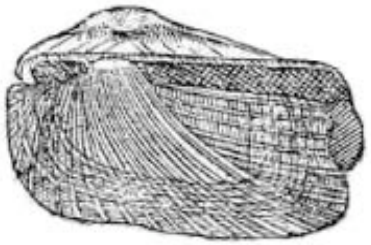


FIGURE 6. An unnamed species of *Arca* published in Aldrovandi (1606).

One of the earliest published records of an arcoid taxon dates back to the early 1600s when Aldrovandi illustrated the unnamed species of *Arca* (Fig. 6) (Aldrovandi, 1606: 513). Descriptions and illustrations of Arcoida appeared in many of the classic Natural History and conchological works, until Linnaeus' formalization of the names in 1758. In pre-Linnean literature, arcoid taxa were ascribed to a multitude of different names, including *Pectunculus* (in Lister, 1687; Sloan, 1725; Gualtherus, 1742); *Ostreum* (in Rumphius, 1705); and *Parallepipedum*, *Anomalocardia* or *Musculus* (in Klein, 1753). None of these names were subsequently used by Linnaeus to form the generic level names of the Arcoida that are in use today, except in the case of *Pectunculus* Lamarck, 1799. In the pre-Linnean literature, *Pectunculus* was a name that encompassed a number of bivalve taxa, and was not exclusive to the Arcoida.

In both the 10th and 12th editions of *Systema Naturæ* (1758, 1767), Linnaeus assigned all of the arcoid taxa to the sole genus *Arca*. These *Arca* species were representative of the present day Arcidae, Noetiidae and Glycymerididae. In 1799,

Lamarck reintroduced the name *Pectunculus* for species that are now referred to *Glycymeris*. For almost a century, this name was used to describe all glycymerid-like taxa. However, Dall (1898) called attention to the fact that the generic name *Glycymeris* Da Costa 1778, had priority over *Pectunculus* Lamarck, 1799. Furthermore, Da Costa (1778) had also used the name *Pectunculus* in 1778, making *Pectunculus* Lamarck a homonym. The result was the immediate substitution of *Glycymeris* for *Pectunculus* (Vokes, 1956). Prior to the mid-1800s, newly described arcoid taxa were ascribed to either *Arca* or *Pectunculus*—by 1843 Reeve had described 174 taxa within the genera *Arca* and *Pectunculus* (Reeve, 1843a, b). By 1935, the majority of the extant genera had been described.

In the past, most attempts to classify the Bivalvia have been based on single character systems or taxobases. These taxobases have been both conchological (e.g. hinge teeth structure and ligament) and anatomical in nature (e.g. siphons, adductor muscles, stomach and ctenidia). Cox (1960: N205-N222) provided an exhaustive review of the history of the classification of the Bivalvia. Unsurprisingly, the higher taxonomic names and the higher order classification of this group have changed extensively (see Table 2 for a synopsis of these names and rankings).

Arcoida was one of the nine orders proposed by Stoliczka in 1871. Stoliczka did not consider it possible to classify natural groups on the basis of single characters systems. He was impressed by the general stability and homogeneity of form and structure of family groupings of bivalves throughout their history, and proposed basing higher classification on an over-all resemblance to a type genus. The families within the order were diagnosed largely on the basis of shell morphology and marginally so on their

ecological diversity. Despite his aversion to classifying bivalves of the basis of single characters, Stoliczka does highlight the most interesting characters for comparison within the orders. Arcoida are 'characterized by entirely disunited mantle-margins and usual total want of siphons' (Stoliczka, 1871: 8). In its original inception the order was comprised of four families—Trigoniidae, Nuculanidae, Nuculidae and Arcidae. These bivalves also shared a similar shell character, with 'numerous denticulations of the hinge-teeth' (Stoliczka, 1871: 307). Of the four families, only Arcidae is attributable to the order, with Trigoniidae, Nuculanidae and Nuculidae being reclassified by subsequent authors. Arcidae was divided into two subfamilies—Axinæinae and Arcinae—the former corresponding to limopsid and glycymerid taxa and the latter corresponding to taxa presently included in Arcidae, Cucullaeidae, Noetiidae and Parallelodontidae.

The characters that have had a large influence on the classification of arcoid taxa have included shell hinge structure, shell microstructure, ligament and gill type. Neumayr (1883) proposed a higher classification system of Bivalvia on the basis of the hinge teeth. This scheme included four orders, wherein arcoids were classified as Taxodonta. Other classification systems founded on hinge structure were that of Dall (1889), with the arcoid taxa being classified as Prionodesmacea and as Eutaxodonta in Grobben's (1892) scheme. MacNeil (1937) introduced the Prionodonta as a suborder of the Filibranchia (see below), which included the Arcoida and Cyrtodontoidea.

Beurlen (1944) introduced the Pteriomorphia to include the Pterioidea, Pectinoidea, Ostreioidea, Anomioidea, Mytiloidea and Arcoidea. Cope (1996), following Korobkov (1954), proposed the subclass Neotaxodonta, which included the superfamilies Arcoidea and Limopsoidea. His justification for the erection of this new subclass was on

the basis of the complex crossed-lamellar shell microstructure and a duplivincular ligament, which are only found in combination in the Arcoidea and Limopsoidea superfamilies. Taylor (1973) believed that the unique combination of simple crossed-lamellar microstructure and an innermost layer of complex crossed-lamellar microstructure warranted separating these superfamilies from the other Pteriomorphia.

Waller (1978) placed the Arcoida in the superorder Prionodonta MacNeil, 1937, thereby restricting the 'superorder' Pteriomorphia to a smaller group than defined by Cox et al. (1969). However, as noted by Scarlato and Starobogatov (1979), the distinction between fossil representatives of the orders Arcoida and Pterioida is not as great as between modern representatives. In 1979, Nevesskaya and co-authors reclassified the Arcoida along with the Cyrtodontoidea and Mytiloidea in the suborder Arcina Stoliczka, 1871 of the newly erected order, Cyrtodontoida.

Pelseneer (1889) put forward his classification of the Bivalvia that was based largely on the soft anatomy of the group, specifically on the gill structure. This resulted in the formation of five orders of which the arcoids were classed within the Filibranchia. Having investigated the gill structure of a great number of bivalve species, Ridewood (1903) put forward his scheme of classification that was somewhat different from Pelseneer's. Ridewood recognized three orders and in this scheme the filibranchs were combined with the majority of pseudolamellibranchs (Mytiloidea, Pectinoidea, and Ostreoidea) to form the Eleutherorhabda. Atkins (1936-38) went further in her investigation of the gill structure and function and believed that the ciliary mechanisms of the gills warranted the erection of two groups, the Microciliobranchia and

Macrociliobranchia. Arcoid taxa, as well as the Pseudolamellibranchia of Pelseneer and the Anomioidea were ascribed to the Microciliobranchia.

TABLE 2. Chronological synopsis of the previously proposed taxonomic ranks of the Arcoida. These ranks have appeared in various classification schemes of the Bivalvia from Stoliczka (1871) to Nevesskaya et al., (1979).

Authority	**Taxonomic Rank and Name**	**Justification**
Stoliczka, 1871	Order Arcacea	Similarity to type
Neumayr, 1883	Order Taxodonta[1]	Hinge teeth
Dall, 1889	Order Prionodesmacea	Hinge teeth
Pelseneer, 1889	Subclass Filibranchia	Ctenidia
Grobben, 1892	Order Eutaxodonta	Hinge teeth
Ridewood, 1903	Order Eleutherorhabda: Suborder Mytilacea	Ctenidia ciliated discs
Atkins, 1936-38	Group Microciliobranchia	Ctenidia filament cilia
Dechaseaux, 1943	Suborder Pseudoctenodonta	Hinge teeth
MacNeil, 1937	Suborder Prionodonta	Hinge teeth
Korobkov, 1954	Subclass Neotaxodonta	Complex crossed-lamellar shell microstructure + duplivincular ligament combination
Waller, 1978	Superorder Prionodonta	Shell microstructure
Nevesskaya et al., 1979	Suborder Arcina	Hinge teeth, typhlosole and stomach

[1] Name Latinized by Fischer, 1886.

Arcoidea, traditionally taken to include Arcidae, Parallelodontidae, Cucullaeidae and Noetiidae (Newell, 1969), are easily recognized by their strong taxodont hinge and duplivincular ligament. These taxa are generally subtrapezoidal in shape and commonly possess radial ribbing. The duplivincular ligament is typically chevron-shaped, except in the Noetiidae, where it is laid down in vertical strips. The Arcidae are epifaunal with byssate (Arcinae and some Anadarinae) and non-byssate (some Anadarinae) forms. They typically nestle in crevices and coral, but also include rock boring (*Litharca*) and sand burrowing forms (*Trisidos*). The mostly extinct family, the Parallelodontidae is distinguished by the presence of pseudolateral teeth (see character 50) on the dorsal hinge (however see the discussion of longitudinal teeth and their presence in other arcoid taxa in the section of 'Character Description'). Members of the Parallelodontidae are elongate and byssate in the Lower Paleozoic and some of these were presumably endobyssate on the basis of shape and form. Other parallelodontids found in the Upper Paleozoic are more quadrate and very similar in shape to Recent epifaunal arcids. The Cucullaeidae possess lateral teeth (see character 50), which are similar in form to pseudolaterals, but differ in their proximity to the umbones. The Cucullaeidae are distinguishable by the presence of a large myophoric flange, an elevated process that flanks the posterior adductor muscle (see character 42). Cucullaeids are byssate burrowers in deeper sandy waters. The Noetiidae are most similar in shell form to the Arcidae, but are easily distinguished from all other arcoids by their possession of alternating vertical strips of fibrous and lamellar ligament. Noetiids are largely abyssate burrowers in shallow waters.

The superfamily Limopsoidea, by tradition include the more ovate forms of this group, and include the Glycymerididae, Limopsidae and Philobryidae (Newell, 1969).

The Glycymerididae being ovate in form, possess a curved hinge line, along which a chevron shaped duplivincular ligament is formed. Glycymerids are non-byssate burrowers consistently found in shallower waters. The Limopsidae and Philobryidae both possess an alivincular ligament (see character 56) and can also be broadly described as being ovate in shape. The Limopsidae have a curved hinge line and generally lack the strong radial sculpture that is seen in many of the Glycymerididae. There were many doubts as to the inclusion of the Philobryidae in the Arcoida—many of their characteristics would seem to be at odds with other arcoid taxa—these minute, inconspicuous taxa, are largely edentate, and many have been observed brooding their young. However, the unique combination of their shell microstructure, in addition to the filibranch gills, justifies their inclusion in this group (Tevesz, 1977, Malchus, 2004a).

Stability within the families has remained relatively solid in comparison to the inter-relationships at higher levels. There have been many alternate classifications of this group with the conflict generally lying in the placement of the Glycymerididae. The general consensus in published studies of the Bivalvia included the Glycymerididae in the Limopsoidea (Vokes, 1967; Newell, 1965, 1969; Boss, 1982; Wilson, 1998; Okutani, 2000; Giribet and Wheeler, 2002). Other classifications have gone further by placing the Glycymerididae in a superfamily of its own, the Glycymeridoidea (originally as the Glycymeracea) (Newton, 1916; Nevesskaya et al., 1971; Coan et al., 2000), while MacNeil (1938) also included the Limopsidae, Cucullaeidae and Noetiidae in this superfamily. The removal of the Glycymerididae from the Limopsoidea was justified on the basis that the Glycymerididae were more closely related to the Cucullaeidae than they were to the Limopsidae. The most extreme position taken in the classification of this

group was by Scarlato and Starabogatov (1979). These authors erected seven superfamilies, including the Bathyarcoidea, Cucullaeoidea, Noetioidea and Philobryoidea in addition to the Arcoidea, Glycymeridoidea and Limopsoidea. This classification has been largely ignored. Believing that the Glycymerididae probably arose from the Cucullaeidae, Carter (1990a) included the Glycymerididae in the Arcoidea. This reclassification was justified on the basis of shell microstructure, dentition and ligament structure between these two families. This classification has been embraced by a number of authors (Amler, 1999; Giribet and Distel, 2003; Oliver and Holmes, 2006 among others.

ORIGINATIONS OF THE ARCOIDA

There have been numerous thoughts on the origin of this group. Hypotheses of relationships within the order have largely taken on a paleontological perspective with descriptions of gradation of one family "giving rise" to another being more the norm (Newell, 1954; Cox, 1959; Tevesz, 1977; Thomas, 1978; Oliver, 1981; Amler, 1989; Carter, 1990a, b, c, d, among numerous others). The general trend in all these studies suggested that the origins of the Arcoida ultimately lay with the cyrtodontoids (Douvillé, 1913). Newell (1954) and later Cox (1959) suggested a gradation from the ancestral Cyrtodontoida to the Parallelodontidae that in turn gave rise to the Cucullaeidae. These authors also suggested that the origins of the Arcidae could be traced to the Cucullaeidae. These propositions were based primarily on temporal relationships and grades of shell dentition: intermediate forms of dentition between members of Parallelodontidae and

Cucullaeidae exist. In the Lower Palaeozoic, parallelotontid taxa were elongate and byssate and some of these were presumably endobyssate on the basis of shape and form. However, parallelodontids from the Upper Paleozoic are more quadrate and very similar in shape to Recent epifaunal arcids and were most likely epifaunal in nature (Stanley, 1972).

While most of these authors supported the idea of cyrtodontoid ancestry, disagreement lay with whether modern arcoids were derived from the Parallelodontidae or the Cucullaeidae. Tevesz (1977) suggested that the Limopsidae and the Arcidae were derived from the Grammatodontinae (Parallelodontidae) via heterochrony, with the Limopsidae giving rise to the Glycymerididae and the Philobryidae and the Noetiidae deriving from the Arcidae. Amler (1989) endorsed this view that the early parallelodontids were the ancestor to both the Arcoidea and the Limopsoidea.

Nicol (1950) and later Carter (1990b) on the basis of microstructural similarities and geographic evidence believed that the cucullaeid *Idonearca* was the ancestor to the Glycymerididae. Nicol later enlarged this idea of ancestry and regarded most, if not all, of the larger group, as having originated either directly or indirectly from the Cucullaeidae Nicol (1954). He considered dividing most living taxodonts (or prionodonts as he referred to them) into two large groups on the basis of life history—whether the taxa were byssate (such as *Arca* and *Barbatia* which are recognized in the Jurassic) or non-byssate (such as *Anadara*, *Glycymeris* and *Noetia*). The arcid genus *Anadara* is a genus of burrowers and is the oldest of the Arcidae being found in the Upper Cretaceous (Newell, 1969). Thomas (1978) based on a consideration of hinge plate structure, posited that the Glycymerididae and Limopsidae to have arisen from the

Cucullaeidae. This trend would necessitate epifaunal arcoids originating from burrowing ancestors (Stanley, 1972). Oliver (1981) postulated that the Limopsidae were derived from the Cucullaeidae and many authors agree that the Philobryidae derived from the Limopsidae (Carter, 1990b; Tevesz, 1977).

Thomas (1978) believed that this early appearance of the Arcoida in the fossil record reflected a direct origination from an ancestral bivalve lineage. This supposition was also proposed by Morton (1982) who posited that the "unique hinge of the Arcoida, the primitive anterior and posterior inhalant streams, the lack of pallial fusions, the ctenidial ciliation and the unusual structure of the digestive tubules when considered in conjunction with the specialization of the outer mantle fold as a photosensory structure all point to the group being a very early offshoot from a primitive bivalve stock."

Debates on the origin or evolution of bivalves are fraught with discussions of one taxon evolving from another. As discussed above, the evidentiary basis for these hypotheses were largely based on the form of ligament or hinge structures and stratigraphic evidence. The "paleontological approach" considers fossil taxa that are of greater geological age, effectively to be the ancestors of taxa found in younger geologic strata and of Recent taxa. This approach is overwhelmingly the view taken in the study of bivalve origins. This is not the approach taken in this analysis. A cladistic analysis, as the kind performed here, cannot identify taxa as the ancestors. If one taxon were to "give rise" to another (the jargon most often used in these studies), then the ancestral taxon would, by definition, be paraphyletic. The idea that one taxa 'gives rise' to another is beyond scientific investigation (Kitching et al., 1998). As to one of the aims of this

study, I aim only to identify monophyletic groups and to elucidate the sister-group relationships within.

PREVIOUS PHYLOGENETIC HYPOTHESES

RELATIONSHIPS WITHIN THE ARCOIDA

There has never been a phylogenetic analysis of this group as a whole, and previous studies are restricted to smaller works. While many of the studies of arcoid taxa have focused on their functional morphology, including comparative studies of small numbers of taxa, few studies have analyzed the morphological characteristics of this group in a cladistic framework. These studies are restricted to those involving Arcidae, Glycymerididae and Parallelodontidae. Sanada and Matsukuma's (1996) analysis centered on Glycymerididae from the Northeastern and Northwestern Pacific. They included 23 characters for 15 glycymerid taxa (no outgroup taxa were included). Simone and Chichvarkhin (2004) analyzed a dataset of 6 arcid taxa for 9 morphological character, including the pterioid taxon *Isognomon bicolor* as the outgroup. Carter et al. (2000) focused on extinct taxa, including six fossil arcoid taxa in a cladistic analysis of extinct bivalves. In this study a monophyletic Parallelodontidae was recovered. Waller's (1998) study of the origins and phylogeny of the Bivalvia, found a monophyletic Arcoida, but this result was not founded on any explicit cladistic analysis, but instead was inferred from the outcomes of previous studies and from his own previous work, with synapomorphies drawn onto the nodes. Giribet and Wheeler's (2002) study of Bivalvia,

which analyzed both morphological and molecular data for the four arcoid taxa included in their analysis and included 183 morphological characters. Steiner and Hammer (2000) simple projected morphological characters onto their molecular trees and so for this reason, their analysis is taken to be strictly molecular, in a phylogenetic context.

A number of studies have investigated arcoid relationships using molecular data. Marko (2002), investigating the divergence times of geminate species pairs, analyzed COI for 27 arcoids from Arcidae, Noetiidae with *Glycimerus* sp. [*sic*] as the chosen outgroup. Using many of the same taxa (and indeed sequences), Marko and Moran (2002) studied divergence of egg size among geminate species pairs, across the Panamanian Isthmus. These authors found a strong correlation between egg size divergence and COI amino acid sequence. Moran (2004b), adding four arcid taxa to the arcid matrix of Marko (2002), found a strong correlation between optimal egg size and productivity plus feeding environment across the Isthmus. Moran projected egg sizes onto her parsimony analysis of 17 arcid species.

In addition to these arcoid-centric studies, arcoid taxa have also been included in broader phylogenetic studies of the Pteriomorphia (Hammer, 2001; Matsumoto, 2003) and Bivalvia (Carter et al., 2000; Campbell, 2000; Steiner and Hammer, 2000; Giribet and Wheeler, 2002; Giribet and Distel, 2003) see (Fig. 68, Chapter 3). Matsumoto (2003) in his study of the Pteriomorphia boasts one of the largest representations of arcoid taxa with 18 species from four families being included in the analysis (the Noetiidae, Parallelodontidae and Philobryidae were lacking from this study). Page and Linse included 6 arcoids from 3 families as outgroup taxa in their study of the Antarctic

limid *Limatula*. (Greater detail of the results of these molecular studies are provided in Chapter 3; Previous Phylogenetic Hypotheses).

The recent molecular analyses of the Bivalvia suggest the need for taxonomic rearrangement within this group (Campbell, 2000; Steiner and Hammer, 2000; Giribet and Wheeler, 2002; Marko, 2002; Giribet and Distel, 2003). As mentioned previously, some of the conflict in the classification of this group lay in the placement of the Glycymerididae in either the Arcoidea (along with the Arcidae, Noetiidae, Cucullaeidae and Parallelodontidae) or in the Limopsoidea (with the Limopsidae and Philobryidae). The Glycymerididae were initially classified in the Limopsoidea, on the basis of shell form—Newell's (1969) described the taxa in this superfamily as including those that were "orbicular to obliquely ovoid, generally without an umbonal ridge; smooth or radially ornamented". However, recent studies have treated this family as an arcoidean taxon, on the basis of the strong taxodont hinge and duplivincular ligament (both the Philobryidae and Limopsidae possess an alivincular ligament) (Nevesskaya et al., 1971, Scarlato and Starabogatov, 1979). Clearly, any discussion of the monophyly of the superfamilies, Arcoidea and Limopsoidea, is entirely dependent on the chosen classification of the group (see the discussion of this below).

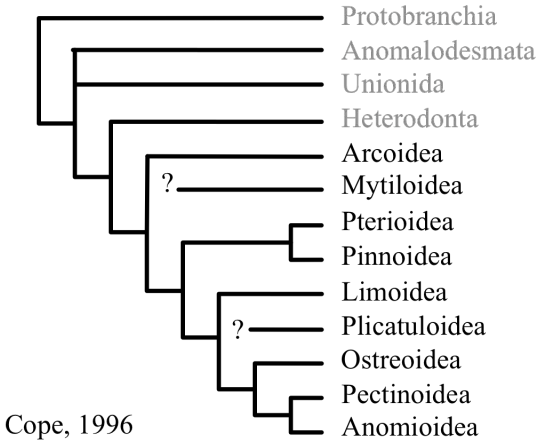
SISTER-GROUP RELATIONSHIP WITH OTHER PTERIOMORPHS

Despite the increased interested in the study of bivalve phylogeny in recent years (Scarlato and Starobogatov, 1978, 1979; Waller, 1990; Starobogatov, 1992; Salvini-Plawen and Steiner, 1996; Cope, 1996; Morton, 1996; Carter, 1990; Campbell et al.,

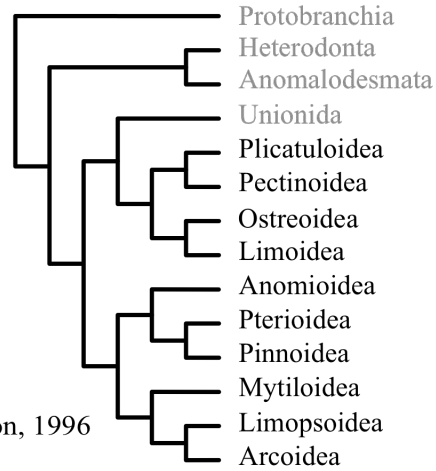
1998; Waller, 1998; Giribet and Wheeler, 2002; Giribet and Distel, 2003), our understanding of the phylogenetic relationships within the group remain poorly understood. Little attention has been paid to the subclass Pteriomorphia and the sister-group relationships within the group remain obscure (Steiner and Hammer, 2000; Hammer, 2001). The selection of published phylogenetic hypotheses of Bivalvia, as illustrated in Fig. 7, markedly illustrate the discordance between the presumed sister-relationships of the higher taxa in the class.

While some studies place the Mytiloidea at the base of the pteriomorphian clade (Waller, 1990, 1998; Campbell, 2000; Hammer, 2001; Giribet and Wheeler, 2002; Matsumoto, 2003), others suggest that the Mytiloidea are the sister-group to the Arcoida (Cope, 1996; Morton, 1996). It should be noted that the Mytiloidea have been excluded from the Pteriomorphia by some authors, being classed as the superorder Isofilibranchia on the basis of shell microstructural and ligament data (Pojeta, 1978; Pojeta and Runnegar, 1985; Waller, 1990; Carter, 1990a). In a number of studies, the Arcoida was the sister-taxon to other Pteriomorphia included in the analyses (Cope, 1996; Campbell et al., 1998; Giribet and Distel, 2003). A variety of sister taxa have been proposed, including Mytiloidea (Morton, 1996), an Anomioidea + Plicatuloidea clade (Hammer, 2001), as well the Arcoida being the sister taxon to non-mytiloid pteriomorphian bivalves (Giribet and Wheeler, 2002).

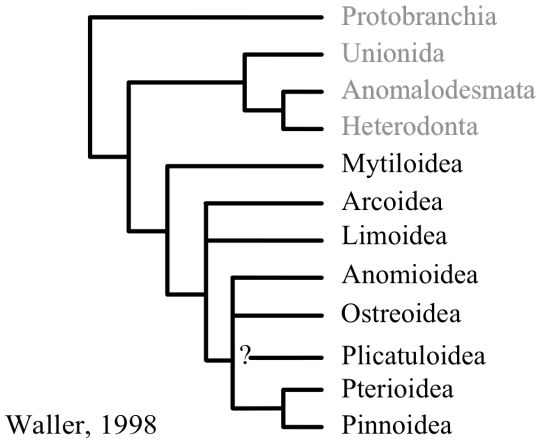
FIGURE 7. High-level phylogenetic relationships of Bivalvia established in previous published studies. Non-pteriomorphian taxa are faded in gray. →



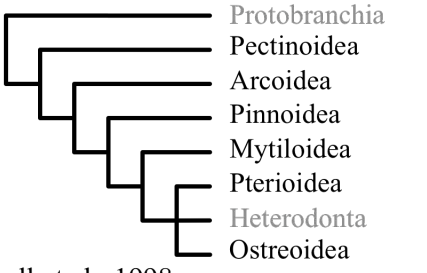
Cope, 1996



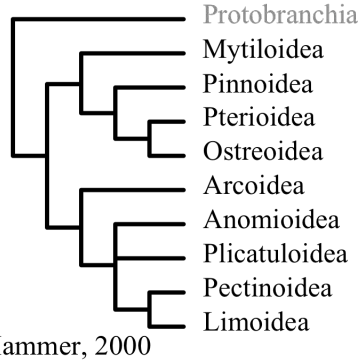
Morton, 1996



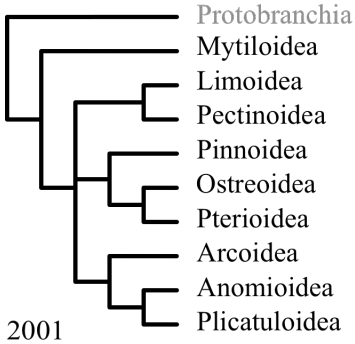
Waller, 1998



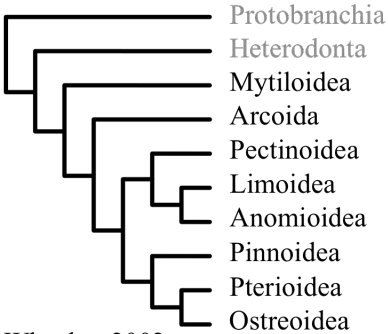
Campbell et al., 1998



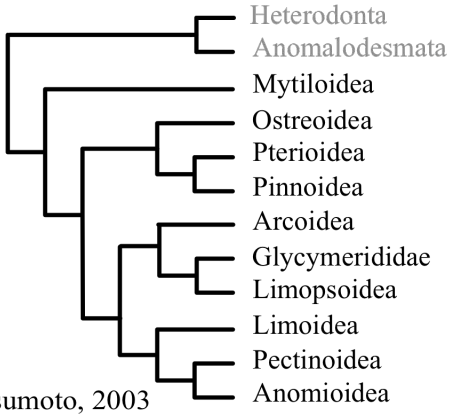
Steiner & Hammer, 2000



Hammer, 2001



Giribet & Wheeler, 2002



Matsumoto, 2003

MATERIALS AND METHODS

TAXONOMIC SAMPLING

The classification system for the Arcoida adopted here generally follows that of Newell (1969: N248-N270) with subsequent adjustments by Morton et al. (1998) and Tevesz (1977) (see Table 3). Eight nominal families in three superfamilies were recognized in Newell's classification. Newell's classification was based largely on gross shell morphology and included few internal anatomical characters. Some exceptions to this classification are taken in this analysis. As mentioned, the superfamily Cyrtodontoidea, originally considered an arcoid, has been regarded as an order (Cyrtodontoida) in recent works (Cope, 1996; Malchus, 2004a). Newell was uncertain as to the placement of two families, the Manzanellidae and the Philobryidae, which he tentatively placed in the superfamily Limopsoidea. The Manzanellidae was removed from the Arcoida by Allen & Sanders (1969) and reclassified as a protobranch, a move confirmed by other authors (Waller, 1990; Turgeon et al., 1998). Nicol (1966) had also questioned the inclusion of the Philobryidae in the Arcoida, however, both Tevesz (1977) and Waller (1978) believed that this family should be included in the Arcoida on the basis of soft anatomy, shell form and shell microstructure. Some genera have been placed in different families since this 1969 classification with the extinct genera *Pichleria* and *Hoferia* being removed from the Limopsidae and placed in the Parallelodontidae. Newell had tentatively placed the genera *Nucunella* and *Vasconella* in the Limopsidae;

these were subsequently removed to the Noetiidae and Arcidae respectively (Tevesz, 1977). *Lissarca,* which had originally been placed in the Limopsidae, is now considered a philobryid. Newell also doubted the inclusion of the freshwater genus *Scaphula* in the Arcidae, but their taxodont hinge and duplivincular ligament confirm their placement in this group. A representative of the valid genus *Stenocista,* described by Oliver & von Cosel (1992b), was also included in the analysis.

This study is the first comprehensive phylogenetic analysis of the Arcoida. While all previous studies that included the Arcoida suffered from limited taxon sampling of this group, representatives of the seven nominal families of the Arcoidea and Limopsoidea of Newell (1969) are included here. Exemplars were chosen to represent the diversity of the approximately 500 species in the order (see Table 4). Newell's (1969) classification of the Arcoida included 32 extant genera and 27 extant subgenera. Since that time, the description of new genera and subgenera has increased greatly. However, there is no current taxonomic revision of any of the major taxonomic groups of the order, including families and superfamilies. Because of this, I would question the erection of some of the taxonomic groups, especially subgenera, and so for this reason representatives were chosen to represent the generic level taxa only. The philobryid genera of Tevesz (1977) (many of which were considered subgenera in Newell's (1969) classification) are considered valid in this study (on the basis of gross shell morphology).

TABLE 3. Classification of the bivalve order Arcoida adopted from Newell (1969). Subsequent emendations to this classification were made by Morton et al., 1998 and Tevesz (1977). Known stratigraphic data for the higher-level is included in parentheses. The symbol ¥ denotes fossil taxa for which no Recent representative has been described.

Phylum Mollusca Cuvier, 1795
Class Bivalvia Linnaeus, 1758
Subclass Pteriomorphia Beurlen, 1944
Order Arcoida Stoliczka, 1871
Superfamily Arcoidea Lamarck, 1809
Family Arcidae Lamarck, 1809 (Triassic - Recent)
Subfamily Arcinae Lamarck, 1809 (Triassic - Recent)
Genus *Arca* Linnaeus, 1758
Genus *Barbatia* Gray, 1842
Genus *Taeniarca* ¥ Olsson, 1965
Genus *Litharca* Gray, 1892
Genus *Trisidos* Röding, 1798
Genus *Ambrogia* Brocchi, 1814
Subfamily Anadarinae Reinhart, 1935 (U. Cret. - Recent)
Genus *Anadara* Gray, 1847
Genus *Lunarca* ¥ Gray, 1857
Genus *Bathyarca* Kobelt, 1891
Genus *Bentharca* Verrill & Bush, 1898
Genus *Larkinia* ¥ Reinhart, 1935
Genus *Samacar* Iredale, 1935
Genus *Scapharca* Gray, 1847
Genus *Scaphula* Benson, 1834
Genus *Senilia* Gray, 1842
Genus *Vasconella* ¥ Boussac, 1911
Family Parallelodontidae Dall, 1898 (L. Ord.- Recent)
Subfamily Parallelodontinae Dall, 1898 (L. Ord.-U. Jur.)

Genus *Parallelodon* ¥ Meek & Worthen, 1866

Genus ?*Carbonarca* ¥ Meek & Worthen, 1870

Genus ?*Curvirostrum* ¥ Buckman, 1882

Genus *Macrodontella* ¥ Assmann, 1916

Subfamily Grammatodontinae Branson, 1942 (?U. Carb. - Recent)

Grammatodon Group

Genus *Grammatodon* ¥ Meek & Hayden, 1861

Genus *Cosmetodon* ¥ Branson, 1942

Genus *Indogrammatodon* ¥ Cox, 1937

Genus *Nanonavis* ¥ Stewart, 1930

Genus *Nordenskjoeldia* ¥ Wilckens, 1910

Genus ?*Cucullopsis* ¥ Chao, 1927

Cucullaria Group

Genus *Cucullaria* ¥ Conrad, 1869

Genus *Nemodon* ¥ Conrad, 1869

Genus *Pleurogrammatodon* ¥ Ichikawa & Maeda, 1958

Catella Group

Genus *Catella* ¥ Healey, 1908

Genus *Torinosulcatella* ¥ Tamura. 1959

Genus *Porterious* Van Winkle, 1918

Genus *Hoferia* ¥ Bittner 1894

Genus *Pichleria* ¥ Bittner 1894

Family Cucullaeidae Steward, 1930 (L. Jurassic, Cret., Recent)

Genus *Cucullaea* Lamarck, 1801

Genus *Idonearca* ¥ Conrad, 1862

Genus *Lopatinia* ¥ Schmidt, 1872

Genus *Pseudocucullaea* ¥ Solger, 1903

Genus *Megacucullaea* ¥ Rennie, 1936

Family Noetiidae Steward, 1930 (L. Cretaceous)

Subfamily Noetiinae Steward, 1930 (U. Cret. - Recent)

Genus *Noetia* Gray, 1857

Genus *Arginopsis* ¥ MacNeil, 1938

Genus *Eontia* Say, 1822

Genus *Incanopsis* ¥ Olsson, 1944
Genus *Noetiopsis* ¥ MacNeil, 1938
Genus *Protonoetia* ¥ MacNeil, 1938
Genus *Sheldonella* Maury, 1917
Genus *Stenocista* Oliver & von Cosel, 1992
Subfamily Striarcinae MacNeil, 1938 (U. Cret. - Recent)
Genus *Striarca* Conrad, 1824
Genus *Arcopsis* Koenen, 1885
Genus *Ovalarca* ¥ Woodring, 1925
Genus *Matsumotoa* ¥ Okada, 1958
Genus *Trigonodesma* ¥ Wood, 1864
Genus *Vetoarca* ¥ Stevenson, 1947
Subfamily Trinacriinae MacNeil, 1937 (U. Cret. - Eocene)
Genus *Trinacria* ¥ Mayer, 1868
Genus *Linter* ¥ Stevenson, 1937
Genus *Pachecoa* ¥ Harris, 1919
Genus *Stenzelia* ¥ MacNeil, 1954
Genus *Nucunella* ¥ d'Orbigny, 1850
Superfamily Limopsoidea Dall, 1895
Family Limopsidae Dall, 1895 (U. Triassic - Recent)
Genus *Limopsis* Brocchi, 1814
Genus *Empleconia* Dall, 1891
Genus *Nipponolimopsis* Habe, 1951
Family Glycymerididae Newton, 1922 (L. Cretaceous)
Subfamily Glycymeridinae Newton, 1922 (L. Cret. - Recent)
Genus *Glycymeris* da Costa, 1778
Genus *Axinactis* Mörch, 1861
Genus *Glycymerella* Woodring, 1925
Genus *Melaxinaea* Iredale, 1930
Subfamily Arcullaeinae ¥ Newell, 1969 (L. Cret. - U. Cret.)
Genus *Arcullaea* ¥ Vokes, 1946
Genus *Peruarca* ¥ Olsson, 1944
Genus *Pettersia* ¥ Nicol, 1953

Genus *Postligiata* ¥ Gardner, 1916
Genus *Protarca* ¥ Stephenson, 1923
Genus *Trigonarca* ¥ Conrad, 1862
Family Philobryidae Bernard, 1897 (Triassic - Recent)
Genus *Philobrya* Carpenter1872
Genus *Adacnarca* Pelseneer, 1903
Genus *Hochstetteria* Vélain, 1877
Genus *Lissarca* Smith, 1877
Genus *Micromytilus* Cotton, 1931
Genus *Neocardia* Sowerby, 1892
Genus *Notomytilus* Hedley, 1916
Genus *Aupouria* Powell, 1937
Genus *Cosa* Finlay, 1927
Genus *Cratis* Hedley, 1914
Genus *Limarca* ¥ Tate, 1886

Representatives from 33 extant genera, for a total of 118 ingroup taxa, were included in the analysis. The only family that did not include Recent taxon representation was the Parallelodontidae. A single extant species *Porterius* dalli, has been described for this family, however it was not possible to acquire a specimen of this species for this study, as they are extremely rare in collections. When possible, the exemplars comprised the type species of each extant genus as well as at least one other congener chosen to be more representative of the breadth of morphological diversity in the genus (see Table 4). When a specimen of the type species was unavailable a congener was chosen.

TABLE 4. Systematic list of the arcoid taxa analyzed in this study. The symbol ŧ represents the types species for the genus, or subgenus (not listed) as the case may be. Fossil taxa are indicated by the symbol †.

Family	Genus	Species
Arcidae		
	Arca	*A. noae* ŧ
		A. ventricosa
		A. avellana
		A. imbricata
		A. mutabilis
		A. navicularis
		A. zebra
		A. bouvieri
	Barbatia	*B. barbata* ŧ
		B. metella
		Barbatia sp. PR01
		B. amygdalumtostum
		B. cancellaria
		B. lacerata
	Barbatia	*B. tenella*
		B. cf. *tenella*
		B. alternata
		B. obliquata (smooth)
		B. obliquata (flaky)
		B. reeveana
		B. foliata
		B. illota
		B. gradata
		B. botanica
		B. candida
		B. domingensis
		B. dubia
		B. iota
		B. rostae
	Barbatia	*B. tenera*
		B. bistrigata
	Litharca	*L. lithodomus* ŧ
	Trisidos	*T. tortuosa* ŧ
		T. semitorta
	Anadara	*A. antiquata* ŧ
		A. trapezia
		A. sp. AMS C.434466
		A. notabilis
		A. geissei
	Larkinia	*L. granosa*
	Scapharca	*S. inaequivalvis* ŧ
		Scapharca pilula
		Scapharca vellicata
		Scapharca sp. PNM03

Family	Genus	Species
	Scapharca	*Scapharca* sp. PNM07
		S. ferruginea
		S. rotundicostata
		S. transversa
		S. ovalis
	Bathyarca	*B. perversidens*
		Bathyarca sp. Brasil
		Bathyarca sp. A
		B. japonica
		B. corpulenta
		B. freileyi
	Bentharca	*B. asperula* †
		B. xenophoricola
		B. nodulosa
	Samacar	*S. strabo* †
	Scaphula	*S. celox* †
		S. pinna
	Senilia	*S. senilis* †
Parallelodontidae		
	Parallelodon	*P. obsoletus* ✝
	Grammatodon	*G. implicatus* ✝
Cucullaeidae		
	Cucullaea	*C. labiata* †
		C. alta ✝
Noetiidae		
	Noetia	*N. ponderosa* †
		N. olssoni
	Arcopsis	*A. adamsi*
		A. solida
		A. afra
	Sheldonella	*S. repenta*
	Striarca	*S. olivacea*
		S. interplicata
		Striarca sp. MNHN101
	Stenocista	*S. gambiensis*
Glycymerididae		
	Glycymeris	*G. glycymeris* †
		G. americana
		G. ovatus
		G. scripta
		G. grayana
		G. holosericus
		G. formosus
		G. reevei
		G. crebreliaratus
		G. pilosa
		G. lividus
		G. striatularis
	Axinactis	*A. inaequalis* †
	Melaxinaea	*M. vitrea*
	Tucetona	*T. pectunculus*

Family	Genus	Species
	Tucetona	*T. flabellata*
		T. gealei
Limopsidae		
	Limopsis	*L. aurita* †
		L. tensioni
		L. loringi
		L. diegensis
		L. soboles
		L. woodwardi
		L. forteradiata
		L. marionensis
	Empleconia	*E. vaginata* †
Philobryidae		
	Adacnarca	*A. nitens* †
		A. limopsoides
	Aupouria	*A. parvula*
	Cosa	*C. costata* †
		C. parallelogramma
		C. waikikia
		C. scabra
	Cratis	*Cratis* cf. *ohasii*
	Lissarca	*L. rubrofusca* †
		L. picta
		L. notarcadensis
	Philobrya	*Philobrya setosa* †
		P. munita
		P. sp. USNM 882226
	Micromytilus	*M. crenulatifera* †
	Neocardia	*N.* sp. USNM 881111
	Notomytilus	*N. rubra* †

For those 14 extant genera where the type is a fossil species, at least one other representative of the genus was included in the analysis. This sampling scheme proved to be well representative of geographic distribution of the order as well as providing a comprehensive suite of characters encompassing the morphological diversity of the arcoids. Ultimately the basic guiding criteria for ingroup exemplar selection rested however, on the availability of specimens in museum collections; while some families, like the Arcidae, were found in many collections, others, such as the Philobryidae, were rare.

The inclusion of fossil taxa increases the amount of missing data that is associated with using fossil taxa in 'soft' morphological and molecular data sets. However, this is not a problem to which extant taxa are immune. The inclusion of extinct taxa in phylogenetic analyses has been a contentious issue in the past, with many authors advocating the unequal treatment of extinct and extant taxa. In this approach, a phylogenetic tree is constructed using extant taxa only and then the fossil taxa are fitted onto this tree (Løvtrup, 1977; Patterson, 1977; Hennig, 1981). There have been many critics of this method (Gauthier et al., 1988; Kluge, 1990; Gatesy and O'Leary, 2001). Unarguable extant taxa can offer a greater number and variety of characters than extinct taxa can, however, the amount of evidence available with extant taxa does not justify the exclusion of extinct taxa from an analysis.

The choice of outgroup taxa was dictated by the sister-group relationships of the Arcoida with other pteriomorphian taxa as established in prior studies (see preceding section on previous hypotheses) (see Table 5). However, no consistent pattern of sister-group relationships was found in these studies. To this end, taxa from each of the four

pteriomorphian orders were included in the analysis. These studies have suggested a sister-group relationship between the Arcoida and each of the other four orders in the Pteriomorphia (Carter, 1990a; Cope, 1996; Morton, 1996; Waller, 1998; Campbell et al., 1998; Steiner and Hammer, 2000; Campbell, 2000; Hammer, 2001; Giribet and Wheeler, 2002; Matsumoto, 2003). Within the orders, the selection of representative species followed a similar rubric to that of the selection of ingroup taxa with regards to specimen availability.

TABLE 5. Systematic list of the outgroup taxa used in the analyses. (See Appendix 1 for sources of specimens).

SUBCLASS	ORDER	FAMILY	SPECIES	GEOLOGIC AGE
Pteriomorphia	Mytiloida	Mytilidae	*Brachidontes domingensis* (Lamarck, 1819)	?Permian
			Mytilus edulis Linnaeus, 1758	Permian
			Lithophaga aristata (Dillwyn, 1817)	?Carboniferous
	Pterioida	Pinnidae	*Pinna carnea* Gmelin, 1791	Late Carboniferous
			Atrina rigida (Lightfoot, 1786)	Late Carboniferous
		Isognomonidae	*Isognomon alatus* (Gmelin, 1791)	Upper Permian
		Malleidae	*Malleus candeanus* (d'Orbigny, 1842)	Upper Cretaceous
		Pteriidae	*Pinctada mazatlantica* (Hanley, 1855)	Triassic
			Pteria colymbus (Röding, 1798)	Triassic
	Limoida	Limidae	*Lima lima* (Linnaeus, 1758)	Late Carboniferous
			Ctenoides scaber (Born, 1778)	Late Carboniferous
	Ostreoida	Gryphaeidae	*Hyotissa hyotis* (Linnaeus, 1758)	Upper Triassic
		Anomiidae	*Anomia simplex* d'Orbigny, 1842	Jurassic

MORPHOLOGICAL DATA COLLECTION

Collection of the exemplars used in this study has come from a number of sources. The vast majority of specimens came from various malacological collections of museums and institutions around the world (see Table 6). Observations were made on dried, formalin-fixed and ethanol-fixed specimens. In addition to providing substantial material for the study of shell characters, dried shells often have dessicated tissue inside the enclosed valves from which it was sometimes possible to extract viable DNA. Moreover, while not desirable, it was still possible to code some of the internal morphological characters from dried tissue, e.g. presence of a hanging rectum.

TABLE 6. Abbreviations and names of cited malacological repositories.

AMNH:	American Museum of Natural History, New York, USA.
AMS:	Australian Museum, Sydney, Australia.
BMNH:	The Natural History Museum, London, England (British Museum of Natural History).
CAS:	California Academy of Sciences, California, USA.
FMNH:	Field Museum of Natural History, Chicago, USA.
LSL:	Linnaean Society of London, London, England.
MNHN:	Muséum national d'Histoire Naturelle, Paris, France.
UCR-InBio:	University of Costa Rica: Instituto Nacional de Biodiversidad, Costa Rica.
USNM:	Smithsonian Institution, Washington, D.C., USA (United States National Museum).

In addition to these museum specimens, specimens were personally collected on a number of expeditions. These include Costa Rica (January, 2003), Puerto Rico and Antigua (July, 2003) and the Great Barrier Reef, Australia (February - March, 2004). Specimens were obtained via direct collecting by snorkeling and SCUBA diving. The animals were photographed and identified following transportation to a laboratory facility/hotel room. Subsequently, the specimens were relaxed using $MgCl_2$ and either fixed in 5% buffered formalin (later transferred to 70% ethanol) for future dissection or were preserved in 95% ethanol to ensure proper preservation of the DNA for further molecular studies. Voucher specimens are deposited in the American Museum of Natural History. For sources of the material used in this study see Appendix 1.

Specimens were photographed using a high-resolution Nikon D40 SLR camera. Smaller bivalves or individual characters were examined using a Nikon SMZ 1500 dissecting stereomicroscope. Features of the ctenidia were examined using an Olympus BX-50 compound microscope.

CHARACTER DETERMINATION

Examination of the characteristics of the chosen representative taxa used in this analysis was performed at gross and microscopic levels and translated into cladistically scorable characters. Morphological data were generally obtained from direct observations of specimens and in some cases from reliable literature accounts of the functional morphology of various taxa. Literature sources were utilized when no specimen with soft tissue preserved was available or when the preservation of the

specimen was poor, such that some characters were obscured or missing. Discrepancies between previously reported observations and the observations made in thus study were noted in the description of the characters and character states (see 'Characters Descriptions' below). Published species descriptions were used for the coding of characters of fossil taxa.

Morphological observations were made from two broad categories: the 'hard' shell morphology, including ligament and the 'soft' internal anatomical features. The 'hard' characters are those that have been most used commonly in historical taxonomic studies of the Bivalvia. These 'hard' characters include shell microstructure and form, hinge formation and ligament. The use of some traditional shell characters were largely abandoned in this study. These characters relate to shell shape and shell form, e.g. the distinction between two taxa may be on the basis of a descriptive characteristic—ovoid in shape as opposed to rectangular. Leaving aside the subjectivity of such characters, it is difficult to translate these features into discrete, objective states. Arcidae, especially taxa within the subfamily Arcinae (e.g. *Arca*, *Barbatia*, *Bathyarca*) are particular plastic with respect to external shell form—many of these taxa are epifaunal burrowers, taking on the form of the coral or rock crevice they inhabit. Such characters reflect adaptations to mode of life and were considered too plastic, representing localized homoplasy at the specific level. A total of 60 shell characters were defined and coded for both the extant and extinct taxa.

The main character groups explored for the 'soft' anatomical features of these organisms included the major organ systems with the Arcoida. These include the musculature (foot, adductor), respiratory and filtration (ctenidia and palps), alimentary

(stomach), circulatory (pericardium) and the sensory and nervous systems. Of these systems, information pertaining to the stomach alone was taken from previous studies of arcoid taxa (Purchon, 1957, 1983, 1987), as it was not feasible to dissect the stomachs for the 131 taxa included in this study. Unfortunately, the determination of the various characters that make up the stomach was not possible without such dissections.

Only discrete characters were coded for each exemplar. In the determination of the character states of some characters, any reference to relative or subjective terms was minimized. An effort was made to move away from the use of character complexes such as ctenidial type (filibranch, eulamellibranch or septibranch) or ligament grade (duplivincular, alivincular, multivincular etc:). The use of these traditional characters systems, which are often a complex of a number of different characters, presumes the unqualified presence of all the characters that make up that type. This absoluteness can introduce unwarranted statements about homology (see Tëmkin's (2006) and Carter et al.'s (2000) treatment of hinge teeth). The only exception to this was with the stomach type where information on all the various characters that make up this character type was not available. Nevertheless, studies of the arcoid stomach have consistently shown that the Arcoida have a stomach of type III (Purchon, 1957, 1983, 1987).

POLARITY DETERMINATION

The polarity of a character specifies the change of character states from plesiomorphic to apomorphic conditions. There are a number of ways to determine character state polarity: these include stratigraphic evidence, ontogenetic precedence of

states or outgroup comparison. Stratigraphic evidence can easily fail since the fossil record is fragmentary and the discovery of fossils from earlier periods has often debunked theories of origins of groups (e.g. as mentioned, the discovery of the philobryid *Eophilobryoidella sinoanisica* from Middle Triassic falsifies any hypotheses of origination of the Philobryidae from the Cretaceous Limopsidae). Ontogenesis, is often complicated, thus its use can also result in misleading information (e.g. pedomorphosis). Moreover, there is no empirical justification for believing that more 'complex' characters or character states are more derived than 'simpler' characters or states. For this reason, the polarity of characters was determined indirectly by comparison with characters found in the outgroup taxa. This method makes no statement of the plesiomorphic nature of any character, nor does it imply that the condition of the character states of the ingroup taxa are necessarily more derived than those present in the outgroup taxa.

DIRECTIONAL TERMINOLOGY

Directional terminology is essential when describing morphological characters in bivalves. The anterior region of the bivalve is directed towards the mouth, while the posterior end lies closer to the anus. The hinge and ligament are located dorsally, while opposite the dorsal hinge is the ventral margin, where the valves open at their widest point. The umbonal region refers to the area of the valve surrounding prodissoconch from where shell growth begins. Terminology for the orientation of the bivalve can be based either on the axis of the hard shell characters—the dorsal hinge axis; or on soft anatomy—the axis of the mouth and anus. The orientation terminology for the characters

herein described relate to hard shell characters. In this study, the anterior-posterior axis is taken in relation to the dorsal hinge as opposed to the line of axis between the mouth and the anus (which in some cases may not be parallel to the hinge). Except for the Philobryidae, the axis of the anterior-posterior dorsal hinge is the same as that of the mouth-anus is the same in all arcoid taxa. The length describes the maximum distance between the anterior and posterior ends of the bivalve, parallel to the dorsal hinge axis. The height is perpendicular to this line. In bivalves, the line of junction of the two valves is known as the commissure plane. Among bivalves where the valves are of equal size, this plane coincides with the sagittal plane.

CHARACTER DESCRIPTIONS

Character descriptions of morphological characters used in the analysis are provided below. Characters have been arranged into general categories according to morphological or organ systems. Characters are numbered as they appear in the data matrix (see Appendix 2). Terms for anatomical structures that have appeared in previous literature sources, but deemed inappropriate or ambiguous, are redefined and appear in *italics.* Similarly, characters that are newly identified in this study appear in bolded ***italics***. The designation a/p indicates the coding: (0) absent; (1) present.

Some of the characters described here have been used in other analyses of Bivalvia, including Waller (1998), Giribet and Wheeler (2002), and Tëmkin (2006) for outgroup sources. Where new terms were introduced or a character is described for the first time, the term is *italicized* in the character descriptions. Character descriptions have

been arranged into categories defined by organ systems and they are numbered as they appear in the matrix. Descriptions of soft anatomical characters pertain to all the arcoid families except the Parallelodontidae for which no Recent representative was examined.

SHELL MICROSTRUCTURE

The outer fold of the mantle edge secretes the adult bivalve shell. The shell is constructed from crystals of either aragonite or and/or calcite, both of which are polymorphs of calcium carbonate. These crystals are bound in a protein matrix of conchiolin. Shell microstructure has been reviewed for a great number of bivalves by Taylor et al. (1969), Taylor (1973), Waller (1980), Carter (1990a, b, c, d) and Carter et al. (1990). Generic groundplan coding has been applied for the terminal taxa when the information was not available: these taxa are mentioned in the character descriptions. Coding for microstructural characters (characters 1-8) was not taken from original observations, but from the previously mentioned literature sources (unless otherwise stated).

1. Mineralogical composition of adult shells: (0) aragonite; (1) aragonite and calcite. Of the Pteriomorphia, only the Arcoida have a shell composed entirely of aragonite, with a few exceptions. An aragonitic and calcite shell is found consistently in the Limoidea, Mytiloidea, Ostreoidea, Pinnoidea and the Pterioidea of the subclass Pteriomorphia (Taylor et al. 1969, 1973). Of the four other subclasses, the Protobranchia, Palaeotaxodonta, and Anomalodesmata are wholly aragonitic, while the Heterodonta are

also wholly aragonitic with the exception of two superfamilies, Chamoidea and the extinct Hippuritoidea that also have a calcite component (Kennedy and Taylor, 1968). A mineralogic composition solely of aragonite is presumed in the mytilid species *Brachidontes domingensis*. While no direct observation of the shell microstructure of this species was undertaken in any previous study, observations of six *Brachidontes* species indicate a shell wholly of aragonite (Carter et al., 1990; Taylor et al., 1969).

2. Shell layers: (0) three; (1) two.

Arcoida have two shell layers, i.e. the outer crossed lamellar and inner complex crossed lamellar layers. Three layers are found in *Lithophaga aristata*, and the chosen limid outgroups, *Anomia simplex* and all the included pterioidean taxa, bar *Malleus candeanus*.

3. Crossed lamellar structure (CL): a/p.

A crossed lamellar structure is one of the most common shell structures and consists of elongate needle-like crystallites, which are arranged into lamellae, with adjacent lamellae having an alignment that differs by about 98° (Taylor, 1973) (see Fig. 2). In extant bivalves it is always aragonitic in structure and consists of two elements, the larger, first order lamellae, which in turn are composed of smaller, second order lamellae. As traditionally used, the term "crossed lamellar" structure excludes complex crossed lamellar (CCL) structure. This occurs in the Arcoida, Limoidea and *Anomia simplex,* comprising the outside shell layer in the Arcoida. Information concerning the shell microstructural content of the Grammatodontinae is scant. Carter (1990b: 325-326) in his limited treatment of the Parallelodontidae indicates the presence of CL, but that of CCL (character 4) is unknown. It should be noted that precarious preservation of

aragonite makes the study of aragonitic shells in fossil specimens from the early Paleozoic almost impossible (Taylor, 1973).

4. Complex crossed lamellar structure (CCL): a/p.

This structure is built up of the same structural elements as crossed lamellar structure, but the arrangement of the lamellae is different (see Fig. 2). With this structure, the alignments of the lamellae are at a right angle to each other. A CCL shell composition is present in all the arcoid families (with the exception of the Parallelodontidae subfamily Grammatodontinae, where the presence of CCL is unknown), as well as *Anomia simplex*, and the limid outgroup taxa. The inner shell region is composed of this shell structure except in areas of muscle attachment, where an irregular prismatic fabric is secreted (myostracum).

5. Shell tubules: (0) absent or restricted to early shell or inner shell layers; (1) present throughout the area within the pallial line and penetrating the shell to the inner surface of the periostracum.

Two types of tubules are found in Bivalvia—differing in the process of formation: shell tubules may occur throughout the whole shell or may be restricted to the inner layer(s). The former type is made after the formation of the ostracum (the calcareous shell layers beneath the periostracum), while the latter are made during shell deposition (Omori et al., 1976). They are formed by epithelial protuberances of the mantle into the shell (Shibata, 1979; Waller, 1980). The tubules may vary in concentration over the shell interior. The function is unknown, but many roles have been posited including, among others, the possibility that they are either sense organs in a broad sense (Omori et al., 1976), increase the surface area for respiration via the 'virtual' expansion of the mantle (Waller, 1980),

assistance in adhering the mantle to the inner surface of the shell (Shibata, 1979; Waller, 1980) or that they may have a placental function in brooding bivalves (Prezant, 1990; Janssen, 1997).

Tubules are found throughout the two shell layers in the Arcoida (see Fig. 5). The presence of tubules throughout the inner and outer shell layers within the pallial line is unique to the Arcoida (Oberling, 1964; Waller, 1998) and are consistently found throughout ontogeny in the Arcoida (Taylor et al., 1973; Shibata, 1979), being most abundant interior to the pallial line, but absent from the adductor myostracum (Shibata, 1979). The tubules are several tens of microns in diameter in all the Arcoida examined (Taylor et al., 1969: 77).

6. Pallial line: a/p.

The pallial line is a scar indicating the line of apposition of the pallial muscles of the outer mantle surface to the inner shell. In the Arcoida, this line also represents the boundary between the outer crossed lamellar shell layer and the inner complex crossed lamellar layer. The shell substance that is laid down beneath these pallial muscles is referred to as myostracum (Taylor et al., 1969). No distinct boundary between the inner and outer shell layers is apparent in the arcid genus *Bathyarca*, and in the large majority of Philobryidae. Among the outgroup taxa, a pallial line scar is absent in the pinnid outgroup taxa and in *Lithophaga aristata*.

7. Nacreous structure (lenticular structure): a/p.

This layer is aragonitic. The tablets of lenticular nacre in the column are at a right angle to the growth lines (Taylor et al., 1969). This is particularly well developed in the middle

shell layer of the Pteriidae and Mytilidae. Nacreous structures of the lenticular and sheet type (see character 9) are consistently absent in arcoids.

8. Nacreous structure (sheet nacre): a/p.

This layer is aragonitic. In sheet nacre, the tablets of nacre are laid down in regular layers parallel to the shell interior. Of the Pteriomorphia, sheet nacre is present in the Mytiloidea, Pinnoidea and Pterioidea (Taylor et al., 1969).

SHELL FORM AND MORPHOLOGY

Classic terms relating to shell shape, such as ovate, rectangular and oval, are avoided, as they are too problematic and subjective. A number of arcoid bivalves have adopted an epibyssate habit, burrowing in either hard substrate or sand. Therefore, the surrounded external environment often influences the form of the shell. Many of the characters described below relate functionally to the habitat within which the bivalve lives. The arcoid shell can be thick and heavy as in *Senilia senilis* (Yonge, 1955) or thin, but sturdy as in *Cucullaea labiata* (Lightfoot, 1786).

9. Periostracum: (0) glabrous or smooth (without bristles or scales); (1) with bristles but not extending beyond shell margins; (2) with bristles extending beyond shell margin.

The periostracum is a thin sheet of quinone-tanned conchiolin that is secreted by the first outer fold of the ventral mantle margin (Hunt & Oates, 1978) and appears on the outer surface of the shell. The functions of the periostracum are many, including its role in subsequent shell deposition and acting as support and substrate for subsequent nucleation

and crystal growth of the outer shell layer. It also plays a protective role in preventing corrosion of the calcified shell by the surrounding acidic waters (Taylor et al., 1969). Furthermore, experiments have shown that projecting elements of the periostracum play a role in stabilizing the shell in sediment (Bottjer & Carter, 1980). Extension of the periostracum beyond the ventral margin is only considered as such when it is extensive and not merely a couple of millimeters beyond the edge. The presence on flaky periostracum should not be mistaken for blunt bristles. A periostracum with scales or bristles is the prevailing condition in the Arcoida. However, a glabrous periostracum is more common among the Philobryidae as well as in some arcid taxa (Fig. 8A). A smooth periostracum was observed in all the outgroup taxa).

10. Periostracal bristle tip shape: (0) blunt; (1) pointed; (2) both blunt and pointed present.

When bristles are found present in both forms over the shell, it is usually the blunt ribs lie over the ribs (Fig. 8B), while the pointed scales are found in the interstices between the ribs (Fig. 8C).

11. Location of periostracal bristles: (0) on the surface of the ribs; (1) on the interstices (or threads) between the ribs; (2) on both the interstices and the surface of the ribs.

Very often the periostracum can be restricted/heavy to the ventral margin of the shell, as in *Glycymeris*, anteriorly, as in *Litharca*, or posteriorly, as in many *Arca* species. In some cases, the shell will lack raised elements, but have this radial threads; scales may be found in these threads and if so are coded as present on the interstices.

FIGURE 8. Form of periostracum found in Arcoida: **(A)** Glabrous or smooth periostracum as seen in *Senilia senilis*; **(B)** Blunt edged periostracum, seen extending over the ventral shell margin in *Arca bouvieri*; **(C)** Pointed bristles of *Scapharca* sp. PNM07. The top arrow indicates the bristles lying within the interstices. The bottom arrow highlights the disjunction between the left and right valve—inequivalve.

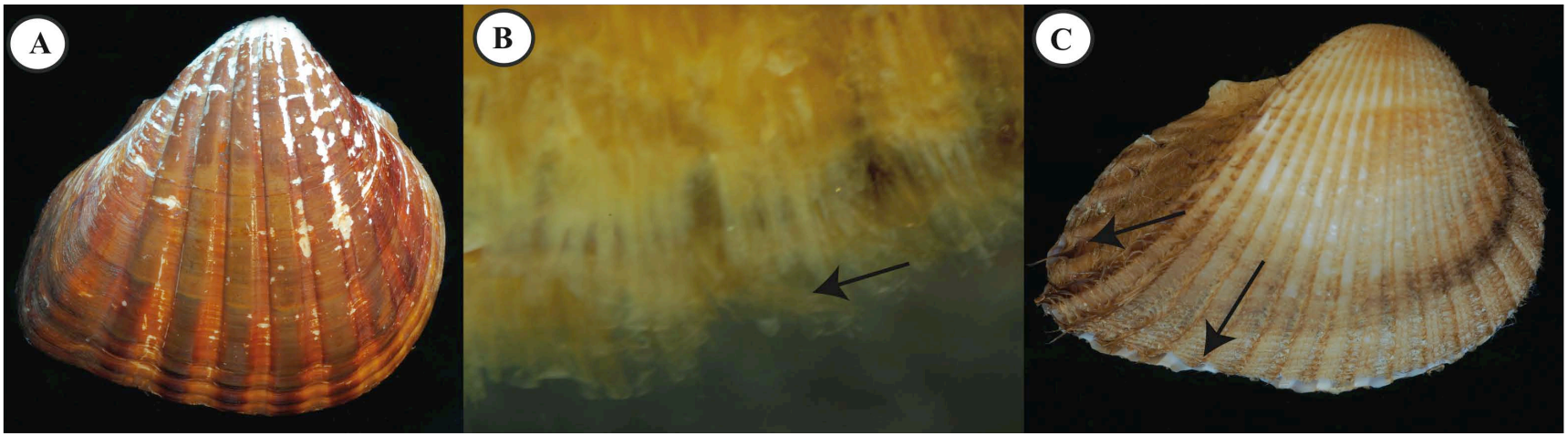
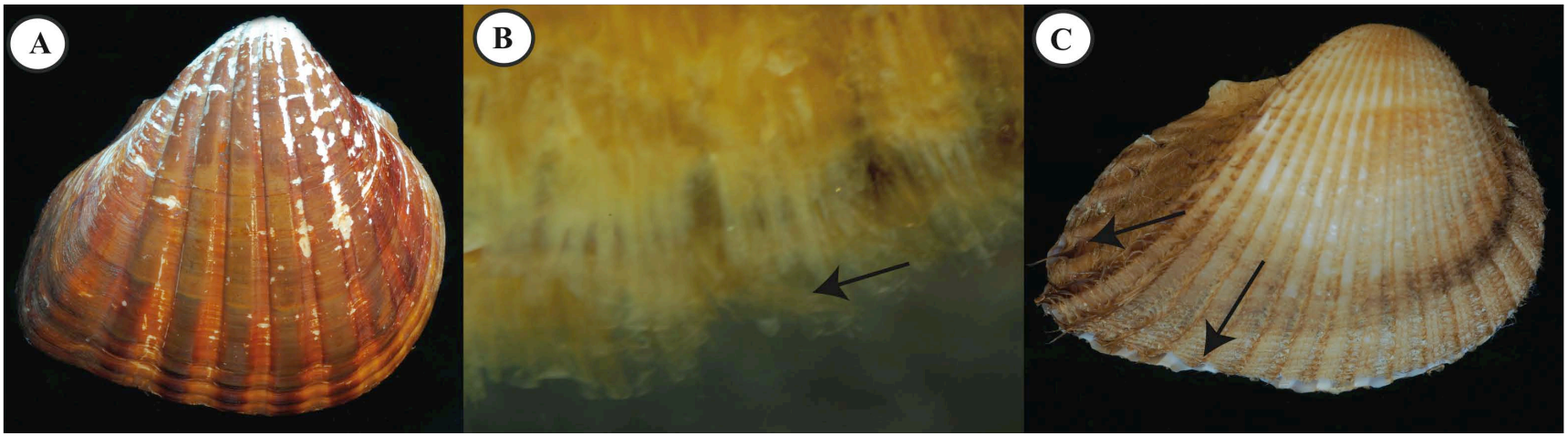


FIGURE 8. Form of periostracum found in Arcoida: **(A)** Glabrous or smooth periostracum as seen in *Senilia senilis*; **(B)** Blunt edged periostracum, seen extending over the ventral shell margin in *Arca bouvieri*; **(C)** Pointed bristles of *Scapharca* sp. PNM07. The top arrow indicates the bristles lying within the interstices. The bottom arrow highlights the disjunction between the left and right valve—inequivalve.



12. Valve size equality: (0) equivalve; (1) inequivalve.

The two valves of a bivalve can differ in a number of respects: size; convexity; shape and sculpture. For the purposes of this study, only size was taken into account. In the majority of bivalve species the valves meet equally at the commissure plane and are of equal size. This is also true of most arcoids. However, in a number of taxa, an inequality exists, wherein the left valve overlaps the right valve. This inequivalvity can be quite considerable as in *Cucullaea,* or slight as in all *Scapharca* species (Fig. 8C). Similar inequivalvity is found in Pterioidea with the left valves overlapping the right, while in some non-pteriomorphs, the right valve is the larger of the two (e.g. Corbulidae, Thraciidae). A pronounced form of this inequivalvity is found in forms where one valve is cemented to the hardened substrate; this is seen in the outgroup taxon *Anomia simplex*.

13. Posterior truncation of shell: a/p.

Truncation of the posterior region of the shell minimizes evacuation of shallow burrowers by turbulence in unstable environments. This truncation of the posterior region of the shell can be quite extreme as in *Cucullaea labiata* and all *Arca* species: the posterior axis forms a sharp angle with that of the ventral axis, or obliquely truncate as in most *Barbatia* species: the angle between the posterior and ventral axes is not as sharp. A truncate posterior region of the shell is seen in Fig. 11B, in the region of the posterior sulcus. Truncation was lacking in all of the Limopsidae and Glycymerididae examined as well as the lone outgroup taxon *Isognomon alatus*.

14. Inflation of valves: (0) present; (1) absent (compressed).

Inflation relates to the relative distance between the two outer planes of the shell that are parallel to the plane of the commissure or junction of the two valves. The great majority

of arcoid taxa exhibit some degree of inflation. The adaptive significance of inflation is unclear, given that this may act as a hindrance to burrowing. Inflated shells are typical of the Arcoida and can be quite extensive as in *Cucullaea labiata* or most Noetiidae or moderate as in most of the Arcidae (Fig. 9A). Lateral compression of the two valves is found in the genera *Philobrya*, *Melaxinaea*, *Empleconia*, most *Limopsis* and *Stenocista* species (Fig. 9B).

15. *Twisting*: (0) absent; (1) deep twist along median axis.

The rotation or turning of the posterior commissure plane at an angle relative to the anterior plane results in the characteristic twisting found in relatively few arcoid taxa (Fig. 10). Twisting of the shell has been described in the arcoid genus *Trisidos* ((McGhee, 1978; Tevesz and Carter, 1979; Morton, 1983), and recently in the extinct arcid *Ambrogia mytiloides* (Brocchi, 1814) (La Perna, 2007). Twisting is also seen in the extinct Bakevellidae (McGhee, 1978). In the extant arcid genus *Trisidos,* the posterior end of the shell has twisted, such that the posterior part of the sagittal plane has turned through approximately 45º in *T. semitorta* and almost 90º in *T. tortuosa*. *Trisidos* was commonly referred to as the "Twisted Ark", until this was replaced with "torted" by McGhee (1978). However, as pointed out by Morton (1983), twisting in *Trisidos* occurs with the contraction of asymmetrical pedal retractors along the sagittal plane. In gastropod, the larvae are torted by contraction of a single pedal larval retractor muscle. For this reason, the term twisting is used to describe this feature.

16. Lateral equality: (0) equilateral; (1) inequilateral.

When the prodissoconch occupies a position close to the middle of the adult hinge line it is said to be equilateral (Fig. 11A), symmetrical or acline and when placed closer to the

margins is inequilateral or prosocline. The Arcoidea typically have an inequilateral shell (Fig. 11B), with the umbones shifted towards the anterior end of the hinge (prosocline). The Philobryidae and Limopsidae, while inequilateral, are only marginally so for most taxa. The only arcoid family that exhibits equilateral symmetry is the Glycymerididae but this pattern is not consistent within the group (Fig. 11B). Placement of the prodissoconch posteriorly on the hinge axis (opisthocline) is not found in any arcoid taxa, or in any of the outgroups. All of the outgroup taxa exhibit some degree of inequilaterality. Shells that are circular or sub-circular in form, as seen in Glycymerididae, Limopsidae and some Philobryidae, are adapted for the anterior-posterior rocking motion used by these shallow burrowers. The elongate, laterally compressed, inequilateral forms as seen in the Arcidae (except *Anadara*) are best equipped as epibyssate nestlers in rocks and crevices (Thomas 1978).

17. Median sulcus: a/p.

A median radial depression is found on the surface of the adult shell in a number of arcoid taxa; originating from the umbonal region, it extends towards the ventral margin. It is commonly found in the Arcidae, Parallelodontidae and Noetiidae, and absent in Cucullaeidae (although a sulcus is evident in juvenile specimens of *Cucullaea labiata*), and the Limopsoidea (*sensu* Dall, 1895) (Fig. 10).

18. Posterior sulcus: a/p.

A posterior radial depression on the surface of the shell is found in a number of Arcidae and Parallelodontidae taxa (Fig. 11B). This sulcus does not lead from the umbonal region of the shell. A posterior sulcus is characteristic of the arcid genus *Arca* (with the

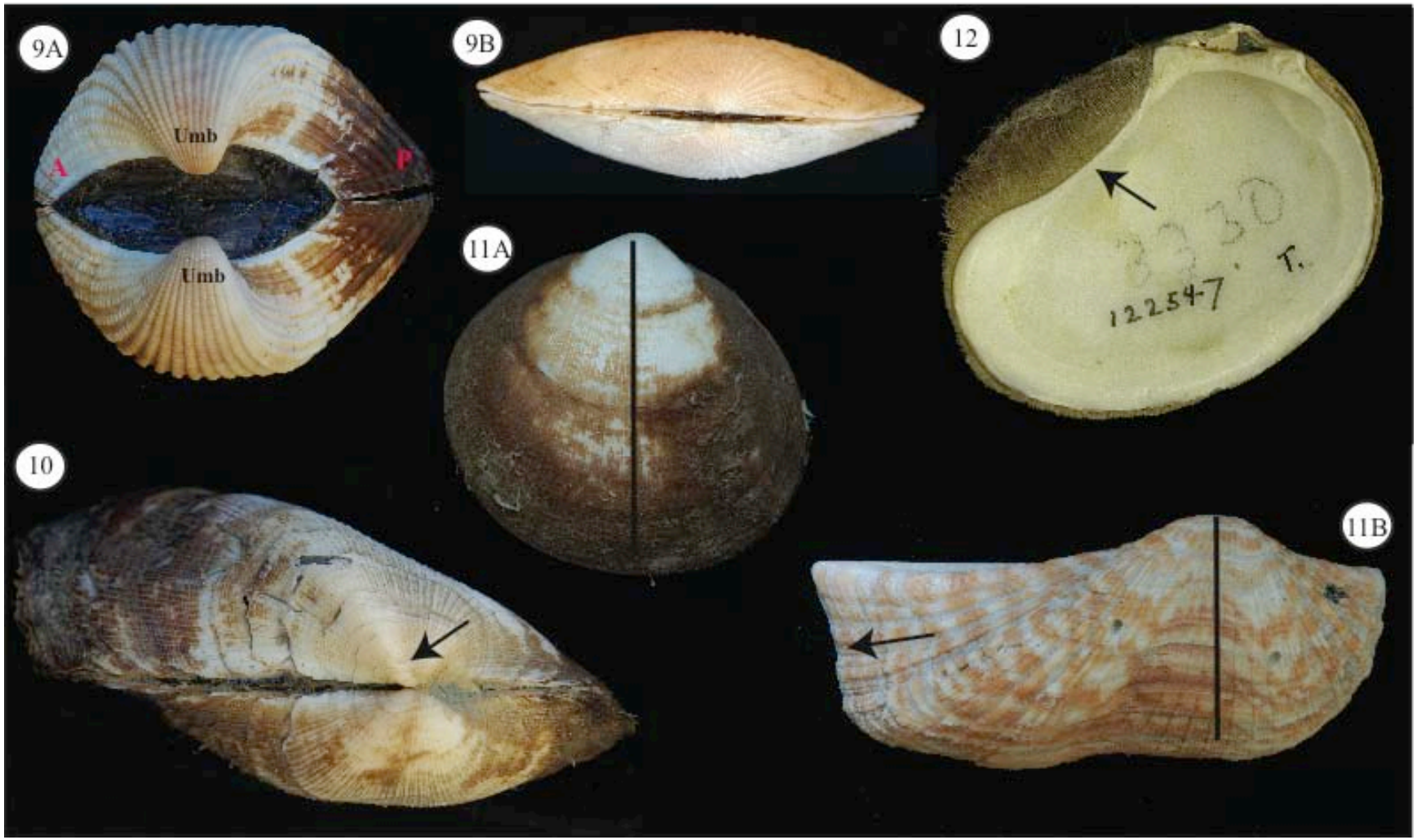
exception of *Arca mutabilis* that lacks this sulcus) and is also found in the noetiid taxon *Noetia olssoni*. A posterior sulcus is absent from all outgroup taxa.

FIGURE 9: Dorsal view of hinge: (**A)** Dorsal view of *Larkinia* sp. AMS C.434466. The notation 'A' and 'P' denote the anterior and posterior region of the organism, Umb = umbones. The prodissoconch is located ventral to the umbones, which in this species are directed towards the posterior region of the animal opisthogyrate; **(B)** Dorsal view of *Melaxinaea vitrea* illustrating the compression of the valves.

FIGURE 10: Dorsal view of the twisted shell form of *Trisidos semitorta*. The arrow highlights the median sulcus.

FIGURE 11: Lateral equality of shell in Arcoida: **(A)** Equilateral valve of *Glycymeris holosericus*; **(B)** Inequilateral valve of *Arca noae*. The line leading from the umbones to the ventral margin illustrates the asymmetry between the anterior and posterior region of the shell. The arrow indicates the posterior sulcus.

FIGURE 12: Dorsal cleft of *Empleconia vaginatus*.


9A
Umb
A
P
Umb
9B
12
12254-7
T.
11A
10
11B

19. Dorsal cleft: a/p.

The posterior dorsal margin is deeply infolded in the limopsid genus *Empleconia* (Fig. 12). This infold forms a deep cleft in the region between the umbones and dorsal posterior margin.

EXTERNAL SHELL SCULPTURE

The external sculpture of arcoid shells is somewhat varied, with no general tendency for a particular form of sculpture across the group. The sculpture is relatively simple and when present, broadly consists of two elements—commarginal (= concentric or conmarginal) and radial sculpture. Both of these orientations can be composed of incised or grooved forms and/or raised projecting elements. When both radial and commarginal elements are present, this may lead to a cancellate, reticulate or costellate appearance. The Arcoida shell sculpture is devoid of any spines, divaricated patterning or extraordinary relief seen in many other bivalve groups. The external sculpture loosely relates to their mode of life (Thomas, 1978).

20. Raised radial sculptural elements: (0) absent; (1) riblets or costellae present; (2) ribs or costae present.

Radial elements are the dominant sculpture of arcoid shells—the heavy commarginal sculpture present in other bivalve groups is lacking. These elements project from the shell surface and run from the umbonal region somewhat perpendicularly to the ventral margin. Ribs are relatively broad, continuous, raised elements on the surface of the shell

(Figs. 13 and 14). The less prominent riblets are much thinner linear projections on the surface of the shell that may or may not originate at the umbones (Fig. 13). Riblets are the predominant sculpture in the Arcoida; however, strong ribs are especially prominent in the arcids *Arca*, *Senilia* and *Anadara*, the Parallelodontidae, the noetiid *Noetia*, and the glycymerid *Tucetona*. Smooth shells predominate the Philobryidae (except *Cosa*). It is believed that this surface relief may assist in stabilization in turbulent sediment and strong currents as well as provide support during digging (Kauffman, 1969; Stanley, 1970; Thomas, 1975).

21. Radial elements: (0) simple; (1) divided.

Simple radial elements are those that do not bifurcate at any region from where they arise at the umbones and end at the ventral margin (Fig. 14). In the Arcoida, this bifurcation generally occurs closer to the ventral margin (Fig. 13); in some taxa the division is complete, arising at the umbonal region (e.g. *Noetia ponderosa*). The presence of this character is dependent on the presence of raised radial elements (character 20, states 1 and 2). Among the outgroup taxa the division of the radial elements is restricted to *Brachidontes domingensis*.

22. Nodules on primary elements (radial or commarginal): a/p.

Nodules are raised protrusions that arise from the radial elements (Fig. 14). In several arcoid taxa, the point of intersection of radial and commarginal costae result in a cancellate appearance (e.g. *Arcopsis adamsi, Striarca olivacea*), however, the presence of nodules is not dependent such an intersection. It is most likely that this surface sculpture assists in their epifaunal life habits. The presence of this character is dependent on the presence of raised radial elements (character 20).

23. Radial scales: a/p.

Scales projecting from the radial elements are found in a number of arcoid taxa (Fig. 15). These scales are directed towards the ventral margin, where a scalloped edge may form (see *Litharca lithodomus*). They always occur at the intersection of radial and commarginal raised elements. The presence of this character is not predicated by the presence of raised radial elements, as seen in *Bathyarca* sp. A (character 20).

24. Radial striae: a/p.

This sculpture, which is less pronounced than ribs, consists of incised radial elements, found on the surface of the shell. While not prevalent, these radial incisions on the surface of the shell are found in a number of taxa, including the arcid genera *Bathyarca* and *Scaphula*, as well as across the Limopsidae and Philobryidae. The faint radial striae are evident in Fig 11A. This sculpture was not seen in any of the outgroup taxa.

25. Emerging radial riblets: a/p.

These radial elements do not originate at the umbones (unlike character 21) (Fig. 13). This form of radial sculpture is frequently seen in all arcoid families with the exception of the Philobryidae. It is noticeably absent from the arcid genus *Anadara*, the sculpture of which is strongly ribbed. Emerging riblets are usually found in taxa that have riblets as opposed to ribs, but this is not an exclusive association. Among the outgroup taxa *Brachidontes domingensis* and *Ctenoides scaber* also possess this form of sculpture.

26. Commarginal riblets: a/p.

Similar to radial counterparts (see character 20), these elements run parallel to the ventral margin. Larger commarginal costae are not found in any of the taxa examined in this

study. A distinction was made between commarginal riblets and commarginal lamellae (see character 27).

27. Commarginal lamellae: a/p.

These are continuous thin projections that extend in the direction of growth and are parallel to the ventral margin (Fig. 16). These lamellae are most often described as ribs in general descriptions, however, the ventral portion of these 'ribs' is not contiguous with the surface of the shell and therefore is considered more lamellae-like than rib-like. These lamellae can be quite flattened as in *Arca* species or somewhat raised as in *Samacar* and *Bathyarca*. When present, the lamellae are far less conspicuous than their radial counterparts/elements.

28. Commarginal striae: a/p.

This sculpture, which is similar to the form of radial striae, is laid down commarginally to the ventral shell margin (Fig. 17). Not to be mistaken with the more irregular growth lines, these striae are evenly laid down along the shell surface and finely inscribed. This shell sculpture is not prevalent in the Arcoida, being restricted to the *Bathyarca*, *Cucullaea* and in some limopsid and philobryid taxa.

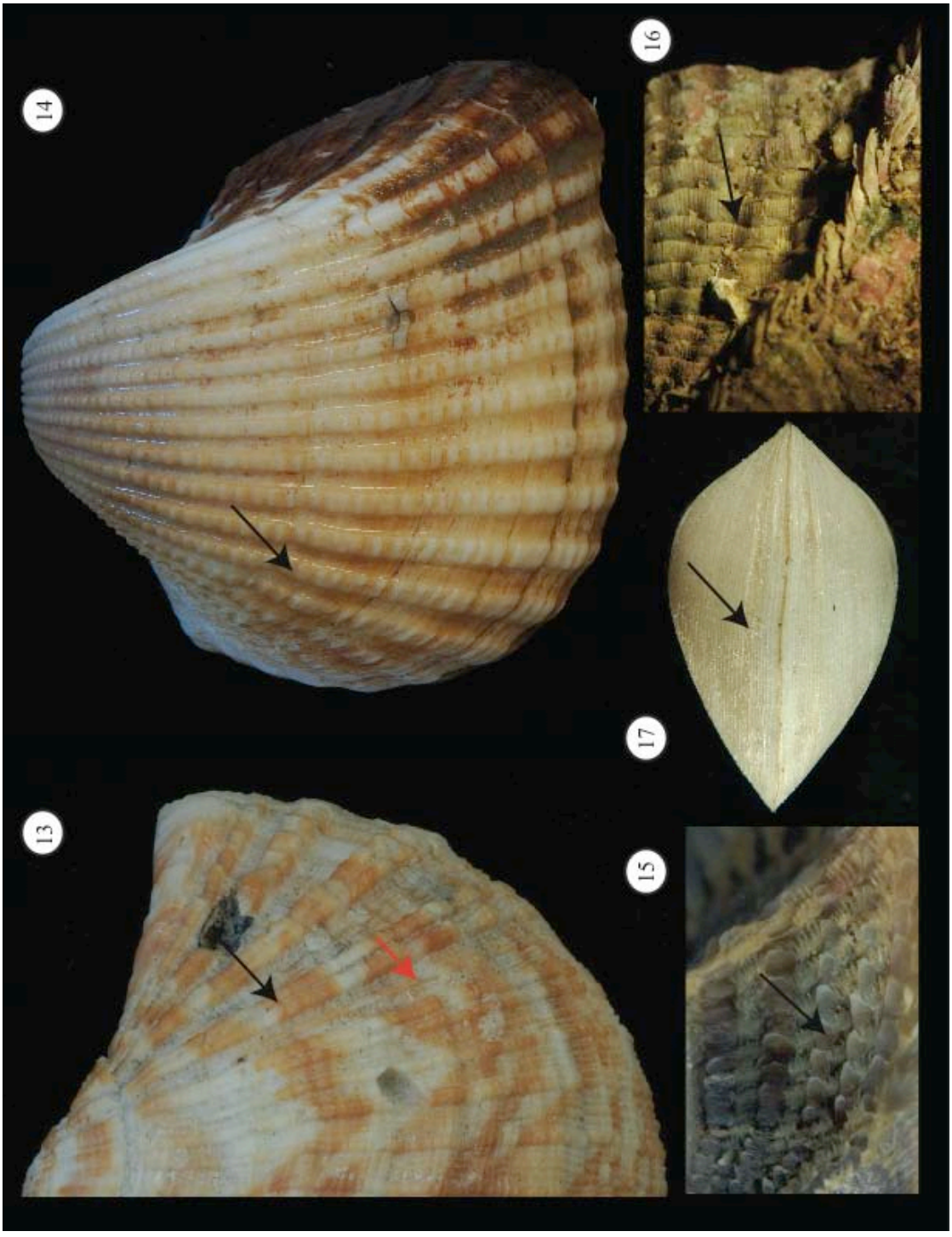
FIGURE 13: External sculpture of *Arca noae* in the anterior region of the shell: The black arrow is highlighting the divided rib; the red arrow is pointing to an emerging riblet.

FIGURE 14: External sculpture of the right valve of *Larkinia* sp. AMS C.434466: Note the strong undivided ribs on the surface of the shell. The arrow indicates the nodules on the surface of these radial elements.

FIGURE 15: Radial scales on the surface of the ribs of *Arca mutabilis*.

FIGURE 16: Commarginal lamellae of *Arca imbricata*.

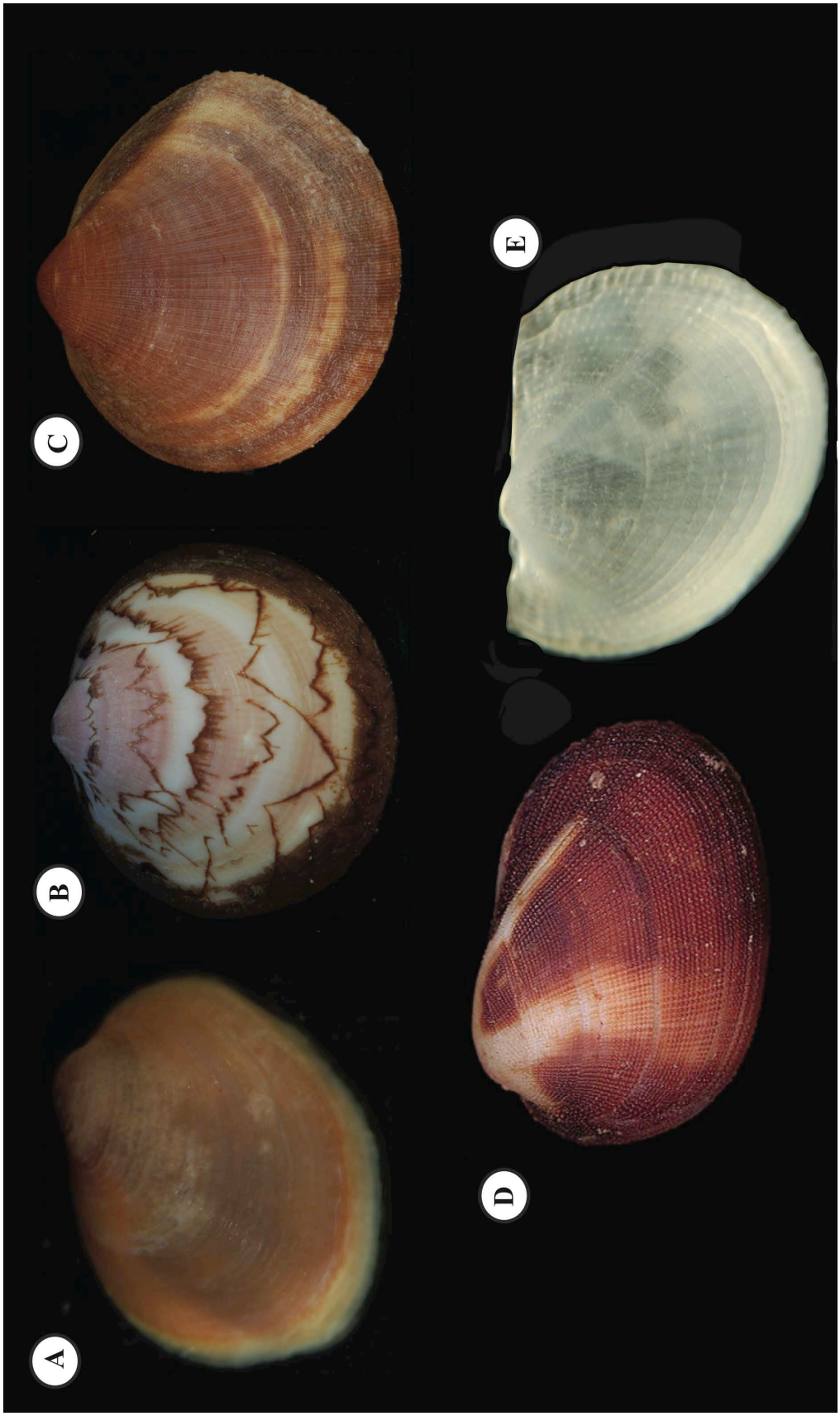
FIGURE 17: Commarginal striae of *Adacnarca nitens*.


14
16
17
13
15

29. Pigmentation on the external shell surface: (0) uniform (Fig. 18A); (1) chevron shaped; (2) radial; (3) irregular; (4) absent.

Pigments in shells are considered to be waste products of metabolism that are secreted into the shell as a means of disposal (Cox et al., 1969). While often considered quite dull, a number of different color patterns are found in the arcoids. While the majority of Arcoida have a uniform shell color (brown tones), some external patterns do exist, including a chevron or zigzag patterning (Fig. 18B) (very common in the Glycymerididae and *Arca* species), a single radiating stripe (Fig. 18D) (*Barbatia amygdalumtostum*, *Barbatia iota*, *Barbatia lacerata*) and irregular mottling (some *Glycymeris* and *Barbatia* species) (Fig. 18C). However, no consistent color pattern is found in any major taxonomic grouping. The Glycymerididae could be described as the most 'colorful' arcoid family, with chevron patterning being found on a great number of taxa. Color is wanting in the Limopsidae and the Philobryidae and in many deep water Bathyarca species (Fig. 18E), of which many species have an Arctic and Antarctic distribution. Nicol (1967) posited that cold-water inhabiting bivalves characteristically lack bright colors on the shells and are absent of any color pattern. Pigmentation is either uniform or largely irregular in the outgroup taxa.

FIGURE 18: Variation of shell pigmentation in Arcoida: **(A)** Uniform pigmentation of *Lissarca rubrofusca*; **(B)** Chevron pattern of *Glycymeris scripta*; **(C)** Irregular pattern of *Glycymeris reevei*; **(D)** Radial pattern of *Barbatia amygdalumtostum* [image from www.femorale.com]; **(E)** Absence of pigmentation on a species of *Bathyarca*.


A
B
C
D
E

30. Calcitic scales: a/p.

These scales are raised and quite distinct from the shell surface. Calcitic scales occur in some species of Pterioidea, as well as in the pinnid outgroup taxa. Such sculpture is absent from the Arcoida.

LARVAL SHELL AND UMBONAL REGION

The prodissoconch is the generally mineralized larval shell and consists of two growth phases (P1 and P2). P1 is the first stage of ontogeny and therefore reflects the size of the egg (Moran, 2004b), whereas P2 is deposited during the veliger stage, usually by planktotrophic larvae. The pre-metamorphic P2 is generally distinguishable by the presence of growth lines. Terminology for the larval shell is taken from Ockelmann (1965) and Malchus (2004a, b). Any discussion of the prodissoconch below refers to P1 and P2, unless otherwise stated.

31. Prodissoconch shape: (0) D-shaped; (1) subtriangular.

The morphology of the prodissoconch can be used to infer larval ecology (Ockelmann, 1965, Ó' Foighil, 1986; Malchus, 2004a; Moran, 2004a,b). The prodissoconchs of lecithotrophic pteriomorphian larvae are typically discoid or D-shaped (Fig. 19, 20) and larvae of this type utilize endotrophic energy sources. The larvae of planktotrophic bivalves, which procure their principal energy supply exotrophically, tend towards a subtriangular-shaped larval shell (Kasyanov, 2001; Malchus, 2004a). However, all larvae, including planktotrophs, obtain some endotrophic energy supply from the egg.

In the Pteriomorphia, a distinct boundary is evident between P1 and P2 in both planktotrophic and lecithotrophic-planktotrophic bivalves. No such boundary is evident in lecithotrophic, embryonic developed bivalves. The shape of the subtriangular prodissoconch is as a result of an elevated P1 and the boundary between the growth phases (Malchus 2004a). Waller (1998) has argued convincingly that the plesiomorphic state of the primitive bivalve larvae was lecithotrophic with this developmental mode being common in all primitive molluscan groups.

The sizes of P1 and P2 and the ratio between these two phases is also suggestive of developmental mode: a planktotrophically-developed bivalve generally has a relatively small P1 and low P1:P2 ratio (P1 < 100 mm, P1:P2 < 0·4); lecithotrophic-planktotrophic types generally have larger P1s and greater ratios (P1 > 100 mm; P1:P2 ≥ 0·6); and the P2 is inconspicuous or absent in lecithotrophic bivalves. In a study of 44 Antarctic bivalves that included 12 arcoid taxa (Hain and Arnaud, 1992), the P1 was a major part of the embryonic shell and the P2 was small or even absent (P1/P2 > 0.90). In all cases where P1 was much greater than P2, the bivalves were directly observed to brood. However, an exception to this was found with *Adacnarca nitens*, where P2 formed more than half of the embryonic shell (P1/P2 ≤ 0.5) and this species was also observed to brood its young. Moreover, contra Hain and Arnaud's assertion otherwise, the prodissoconch of *A*. *nitens* is not oval-shaped, but conforms to the D-shaped form of all other philobryids examined. A D-shaped rimmed prodissoconch was also observed in *Bentharca decorata* (Hayami and Kase, 1993), *Acar plicata* (Barnard, 1964) and in the arcid *Barbatia* (*Acar*) *bailyi* (Moran, 2004a) and in the arcid taxa *Barbatia* (*Acar*) *dubia*

and *Barbatia* (*Acar*) *botanica* (observed in this study). Of the previous studies, brooded young were only observed in *Barbatia* (*Acar*) *bailyi* (Moran, 2004a).

32. Prodissoconch rim: a/p.

In the majority of Philobryidae the prodissoconchs terminate with a raised rim, giving the umbonal region an appearance of a pakol or Afghani hat (Fig. 21). A rim is absent in *Lissarca*, *Micromytilus* and *Notomytilus*. This hat-shaped prodissoconch has been previously observed in the arcid taxa *Bentharca decorata* (Hayami and Kase (1993), *Barbatia* (*Acar*) *plicata* (Barnard, 1964), *Barbatia* (*Acar*) *marsupialis* (Oliver and Holmes, 2004), *Barbatia* (*Acar*) *pentasion* (Kilburn, 1983) and *Barbatia* (*Acar*) *bailyi* (Moran, 2004a). The adaptive significance of this structure is unknown, however, it is thought that is linked with non-planktotrophic development.

33. Pigmentation of the prodissoconch in adult shell: a/p.

In a number of species, the prodissoconch is pigmented such that it is a different color from the dissoconch or the adult shell. The pigmentation varies from purple in *Glycymeris glycymeris* to a rusty orange color in *Barbatia tenella*.

34. Direction of prodissoconch coiling: (0) orthogyrous (prodissoconch coils towards center or ventralward); (1) prosogyrous (prodissoconch coils in anterior direction); (2) opisthogyrous (prodissoconch coils in posterior direction).

In the Arcidae and Noetiidae, all three conditions of direction of prodissoconch coiling were seen. *Cucullaea labiata* was observed to have a prosogyrous prodissoconch. The Glycymerididae in this study were seen to have a prodissoconch that was either orthogyrous (Fig. 22A) or opisthogyrous (Fig. 22B). The limopsids are overwhelmingly orthogyrate, except for *Limopsis tensioni*. In all the philobryid taxa examined, the

prodissoconchs were exclusively orthogyrate, with the prodissoconch of the left valve directly facing that of the right valve. In the outgroup taxa the mytiloids, the limid *Ctenoides scaber*, as well as all pterioids (except *Malleus candeanus*) possessed a prosogyrate prodissoconch. *Lima lima* was the sole outgroup taxon possessing an orthogyrous prodissoconch. All other outgroup taxa were observed to have opisthogyrate prodissoconchs.

35. Prodissoconch position relative to the adult hinge line: (0) terminal; (1) non-terminal.

A terminal prodissoconch is one that is formed at the anteriormost or posteriormost point of the hinge line (Fig. 23). In all but one a few arcoid taxa (*Litharca lithodomus*, *Cosa costata*, *Philobrya munita* and the philobryid genera *Philobrya*, *Neocardia*, *Notomytilus* and *Cratis*), the prodissoconch is not terminal and instead are located closer to the center of the hinge line. The terminal prodissoconch of these taxa is found anteriorly on the hinge line in all cases except *Litharca lithodomus*, where it is placed posteriorly.

36. Evidence for larval hinge teeth present in adult hinge: a/p.

Interlocking teeth-like structures are evident on the adult hinge of the majority of Philobryidae (Fig. 24). These 'teeth' represent the hinge structures found in the provinculum (larval shell) (Malchus, 2004a). They have been described as denticles in earlier works (Tevesz, 1977; Malchus, 1995). When present, they are found on the adult hinge located anteriorly and/or posteriorly. Larval hinge teeth were found in all examined Philobryidae except *Philobrya munita* and *Philobrya* sp. (USNM 882226). Surprisingly this character was also seen in two arcid taxa, *Bathyarca perversidens* and *Bathyarca* sp. A. Larval hinge teeth were absent in all outgroup taxa.

FIGURE 19: Dorsal hinge of *Adacnarca nitens*: The box highlights the D-shaped prodissoconch of this taxon.

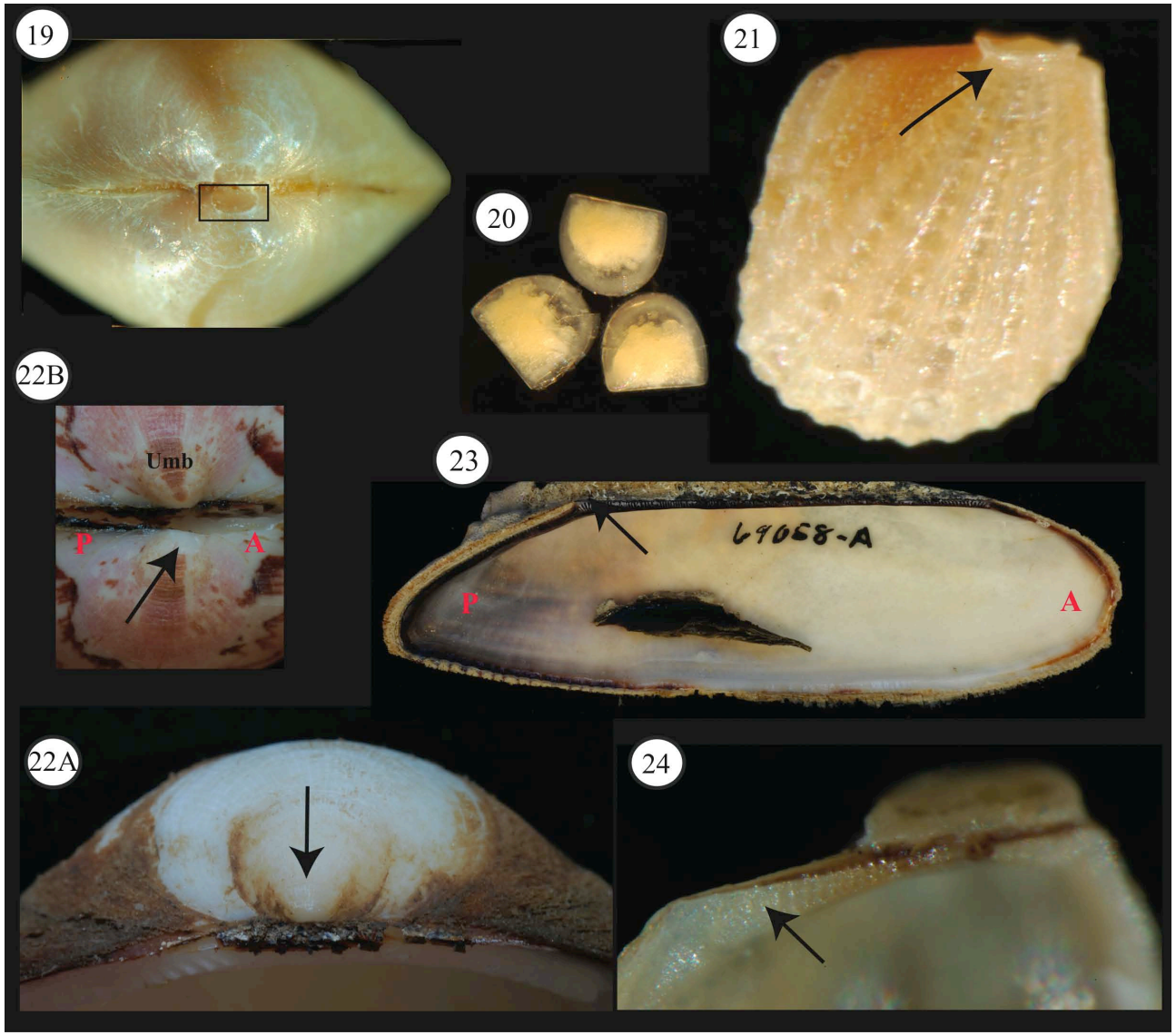
FIGURE 20: D-shaped larvae of *Adacnarca nitens*.

FIGURE 21: Prodissoconch rim of *Cosa costata*.

FIGURE 22: Direction of prodissoconch coiling: **(A)** Orthogyrous prodissoconch of *Glycymeris holosericus*; **(B)** Prosogyrous prodissoconch of *Glycymeris scripta*.

FIGURE 23: Terminal prodissoconch position of *Litharca lithodomus*: The arrow points to the distal end of the hinge line, above which lies the prodissoconch.

FIGURE 24: Larval hinge teeth of *Cosa costata*.


19
21
20
22B
Umb
P
A
23
69058-A
P
A
22A
24

37. Umbonal keel (carina): (0) absent; (1) low; (2) sharp.

In many Arcoidea (sensu Newell, 1969), a prominent, sharp-edged or keel-like radial ridge runs diagonally from the umbones towards the posteroventral margin, this ridge can almost be razor sharp as evidenced in *Trisidos tortuosa* and *Scaphula* species (Fig. 25). A low keel is characteristic of *Barbatia* species for example. This ridge is mostly lacking in the Limopsoidea (sensu Newell, 1969).

38. Umbonal arching: (0) absent; (1) present; (2) overarched.

Arching of the dorsal umbonal region is the typical situation in the Arcoida. With an arched umbonal region, the face of the prodissoconch of each valve is directed towards other. The umbones in the Philobryidae are devoid of any curvature and the prodissoconch (P1+P2) is directed dorsally (Fig. 26A). The umbones are considered to overarch when the prodissoconchs curve sharply ventralward and continue to curve away from the dorsal midline (Fig. 26B).

39. Umbonal separation: a/p.

Separation of the umbones was measured at the umbones. When separation was absent, the umbones touch (Fig. 26a), a condition usually found in the Limopsoidea (sensu Newell, 1969). Inter-umbonal growth is frequently found in the Arcoidea (Fig. 26b) (sensu Newell, 1969) and facilitates the shell valves to gape widely (Morton, 1981). This can lead to breakage of the earlier formed ligament (Thomas, 1976). The region between the two umbones is generally equidistant at both the anterior and posterior extremities of the hinge. However, in *Litharca lithodomus*, this region of the hinge is unsymmetrical, being the widest at the umbones (which are terminal) and taper to point at the anterior

end. Umbonal separation was absent in all the outgroup taxa, with the exception of the Limidae and *Hyotissa hyotis*.

INTERNAL SHELL FORM

40. Inner margin crenulations: (0) absent; (1) restricted to the anterior and posterior extremities; (2) restricted posteriorly; (3) present.

Crenulations are raised elements on the inner ventral margin of the shells (Fig. 27). In conjunction with the hinge teeth, they serve to align and interlock the valves (Thomas, 1975). Very often they reflect the interstices between radial ribs on the outer surface of the shell in the case of *Tucetona* and *Melaxinaea*. There is no such reflection in *Glycymeris*, where the external surface is smooth (contra Thomas (1975) who described the external surface as ribbed). It is possible that these internal crenulations correspond to radial structural elements in an inner layer of the shell (Newell, 1969). This inner margin ornamentation has also been described as scalloped (Newell, 1969) and denticulations (Nicol, 1954, 1967).

41. Posterior tubercles on ventral margin: a/p.

Tubercles are here defined as raised internal elements extending from the distal end of the posterior carina (and/or anterior margin in *Cratis*) dorsally towards the central portion of the shell (Fig. 28). These are distinguished from inner crenulations, which are limited to the ventral margin. Restricted to the philobryid genera *Micromytilus*, *Notomytilus* and *Cratis*, these tubercles, do not necessarily reflect external sculpture, given that the genera *Micromytilus* and *Notomytilus* are externally smooth. As with inner margin crenulations,

the tubercles interlock, possibly reflecting an alignment function between the two valves. These tubercles have been described elsewhere as crenulations (Tevesz, 1977) or denticles (Kauffman, 1969).

42. Posterior myophoric process: (0) absent; (1) buttress; (2) well-developed flange.

A myophore is a calcareous process that aids in the attachment of the adductor muscle, and in inflated taxa, assists in reducing the effect of shearing on the adductor muscle (Kauffman, 1969). This process extends from the anteroventral margin of the posterior adductor muscle dorsally towards the umbonal region of the shell. When present, it appears as a faintly raised ridge, or buttress, or may be more extensive, forming a well-developed raised flange (in larger individuals it can extend up to 0.5 cm) (Fig. 29A). A posterior buttress is characteristic of the Glycymerididae and Noetiidae, with sporadic presence in the other families (Fig. 29B). A projecting myophoric flange is associated with inflated valves and truncated posterior shells. This is characteristic of many Cucullaeidae. A posterior myophoric process is generally absent from the Arcidae, and with the exception of *Lissarca picta,* is absent from all Philobryidae. Myophoric processes (anteriorly and posteriorly) are absent from all the outgroup taxa.

43. Raised anterior buttress: a/p.

The anterior buttress is similar in structure to the faint ridge in character 42 (Fig. 29B). Coding of this character is restricted to those bivalves with an anterior adductor muscle (see character 77). It functions in the attachment of the anterior adductor muscle. As with the posterior myophore, it extends from the internal margin of the adductor muscle dorsally towards the umbones. This buttress is commonly found in the Glycymerididae, Limopsidae and Noetiidae, as well as a minority of Arcidae. *Aupouria parvula* is the sole

philobryid that possess an anterior buttress, however faint this may be (although it is worth noting that it is the only philobryid in this study that possessed an anterior adductor muscle).

44. Elevated adductor muscle scars: a/p.

The site of attachment of the adductor muscles is elevated, such that it forms a slightly elevated platform in some species of *Barbatia*, namely those taxa in the subgenus *Acar* (Fig. 30).

FIGURE 25: External view of the right valve of *Scaphula pinna*: The arrow is pointing to the strong umbonal keel running form the dorsal umbones to the postero-ventral margin.

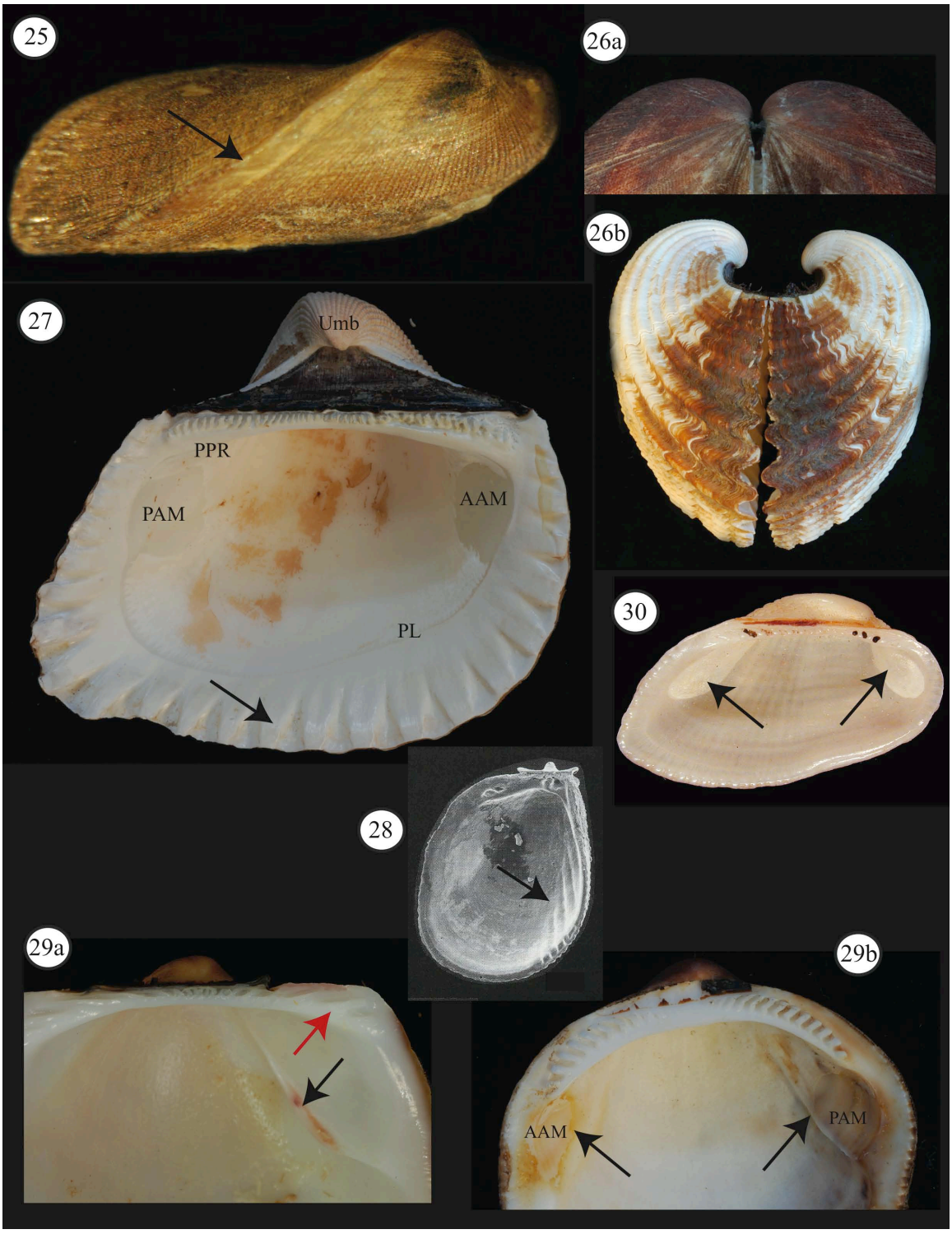
FIGURE 26: Lateral view of hinge illustrating umbonal separation and degree of arching: **(A)** Lateral view of the hinge of *Glycymeris pilosa*. There is no separation between the left and right umbo. The umbones do not arch; **(B)** lateral view of *Larkinia* sp. AMS C.434466; note the overarching umbones.

FIGURE 27: Internal view of *Larkinia* sp. AMS C.434466 illustrating muscle scars: The anterior (AAM) and posterior (PAM) adductor muscles, posterior pedal retractor muscle (PPR), pallial line (PL) and umbones (Umb) are highlighted. The arrow points to the central margin crenulations.

FIGURE 28: Posterior tubercles on the ventral margin of *Cosa waikikia* [image taken from Hayami and Kase, 1993].

FIGURE 29: Longitudinal teeth and myophoric processes: **(A)** Internal view of *Cucullaea labiata*. The black arrow is pointing s to the posterior myophoric flange. The longitudinal teeth on the posterior dorsal hinge ('laterals') are indicated by the red arrow; **(B)** Internal view of *Glycymeris pilosa* highlighting the antererior and posterior adductor muscle scars, with the arrows highlighting the position of the buttresses.

FIGURE 30: Elevated adductor muscle scars: internal view of *Acar dubia kerma* AMS C.62578.


25
26a
26b
27
Umb
PPR
PAM
AAM
PL
30
28
29a
29b
AAM
PAM

HINGE STRUCTURES

The hinge teeth, hinge plate and structures for ligament attachment are dorsally placed, beneath the area of the umbones. While the ligament (in conjunction with the adductor muscles) connects the two valves dorsally and assists in the opening and closing of the valves, it is the hinge teeth that serve to guide the valves into complete and precise apposition. Once the valves are shut, the teeth aid in reducing the shear along the commissure plane. The Arcoida have been described as having taxodont teeth, a configuration of the teeth that are characterized by the presence of numerous relatively undifferentiated interlocking teeth originally described by Neumayr (1883). However, the number and orientation of the teeth in relation to the hinge line varies a great deal across the order and in fact can vary within a species. In this study, the hinge teeth are characterized by their relative position on the hinge line and by their proximity to the umbos. This characterization of teeth in part follows Tëmkin's (2006) treatment of pterioidean teeth. Terminology relating to the hinge structures was taken from Cox et al. (1969).

45. Pseudonymphae: a/p.

Pseudonymphs are modified ostracum that is secreted in advance of the lamellar ligament. They are laid down posteriorly along the border between the fibrous ligament and ostracum (Waller, 1990) and separate the fibrous ligament from the shell. Unlike true nymphae, pseudonymphae do not trap the lamellar ligament in the groove along the dorsal margin. These ligament-support structures appear to be present in all mytiloids

except for those such as *Dacrydium*, which have modified ligament systems consisting only of a resilium, possibly resulting from neoteny (Carter, 1990a). The presence of pseudonymphs is restricted to the pinnid and mytilid outgroup taxa.

46. Hinge line: (0) straight; (1) curved or arched.

The hinge line refers to the ventral edge of the hinge plate from the anterior to posterior ends. In general, the Arcoidea (*sensu* Newell, 1969) possess a straight hinge line (Fig. 3B), while the line curves in the Limopsidae and Glycymerididae (Fig. 3A). No such generality can be seen in the Philobryidae, where both hinge line types are equally prevalent.

47. Teeth series: (0) complete (one continuous series along the hinge plate); (1) two series.

When present, arcoidan teeth are typically laid down in either one or two series along the hinge plate. In those taxa that possess two series, the junction between the series generally occurs ventral to the umbones (except in *Litharca lithodomus*, where the umbones are terminal and the intersection occurs midway along the hinge plate). By and large the distal teeth are larger in size to those placed proximally beneath the umbones. An edentulous gap (see character 51) may or may not separate the two teeth series. When no gap is evident (Fig. 31), the proximal teeth form an oblique crossover between the anterior and posterior series. The teeth in Arcoida are generally laid down in two series; a single continuous series of teeth was observed in a small number of species of *Barbatia*, and in some noetiid and glycymerid taxa. The presence of a complete series is restricted to taxa with both anterior and posterior teeth—the teeth in the philobryid *Aupouria parvula* are present on the anterior end of the hinge plate only. The presence of

this character is dependent on the presence of both anterior and posterior adult teeth (characters 48 and 49).

48. Subumbonal adult anterior teeth configuration: (0) multiple interlocking; (1) single tooth in one valve interlocks with socket in other valve; (2) absent (edentulous).
See character 49.

49. Subumbonal adult posterior teeth configuration: (0) multiple interlocking; (1) single tooth in one valve interlocks with socket in other valve; (2) absent (edentulous).
The microstructure of arcoid hinge teeth is comprised of simple crossed lamellar material. As pointed out by Thomas (1978), the arcoid hinge consists of innumerable variations on a single theme: interlocking simple, relatively undifferentiated teeth that run anteriorly and posteriorly from the umbonal region. The shape of the teeth often conforms to the shape of the hinge line—arcoids with a straight hinge line, will often have thin, simple straight vertical teeth that are perpendicular to the ventral hinge line (as seen in the Arcidae and Noetiidae), while the curved hinge plate of the Glycymerididae and Limopsidae possess somewhat straight teeth, becoming chevron-shaped towards the hinge extremities, where the hinge line curves. In some arcoids (e.g. glycymerids), the teeth have a superficially parallel appearance at the hinge extremities, where the hinge line curves towards the ventral margin. These teeth nevertheless maintain an alignment perpendicular, or obliquely so, to the hinge line. Very often the subumbonal teeth will be perfectly vertical becoming more oblique towards the edges of the hinge plate. The presence of these teeth does not preclude the presence of longitudinal teeth (see characters 49), as both forms may be found on the hinge plate.

The number of multiple interlocking teeth varies greatly across the order. In the Arcidae, we see taxa with as many as 40 teeth in the posterior region of the hinge plate (cf. *Arca noae* and *Barbatia barbata*), while many of the Philobryidae are wanting—this family is the only arcoid family with edentate taxa, and in fact when teeth are present, they rarely exceed five in number of either side of the hinge plate (cf. *Lissarca picta* and *Cratis* cf. *ohasii*). The lack of need for teeth is connected to life habits that have reduced the need to have precision closing of the two valves (Carter et al., 2000). In the outgroup taxa, the teeth configuration, when present, consisted of a single tooth in one valve interlocking with a socket in the other valve. The multiple interlocking teeth of the mytiloid taxa are not considered true cardinal teeth (see character 54) and so were coded as absent.

50. Longitudinal orientation of teeth: (0) present in both anterior and posterior sides of hinge plate; (1) restricted to posterior end of hinge plate; (2) anterior only; (3) absent. In defining bivalve hinges, Cox et al. (1969) described two forms of teeth with a longitudinal orientation, based on their proximity to the umbones—lateral and pseudolateral teeth (see character 51). Here, this definition is further refined by the relative alignment of the teeth to the dorsal hinge line. Longitudinal teeth are parallel to the dorsal hinge axis as opposed to the ventral hinge axis, as acutely oblique teeth on a curved hinge line will appear superficially like longitudinal teeth (cf. *Scaphula pinna*). These teeth are few in number, with no more than five being found on either side of the hinge plate.

Longitudinal teeth are typical of the Parallelodontidae and the Cucullaeidae (Fig. 29A: red arrow), with the teeth often being found on both sides of the hinge plate. In the

Arcidae, the longitudinal teeth, like those seen in some species of *Bathyarca*, *Bentharca* and *Samacar*, are mostly restricted to the posterior margin. This character is not applicable to edentate taxa. Longitudinal teeth are seen in the limid outgroup taxa only.

51. Growth of longitudinal teeth relative to the umbones: (0) proximal; (1) distal.

The proximal end of 'lateral' teeth is well separated from the umbonal region and is placed closer to the anterior and/or posterior extremities of the hinge (Fig. 29A). 'Pseudolaterals' have a similar longitudinal orientation to lateral teeth, but in this case, the proximal end of the teeth extends to the cardinal region beneath the umbones. This character is restricted to teeth with a longitudinal orientation (see character 49).

52. Edentulous space: a/p.

A gap in the hinge line is found in some arcoid taxa (Fig. 32). When present, this space divides the two teeth series on the internal dorsal hinge, below the central umbonal region. The presence of two teeth series does not compel the occurrence of an edentulous space—there are many cases where there are two series and yet a gap is absent e.g. *Litharca lithodomus*. The edentulous spaces can be minor as in *Barbatia* or quite extensive, spanning up to a third of the hinge axis, as in many *Bathyarca* species. This character applies to bivalves with a two series hinge only (characters 48 and 49).

53. Teeth striation: a/p.

Minute striations are found on taxodont teeth (Fig. 33). These striations, present on both sides of the teeth, are characteristic for all 'Eutaxodonta' and have been described as radially arranged fibrous structure (Omori et al, 1976). This striate sculpture on the anterior and posterior surface of the teeth was present in all the examined arcoid taxa except *Lissarca rubrofusca* and *Lissarca notorcadensis.*

54. Oblique furrow: a/p.

On the crest of the hinge teeth a small oblique furrow may be found in some taxa (Fig. 33). The corresponding socket does not have a ridge reflecting this depression (Tschudin, 2001). An oblique furrow is found in the arcid taxa *Arca noae*, *Barbatia aymgdalumtostum* and *Trisidos*, the noetiid *Striarca* sp. MNHN101, and in all Glycymeridiidae, with the exception of *Glycymeris grayana*. The presence of this furrow is a product of sequential growth of ridges on the anterior and posterior sides of the tooth (Tschudin, 2001). The presence of this character is dependent on the presence of anterior and/or posterior adult teeth (characters 48 and 49).

55. Simple teeth: a/p.

Simple teeth are not true cardinal teeth (Le Pennec, 1980) but merely small teeth situated on either side of the ligament, ventral to the umbones. It is thought that these 'teeth' are external manifestations of internal radial ribs. This has been described as 'dysodont' (Cox et al., 1969) and is restricted to the Mytilidae outgroup taxa.

LIGAMENT

The ligament is an almost uncalcified part of the shell that in conjunction with the relaxed adductor muscles abducts the valves. It is secreted by the mantle and consists of two parts: an upper lamellar band; and a lower fibrous layer. An antagonistic relationship exists between the ligament and the adductor muscles—when the valves are closed the lamellar band of the ligament is stretched and the fibrous part beneath is compressed. Upon relaxation of the adductor muscle, the stress on the lamellar and fibrous bands is

released and the valves open (Trueman, 1969; Thomas, 1976). Shallow burrowers have relatively weak ligaments (the foot aids in opening the valves), while swimmers have stronger more efficient ligaments (Newell & Boyd, 1987).

Ligament systems in bivalves are highly complete and exhibit a great range of systems and subsystems (Malchus, 2004a). Definitions of the bivalve ligament terminology used in these analyses are mostly taken from Newell & Boyd (1984), Carter (1990), Ubukata (2003) and Malchus (2004a). The ligaments of the Arcoida have been reviewed in depth by Thomas et al. (2000).

56. External ligament: a/p.

External ligaments either attach above the hinge dentition or at or near the dorsal shell margin in edentulous species (Carter, 1990a). Ligaments of this type, located near the ventral margin of the hinge plate, are predominant in the Arcoida. The fibrous portion of the larval ligament continues growing ventrally down the hinge plate, becoming an internal ligament in the Philobryidae. Of the outgroup taxa, *Anomia simplex* is the sole taxon in possession of an internal ligament.

57. Restriction of fibrous portion of ligament to resilifer: a/p.

The ligaments in the Arcoida generally attach to the surface of the hinge and lack any support structures (Malchus, 2004a). Simple ridges and/or grooves are present in the majority of Arcoida, with the fibrous portion generally being laid down in the grooves. Resilifers are hollowed out depressions in which the fibrous portion (the resilium) of an alivincular (or multivincular ligament: see character 58) ligament resides. Alivincular ligaments can be external or internal ligaments (Fig. 32). The Philobryidae possess

internal alivincular ligaments. The Limopsidae have been considered to possess a 'secondary alivincular' ligament, which has been regarded as a pedomorphic derivative of the duplivincular ligament (Ubukata, 2003). Resilifers are seen in the pterioidan and limid outgroup taxa.

58. Serial repetition of resilifer (resilium): a/p.

Serial repetition of resilifers of the alivincular type is not seen in any of the ingroup taxa. As with alivincular ligaments, the pad of fibrous ligament (resilium) is flanked on either side by lamellar ligament and restricted to the triangular resilifer. This external ligament is generally opisthodetic and is characteristic of Isognomonidae). Ligaments of this type are classed as multivincular.5

59. Ligament position relative to the prodissoconch: (0) opisthodetic (Fig. 34A); (1) elongate amphidetic (extending on either side of the beak) (Fig. 34B) (Yonge, 1978); (2) central amphidetic (small diamond or triangle shaped area just ventral to the umbones) (Fig. 34C); (3) prosodetic.

There has been much disagreement as to the primitive condition of the bivalve ligament. Yonge (1978) suggested that primitive bivalves were more or less equivalve with an amphidetic external ligament. He asserted that the ancestral ligament would have been two-layered, but covered additionally by an external periostracal layer. However, other authors have concluded that the primitive ligament was opisthodetic (Newell and Boyd, 1987; Waller, 1990, 1998). Given that the Protobranchia, the most primitive of the bivalves, possess an opisthodetic ligament, this was taken as the most primitive state in this analysis.

60. Ligament growth: (0) new elements laid down at or near the middle of the pattern; (1) new elements laid down anteriorly and posteriorly; (2) new elements laid down anteriorly and extends posteriorly.

In most arcoids, the zone where the lamellar ligament is secreted lies near the umbones. As the shell grows, this sheet migrates anteriorly and posteriorly. The tracks of these zones form two sets of oblique ridges and grooves on the ligamental areas where they are attached. The pattern of ligamental growth is found in most Paleozoic arcoids. The Noetiidae depart from this pattern in that the insertion of the lamellar ligament is laid down in vertical strips as opposed to the oblique strips of other arcoids (Fig. 35). The lamellar strips are embedded into the sheet of fibrous ligament and are laid down at the anterior and posterior ends of the dorsal hinge. This is accomplished by fixing the site of secretion of the lamellar strips, instead of migrating it along the axis (Thomas et al., 2000). Ligament growth of alivincular ligaments begins beneath the umbones, with a central fibrous band flanked on both sides by lamellar material. The ligament emerges beneath the umbones also in the pteriid outgroups and extends towards the anterior nad posterior ends of the hinge. In the Pinnidae and Mytilidae, the post larval ligament is laid down anterocentrally and extends towards the posterior end of the hinge (Malchus, 2004a).

61. Ligament striation of duplivincular ligament: (0) oblique ligamental grooves (Fig. 34B); (1) vertical ligamental grooves (Fig. 35).

Duplivincular ligaments are external ligaments wherein pairs of lamellar and fibrous conchiolin sublayers are repeated. These repetitions take two forms—perpendicular to the hinge plate, with each sublayer being parallel to the next; or the sublayers appear as

oblique or sub-oblique bands along the cardinal area. The former is unique to the Noetiidae, while oblique ligamental grooves are found in all other arcoids with a duplivincular ligament. A duplivincular ligament is found in all arcoid taxa except the Limopsidae and Philobryidae.

The duplivincular ligament is considered primitive because its components simply alternate rather than being segregated in positions appropriate to their functional roles. This serial construction is the simplest of several strategies that emerged early in the evolutionary radiation of the bivalves to offset the effects of breakage of lamellar ligament in animals of increasingly larger size.

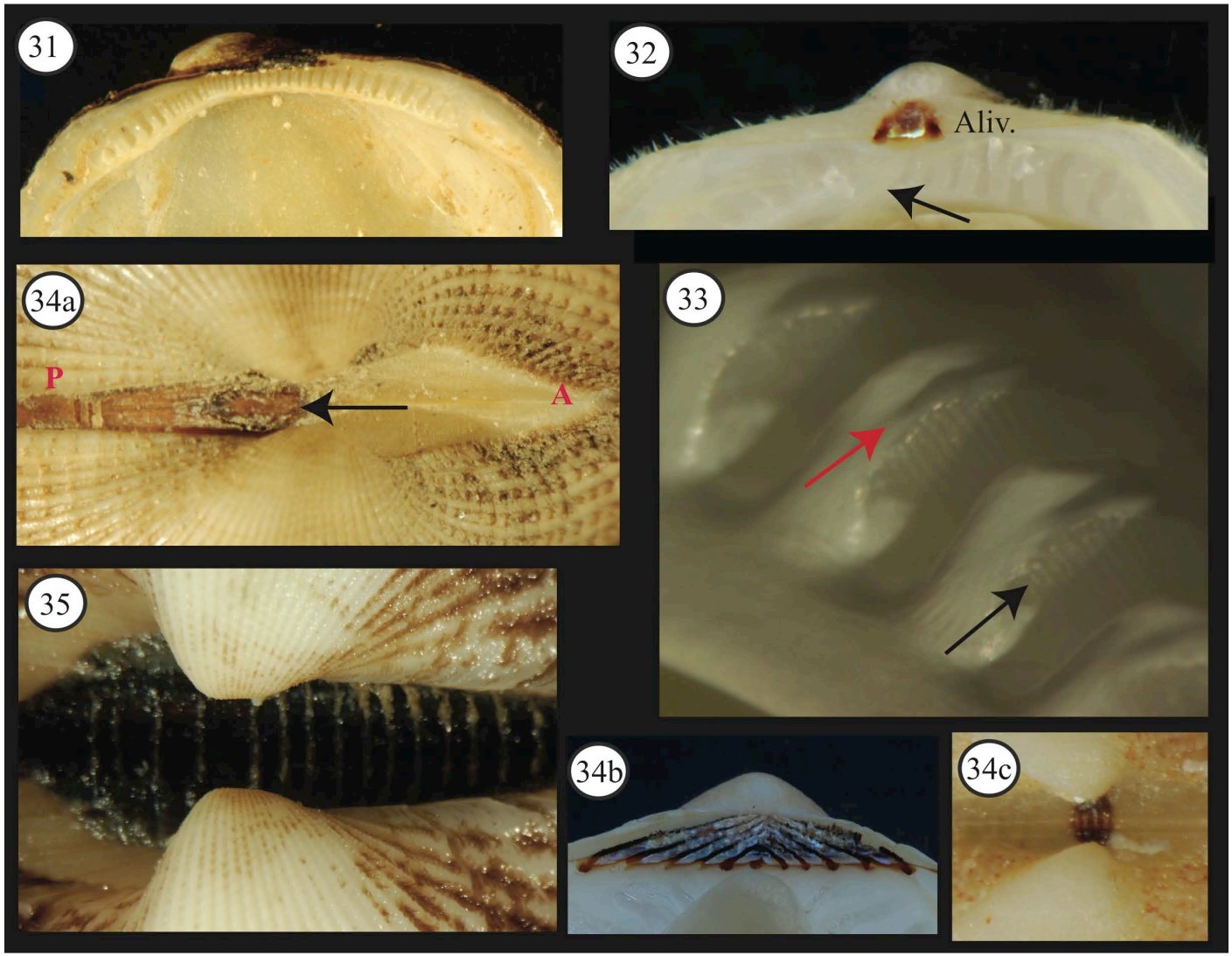
FIGURE 31: Internal view of *Sheldonella repenta*: the hinge lie is comprised of a single row of teeth, with no edentulous gap.

FIGURE 32: Internal view of hinge of *Limopsis aurita*: the arrow is pointing to the edentulous gap that separates the anterior from the posterior row of teeth. The ligament is of the alivincular type, resting in a resilfer.

FIGURE 33: Magnification of teeth of *Tucetona pectunculus*: striations (black arrow) and oblique furrow (red arrow) are highlighted.

FIGURE 34: Ligament position relative to the prodissoconch: **(A)** Opisthodetic, duplivincular ligament; **(B)** amphidetic, duplivincular ligament; **(C)** central amphidetic ligament of *Arcopsis adamsi*.

FIGURE 35: Transverse, amphidetic ligament of *Noetia ponderosa.*


31
32
Aliv.
34a
P
A
33
35
34b
34c

FOOT AND BYSSUS

In bivalves, the foot is the primary organ for locomotion, burrowing and attachment, although its primary function in the Anomioidea is in cleaning the mantle cavity (Yonge, 1977). In the Pteriomorphia, the sole of the foot is distinct from the lateral walls of the foot, even when the foot is withdrawn (Waller, 1998). The byssus is a structure associated with the foot that enables attachment of the bivalve to features such as rocks and corals. Secreted by the byssal gland in the foot, it is comprised of proteinaceous thread(s).

62. Foot: (0) present; (1) present with two distinct components (2) absent.
The presence of a foot is considered to be the plesiomorphic condition and is found in all bivalve larvae, only becoming lost in some adults, namely those that cement to a hard substrate (although some cementing bivalves retain the foot) (Cox et al., 1969). It is found in all arcoid adults and is laterally compressed. The presence of a foot is presumed present in the extinct taxon Parallelodontidae. Given the shape of the shell, the foot is considered to have an orientation that is parallel to the ventral margin of the shell (character 63). The foot is divided into two parts in the outgroup taxon *Malleus candeanus* (Pelseneer, 1911), with a shorter primary foot associated with byssal secretion and an 'accessory' foot associated with cleaning of the mantle cavity. The absence of an adult foot is restricted to the outgroup taxon *Hyotissa hyotis*.
63. Orientation of the foot axis: (0) 0°—parallel or subparallel to the ventral margin of the shell (Fig. 36); (1) 45°-90°—at an angle between 45° and 90° to the ventral margin of

the shell (Fig. 37); (2) 180°—the foot is rotated at an approximate angle of 180° relative to the ventral margin of the shell.

Two major trends in the orientation of the foot, relative to the ventral margin, are seen in the Arcoida. The foot is parallel or subparallel to the ventral margin in the Arcidae, Noetiidae, Cucullaeidae and Parallelodontidae, while it is orientated at an angle between 45° and 90° to the ventral margin in the Limopsidae and Philobryidae. The foot is often wedge or anvil shaped in those taxa with a 0° orientation and slender with distinct anterior (toe) and posterior (heel) regions. The foot is parallel to the ventral margin in the pinnid outgroup taxa. All other outgroup taxa have a foot that is orientated at an angle between 45° and 90° to the ventral margin, with the exception of *Anomia simplex* and *Malleus candeanus*, which have a foot orientated at 180° to the ventral margin, such that the ventral groove of the foot is facing anteriorly. This character is dependent on the presence of a foot and so therefore does not apply to the sole bivalve in this study that does not possess a foot, *Hyotissa hyotis*.

64. Pigmented cells on the foot: a/p.

Pigment granules are known to form in bivalves in response to light (List, 1899). These granules are evident on the foot of many arcid and glycymerid taxa and are embedded in the tissue of this organ. Given that the pigment is embedded into the tissue, this is distinguished from the pigmented epithelial sheath around the visceral mass present in some arcoid taxa (see character 94). *Pteria colymbus* was the lone outgroup taxon to exhibit this characteristic.

65. Byssus: (0) absent; (1) present in larvae and adults; (2) lost in adults.

In animals that produce a larval but not an adult byssus, it is assumed that the animal lost the adult byssus secondarily, and therefore the character is treated as additive. In cases where a byssal gland is evident, but the byssus is found lacking, this is considered 'lost in adults'—this is found in Limopsidae and Glycymerididae. The emergence of the byssus from the bivalve is dependent on the orientation of the foot. In the arcid taxon *Senilia senilis*, a small number of byssal threads have been observed in spat sized individuals that assisted in anchoring them to sand particles (Yoloye, 1975). Given the presence of a byssal gape in the ventral region of the shell in the Parallelodontinae, the presence of a byssus is considered to be present.

66. Form of byssus: (0) thread-like (Fig. 38A); (1) sheet-like (Fig. 38B); (2) calcified. The form of the byssus in Arcoids is in two forms: it may be in the form of threads that are either discrete or fused, or it may be sheet-like (see character 67). The outgroup taxon *Anomia simplex* has a calcified byssus, by which is adheres to hard substrates.

67. Fusion of byssal threads: (0) threads discrete (Fig. 38A); (1) byssal threads fused, but tips of individual threads are free; (2) byssal threads completely fused (Fig. 38B). The degree of fusion of the byssal threads is somewhat reflective of the mode of life. In *Arca* the byssus is hypertrophied and extends along much of the ventral surface of the animal. These animals restrict their movement to wedging into deep crevices and so the foot has lost a lot of its locomotary function. The byssus holds the animal firmly in place. Thin thread-like byssi are easily re-secreted if the animal is detached from its resting place.

68. Byssal gape: a/p.

An opening passage for the byssus when the shell is closed is present in a number of arcoid taxa (Fig. 39). The gape can be quite expansive, allowing passage of a large thickened byssus as seen in *Arca* or can be a slight opening as in *Neocardia* sp. A. This byssal gape is present in both juveniles and adults. A gape is absent from all other arcoids except the philobryid taxa *Philobrya munita* and *Neocardia* sp. A. In the Arcidae, this gape lies at the ventral margin of the shell, reflecting the positioning of the foot inside. Given that the orientation of the foot in the Philobryidae is between 45°-90° relative to the ventral shell margin, the byssus emerges dorsally. A gape is found in all the outgroup taxa except *Lithophaga aristata* and the ostreid *Hyotissa hyotis*, which lacks a foot. It is not surprising that *Lithophaga* lacks a byssus, given that this taxon is a known borer of calcareous substrates.

69. Byssal groove: (0) slit-like; (1) pear-shaped.

This groove runs along the underside of the foot. The groove is found in all arcoid adults, irrespective of whether they have a byssus. The groove can be shallow in the case of *Limopsis loringi* or deep as in the philobryids and can extend along the entire undersurface of the foot or can be limited to the extremities (see character 71). In *Bathyarca pectunculoides,* the byssal groove consists of a single channel, while that of *Trisidos* is composed of a number of radiating channels, surrounded by a very large byssal gland. A pear-shaped byssal groove was limited to the outgroup taxon *Anomia simplex*.

70. Byssal gland: (0) indistinct (1) distinct.

The byssal gland, located around the ventral byssal groove of the foot, is involved in the secretion of the byssus. When present, this gland can be quite distinct (pink or yellow in

color) or indistinct and not discernible from the surrounding tissue (the pink gland is visible in Fig. 40). In many arcoid taxa, a distinct byssal gland is evident at the ventral base of the foot. This character is dependent on the presence of a slit-like byssal groove (character 68).

71. Extension of byssal groove: (0) extends all the way along the undersurface of the foot; (1) partial extension along the undersurface of the foot.

Partial extension can be from the anterior end to the center or from the posterior end to the center.

72. Pedal papillae: a/p.

Pedal papillae lies in a pit at the undersurface of the foot. These papillae mark the site of attachment of the byssus to the foot (Fig. 38B). The papillae are present in those species with a thickened, large byssus but absent in species with singular thread-like and sheet-like byssus. This character is coded in species with a ventral byssal groove only (character 64).

FIGURE 36: Internal view of whole body of *Tucetona flabellata*: The anterior (AAM) and posterior adductor muscle (PAM), the ctenidia, ctenidial suspensory membrane (CSM) and the hanging anus (red arrow) are highlighted. The line along the ventral foot illustrates the near 0° angle of the ventral margin of the foot. The posteroventral margin of the mantle is pigmented.

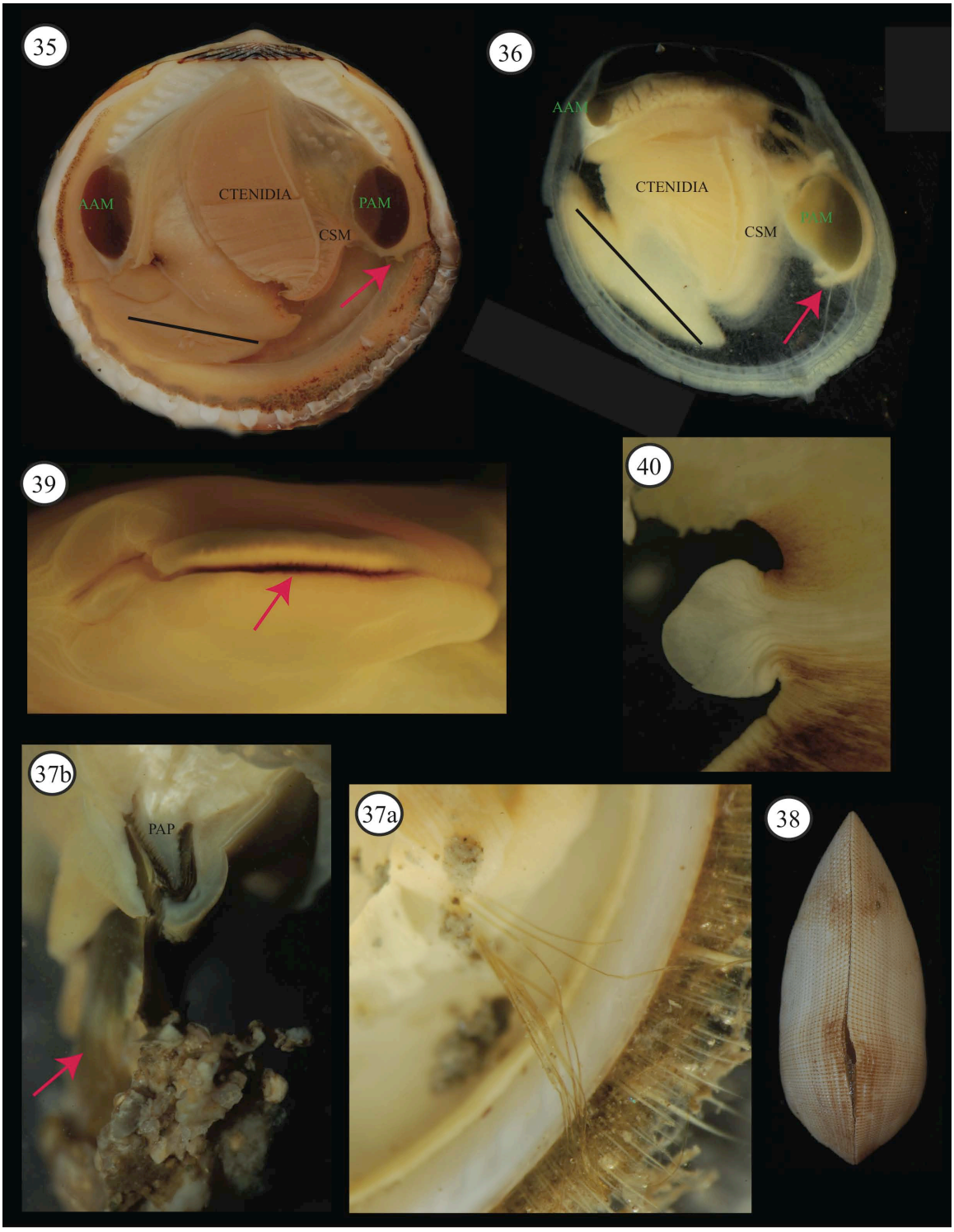
FIGURE 37: Whole body of *Limopsis aurita*: Highlighted are the anterior (AAM) and posterior adductor muscle (PAM), the ctenidia, ctenidial suspensory membrane (CSM) and the hanging anus (red arrow). The line along the ventral foot illustrates the near 45° angle of the ventral margin of the foot.

FIGURE 38: Byssal form in Arcoida: **(A)** Thread-like byssus of *Limopsis aurita*; **(B)** lateral view of the foot *Barbatia candida*. The sheet-like byssus (indicated by the red arrow) is attached to the byssus by the pedal papillae (PAP).

FIGURE 39: Ventral byssal gape of *Barbatia tenella*.

FIGURE 40: Ventral byssal groove or furrow of *Barbatia tenella*: located on the undersurface of the foot of *Barbatia tenella*, the pink byssal gland is highlighted.

FIGURE 41: Posteriorly directed process on the visceral mass of *Glycymeris crebreliratus*.


35
AAM
CTENIDIA
PAM
CSM
36
AAM
CTENIDIA
CSM
PAM
39
40
37b
PAP
37a
38

COMPONENTS OF THE VISCERAL MASS

73. ***Posteriorly directed process on the visceral mass***: a/p.

A non-muscular protuberance on the posterior edge of the visceral mass and dorsal to the foot is found in all glycymerid species and in some arcids (Fig. 41) (e.g. *Arca noae*). In the vast majority of glycymerid species examined, this appeared as an inconspicuous bump at the side of the posterior visceral mass, directly opposite the area where the posterior mantle margins appose to form the exhalent current. However, in *Glycymeris formosus*, this extension from the visceral mass was quite extensive and the epithelial cells appear ciliated. The function is unknown, but given the location and ciliation, it is likely to have a sensory function. This process was only found in one outgroup taxon, *Brachidontes domingensis*.

74. Pallial organ: a/p.

The pallial organ as defined by Yonge (1953) (the mantle organ or gland of Grave, 1911), is a highly prominent stalk-like organ, divisible into a tube and a more swollen head that projects posteriorly from the posterodorsal region of the visceral mass. This organ functions in chemical defense and to a lesser degree 'house-keeping' of the mantle cavity (Liang & Morton, 1988), this organ is confined to the pinnid outgroup taxa.

MUSCULATURE

Molluscan muscles leave conspicuous scars at the point of contact of the muscle and the inner shell layer or inner ostracum. The adductor muscles extend between the two valves

and serve to draw the two valves together. Bivalves can have either one (monomyarian) or two (dimyarian) adductors (Lamarck, 1812). When the anterior and posterior muscle scars are approximately of the same size, the shell is said to be isomyarian or homomyarian**.** When they are significantly unequal the shell is anisomyarian or heteromyarian. The anisomyarian condition is reflective of an epibyssate lifestyle with the anterior adductor muscle being reduced in size relative to the posterior adductor muscle (Fig. 36) and a corresponding reduction in the anterior region of the shell, as well as an anterior shift of the umbonal region. Species that have been described as having sub-equal adductors (e.g. *Tutecona* species: Fig. 36) are considered to be isomyarian and only those that show a significant difference in the size of the adductors as anisomyarian (e.g. *Arca* species).

75. Anterior adductor muscle (or scar) (AAM): (0) present (isomyarian); (1) reduced (anisomyarian); (2) absent (monomyarian).

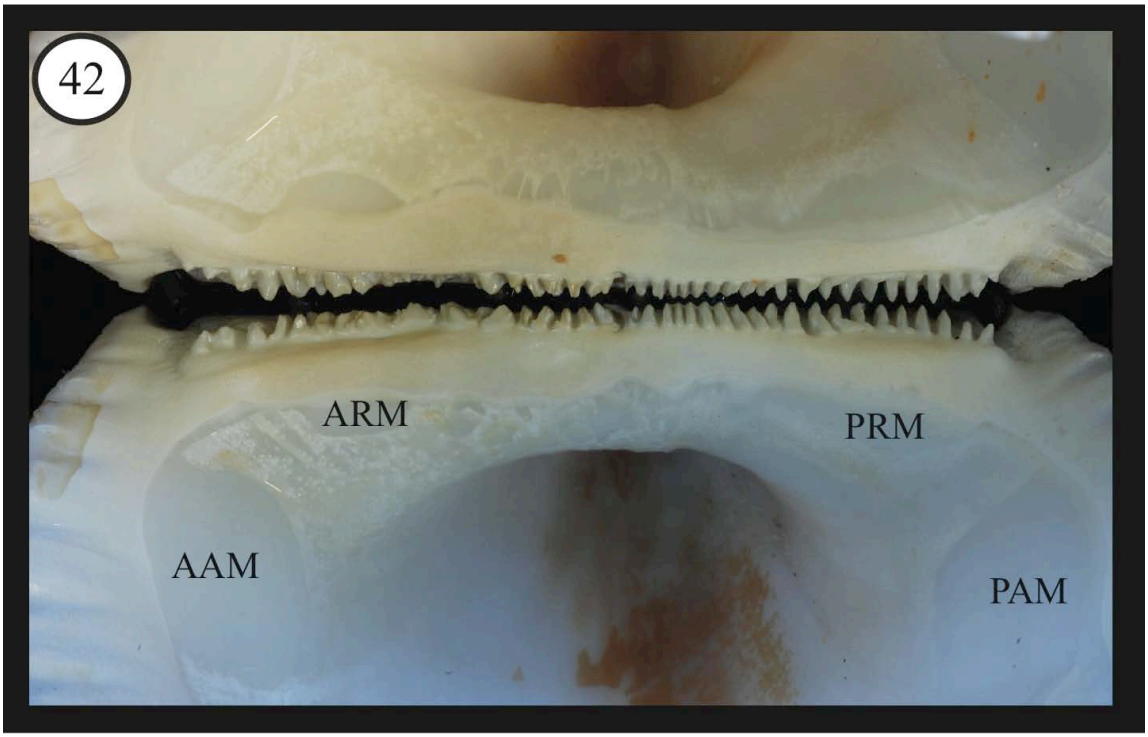
All bivalves have two adductor muscles when they are juveniles, however, the anterior adductor may be lost as adults. The presence of two muscle scars of similar size (isomyarian condition) seems to be the plesiomorphic state for bivalves. The monomyarian condition is restricted to members of the Philobryidae and outgroup taxa. On the basis of ontogenetic criteria, this character is treated as additive.

76. Posterior adductor muscle or scar (PAM): (0) present; (1) reduced in size with respect to the anterior adductor (anisomyarian condition).

77. Crescent-shaped posterior adductor muscle: a/p.

In all arcoid taxa the PAM is either subcircular or subrectangular in shape. The former is generally found in the Arcidae, Glycymerididae, while the latter in the Noetiidae, Cucullaeidae. A crescent-shaped PAM is restricted to the outgroup taxa *Atrina rigida*, *Isognomon alatus*, *Malleus candeanus* and *Pinctada mazatlantica*. A crescent shaped PAM can range in extremity from a bean-shaped PAM to a moon-like crescent.

FIGURE 42. Internal view of the hinge line of *Anadara trapezia* from a ventral perspective. Anterior and posterior adductor and pedal retractor muscles are highlighted.



78. Posterior adductor muscle scar distinctly pigmented: a/p.

Pigmentation of the posterior adductor muscle is found in some glycymerid taxa *Tucetona flabellata* and *Glycymeris crebreliratus*.

79. Pedal retractors equal in size: (0) equal; (1) unequal.

The symmetry of the anterior and posterior pedal retractors is generally unequal in the Arcoida (unequal in Figs. 37, 42). The posterior pedal retractor is usually much larger, at least two to three times larger in *Arca zebra*.

80. Position of posterior pedal retractor muscle (or scar) (PPR) relative to PAM (or scar): 0) anterodorsal; (1) ventral.

Throughout the Arcoida, the posterior pedal retractor muscle is in a position that is anterodorsal to the PAM. The relative position of these muscles is discussed below (see character 81). It is only in the limid outgroup taxa that the muscles were placed ventral to the PAM.

81. Relative position of PPR (or scar) to PAM (or scar): separate (Fig. 42); (1) confluent.

The PPR and PAM are generally separated in the Arcoida, such that they form two distinct scars on the inside of the valve. In the Philobryidae, however, the PPR is adjacent to the PAM such that this two muscles form one posterior scar on the inside of the shell valve. This condition is also prevalent in the outgroup taxa bar Isognomon alatus and Ctenoides scaber where they are separate.

82. Position of posterior adductor muscle scar relative to the pallial line: (0) postero-ventral margins of adductor confluent with the pallial line (see Fig. 27); (1) posteroventral margin separated from the inside of the pallial line or the adductor scar is entirely within the pallial line.

A posterior adductor muscle scar that is confluent with pallial line is the prevalent condition in the Arcoida, but is separate from the pallial line in the arcid taxa *Arca*,

Trisidos, *Litharca* as well as some *Barbatia* species and in the philobryid taxon *Aupouria parvula*. This character is dependent on the presence of a pallial line and so does not apply to any of the species of *Bathyarca*, which lacked a pallial line.

MANTLE

The bi-lobed mantle surrounds the organs and visceral cavity. Historically the plesiomorphic condition of the bivalve mantle edge was considered to consist of three folds that take the form of an inner (muscular), middle (sensory) and outer (secretory) fold (Yonge, 1957), with the periostracal groove placed between the middle and outer fold. While many bivalve workers still cling to this traditional view of mantle classification, the number of folds and their functions in actuality vary greatly across the Bivalvia, making it difficult to establish homology, especially for distantly related taxa. The periostracal groove alone appears to be homologous across Bivalvia. To circumvent this problem, Waller (1978) adopted a system whereby the folds are described as either outer (OF) or inner (IF) relative to their position to the periostracal groove, and they are numbered consecutively outward from the periostracal groove. The adoption of this system of categorizing the folds reduces the confusion in the establishment of homologies across the mantle layers—Yoloye (1975) believed that *Senilia senilis* had a unique mantle condition in that the periostracum was secreted by the inner surface of the middle mantle lobe as opposed to the inner surface of the outer mantle lobe, the lobe that was customarily believed to secrete the periostracum. Using Waller's system, the periostracal groove for this taxon in fact lies between OF-1 and IF-1 (with an additional outer fold,

OF-2, distally). Terminology for the mantle margin follows that of Waller (1978, 1980). It is likely that the confusion surrounding the number of folds in the mantle edge might relate to the presence of sub-folds—it is believed that distinguishing between a fold and a sub-fold is a subjective determination and so all folds, whether sub- or otherwise are considered as folds in this study.

83. Multiplication of the outer mantle fold: (0) absent (OF-1); (1) duplicate (OF-1/OF-2) (Fig. 43); (2) triplicate (OF-1/OF-2/OF-3) (Fig. 44).

The first outer fold (OF-1) is prominent in all arcoid species. The compound eyes, if present, are found on the crest of this fold and exist under the transparent periostracum. The second fold (OF-2), when present, has the classic secretory function. This fold is always shallow. It is unclear what the function of the third outer fold.

Waller (1980) examined the shell microstructure and mantle fold condition of a number of arcoid taxa. In this exceptional work he described the Arcoida as having two patterns of mantle fold arrangement: a three fold condition: with two outer and one inner fold (as seen in *Arca* and *Glycymeris*); and a four mantle fold condition, with two inner and outer folds (as seen in *Barbatia*) (although he does mention the existence of a two fold condition, but does not say in which taxon this condition is found). However, no consistent pattern in the arrangement of the mantle folds was observed in the Arcoida in this study—a triplication of the outer mantle was evident in all the *Arca* species examined in this study, with the exception of *Arca ventricosa* that had two outer folds. The majority of the other arcid genera have two outer folds (except *Barbatia tenella*, *Barbatia candida*, *Senilia senilis*, *Litharca lithodomus* and *Fugleria* species, which had two outer

mantle folds). *Cucullaea labiata*, Noetiidae, and all limopsids (except *Limopsis forteradiata*: OF-1 only) possess a duplication of the outer mantle fold. The great majority of Glycymerididae have three outer folds (except the genus *Melaxinaea*). The Philobryidae exhibit all of the three character states. *Lissarca picta* and *Micromytilus crenulatifera* were the only taxa seen to exhibit the two fold condition of Waller (this taxa were not included in his examination). A single outer mantle fold is found in *Anomia simplex*, *Pinctada mazatlantica*, *Hyotissa hyotis* and the mytiloid and pinnid outgroup taxa. A duplication of the outer fold is also found in the remaining outgroup taxa.

84. Multiplication of inner mantle fold: (0) absent (IF-1) (Figs. 43, 44); (1) double (IF-1/IF-2); (2) triple (IF-1/IF-2/IF-3).

A similar inconsistency across higher taxonomic groupings in mantle fold arrangement is also seen with the inner mantle folds. Species of the genus *Arca* possess a single inner mantle fold. A single or double mantle fold is observed in the Arcoida. A three fold inner mantle condition was evident only in the outgroup taxon *Lithophaga aristata*. A second inner fold has been described previously for *Senilia senilis*, *Anadara notab*ilis, *Anadara planicostata* and for a *Barbatia* sp. (Waller, 1980), however, contra Waller's assertion otherwise, no evidence of a second inner fold was found in *Anadara notabilis*. The inner folds of the mantle are very often thrown into folds in the posterior region of the animal giving it an overall scalloped appearance. It is likely that these folds interlock, effectively forming a mantle curtain, a condition that is similarly found in scallop bivalves (Waller, 1976).

85. ***Pustules present on innermost mantle fold***: a/p.

On the distal edge of the innermost mantle fold, the surface is lined with somewhat circular unpigmented pustules (Fig. 47). These pustules are especially prominent in the posteroventral region of the mantle edge. Waller (1980) described a similar structure on the distal edge of the second outer fold in some of the arcoid taxa he examined. He described these structures as adhesive pads, which would make sense in assisting the outer mantle edge in sticking to the inner shell margin. The need for an adhesive pad on the innermost mantle margin seems unlikely. Pustules were observed only in the arcid taxa *Barbatia cancellaria*, *Barbatia* sp. PR01, *Anadara antiquata*, *A. notabilis* and in the philobryid *Adacnarca limopsoides*.

86. ***Commarginal ridges on mantle folds***: a/p.

Commarginal grooves or ridges on the proximal side of the mantle folds are prevalent in the Arcoida (Fig. 45). These ridges give the mantle folds a wrinkled appearance. It is unclear what the adaptive significance of these grooves may be.

87. Tentacles IF-1: (0) absent; (1) simple; (2) complex.

See character 88.

88. Tentacles IF-2: (0) absent; (1) simple; (2) complex.

Tentacles on the inner mantle folds are prevalent in many pteriomorphian taxa (Waller, 1978). Sensory in nature, these are restricted to the outgroup taxa (except the mytilid *Lithophaga aristata*).

89. Mantle flap or extension: a/p.

First described by Pelseneer (1911), the inner mantle fold is enlarged posteriorly, such that each mantle forms an extensive flap. When extended, these flaps essential form very

simple siphons (Fig. 46). There is an associated gland for these flaps, situated posteroventrally. This character is autapomorphic for *Bathyarca*.

90. Mantle fusion: (0) ventral margin open, unfused; (1) single mantle fusion at posterior end of ventral margin; (2) siphons.

The vast majority of bivalves have some degree of mantle fusion along the ventral mantle margin (Newell, 1969). Yonge (1939, 1957) proposed that the presence of an anterior incurrent flow and the lack of fusion of the mantle lobe ventrally are plesiomorphic characters for bivalves and for the Pteriomorphia. This condition is also typical of juvenile bivalves. With the anisomyarian condition, the incurrent and excurrent apertures have moved to the posteroventral position and it is this area that lies close to the substratum (Morton et al., 1998). Freedom of the mantle lobes is found in all arcoid as well as pterioidean outgroup taxa. While fusion of the mantle margin in lacking in the Arcoida, the mantle is intimately apposed, such that inhalant and exhalant currents are produced. Fusion at a single place at the posterior margin allows the formation of a small opening through which the exhalent current passes. This condition is found in most Mytilidae. Siphons are tube-like extensions of the mantle that function in the movement of water and wastes into and out of the body. Found in most heterodont taxa, they are also present in outgroup genus *Lithophaga*, which exhibits extensive fusion both above and below the excurrent opening that results in an excurrent siphon.

91. Waste canal: a/p.

Lying parallel to the mantle margin, the waste canal consists of a ciliated groove bound by folds above the surface of the mantle. This canal lies close to the upper edge of the

ascending lamellae of the outer demibranchs of the gill (Grave, 1911; Yonge, 1953). This is restricted to the pinnid outgroup taxa.

92. Glandular development of mantle tissue: a/p.

The mantle tissue is quite glandular and thick in the Arcoidea + Glycymerididae (sensu Newell, 1969), but virtually transparent in the Limopsidae and Philobryidae.

93. Pigmentation of mantle margin edge: a/p.

On the edge of the mantle is often pigmented dark brown-black in arcoid taxa (Fig. 36). This pigmentation can be irregularly speckled (as in *Barbatia obliquata*) or quite heavy, especially in the posteroventral region of the mantle (as in *Arca noae*). This pigmentation is in deep contrast to the rest of the mantle tissue (*Ctenoides scaber* is entirely pigmented red).

94. ***Epithelial sheath of pigmented cells on mantle surface***: a/p.

When present, the entire face of the external mantle surface is covered with a thin sheath of epithelial cells that are conspicuously pigmented, given it a somewhat speckled appearance (when examined with a microscope). It is unclear why pigmented cells, which are sensitive to light, would be seen on the anteriormost portion of the mantle, beneath the umbones, where the mantle is unlikely to see much light.

95. Tumescent spots on mantle edge: a/p.

White opaque spots are found on the posterior region of the inner-most mantle fold (Fig. 61). Described by Waller (1980) as tumescent spots or papillae, it was postulated that these blotches formed in areas that were reachable by light (Atkins, 1936; Sullivan, 1961). This has been observed in a number of taxa, e.g. *Anadara trapezia* and *Glycymeris glycymeris*).

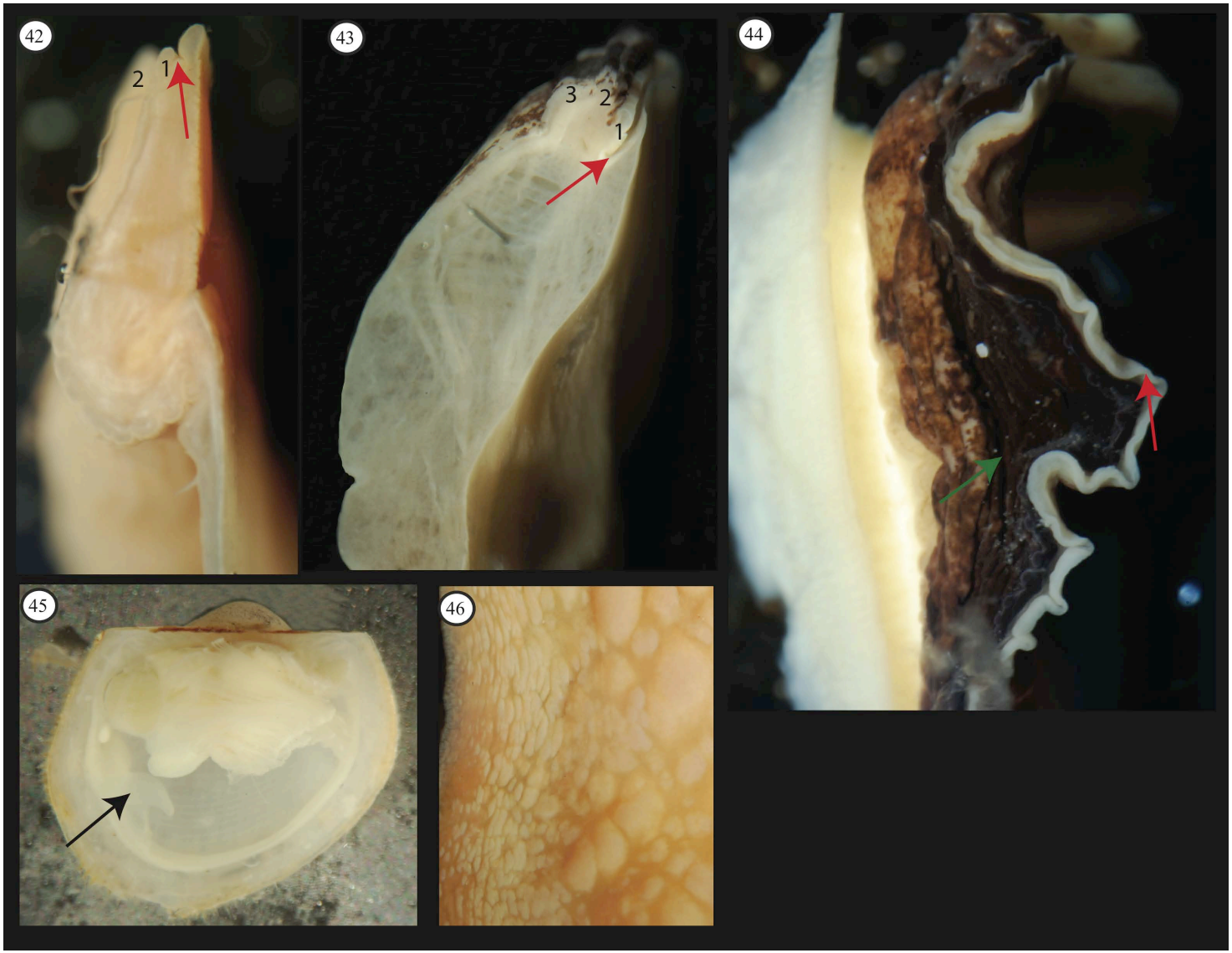
FIGURE 43: Cross section of mantle of *Anadara trapezia*: the red arrow indicates the periostracal groove and also the junction between the outer and inner mantle fold. 1 = OF-1, 2 = OF-2

FIGURE 44: Cross section of mantle of *Arca noae*: the red arrow indicates the periostracal groove and also the junction between the outer and inner mantle fold. 1 = OF-1; 2 = OF-2; 3 = OF-3.

FIGURE 45: Ventral view of mantle edge of *Arca avellana*: the green arrow points to the commarginal folds; the red arrow indicates the junction between the outer and inner folds.

FIGURE 46: Mantle extension of *Bathyarca* sp. MNHN 03.

FIGURE 47: Tumescent spots on the inner mantle surface of *Anadara antiquata*.


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CTENIDIA, LABIAL PALPS AND LIPS

In bivalves, as in all mollusks, the ctenidia or gills are multifunctional. As might be expected, they perform both respiratory and ventilation functions, however, they are also involved in filter feeding and food sorting. Moreover, they also play a role in brooding of larvae in some groups (e.g. Paleoheterodonta, Corbiculoidea, Teredinidae, and in the arcoid family, the Philobryidae). The terminology for gill morphology follows Ridewood (1903) and Atkins (1937) unless otherwise stated.

The ctenidia of the Arcoida are found on either side of the visceral mass and consist of a series of lath-like filaments that are attached to a hollow suspensory membrane, which extends posteriorly into a pointed flexible tip. Each ctenidium is composed of two demibranchs that are termed inner and outer according to their proximity to the sagittal plane. The series of filaments form a sheet-like lamella, such that a typical ctenidium consists of four lamellae, an ascending and descending lamellae in each demibranch.

Water, carrying food particles, enters the bivalve through the inhalant current. These food particles are passed over the ctenidia and sieved through the cilia of on the surface of the filaments. The food is either transported dorsally and anterior towards the mouth or ventrally to and posteriorly to be rejected. The food particles go through a final sorting by the labial palps, before they are taken into the mouth. There are two pairs of labial palps on either side extending from the ventral margin of the anterior adductor muscle to the anterior region of the gills. Any particles that are not taken into the mouth

are passed ventrally to be ejected posteriorly as pseudofaeces. The labial palps of bivalves have been examined in detail by Thiele (1886).

96. Ctenidial filament morphology: (0) ordinary filaments (Fig. 48); (1) principal filaments; (2) principal and apical filaments.

Arcoid filaments are exclusively ordinary (Atkins, 1937). This corresponds to the homorhabdic gill condition of Lankaster (1883). Ordinary filaments are those where all the gill filaments are alike and plicae or vertical folds are absent. The lamellae of heterorhabdic gills (Lankaster, 1883) are thrown into vertical folds and the filament at the base of this plica is generally of greater size than those at the apex of the fold. Principal and apical filaments comprise heterorhabdic gills. Ordinary filaments are found in the mytilioid outgroup taxa *Mytilus edulis*, *Brachidontes domingensis* and *Lithophaga aristata*, as well as the pterioid taxa *Isognomon alatus* and *Malleus candeanus.* Principal filaments only are found in all other outgroup taxa except for the pinnid taxa *Atrina rigida* and *Pinna carnea*, which possess both principal and apical filaments.

Ridewood (1903) showed that the formation of ordinary filaments ontogenetically precedes that of principal filaments. Apical filaments are only found in plicate ctenidia, as their formation is dependent on the prior differentiation of principal filaments. The ordering of this character did not affect the relationships of the ingroup taxa, which possess ordinary filaments only.

97. Ciliated discs between filaments: a/p.

Gills of the Arcoida are eleutherorhabdic in form; connection of individual filaments is made via concentration of cilia projecting from discs placed laterally on the filament (Fig.

49). Gills of this type correspond to the filibranch gill grade of Pelseneer (1889). Filibranch ctenidia are W-shaped in which the filaments are loosely connected by ciliary junctions and are not united ventrally. This connection is so loose such that easily causes the ctenidia to break apart and fray (Atkins, 1937).

98. Ciliated discs projecting from spurs: a/p.

In eleutherorhabdic taxa, the ciliated discs generally project from the anterior and posterior sides of the filament (Fig. 50). However, in some instances they arise from lateral outgrowths or 'spurs' (Ridewood, 1903). These spurs are found only in a few arcoid taxa (e.g. *Barbatia foliata*).

99. Tissue junction between filaments: a/p.

Lateral tissue junctions between ctenidial filaments are absent in the Arcoida; ciliated discs unite the filaments together in the arcoid demibranch. Organic interfilamental junctions are referred to the term synaptorhabdic. Gills of this type correspond to the Eulamellibranchia gill grade of Pelseneer (1889) and are found in the Pinnidae, Limidae, *Pteria*, *Pinctada*, and *Hyotissa* outgroup taxa. In eulamellibranch ctenidia, the filaments are more intimately united ventrally (Atkins, 1937).

100. Interlamellar septum: (0) absent; (1) ventral septum; (2) fenestrated septum; (3) dorsal septum; (4) complete septum.

An interlamellar septum refers to a sheet of either continuous or fenestrated membrane that connects the descending and ascending filaments of the demibranchs. When present in the Arcoida, it is usually ventrally placed between the two lamellae. The extension of this membrane is no more than a quarter to a third of the height of the demibranch. This septum can also take the form of a complete septum, extending from the base of the

demibranch to its dorsal most extremity (Pterioidea), a restricted dorsal septum (*Isognomon alatus*) or a fenestrated septum (multiple cross bars of Tëmkin, 2006) (*Mytilus edulis* and the pinnid outgroups). A ventrally placed septum is also found in both the limid outgroups as well as *Lithophaga aristata* and *Brachidontes domingensis*.

Interlamellar extensions are found in a number of Arcoida, e.g. *Glycymeris americana*, *Anadara granosa.* These tissue extensions are generally found dorsally on the descending lamellae (Ridewood, 1903). A distinction is made between this type of membrane and that of the septum that connects the ascending and descending lamellae.

101. Ctenidial reflection: a/p.

Each ctenidial filament consists of outer ascending and inner descending limb (Fig. 48). In the vast majority of arcoid, except *Adacnarca*, the ascending limb of the filaments are recurved or reflected, such that they form a food groove which convey food particles to the anteriorly placed labial palps. Reflected filaments are also found in the mytilid, *Isognomon alatus*, *Anomia simplex* and the limid outgroup taxa.

102. Food groove on ventral margin of outer demibranch: a/p.

A food groove is lacking in all homorhabdic arcoids examined. Found in a number of outgroup taxa, this groove transports sorted food particles anteriorly towards the mouth.

103. Swelling of anterior filament of inner demibranch: a/p.

This swelling of the anterior filament has been described in *Lissarca*, *Philobrya* and *Adacnarca* (Burne, 1920) (Fig. 52). Its function is unknown (Morton, 1978).

104. Ctenidial suspensory membrane (CSM): a/p.

In the Arcoida, the ctenidia attach to the anteroventral region of the posterior adductor muscle via a suspensory membrane (Figs. 36, 37, 53). A CSM is absent in some philobryid taxa as well as in *Mytilus edulis* and in the pinnid outgroup taxa.

105. ***CSM folds***: a/p.

Vertical folds along the CSM were present in a number of taxa. This folds manifests as slight creases in the arcid taxa *Barbatia tenella, Litharca lithodomus Fugleria tenera* and the limopsid *Limopsis marionensis* or were quite deep as in *Senilia senilis.* These folds were restricted to the ingroup taxa.

106. ***CSM papillae***: a/p.

The arcid *Anadara antiquata* possesses distinctive large papillae on the CSM (Fig. 53). These papillae are evenly spaced along the CSM. This character was not seen in another other taxa. It is unclear what is the function of these fleshy protuberances.

107. ***Ctenidial pigmentation***: a/p.

The CSM and the posterior-most filaments are conspicuously pigmented in a number of arcoid taxa. This pigmentation sometimes forms bands along the CSM (Fig. 62). This was evident in a great majority of arcid taxa including the borer *Litharaca lithodomus*, as well as all *Tucetona* species and *Glycymeris* cf. *lividus*. Pigment in the mantle tissue is deemed to have a sensory function (Waller, 1980) and it is likely that this is the case with the ctenidia, given that the pigment was heaviest in the posterior region where the bivalve has the maximum exposure to the external environment in a lot of arcoid taxa.

108. Adult incurrent: (0) anterior and posterior: (1) posterior only; (2) anterior.

The anterior current is typical of byssally attached, nestling bivalves, but lost in many burrowing forms (Lim, 1966). The anterior inhalant current is lost in more derived

bivalves and the point of entry of the posterior inhalant current is distant from the sediment surface (Oliver & Allen, 1980a). Direct observations of the currents was not possible and so groundplan coding for this character (and character 109) was taken. The presence of this anterior current is thought to be the primitive bivalve condition (Yonge, 1953, 1955). An inhalant current that is restricted to the anterior region of the animal is present in the outgroup taxon *Malleus candeanus* only.

109. Rejection current on ventral edge of ctenidium: (0) anteriorly; (1) posteriorly.

In arcoids the current direction along the ventral edge of the ctenidium is a posteriorly directed rejection current (Atkins, 1936) (the principal literature sources in Appendix 1 confirm this current in the various taxa studied). Yonge's (1955) observation of an anterior-ward current in *Senilia senilis* was rejected by Yoyole (1975), who observed the posterior-ward current typically found in the Arcoida. In most bivalves, the current passes anteriorly towards the mouth and is therefore a feeding current. This rare form of rejection is also found in the Anomiidae (Atkins, 1936).

110. Insertion of ventral tips of anterior-most filaments into distal oral groove: (0) present; (1) absent.

In the Arcoida, the ventral tips of the anterior filaments of the inner demibranch are not inserted into the distal oral groove of the labial palps (Fig. 51). This corresponds to type III of Stasek's (1963) categories of associations between the ctenidia and the labial palps of bivalved mollusks. This condition is also found in all outgroup taxa except the Mytilidae. Insertion of the ventral tips of the anterior filaments is found in the mytilid outgroup, corresponding to Stasek's type I. Category II, in which the ventral tips of the

anterior-most filaments of the inner demibranch are inserted and fused to a distal oral groove is not found in any of the taxa of this study.

111. Fusion of labial palps to visceral mass: (0) restricted to small area proximal to the lips; (1) along the proximal edge of the dorsoventral axis; (2) along the complete dorsoventral axis.

In the Arcoida, the palps extend from the ventral margin of the anterior adductor muscle dorsally from the lips to the anterior region of the ctenidia. They are fused along the entire dorsoventral axis of the palps to the visceral mass. The fusion is complete, such that they lack a free-pointing extremity. Fusion of the palps to the visceral mass is restricted to the proximal region of the dorsoventral axis in a number of outgroup taxa, as in seen in the Pterioidea. Extension of these palps is ventralward from the lips. The distal edge of the palps is free. In the Mytiloidea, the palps are fused to the visceral mass in a small region close to the lips only. In these outgroup taxa, fusion between the inner and outer palps is limited to the anterior only and the ridges run parallel to this line of fusion.

112. Tips of labial palps: (0) broad; (1) angled.

Angled labial palp tips are found in *Glycymeris* and *Cucullaea*, while broad tips are found in *Barbatia*, as well as some outgroup taxa (*Malleus candeanus*, *Pinctada mazatlantica*, *Isognomon alatus* and *Pinna carnea*).

113. ***Tentacles on distal free edge of inner labial palp***: a/p.

Tentacles were evident along the free edge of the inner labial palp in *Cucullaea labiata* only. As with all tentacles, it is likely to have a sensory function. This is autapomorphic for this taxon.

114. Inner folds or grooves of palps: (0) distributed along the entire inner edges of the palps; (1) restricted to the distal half of palps; (2) absent.

Transverse ridges on the inner palps function in channeling food towards the oral groove, which leads ventrally to the mouth. The inner folds, which typically are distributed along the entire inner edges of the palps, are mostly restricted to the dorsal half of palps in arcids (Simone and Chichvarkhin, 2004). Taxa with a minimal number of folds (as few as three) are restricted to habitats with clear water and gravely substrate (Thomas, 1975), while those taxa that inhabit fine-grained substrates and turbid water, like muddy or estuarine waters, possess many folds (as many as 35-40). Reduction in the number of folds of grooves in the palps is correlated with an efficient sorting mechanism found on the ctenidia (Atkins, 1937). Moreover, the numbers of folds along the palps are reduced in suspension feeders that do not want a high filtration rate of food. Such is the case with the limopsid taxa in this study, which are known suspension feeders. Folds were absent in the philobryid taxon *Neocardia* sp. A.

115. Palp ridges thrown into a series of vertical folds: a/p.

The ridges of the labial palps are thrown into a series of fold. This enhances the sorting capability of the palps and were prominent in arcid taxa. The Glycymerididae, in comparison with the Arcidae, have few folds, distally placed on the palp; these palp folds are not thrown into folds.

116. Oral groove: a/p.

When present, this groove extends from the dorsal extremity of the palps ventrally to the mouth, forming at the junction of the inner and outer palp. This term was introduced by Kellogg (1915) who differentiated between the ‘lateral oral groove’ that lies between the

ridged areas of the inner and outer palp and the 'proximal oral groove' that passes between the smooth portions of the mouth. A groove is lacking when the folds of the inner and outer palps are almost united.

117. Lateral extension of labial palps: a/p.

At the smooth ventral portion of the outer labial palp, the tissue is expanded laterally such that it extends over the inner palps. It is likely that the resulting enclosure prevents food loss as it moves towards the mouth. This extension was observed in *Anadara, Bathyarca corpulenta, Striarca interplicata* and some limopsid taxa. A similar membrane is found in *Atrina rigida*, however this originates from the inner palp. Given the similar function of this flap, it is coded as present in the pinnid outgroup taxon.

118. Lip overlap: (0) absent; (1) ventral lip wrapped up and over the dorsal lip; (2) dorsal lip wrapped down and around the ventral lip.

The lips of the Arcoida are simple in structure (Gilmour, 1974). Surround the mouth, they continue up dorsally towards the paired palps forming a contiguous line. In the Arcoida, the mouth and lips are positioned at the ventral margin of the anterior adductor muscle. Two conditions for this character are found in the Arcoida: the dorsal lips are perfectly in line with the ventral lips (therefore overlap is absent) or the dorsal lip folds over and under the ventral lip. An opposite situation with the ventral lips folding up and over the dorsal is seen in *Anomia simplex* and the pinnid outgroups. The oral region of Bivalvia has been examined in detail by both Gilmour (1974) and Bernard (1972).

119. Longitudinal folds on the inner surface of lips: a/p.

These folds extend from the distal portion of lips ventrally to the mouth.

120. Transverse folds or grooves on the inner surface of lip margins: a/p.

Transverse folds or grooves were detected in *Anadara antiquata*.

121. Labial caecum: a/p.

A caecum lying in the angle between the inner lip and the body wall was observed in the philobryid taxa *Lissarca*, *Philobrya* and *Adacnarca* (Burne, 1920; Morton, 1978). The function of the caecum is unknown.

FIGURE 48: Ordinary filaments found in Arcoida: the dorsal region of the filament is reflected.

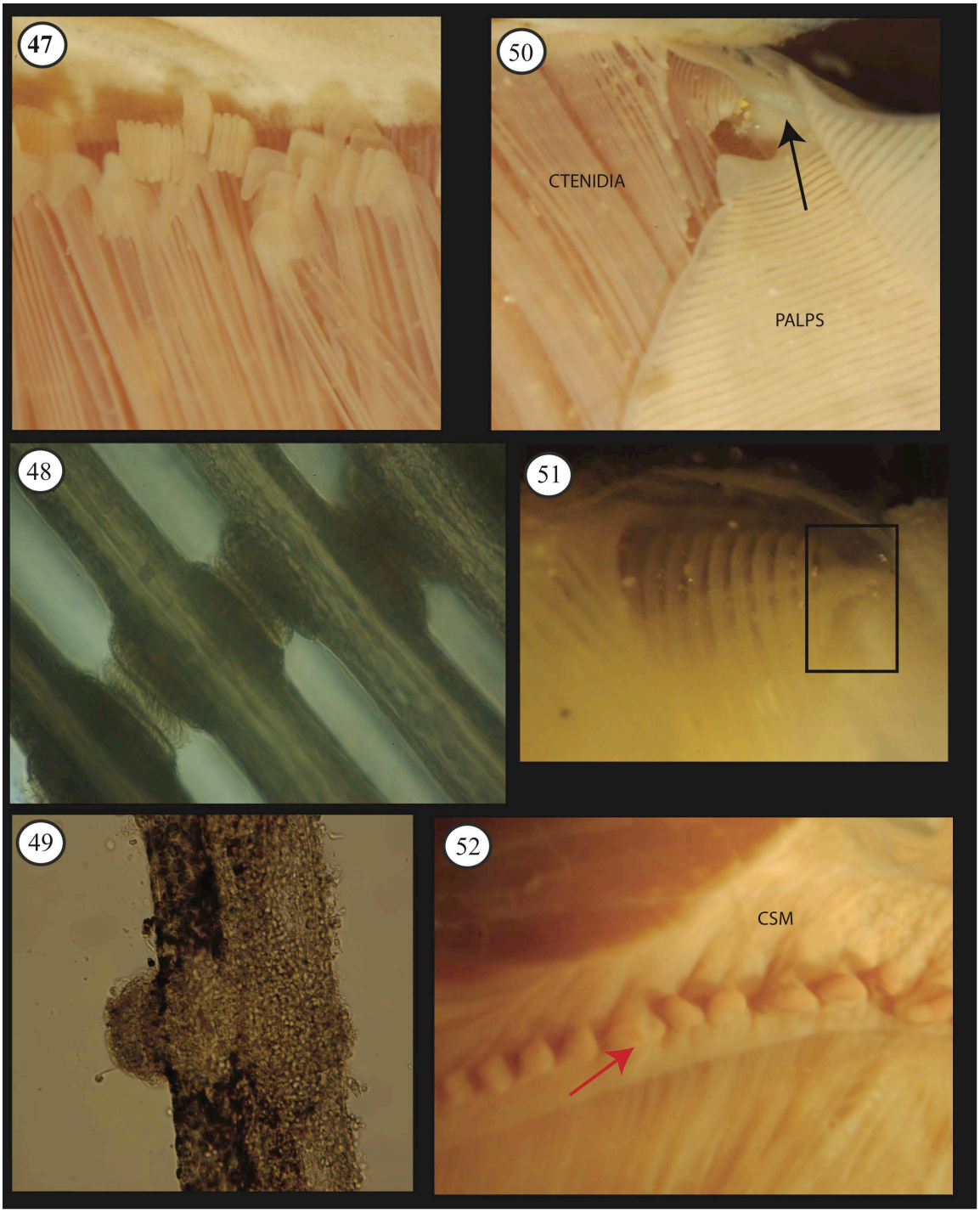
FIGURE 49: Eleutherorhabdic ctenidia of Arcoida: ciliated disks project laterally connect adjacent filaments.

FIGURE 50: Ciliated discs on spurs of *Barbatia foliata*.

FIGURE 51: Stasek's Type II association of ctenidia and labial palps: the ventral tips of the anterior filaments of the inner demibranch are not inserted into the distal oral groove of the labial palps.

FIGURE 52: Swelling of anterior filament of inner demibranch of ctenidium.

FIGURE 53: Papillae along the ctenidial suspensory membrane in *Anadara antiquata* (red arrow).


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CTENIDIA
PALPS
48
51
49
52
CSM

ALIMENTARY SYSTEM

The digestive system within Bivalvia is broadly consistent. The stomach in bivalves is quite complex, with many associated structures.

122. Esophageal ridges and grooves: a/p.

Distinct grooves and ridges circle the mouth and continue posteriorly along the esophagus. The mouth holds a position ventral to the anterior adductor muscle, when an anterior adductor is present. These ridges and grooves are found in *Anadara notabilis*, *Scapharca vellicata*, *Anadara rotundicostata*, *Barbatia reeveana*, *Trisidos semitorta* and *Cucullaea labiata*, as well the pinnid outgroups taxa. These folds do not extend into the lips surrounding the mouth. This character has been used in a number of studies of higher-level analyses including Salvini-Plawen & Steiner's (1993) higher-level analysis of Bivalvia, Giribet & Wheeler's (2000) analysis of Bivalvia. In both these studies, the esophageal ridges were coded as absent in all the pteriomorphian taxa as well as in many of the outgroup taxa included in this study. Tëmkin (2006) coded esophageal ridges as present in the pterioid taxa *Isognomon alatus*, *Malleus candeanus* and the non-pterioids *Mytilus edulis*.

123. Stomach type: (0) type I; (1) type III; (2) type IV.

The stomach is the chief organ for processing food in bivalves. It lies within the visceral mass and generally entails ciliated sorting areas, ducts to the digestive diverticula and a rotating crystalline style or protostyle that in conjunction with the gastric shield, grinds up food particles. Purchon (1956, 1957, 1958, 1987) in his numerous investigations of

bivalve stomach, broadly categorized the stomachs into five morphological types. Type III stomach are consistently found in the Arcoida and generally correspond to those with a long, slender tongue of the major typhlosole penetrating the food-sorting caecum to its apex, accompanied throughout by the intestinal groove (Purchon, 1957). The stomach is comprised of an oval dorsal chamber with an elongate combined style sac and midgut. Numerous scattered ducts to the digestive diverticula, a crystalline style, and a gastric shield are also present. This stomach type is also found in the Mytiloidea, Pterioidea, Pinnoidea and Ostreoidea outgroups. The stomach of *Malleus candeanus* (corresponding to Purchon's (1956) type I), are bipartite in nature, with a rounded dorsal region with no more than 3 ducts leading to the digestive diverticula. Stomachs of type IV (Purchon, 1957, 1958) feature a major typhlosole that passes through the floor of the stomach, terminating close to the left pouch. The ducts to the digestive diverticula are clustered and numerous in number. Type IV stomachs are characteristic of the Limidae and Anomiidae.

124. Typhlosole shape: (0) absent (Fig. 54A); (1) ventral median furrow; (2) heart-shaped (Fig. 54B); (3) simple T-shaped; (4) multiple folds median bar; (5) simple median bar; (6) multiple folds.

The typhlosole is an internal ridge or fold in the intestinal wall. The presumed function of this ridge is to increase the area of absorption during digestion. No consistent pattern in shape was seen across the Arcoida. In cross section, they appeared as a simple ventral median furrow (as in Tucetona pectunculus) to simple heart shaped (*Trisidos tortuosa*) to more complex ridges with multiple folds (*Limopsis soboles*). The shape of the typhlosole was examined at the point where the intestine passes the ventricle.

125. Rectum: (0) free-hanging (Fig. 36, 37); (1) attached to the ventral surface of the posterior adductor muscle (Figs. 58, 59).

The intestine passes along the dorsal surface of the posterior adductor muscle and continues down towards rectum that lies at the ventral surface of the muscle. Both rectal forms are equally prevalent in the Arcoida. The opening of the rectum (anus) is directed anteriorly towards the visceral mass.

126. ***Tissue folds leading from the anus to the abdominal sense organs***: a/p.

A conspicuous fold of tissue leads from the anus to each of the abdominal sense organs in some arcoid taxa. These folds connect medially such that they fuse along the under surface of the posterior adductor muscle.

127. *Anal process*: a/p.

A conspicuous somewhat lanceolate-shaped membrane extends from the tip of the anus in some arcoid taxa (Fig. 55). It has been originally referred to as an anal process by Herdman (1904), and subsequently as an anal flag or ear (Pelseneer, 1911) and anal funnel (Tëmkin, 2006) among others. Given that this growth of tissue is neither ear-shaped, flag-shaped nor funnel-shaped, a simple process is deemed more descriptive. Its likely function is that of directing the current of fecal pellets away from the mantle cavity. This process is found in a number of arcid, glycymerid and philobryid taxa as well as the pinnid, and pterioidean outgroup taxa (Tëmkin, 2006) and *Lima lima*.

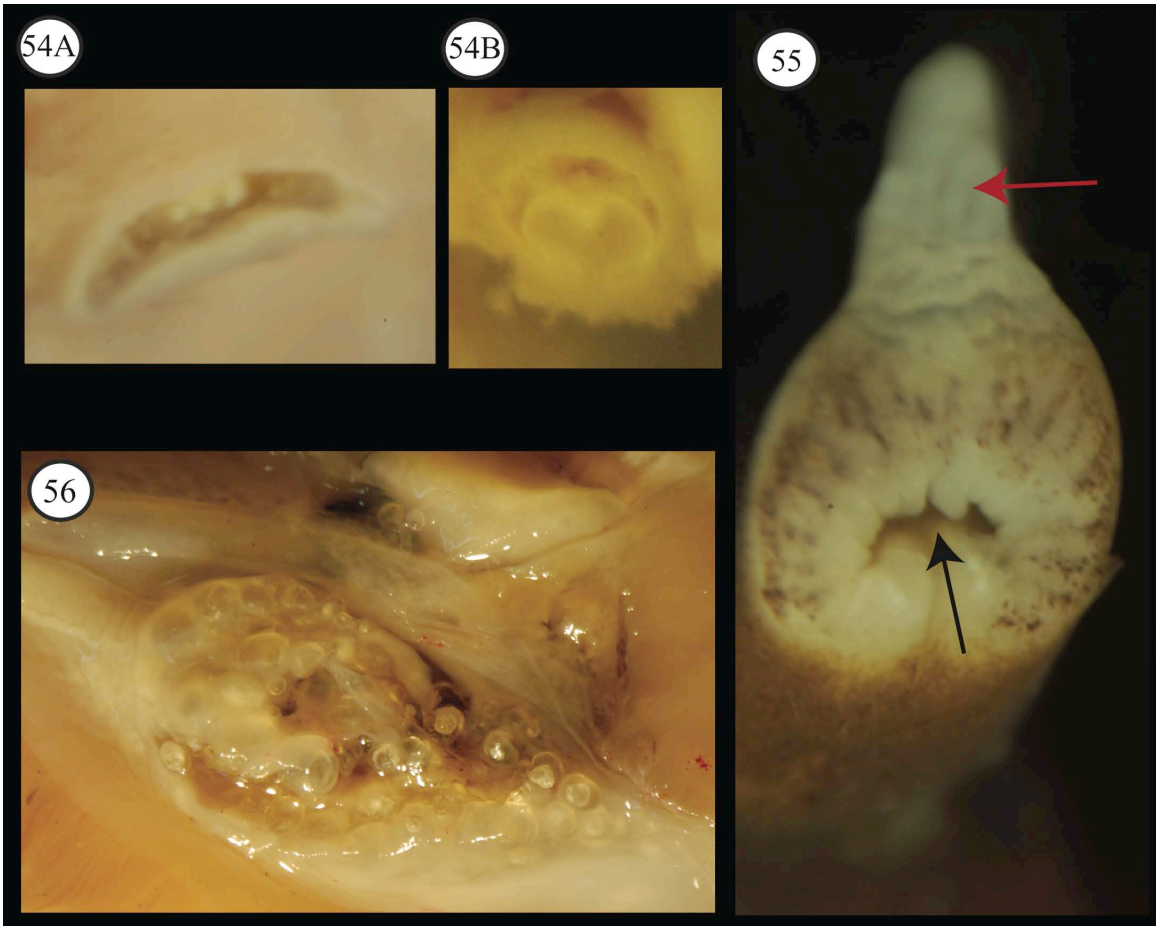
128. Anal papilla: a/p.

The papilla found protruding from the opening at the anus is an extension of the typhlosole (Fig. 55). This papilla is prevalent among glycymerid and arcid taxa. It was also observed among the pterioidean outgroup taxa and in *Pinna carnea*.

FIGURE 54: Intestinal cross-section: (A) Cross section of intestine of *Litharca lithodomus* at region immediately posterior to the heart. No typhlosole is evident; (B) cross section of intestine of *Trisidos tortuosa* illustrating the heart-shaped typhlosole.

FIGURE 55: Anal process: the anal process of *Arca avellana* (red arrow), the anal papilla is also evident (black arrow).

FIGURE 56: Renal concretion of *Glycymeris crebreliratus*.



EXCRETORY SYSTEM

In bivalves, the heart is intimately associated with the excretory system and is often considered an organ of the excretory system. In fact, hemocytes play an active role in scavenging waste material and eliminating them from the body (Morse, 1987). The bivalve-heart complex lies ventral to the dorsal hinge. The excretory system is comprised of the pericardial glands and kidneys or nephridia. These organs function to filter, transport, accumulate and excrete the products of metabolism into the mantle cavity. Ammonia is the principle end product of amino acid metabolism and is readily excreted into the surrounding aqueous environment. Uniquely, bivalves accumulate granular and crystalline deposits or concrements, primarily by cellular lysosomal systems in the kidneys and pericardial gland cells (Morse, 1987). The paired kidneys of arcoids are large, separate and subtriangular, they excrete waste matter into the pallial cavity, which are them removed to the exterior. They are located inside the pedal retractors and are connected with the pericardial cavity in front via a renopericardial canal, posterior to the ventricle.

129. Renal concretions or nephroliths: a/p.

These extracellular concretions are calcium in composition. Restricted to the Glycymerididae they lie beneath the CSM (Fig. 56). First described in *Pectunculus* by Pelseneer (1911) as ‘cornée’, these concretions can reach up to 2.5 mm in diameter and are often quite numerous.

CIRCULATORY SYSTEM

In Mollusca, the heart is formed by an invagination of the wall of a coelomic pericardial cavity. The heart generally consists of a medial ventricle and at least one pair of auricles, and an anterior aorta connecting with an open hemocoelic blood circulation system (Waller, 1998). In bivalves, the heart is usually dorsally placed. The pericardial cavity of arcoids may be single, dorsally or ventrally septate, or completely divided into two chambers. The pericardial cavity of bivalves, including those of seven arcoids, has been examined in depth by White (1942).

Typically in bivalves, oxygen is absorbed from the water directly into the tissues, without the aid of respiratory pigments; however, hemoglobin, myoglobin and hemocyanin-like molecules are known in some bivalve groups (Terwilliger and Terwilliger, 1985). These pigments are not carried in cells, but in solution around the body cavity (Morton et al., 1998). Bivalves that live in muddy substratum may be deficient in oxygen in which case these pigments facilitate oxygen transport into the tissue. However, as pointed out by Terwilliger and Terwilliger (1985), poor oxygenation in the surrounding environment of the organism does not correlate with the presence of this respiratory protein. Oxygen diffuses into the blood across the lamellae of the ctenidia providing an adequate amount of oxygen of sedentary bivalves (Morton et al., 1998).

Arcoid blood has been extensively examined at both the molecular and biochemical level (San George and Nagel, 1985; Suzuki et al., 1992; Piro et al., 1998) but only in a few arcoid taxa. While intracellular hemoglobin has been observed in

erythrocytes of some members of the families Arcidae and Glycymerididae (Booth & Magnum, 1978; Boyd, 1998; Morton et al., 1998), they have not been consistently found in these groups. In the Arcidae, the genus *Anadara* is known for its hemoglobin-laden erythrocytes, earning it the common name Blood cockle. A number of arcids (e.g. *Scapharca inaequivalvis*, *A. trapezia* and *A. broughtonii* possess two types of hemoglobin that bind oxygen in a cooperative manner (Piro et al., 1998). Red, hemoglobin enriched tissue was observed in the many arcid and all glycymerid taxa as well as the noetiid *Noetia ponderosa* and the cucullaeid *Cucullaea labiata.* No such evidence for the presence of hemoglobin was seen in the Limopsidae or Philobryidae. Given the inconsistent distribution of this character across the group, and the inability to observe the hemoglobin directly (fresh specimens are necessary), it was not possible to code nor groundplan for this character.

130. Ventricle form: (0) single (Fig. 57A); (1) bi-lobed (Fig. 57B); (2) double (Fig. 57C). A bi-lobed ventricle is typical of the great majority of Arcoida, and has been attributed to the greater development of the pedal retractor muscles, which have pushed the heart aside in order to occupy its position (see White, 1942). With this doubling of the ventricles, we also see a duplication of the surrounding pericardium. Doubling of the ventricles was found in all the *Arca* species examined. A single ventricle was observed in all the Philobryidae studied. A single ventricle was found in all the outgroup taxa except the chosen limid outgroups.

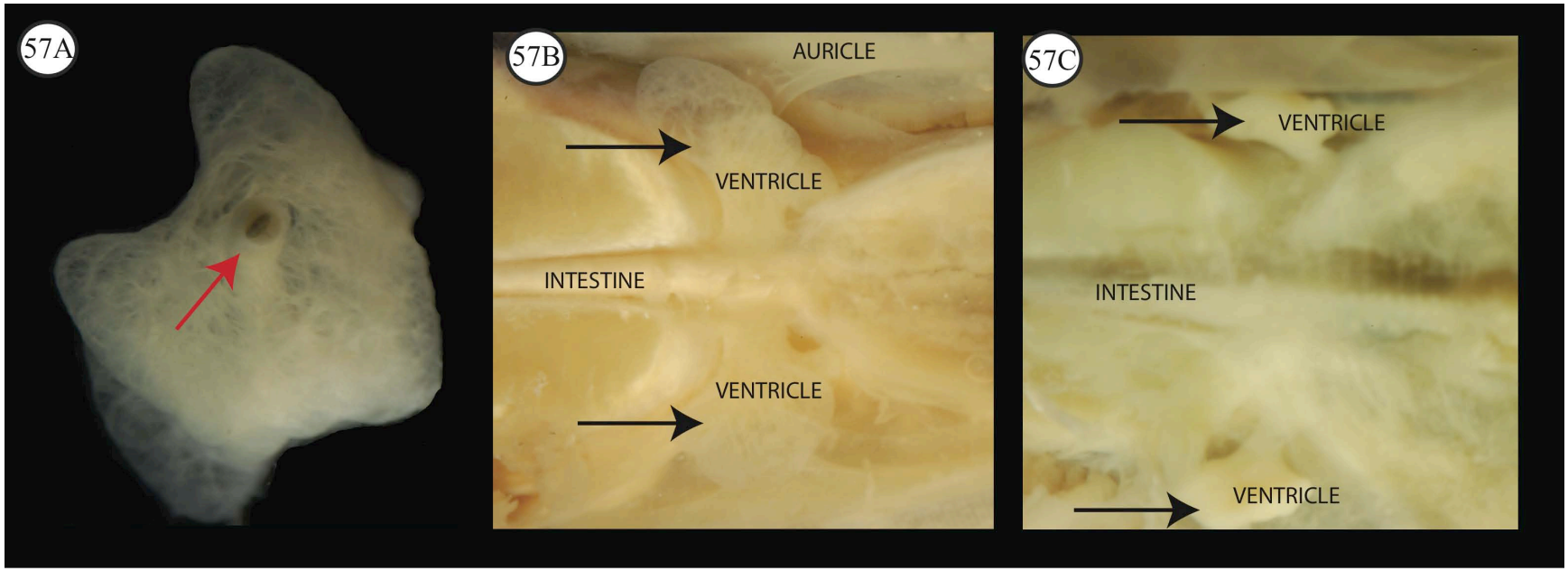
131. Penetration of ventricle by the intestine: (0) present (Fig. 57A); (1) intestine passes ventral to the ventricle; (2) intestine passes dorsal to the ventricle.

FIGURE 57: Variation of heart types of Arcoida:

(A) Single lobed heart illustrating the penetration of the intestine through the ventricle.

(B) Bi-lobed heart, separated by the intestine.

(C) Double heart found in *Arca* species.



In the Arcoida, penetration of the ventricle by the rectum is the most common condition. The intestine was rarely observed to pass dorsally above the ventricle (*Adacnarca ntiens*, *Scaphula celox*, *Barbatia* sp. PR01 (and *Pinctada mazatlantica* among the outgroups)). The rectum does not perforate the ventricle of the heart, but it is embedded in the tissues of its ventral wall in *Arcopsis*, *Stenocista*, *Noetia ponderosa*, *Lissarca*, *Empleconia*, as well as a few arcids (and the limid outgroups). The intestine of all other outgroup taxa penetrates the heart. This only applied to species with character states 0 and 1 in character 139.

SENSORY AND NERVOUS SYSTEM

Commensurate with their sessile lifestyle, bivalves lack a head and therefore sensory functions are restricted to the mantle edges and to distal regions near the shell margin. The mantle margin of bivalves can have photoreceptors, pigmentation, tentacles and papillae. The mantle margin is tactile and even if the mantle lacks eyes, it will respond to sudden changes in light intensity by contracting the mantle, withdrawing the foot and adducting the shells. A detailed review of bivalve eyes is provided in Morton (2001) and of arcoid eyes in Waller (1980) and Nilsson (1994). Photoreceptors at the mantle margin are referred to as pallial eyes and they possess a wide range of complexity. Pallial eyes can be simple cups consisting of sensory and pigment cells or are more complex, compound eyes with multifacets. The presence of one time of pallial eye does not restrict that of the other. In the pteriomorphs, these photoreceptors develop on the outer fold

(OF-1) of the mantle margin. In a number of pteriomorphian genera, additional photoreceptors are found in the region of the ctenidia (Pelseneer, 1911).

132. Abdominal sense organ (ASO): a/p.

ASOs are paired mechanoreceptors that are consistently found across the Pteriomorphia. Situated on the ventral surface of the posterior adductor muscle (Thiele, 1887, 1889; Haszprunar, 1983, 1985), they manifest as ectodermal thickenings in this region (Figs. 58, 59). This character was coded as present in all of the taxa (both ingroup and outgroup) included in the analysis, except for the Parallelodontidae, where no information can be available as to the presence of these organs in these fossil groups. The parallelodontid taxa were coded as '?' for this character and all other characters (characters 132-134) relating to this organ.

133. Position of ASO relative to the anus: (0) far from anus, placed more anteriorly (Fig. 59); (1) close to anus (Fig. 58).

134. Symmetry of paired ASO: (0) symmetrical; (1) asymmetrical, with the right large and more conspicuous relative to the smaller or vestigial left ASO; (2) asymmetrical, with the left absent.

In the Arcoida and the outgroup Mytilidae, the ASOs are typically symmetrical, with the exception of the Glycymerididae and the twisted ark *Trisidos*, where the left ASO is significantly smaller than the right. This asymmetry was observed in condition is also found in some outgroup taxa (Pteriidae, Pinnidae). The asymmetrical condition is taken to the extreme in *Cratis* cf. *ohasii* and the outgroup taxon *Hyotissa hyotis*, where the left ASO is absent (Haszprunar, 1983).

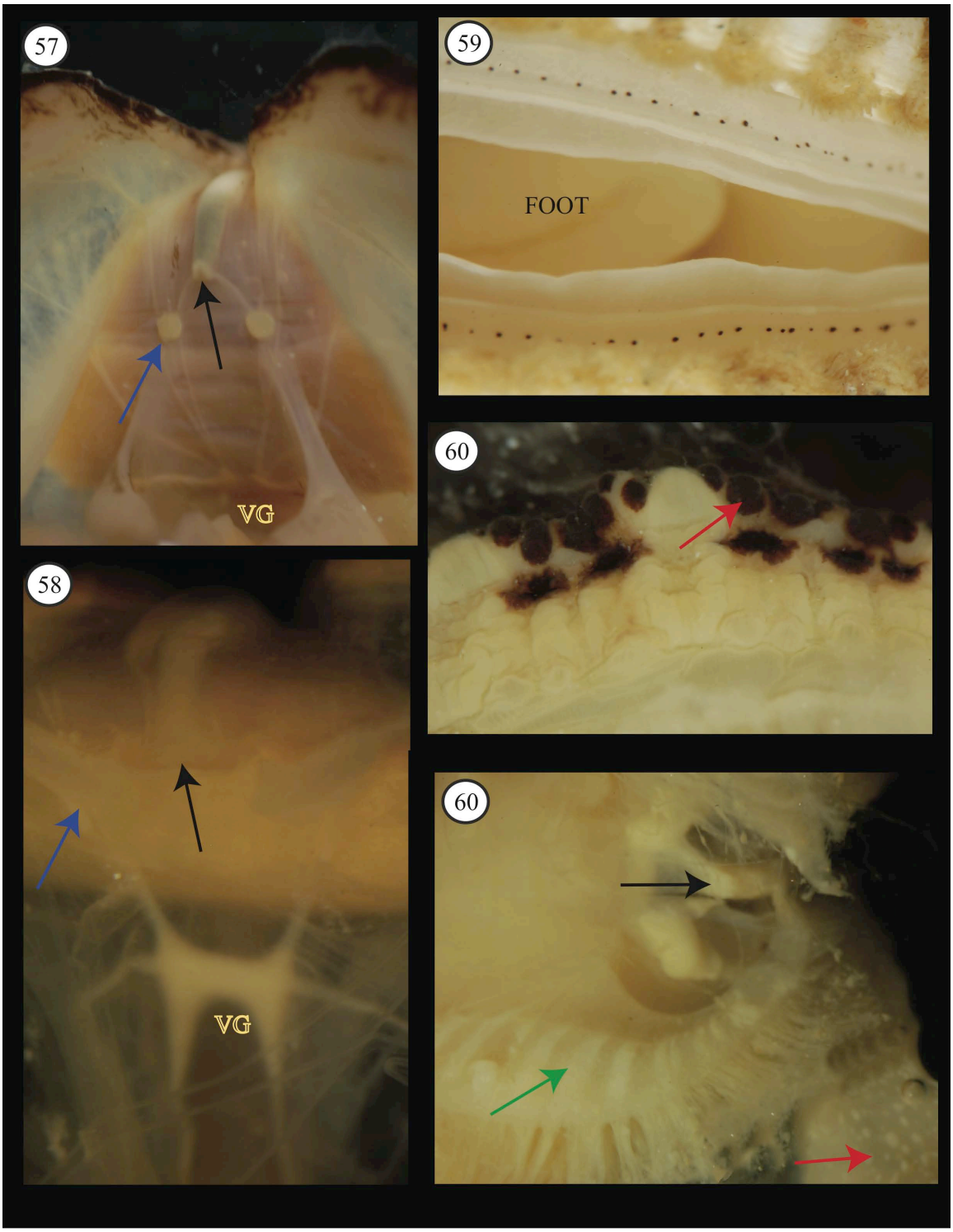
FIGURE 58: Ventral of posterior adductor muscle of *Arca navicularis*: the blue arrow indicates the circular abdominal sense organs, on either side of the attached anus (black arrow). The visceral ganglia, at the bottom of the image are coalesced.

FIGURE 59: Ventral of posterior adductor muscle of *Anadara granosa*: the blue arrow indicates the abdominal sense organ, which is this species are elongate. The anus is also attached, as are the visceral ganglia coalesced.

FIGURE 60: Simple pallial eyes on the ventral mantle margin of *Barbatia gradata*.

FIGURE 61: Compound eyes on the ventral mantle margin of *Barbatia cancellaria*: the mantle is heavily pigmented.

FIGURE 62: Ventral view of posterior region of *Anadara notabilis*: the anus is attached (black arrow). White pigmented bands are seen along the ctenidial suspensory membrane (green arrow) as are the white pigmented spots on the inner mantle surface.


57
VG
59
FOOT
60
58
VG
60

135. Relative position of left and right ASOs: (a) both ASOs on the same plane; (1) left ASO ventral to the right ASO.

The relative positions of the left and right ASOs were found to be on the same plane in all the arcoid taxa examined except *Barbatia amygdalumtostum*, *Glycymeris americana* and *Glycymeris scripta*. A similar asymmetry in the positioning of the ASOs on the posterior adductor muscle was observed in the pinnid outgroup taxa as well as in *Isognomon alatus*.

136. Osphradia: (0) present; (1) absent.

Originally described by Spengel (1881) in the arcid taxon *Arca noae* (L.), it was homologized with the 'Geruchsorgan' of gastropods. In bivalves, these organs are located in the posterior mantle cavity, ventrally placed to the visceral ganglia and follow the branchial nerves. Epithelial in form, they often appear as a pigmented ridge innervated by the visceral ganglia. In the Arcoida, these organs are located close to the visceral mass and lie within the ctenidial axes. There has been great speculation as to their function, including an association with respiratory organs, chemoreception, mechanoreception, light reception, and osmoreception (see Haszprunar, 1987: 55 and references therein). Given its posterior position opposite the region of mantle opposition, these organs most likely have a function in chemo- or mechanoreception.

137. Ctenidial eyes: a/p.

Ctenidial eyes consist of a shallow cup of ciliated, pigmented cells that are located at the base of the anteriormost filament of the inner demibranch of the ctenidia. They are considered to be "true" eyes as they maintain a nervous connection with the cerebral ganglia (Morton, 2000, 2001). They have been described as branchial, cephalic or

cerebral eyes (Morton, 2001). The term ctenidial is adopted here (following Tëmkin, 2006) given that this term unambiguously describes the location of these eyes (bivalves are acephalic so a term like cephalic is quite confusing). Pelseneer (1911) observed that cephalic eyes did not occur in species inhabiting depths of greater than 250-300 meters. Moreover, contra Pelseneer's observations, species of *Adacnarca* that were subsequently dissected by Burne (1922) that were found to have cephalic eyes and that were collected between 90-450 meters. This was confirmed in this study. Furthermore, not all taxa that live in habitats where there is penetrable light possess these eyes.

Ctenidial eyes were observed in the noetiids *Arcopsis adamsi* and *Arcopsis afra*, in a great number of arcid taxa, and all the philobryid taxa examined in this study. They were also found in the mytilid outgroup taxa, except *Lithophaga aristata*, in all the pterioidean taxa except *Pinctada mazatlantica*, as well as *Anomia simplex*.

138. Simple pallial eyes: a/p.

When present, they are generally found on the posterior mantle margin and have nervous connection with the visceral ganglia (Fig. 60). Pallial eyes consist of a cup-shaped depression of columnar sensory cells surrounded by pigmented cells. Cilia arise from these cup cells. These eyes are found on the innermost outer mantle fold (OF-1) in some Arcoida and Pterioidea, which because of their position on the mantle, the eyes are beneath the newly generating periostracum. This is in contrast to the condition of other bivalves, where they are positioned on the middle mantle fold (Waller, 1980, Morton, 2001). Pallial eyes have been lost in 'higher' bivalves with the alternative evolution of more complex eyes (Morton, 1978). Simple pallial eyes were observed across the Arcoida and seen in members of all families except the Limopsidae. A single

anterodorsal simple eye was seen in all the *Arcopsis*, *Striarca* and *Sheldonella* species examined. This eye was dark brown in color, but in the absence of histological sectioning, it was not possible to discern whether these eyes were different from the simple pallial eyes seen along the ventral margin, and so these eyes are coded as simple pallial.

139. Compound pallial eyes: a/p.

Compound photoreceptors sit on a short stalk and are ommatidium-like in nature, with a faceted arrangement analogous to that of the Arthropoda. The number of ommatidia can range between 100-160 per eye (Nilsson, 1994). Ommatidia are funnel-shaped pigments tubes with a photoreceptor cell at the base that lack lenses or other focusing structures. Details of the structure and form of these photoreceptors in many arcoid taxa are provided in Nilsson (1994). These compound photoreceptors are found on the crest of the first outer fold of a number of arcoid taxa, sitting beneath the transparent periostracum (Fig. 61). They also vary in size (the diameter of the eye ranges between 180-300 μm) and number along the ventral margin, being larger posteriorly, smaller or absent mid-ventrally (where the byssus emerges if present) and anteriorly which is deeper into the substrate (see Waller, 1980: 23). Nilsson has observed as many as 300 compound eyes scattered along the ventral margin a *Barbatia cancellaria* (Nilsson, 1994).

These complex eyes were observed in all species of *Arca* examined, as well as in *Litharca lithodomus*, many *Barbatia* species, *Cucullaea labiata*, all glycymerid taxa except *Glycymeris grayana*, and the philobryid. Compound photoreceptors were absent notably absent from the Noetiidae, Limopsidae and Philobryidae, with the exception of

Cratis cf. *ohasii* and *Philobrya setosa*. Compound eyes were not observed in any of the outgroup taxa.

140. Relative position of visceral ganglia: (0) coalesced, adjacent to each other; (1) not adjacent, separated by commissure.

The visceral ganglia are generally closely associated in the Arcoida (Fig. 59: VG). However, exceptions are found across the group (e.g. *Limopsis aurita* and *Litharca lithodomus*), wherein the visceral ganglia are widely separated. Wide separation of the ganglia is found throughout the pterioidean outgroup taxa (Tëmkin, 2006).

REPRODUCTIVE STRATEGIES

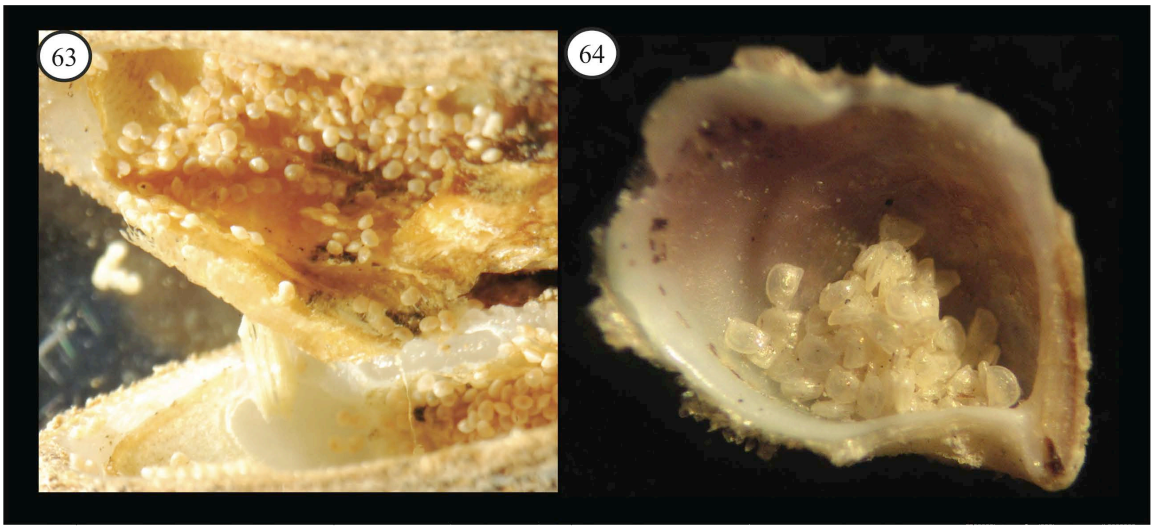
Bivalves exhibit a wide variety of reproductive strategies throughout their lifecycle. Separation of sexes or dioecity is found in the vast majority of bivalves, however some degree of hermaphroditism is not uncommon (e.g. simultaneous, consecutive) (e.g. anomalodesmatan species, *Corbicula fluminalis, Crassostrea virginica*). Hermaphroditism reveals a tendency towards protogyny in some species, but a more prevalent trend towards protandry exists (e.g. *Pisidium* species, *Ostrea edulis*). Sex determination is virtually impossible without internal examination and few exhibit sexual dimorphism (e.g. Galeommatoidea). Reproduction in bivalves is generally through external fertilization with a wide variety of developmental modes. The great majority of arcoids are dioecious bivalves that directly release their gametes into the water column. However, hermaphroditism has been observed in some arcoids e.g. *Senilia senilis*

(Yoloye, 1974). Insufficient information on the reproductive system was available for this study.

141. Reproductive mode: (0) free-spawning; (1) brooding to larvae (Figs. 63, 64). Brooding is often correlated with benthic lecithotrophy and planktotrophic larvae are generally pelagic (see character 31). The Philobryidae have categorically been described as infra-branchial brooders (Dell, 1964; Tevesz, 1977; Prezant, 1990; Prezant et al., 1992; Stiller and Jinhua, 2004; Malchus, 2006). This would appear to be an assertion rather than a fact as direct evidence of brooding for the ca. 80 species of Philobryidae has not been recorded for all. The straight-hinged prodissoconch is no guarantee for internal brooding; in the case of Limopsidae (see Malchus and Warén, 2005), evidence of brooding was never found despite the examination of thousands of samples (Malchus *pers*. *comm*., 2008). Nevertheless the competent larvae of Limopsidae have straight hinges. It light of this, brooding behavior is recorded as present when embryos or juveniles were visible inside the visceral cavity, or where records of brooding were recorded in the literature. However, their straight-hinged D-shaped prodissoconch and sculptural elements in the umbonal region are strongly suggestive of brooding. Given this fact, the presence of brooding was ambiguously coded (?) for the philobryids where brooding behavior was not directed.

FIGURE 63: Brooded young inside the valves of *Barbatia dubia*.

FIGURE 64: Brooded young inside *Philobrya setosa*.



CHARACTER CODING

The final complete dataset included 141 characters for the 131 taxa. Of these 141 characters, 37 (~26%) were multistate with the remaining 113 being treated as binary. In total, 133 characters were parsimony informative, the remaining being autapomorphic. Autapomorphic characters were excluded from calculation of the CI and RI, but were maintained in the data matrix for diagnostic and descriptive purposes. All but two characters were treated as non-additive. These characters, byssal presence throughout ontogeny (character 64) and differentiation of gill filaments (character 95), were treated as ordered on the basis of ontogenetic evidence (see character descriptions of these characters for justification for additive coding). All characters were treated as equally weighted. Characters are coded in adult specimens only. For the purpose of brevity in the description of overall superfamilial characteristics, such as shell form, the Arcoidea here are taken to include Arcidae, Noetiidae, Cucullaeidae and Parallelodontidae (sensu Newell, 1969), and the Limopsoidea include Glycymerididae, Limopsidae and Philobryidae (*sensu* Newell, 1969), unless otherwise stated.

In constructing trees, observations are translated into characters and states and a matrix is created in which each taxon is scored for all characters. Not all characters, however, are relevant for all taxa—these inapplicable characters occur when a feature is reduced or absent in some taxa. Inapplicable data constituted 607 of 18,471 total cells. Missing data constituted 1028 of the total data matrix and usually occurred when no soft tissue for a taxon was available. It was also not possible to code for soft anatomical features in a number of the Philobryidae—members of this family are conspicuously

small and the preservation of the tissue was such that it was impossible to code a large majority of the anatomical characters. Moreover, the preservation of many samples was such that the soft tissue was completely hardened making dissection extremely difficult. Obviously, the scoring of internal anatomical characters was not possible for the three fossil taxa included in this analysis. Missing data were coded as '?' in the data matrix and inapplicables as '-'. The matrix of morphological characters was maintained and edited using the program Winclada v.1.00.08 (Nixon, 2002) (see Appendix 2).

PHYLOGENETIC ANALYSES

The morphological dataset was analyzed with parsimony as the optimality criterion. All analyses were performed using the computer programs POY version 4.0.2906 (Varón et al., 2008) and in TNT (Goloboff et al., 2000) [commands follow the description of the search strategy in square brackets]. Both of these phylogenetic programs were utilized to assess the different algorithmic approaches employed in these phylogenetic programs in searching for the most optimal tree.

With POY, the initial heuristic search was carried out using the automated 'timed search' option. The timed search performs an initial build, followed by multiple rounds of TBR branch swapping that is further followed by parsimony ratchet and tree fusing. The maximum time for this search was set to 2 hours [**search** (max_time:00:02:00, min time:00:01:00, hits:20, memory:gb:2]. Following this initial search, unique [**select** unique)] trees were subjected to two further rounds of ratcheting, with branch swapping in between. The parsimony ratchet randomly reweights a defined fraction of the

characters by an arbitrary factor, performs branch swapping, returns the weights to the original value, reswapping the trees again. This algorithm allows you to further traverse the tree space in search of a global optimum [**perturb** (iterations: 3, ratchet: (0.2, 3) **swap** (trees: 1000) **perturb** (iterations: 3, ratchet: (0.2, 3) **select** ()]. All trees were rooted on the ostreid taxon *Hyotissa hyotis*. A strict consensus was reported from all the unique trees in memory.

In TNT, an automated search was also employed, wherein a 1000 replications of RAS and TBR were performed, with rounds of the parsimony ratchet, tree drifting, and tree fusing being performed during each replicate [**xmult**=replications1000 **ratchet**200 **drift**200 **fuse**100].

The analyses were either carried out on a Mac Pro 2.66 GHz Intel Xeon 4-Core, 16Gb 667 MHz or a Mac Pro 2 x 3.2 GHz Intel Xeon 4-Core, 32 GB 800 MHz and were run in parallel. Because these analyses were run in parallel, the total run time is equivalent to the time of the search times the number of processors, thus, a search that took 2 hours to complete, on a 4-core machine, ostensibly ran for 8 hours.

In addition to the complete morphological dataset, a sub-matrix containing 'hard' characters only, was also analyzed. Shell morphological features have traditionally been used to describe new species, as well as determining the higher taxonomic groups—especially genera and families—in the Bivalvia. This sub-matrix contained 73 shell characters pruned from the original matrix (see Appendix 2; shell characters appear in bold). These 'hard' characters included those that relate to the shell microstructure (characters 1-8), shell morphology and form (characters 9-30), prodissoconch (31-36),

ligament and hinge area (37-39; 45-61), byssus (characters 65-68) as well as other internal shell features (40-44; 75-82).

Given that the shell characters included in this analysis were analyzed separately in order to determine their value in describing higher taxonomic groups, a sub-matrix containing all other, non-shell characters, was also analyzed, to evaluate their ability to recover traditional groups. These characters included those of the foot and visceral mass (characters 61-63; 68-73), mantle (characters 82-94), ctenidia, palps and lips (characters 95-120), alimentary and excretory system (characters 119-128), circulatory system (characters 129-130), sensory and nervous system (characters 131-139) and reproductive strategies (character 140). Hereto, for the sake of brevity, the three analyses will be referred to as 'complete', 'hard' and 'soft'.

Character optimizations were traced on to the branches of the tree using Winclada (Nixon, 2002). The apomorphies were mapped such that the optimizations were delayed and non-homoplastic synapomorphies would appear as black circles along the branches. Homoplastic reversed characters appear as white circles. When mapped onto the tree, the numbers above and below the circles represent the character number and state respectively.

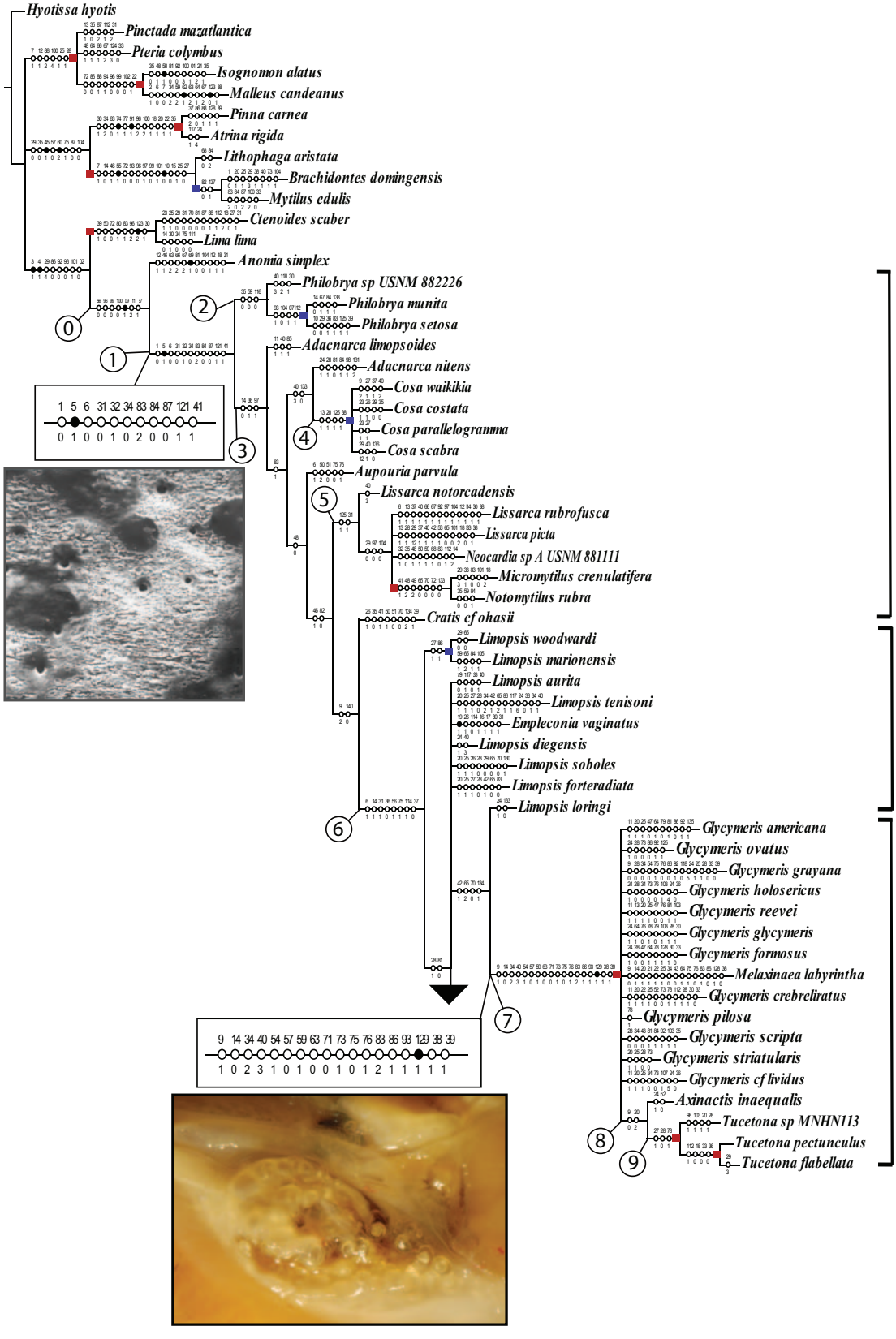
The robustness of the clades was evaluated using both parsimony jackknife (Farris et al., 1996) and Bremer support (Bremer, 1994). Through reiterative random resampling of the character matrix without replacement, jackknifing provides a support measure for each clade. The Bremer support index for a clade is the number of extra steps required to lose a branch in the consensus of the nearly most parsimonious trees. Detailed descriptions of these methods are provided in Chapter 3.

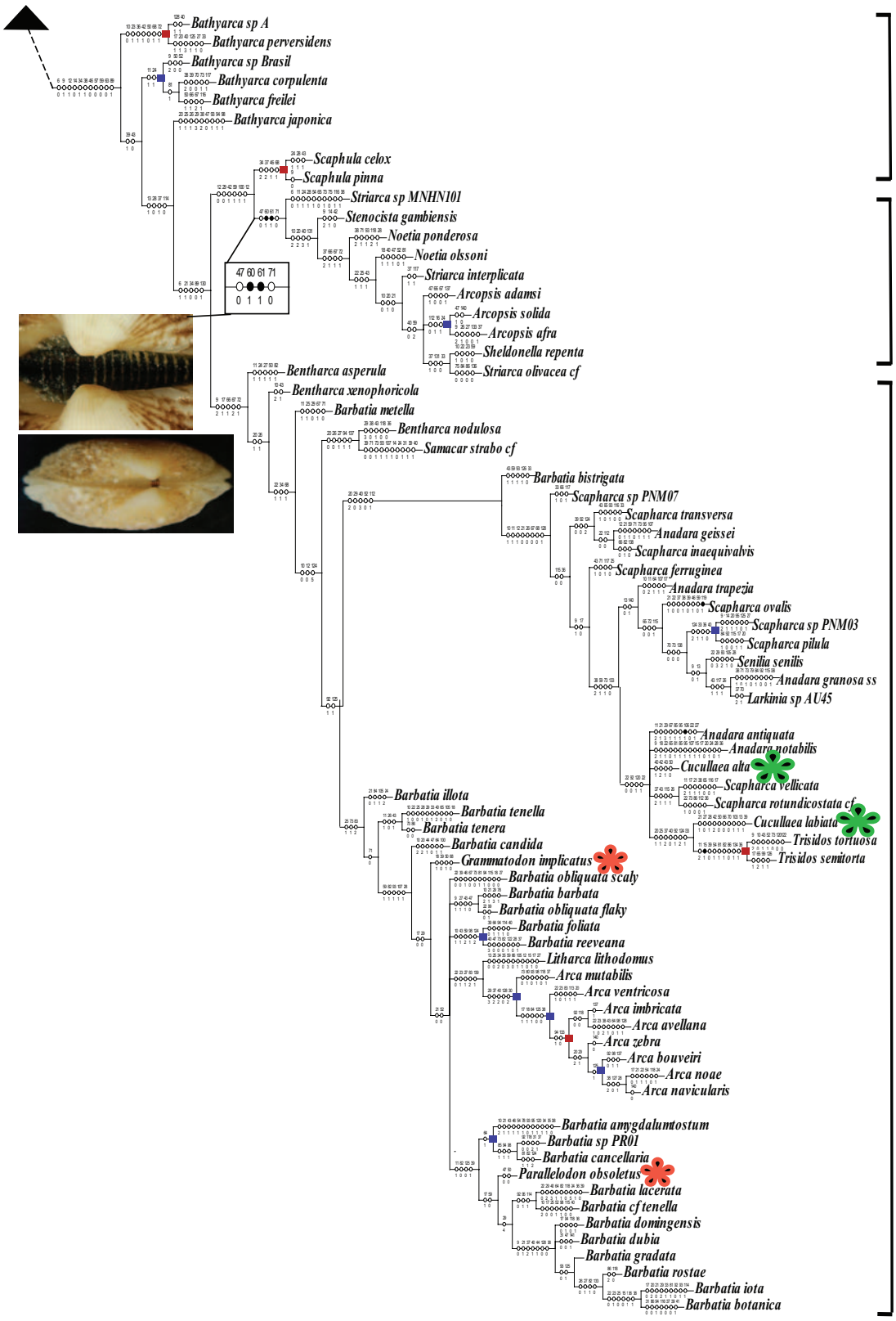
Finally, a test of the previously proposed classification schemes of Newell (1969) and Amler (1999) was performed using POY. In these analyses, the search topologies were constrained such that they reflected these previous classifications. The difference in the length of these constrained trees and those obtained from the phylogenetic analysis of all the morphological data is reported. In order to achieve this, characters were added to the matrix, such that all the member of a family were scored for the same character; these additional characters were given a weight of 100 in order to force a sister-group relationship within these taxa. In order to differentiate between Newell (1969) and Amler's (1999) classifications, the weighted family level clades scored for an additional weighted character, with the Glycymerididae receiving the same character weight as the Arcidae, Noetiidae, Cucullaeidae and Parallelodontidae to liken the classification scheme of Amler (1999) and the same weight as the Limopsidae and Philobryidae to reflect that of Newell (1969).

RESULTS

Comparable results were obtained with the POY and TNT analyses, with trees of identical lengths being found. The overall structure of the trees found with POY and TNT are the same. For this reason, only the trees gained from one of the computer programs, those done with POY, are shown.

FIGURE 65. *Complete Morphology*: The strict consensus of 49 most parsimonious trees of length 1287. The apomorphies were mapped using Winclada (Nixon, 2002) such that only unambiguous non-homoplastic synapomorphies would appear as black circles along the branches. Homoplastic reversed characters appear as white circles. The red and green asterisks highlight the parallelodontid and cucullaeid taxa respectively. The numbers above and below the circles represent the character number and state respectively. Jackknife values between 50-74 are indicated by blue box on the branch and between 75-100 are indicated by a red box. The tree continues on the following page. The complete morphology tree for which Bremer support values were calculated can be found in Appendix 3. [Image of shell tubules from Waller, 1978; image of renal concretions from *Glycymeris scripta*; images of noetiid traverse hinge from *Noetia* (top) and *Arcopsis* (bottom)]. →


Hyotissa hyotis
Pinctada mazatlantica
Pteria colymbus
Isognomon alatus
Malleus candeanus
Pinna carnea
Atrina rigida
Lithophagа aristata
Brachidontes domingensis
Mytilus edulis
Ctenoides scaber
Lima lima
Anomia simplex
Philobrya sp USNM 882226
Philobrya munita
Philobrya setosa
Adacnarca limopsoides
Adacnarca nitens
Cosa waikikia
Cosa costata
Cosa parallelogramma
Cosa scabra
Aupouria parvula
Lissarca notorcadensis
Lissarca rubrofusca
Lissarca picta
Neocardia sp A USNM 881111
Micromytilus crenulatifera
Notomytilus rubra
Cratis cf ohasii
Limopsis woodwardi
Limopsis marionensis
Limopsis aurita
Limopsis tenisoni
Empleconia vaginatus
Limopsis diegensis
Limopsis soboles
Limopsis forteradiata
Limopsis loringi
Glycymeris americana
Glycymeris ovatus
Glycymeris grayana
Glycymeris holosericus
Glycymeris reevei
Glycymeris glycymeris
Glycymeris formosus
Melaxinaea labyrintha
Glycymeris crebreliratus
Glycymeris pilosa
Glycymeris scripta
Glycymeris striatularis
Glycymeris cf lividus
Axinactis inaequalis
Tucetona sp MNHN113
Tucetona pectunculus
Tucetona flabellata
Philobryidae
Limopsidae
Glycymerididae


Bathyarca sp A
Bathyarca perversidens
Bathyarca sp Brasil
Bathyarca corpulenta
Bathyarca freilei
Bathyarca japonica
Scaphula celox
Scaphula pinna
Striarca sp MNHN101
Stenocista gambiensis
Noetia ponderosa
Noetia olssoni
Striarca interplicata
Arcopsis adamsi
Arcopsis solida
Arcopsis afra
Sheldonella repenta
Striarca olivacea cf
47 60 61 71
0 1 1 0
Bentharca asperula
Bentharca xenophoricola
Barbatia metella
Bentharca nodulosa
Samacar strabo cf
Barbatia bistrigata
Scapharca sp PNM07
Scapharca transversa
Anadara geissei
Scapharca inaequivalvis
Scapharca ferruginea
Anadara trapezia
Scapharca ovalis
Scapharca sp PNM03
Scapharca pilula
Senilia senilis
Anadara granosa ss
Larkinia sp AU45
Anadara antiquata
Anadara notabilis
Cucullaea alta
Scapharca vellicata
Scapharca rotundicostata cf
Cucullaea labiata
Trisidos tortuosa
Trisidos semitorta
Barbatia illota
Barbatia tenella
Barbatia tenera
Barbatia candida
Grammatodon implicatus
Barbatia obliquata scaly
Barbatia barbata
Barbatia obliquata flaky
Barbatia foliata
Barbatia reeveana
Litharca lithodomus
Arca mutabilis
Arca ventricosa
Arca imbricata
Arca avellana
Arca zebra
Arca bouveiri
Arca noae
Arca navicularis
Barbatia amygdalumtostum
Barbatia sp PR01
Barbatia cancellaria
Parallelodon obsoletus
Barbatia lacerata
Barbatia cf tenella
Barbatia domingensis
Barbatia dubia
Barbatia gradata
Barbatia rostae
Barbatia iota
Barbatia botanica
Arcidae
Noetiidae
Arcidae

All Taxa – All Data

Relationships of the Arcoida

An analysis of the complete morphological dataset (131 taxa for 141 characters), recovered 49 most-parsimonious trees (mpts). The length of each of these trees was 1287 (consistency index = 0.14; retention index = 0.66). In all analyses performed, autapomorphic characters were removed in the calculation of the consistency index so as not to inflate it. The Arcoida was clearly seen to form a monophyletic clade in each of the mpts. The strict consensus of these trees, with the collapse of 32 nodes is shown in Fig. 65. In this analysis, two of the seven families were monophyletic—the Glycymerididae and the Noetiidae—the Cucullaeidae, represented by the Recent taxon *Cucullaea labiata* and the Miocene *Cucullaea alta,* were polyphyletic, placing on different parts of the tree (these taxa are highlighted with a green asterisk), within the Arcidae: *Cucullaea labiata* formed a sister-group relationship with *Trisidos* spp, while *C. alta* placed among anadarine taxa. A similar result was seen with the Parallelodontidae, represented by the parallelodontine *Parallelodon obsoletus* and the grammatodontine *Grammatodon implicatus*, which was rendered polyphyletic, falling at different places within the Arcidae, among Arcinae taxa (these taxa are highlighted with a red asterisk). Both the Limopsidae and Philobryidae were paraphyletic with respect to the Arcoidea sensu Amler (1999).

Of the 36 nominal genera included in this analysis, the following were recovered as monophyletic groups in all the shortest trees: the philobryid taxa *Philobrya* and *Cosa*;

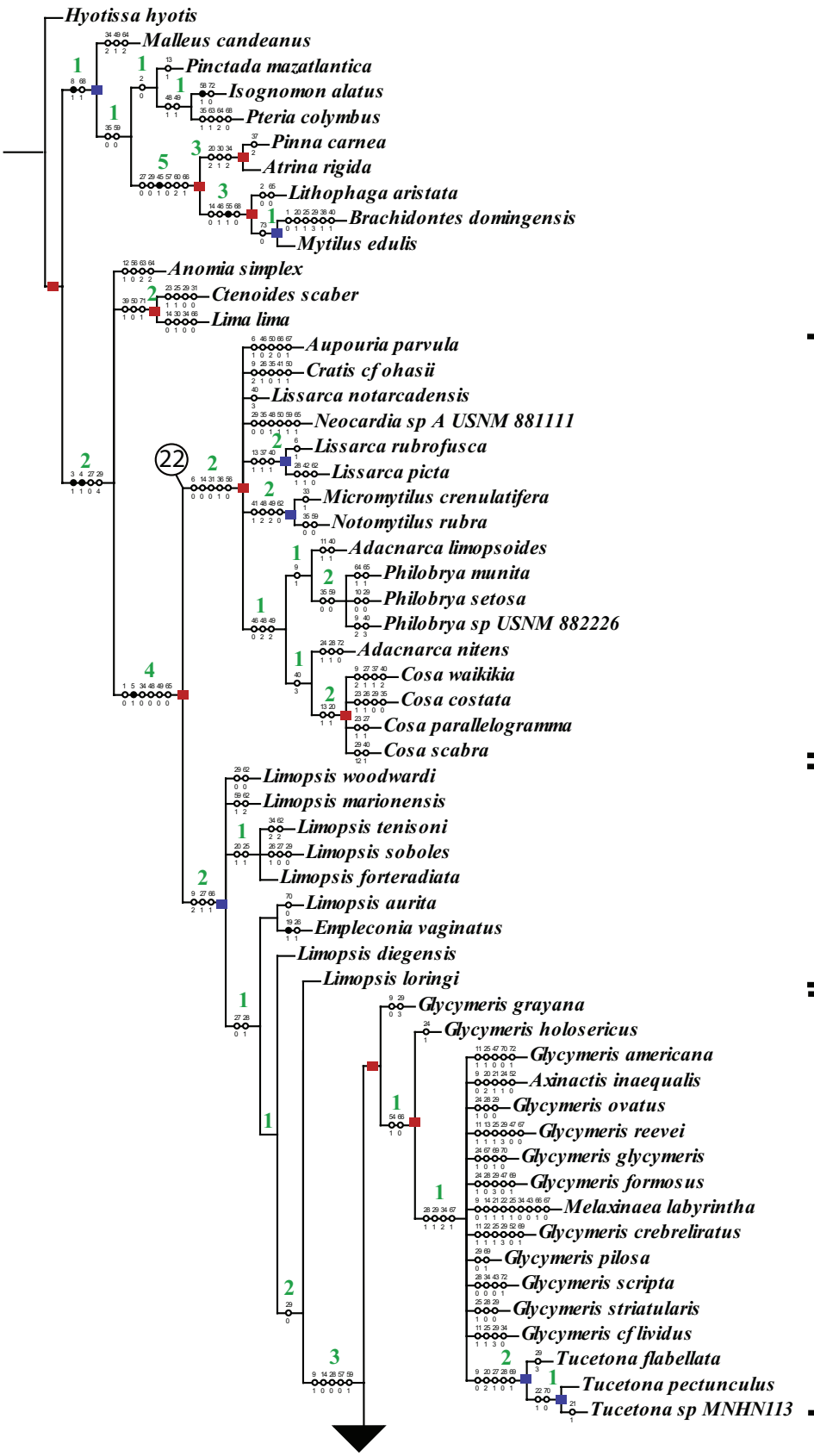
the glycymerid *Tucetona*; the arcids *Scaphula, Trisidos and Arca*. Due to limited availability of some taxa in collections, it was not possible to include more than a single taxon for 15 of the genera; these include the philobryid taxa *Aupouria*, *Cratis*, *Neocardia*, *Micromytilus*, *Notomytilus*, the noetiids *Sheldonella* and *Stenocista,* the glycymerids *Melaxinaea* and *Axinactis,* the limopsid *Empleconia* and the arcids *Larkinia, Samacar, Senilia* and the monotypic *Litharca*.

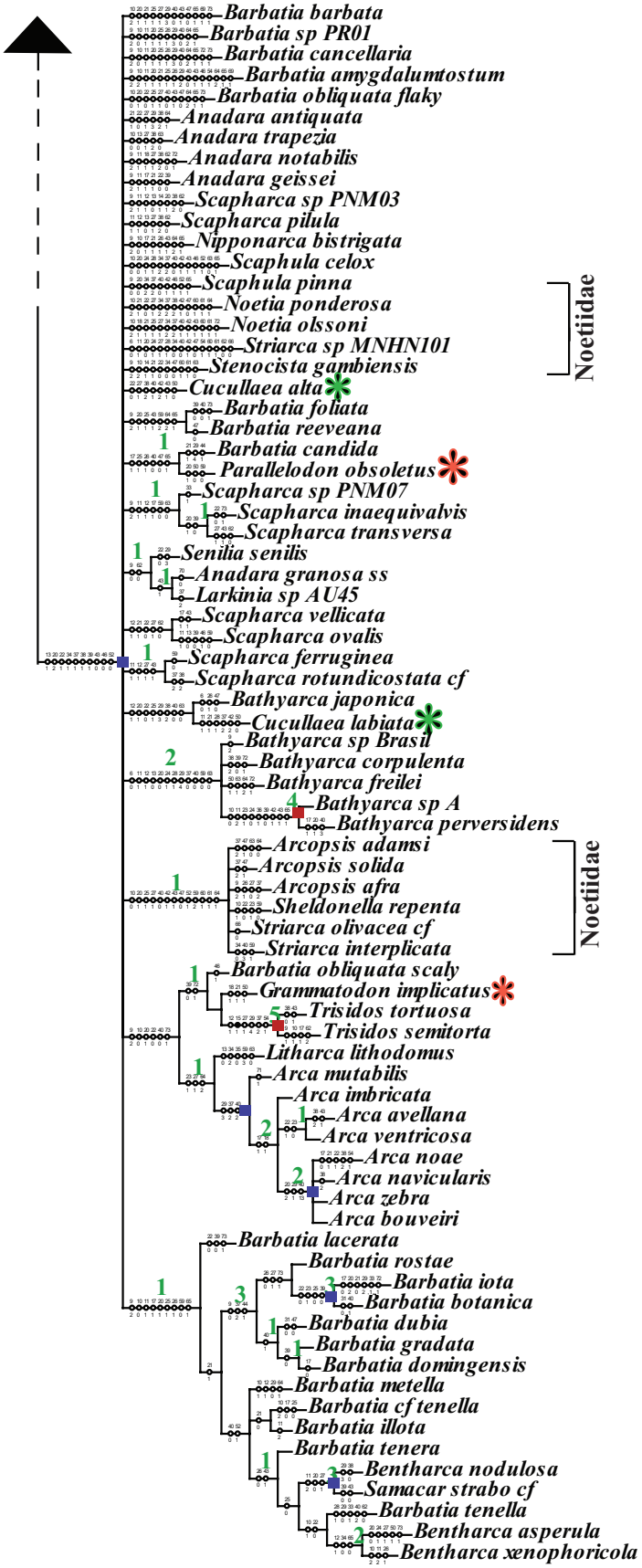
In each of the shortest trees, the constituent taxa within the major clades remained the same, but it was the movement of taxa within these clades that resulted in the recovery of 79 mpts.

Sister-Group Relationships of Higher Taxa

The anomiid *Anomia simplex* was found to be the sister-taxon to the Arcoida in this analysis. In the 'complete' analysis, the limid taxa *Ctenoides scaber* and *Lima lima* form a clade, which is the sister taxon to the Anomiidae + Arcoida clade. A monophyletic Pterioida was not recovered—the Pinnidae was not the expected sister-taxon to the Pteriidae, but formed a monophyletic group with the Mytilidae.

FIGURE 66. *Shell Characters Only*: The strict consensus of 3058 most parsimonious trees of length 611. Tree continues on the following page, all taxa that are not indicated by an asterisk or a bar are Arcidae. Jackknife values as in previous tree. Bremer support values are in green above the branches. →


Hyotissa hyotis
Malleus candeanus
Pinctada mazatlantica
Isognomon alatus
Pteria colymbus
Pinna carnea
Atrina rigida
Lithophaga aristata
Brachidontes domingensis
Mytilus edulis
Anomia simplex
Ctenoides scaber
Lima lima
Aupouria parvula
Cratis cf ohasii
Lissarca notarcadensis
Neocardia sp A USNM 881111
Lissarca rubrofusca
Lissarca picta
Micromytilus crenulatifera
Notomytilus rubra
Adacnarca limopsoides
Philobrya munita
Philobrya setosa
Philobrya sp USNM 882226
Adacnarca nitens
Cosa waikikia
Cosa costata
Cosa parallelogramma
Cosa scabra
Limopsis woodwardi
Limopsis marionensis
Limopsis tenisoni
Limopsis soboles
Limopsis forteradiata
Limopsis aurita
Empleconia vaginatus
Limopsis diegensis
Limopsis loringi
Glycymeris grayana
Glycymeris holosericus
Glycymeris americana
Axinactis inaequalis
Glycymeris ovatus
Glycymeris reevei
Glycymeris glycymeris
Glycymeris formosus
Melaxinaea labyrintha
Glycymeris crebreliratus
Glycymeris pilosa
Glycymeris scripta
Glycymeris striatularis
Glycymeris cf lividus
Tucetona flabellata
Tucetona pectunculus
Tucetona sp MNHN113
Philobryidae
Limopsidae
Glycymeridae


Barbatia barbata
Barbatia sp PR01
Barbatia cancellaria
Barbatia amygdalumtostum
Barbatia obliquata flaky
Anadara antiquata
Anadara trapezia
Anadara notabilis
Anadara geissei
Scapharca sp PNM03
Scapharca pilula
Nipponarca bistrigata
Scaphula celox
Scaphula pinna
Noetia ponderosa
Noetia olssoni
Striarca sp MNHN101
Stenocista gambiensis
Noetidae
Cucullaea alta
Barbatia foliata
Barbatia reeveana
Barbatia candida
Parallelodon obsoletus
Scapharca sp PNM07
Scapharca inaequivalvis
Scapharca transversa
Senilia senilis
Anadara granosa ss
Larkinia sp AU45
Scapharca vellicata
Scapharca ovalis
Scapharca ferruginea
Scapharca rotundicostata cf
Bathyarca japonica
Cucullaea labiata
Bathyarca sp Brasil
Bathyarca corpulenta
Bathyarca freilei
Bathyarca sp A
Bathyarca perversidens
Arcopsis adamsi
Arcopsis solida
Arcopsis afra
Sheldonella repenta
Striarca olivacea cf
Striarca interplicata
Noetiidae
Barbatia obliquata scaly
Grammatodon implicatus
Trisidos tortuosa
Trisidos semitorta
Litharca lithodomus
Arca mutabilis
Arca imbricata
Arca avellana
Arca ventricosa
Arca noae
Arca navicularis
Arca zebra
Arca bouveiri
Barbatia lacerata
Barbatia rostae
Barbatia iota
Barbatia botanica
Barbatia dubia
Barbatia gradata
Barbatia domingensis
Barbatia metella
Barbatia cf tenella
Barbatia illota
Barbatia tenera
Bentharca nodulosa
Samacar strabo cf
Barbatia tenella
Bentharca asperula
Bentharca xenophoricola

All Taxa – Traditional Shell Characters

Relationships of the Arcoida

A reduced matrix, with 131 taxa and 73 traditional characters (shell characters only), yielded 3058 mpts. The length of each of these trees was 611 (consistency index = 0.15; retention index = 0.72). The strict consensus of these trees with the collapse of 61 nodes is shown in Fig. 66. As in the previous analysis, the Arcoida forms a monophyletic clade with respect to the outgroup taxa. Only the Philobryidae and Glycymerididae were recovered as monophyletic clades in each of the mpts. In this analysis, as in the complete morphological analysis, the Limopsidae were rendered paraphyletic with respect to the Arcoidea *sensu* Amler (1999). The Arcidae were rendered polyphyletic by the inclusion of the Noetiidae, Cucullaeidae and Parallelodontidae, which were all polyphyletic. The Cucullaeidae and Parallelodontidae are highlighted on the tree as in the previous figure.

In this analysis, with the exception of *Scaphula,* the same monophyletic genera were recovered as in the previous 'complete' analysis, i.e. *Philobrya, Cosa, Tucetona, Trisidos* and *Arca*. No other monophyletic genera were recovered. Higher-level taxonomy of Bivalvia has equally been defined by soft anatomical characteristics (e.g. ctenidial type or stomach grade) as by shell characters. However, the classification of genera and families was largely based on shell features (e.g. ligament and hinge). Despite the fact that all of the arcoid genera were originally defined and erected on the basis of such characters, the majority of these genera do not form monophyletic clades in this analysis of shell characters only.

Sister-Group Relationships of Higher Taxa

In this analysis, a polytomy consisting of *Anomia simplex* and the limid taxa *Ctenoides scaber* and *Lima lima* were found to be the sister-taxon to the Arcoida. The sister group relationships among the outgroup taxa were highly similar to those found in the previous analysis. The analysis of shell characters only again recovered a sister-group relationship between the pinnid and mytilid taxa. Unlike the previous analysis, however, the pterioidean taxon *Malleus candeanus* did not place with the other pterioidean taxa, but instead was the sister taxon to these smaller clades (i.e. the non-malleid pterioids, the pinnid + mytilids).

All Taxa – Soft Anatomical Characters Only

Surprisingly, little can be said about both the interrelationships of the Arcoida and of their relationships with other pteriomorphian taxa from the analysis of soft anatomical characters only. The analysis of these anatomical features did not recover a monophyletic Arcoida, nor did it recover any of the higher taxonomic groups. A virtual comb was recovered from this analysis (see Fig. 67). In this analysis, the outgroup taxa (highlighted in red) are polyphyletic, placing at the base and the tip of the tree. The *only* taxa that show any sister group relationships are the pinnid, limid and mytilid outgroup taxa.



FIGURE 67. *Soft Anatomy Only*: The strict consensus of 3556 most parsimonious trees of length 568, CI = 0.16, RI = 0.67. Outgroup taxa are highlighted in red.

Apomorphies

The synapomorphies that define the major clades recovered from the 'complete' analysis are listed below. These include a small number of non-homoplastic synapomorphies (black circles) and a majority of homoplastic synapomorphies (white circles). The non-homoplastic synapomorphies are distinguished from those that are homoplastic by bold font. These non-homoplastic synapomorphies are further distinguished on the basis of ambiguity, with unambiguous, non-reversed synapomorphies being italicized. These non-reversed synapomorphies appear as black circles on the branches and are illustrated in Figs. 65 and 66. Homoplastic synapomorphies are visible as white circles on the branches. As evidenced by both these figures, the majority of clades are defined by homoplastic characters. The homoplastic synapomorphies that define major clades but that are later reversed in the tree are discussed in some detail below; this clade is highlighted in square brackets [ ]. The synapomorphies that recovered a monophyletic Philobryidae in the analysis of shell characteristics only are also discussed (Node 22). As a general rule, only those homoplastic synapomorphies that are not further reversed within a clade are discussed, unless otherwise noted. Autapomorphies have already been discussed in the 'Character Description'.

‘Complete’ Analysis

Node 0: *Anomia simplex* + Arcoida

» **External ligament** (character 56, state 0).

An external ligament is absent in *Anomia* and in the Philobryidae. An internal ligament is a defining characteristic of the Philobryidae. All other arcoids possess an external ligament.

» Ctenidial filament morphology (character 96, state 0).

The ctenidia of the Arcoida are comprised exclusively of ordinary filament, giving them the flat homorhabdic gill condition.

» Tissue junction between filaments (character 99, state 0).

The gills of the Arcoida lack tissue junctions between the ctenidial filaments, instead being united via lateral ciliated discs.

» ***Rejection current on ventral edge of ctenidium*** (character 109, state 1).

The rejection current on the ventral edge of the ctenidium is directed posteriorly in Arcoida and its sister-taxon, *Anomia simplex*. The rejection current is directed anteriorly towards the mouth in all other taxa included in this analysis.

» Fusion of labial palps to visceral mass (character 111, state 1).

The labial palps of the Arcoida attach along their entire dorsoventral axis to the visceral mass, such that there are no free edges. A similar condition is found in *Anomia simplex* and in the pinnid outgroup taxa.

» Ctenidial eye (character 137, state 1).

Ctenidial eyes are located at the base of the anteriormost filament of the inner demibranch of the ctenidia. These eyes are predominantly found in the Philobryidae, Noetiidae and Arcidae.

Node 1: Arcoida

» Shell microstructure: The mineralogical composition of the arcoidan adult shell is aragonitic in nature (character 1, state 0). This microstructural form is also found in the mytilid *Brachidontes domingensis*. While not unique to this group, all arcoids possess two shell layers (character 2, state 1) that is comprised of an outer layer of crossed lamellar structure (character 3, state 1) and an inner shell layer composed of complex crossed lamellar structure (character 4, state 1). Nacreous structure (characters 7 and 8, states 1) is never present in this group.

» ***Shell tubules*** (character 5, state 1).

The presence of shell tubules throughout the two shell layers within the pallial line is the defining characteristic of the Arcoida. When present in the outgroup taxa, they are found only in the inner shell layers. They are restricted to the inner shell layers in Mytilidae, and Pinnidae.

» Pallial line (character 6, state 0). [Philobryidae]

The pallial line marks the point of apposition of the pallial muscles of the outer mantle surface to the ventral wall of the inner shell surface. A well-defined wall is absent in the majority of Philobryidae (as well as in the arcid *Bathyarca*), but present in all other arcoid taxa.

» Prodissoconch shape (character 31, state 0). [Philobryidae]

An in depth discussion of the prodissoconch shape and its relationship to larval ecology is provided in the section on character descriptions. Briefly, a D-shaped prodissoconch is characteristic of all the Philobryidae, however, as with characters 32 and 140 (see below), this character is not unique to this family, with some arcids, such as *Barbatia dubia*, also possessing a prodissoconch of this form.

» Prodissoconch rim (character 32, state 1). [Philobryidae]

A raised rim around the prodissoconch is present in the majority of the Philobryidae; with the exception of *Lissarca*, *Micromytilus* and *Notomytilus*. This characteristic is not unique to the Philobryidae, but is found in a small number of arcid taxa. The significance of this is that while the function of this character is not definitively known, it is likely to play a role in non-planktotrophic development, given that a rim is only found in those taxa that exhibit this form of larval development.

» Direction of prodissoconch coiling (character 34, state 0). [Philobryidae]

The prodissoconch of the Philobryidae is consistently orthogyrous, with the beaks of each valve pointing directly towards each other.

» The tentacles (character 87, state 0) present on the outer and/or inner mantle layers, as seen in some of the outgroup taxa, are absent in the Arcoida. In the Arcoida, the sensory structures of the mantle are restricted to eyes and pigmentation.

» **Labial caecum** (character 121, state 1). [Philobryidae]

A caecum lying in the angle between the body wall and the inner lip has been observed in a number of philobryid taxa; *Lissarca*, *Philobrya* and *Adacnarca*. It was not possible to record its presence of absence in the other philobryid groups, due to poor preservation of the tissues. The adaptive significance of this feature is unknown, but given its proximity to the mouth, it is likely to play some role in digestive functions.

» Reproductive mode (character 141, state 1). [Philobryidae]

As mentioned previously, the Philobryidae have categorically been described as organisms that brood their larvae in their infra-branchial chambers. This assertion was based on direct observations of brooded young in some taxa, but was inferred for other taxa. For these taken where brooding was inferred from the presence of a straight-hinged prodissoconch, which some authors believed guaranteed internal brooding. Brooded young have been observed by some authors in *Barbatia* species (e.g. *Barbatia bailiyi:* Moran, 2004a) and in *Barbatia dubia* by this author.

Node 2: *Philobrya*

» The prodissoconch of *Philobrya* is terminal, with a position at the anteriormost end of the hinge line (character 35, state 0). Such a position on the hinge line, is common among the Philobryidae. Because of the positioning of the prodissoconch, the ligament is

restricted to growing posterior to the PD (opisthodetic) (character 59, state 0). In addition, an oral groove is lacking at the junction between the outer and inner labial palps (character 116, state 0). While not unique to the Philobryidae, *Philobrya* possess distinct osphradia (character 136, state 1).

Node 3: Arcoida except *Philobrya*

» Evidence for larval teeth in the adult hinge (character 36, state 1).

Larval teeth are present in the adult hinge of all Philobryidae, with the exception of *Philobrya munita* and *Philobrya* sp. USNM07. These teeth are remnants of the teeth found in the larval shell that have not been eradicated with the growth of the adult hinge, as is the case with all other arcoids.

Node 4: *Cosa*

» The philobryid genus *Cosa* is characterized by the presence of the following: posterior truncation of the shell (character 13, state 1); raised radial sculptural elements in the form of riblets (character 20, state 1); an attached rectum (character 125, state 1); and presence of simple pallial eyes (character 138, state 1).

Node 5: *Lissarca* + *Neocardia* + *Micromytilus* + *Notomytilus*

» These taxa form a clade on the basis of an attached rectum to the undersurface of the posterior adductor muscle (character 125, state 1) and by passing of the intestine ventral to the ventricle (character 131, state 1). Within this group, we see a larger clade (except *Lissarca notorcadensis*) that are united by uniformity in the pigmentation of their

external shell surfaces (character 29, state 0), by the absence of ciliated discs between filaments in all taxa except *Lissarca rubrofusca* (character 97, state 0) and by the absence of a ctenidial suspensory membrane (character 104, state 0).

Node 6: Arcoida except Philobryidae

» Pallial line (character 6, state 1).

The pallial line is a scar found on the inside of the shell that marks the line of attachment of the mantle to the inner shell surface. It also represents the boundary between he outer crossed lamellar and inner complex crossed lamellar structure of the shell. A pallial line is found in all arcoids except the Philobryidae and in all *Bathyarca* species examined in this study.

» Inflation of the valves (character 14, state 1). [Limopsidae]

The relative distance between the two outer planes of the shells, parallel to the commissure plane, is generally great in the Arcoida, such that the valves appear inflated. The valves of the Limopsidae exhibit some degree of compression.

» Prodissoconch shape (character 31, state 1) and rim (character 32, state 0).

The shape of the prodissoconch in virtually all the Arcoida is subtriangular. As mentioned previously a D-shaped prodissoconch is seen in the Philobryidae and some *Barbatia* species that are known to brood their young. All non-philobryid arcoids lack a prodissoconch rim, with the exception of some *Bentharca* and *Bathyarca* taxa that are known to brood their young.

» External ligament (character 56, state 1).

An external ligament is present in all Arcoida bar the Philobryidae, which possess an internal alivincular ligament.

» Anterior adductor muscle (or scar) (character 75, state 1).

In the majority of the Arcoida, with the exception of the approximately equilateral form of the Glycymerididae, the shell form tends towards a shortened more restricted anterior end and a broader posterior end. Therefore, the size of the anterior adductor muscle is restricted and reduced in comparison with the posterior adductor muscle.

» Inner folds or grooves on the palps **(**character 114, state 1).

Transverse ridges on the inner palps direct the incoming food towards the oral groove, which leads ventrally to the mouth. In the Limopsidae and Glycymerididae, these folds are restricted to the distal portion of the palp. These taxa are generally restricted to habitats with clear water and gravely substrate (Thomas, 1975). This is correlated with an efficient sorting mechanism found on the ctenidia (Atkins, 1937) and is prevalent in suspension feeders, where a high filtration rate of food is not needed. Such is the case with the limopsid taxa in this study, which are known suspension feeders.

Node 7: Glycymerididae

» Inner margin crenulations (character 40, state 3).

The Glycymerididae possess raised shell elements on the inner ventral margin of the shell. These crenulations may or may not correspond to the external radial structure.

Crenulations assist in keep the valves aligned, an important feature for these burrowing organisms.

» Oblique furrow (character 54, state 1).

With the exception of *Glycymeris grayana*, all Glycymerididae possess a small oblique furrow on the crest of the hinge teeth.

» Restriction of fibrous portion of filament to resilifer (character 57, state 0).

The fibrous portion of the Glycymerididae is not restricted to a hollowed out depression on the hinge surface. A resilifer bound ligament is characteristic of the Limopsidae and Philobryidae, which possess a ligament of the alivincular type. The presence of a resilifer has not been observed in any other arcoidean taxa.

» Ligament position relative to the prodissoconch (character 59, state 1).

All the glycymeridid taxa in this study possess a ligament that extended anteriorly and posteriorly (elongate amphidetic).

» Orientation of the foot axis (character 63, state 0).

The glycymeridid foot is orientated such that it is parallel to the ventral margin of the shell. This anvil shaped foot is a powerful tool employed by these organisms for burrowing into sand.

» Extension of byssal groove (character 71, state 0).

The byssal groove on the ventral surface of the foot, marks the place from within which the byssus emerges. In the Glycymerididae the byssal groove extends along the entire

surface of the anvil shaped foot. The presence of such an extensive groove in the Glycymerididae is somewhat perplexing given the fact that the byssus, which is thread – like, is lost in adults.

» Posteriorly directed process on the visceral mass (character 73, state 1).

The majority of the Glycymerididae possess a posteriorly directed process on the visceral mass. The function of this newly described character is unknown.

» Adductor muscle (or scar) (character 75, state 0; character 76, state 1).

Given their almost equilateral shape, the anterior adductor muscles of the animals are approximately equal in size to the posterior muscles. *Glycymeris grayana* and *Melaxinaea labyrintha* are the only exception to this state, having reduced anterior adductor muscle.

» Multiplication of outer mantle fold (character 83, state 2).

With one exception, *Melaxinaea labyrintha*, all Glycymerididae exhibit three mantle folds outside the periostracum. This finding is contrary to any previous finding (see discussion in character descriptions). Evidence for pigmentation of this outer fold was seen in all the Glycymerididae examined, again with the exception of *Melaxinaea labyrintha.*

» Pigmentation of mantle margin edge (character 93, state 1).

The mantle edge of the Glycymerididae is pigmented.

» ***Renal concretions*** (character 129, state 1).

Extracellular deposits of calcium lie beneath the ctenidial suspensory membrane in the Glycymerididae). First described by Pelseneer (1911), this feature has never been described as a defining characteristic of this family. However, as previously mentioned, members of this family have been exclusively circumscribed by characteristics of the shell and anatomical studies of this family are rare.

» Eyes: With few exceptions (*Melaxinaea labyrintha* and *Glycymeris grayana*), the mantle edge of the Glycymerididae is lined with both simple (character 138, state 1) and compound (character 139, state 1) eyes.

Node 8: *Axinactis* + *Tucetona*

» Both *Axinactis* and *Tucetona* are distinguished from other glycymeridids by their glabrous shell surface (character 9, state 0) and possession of strong radial ribs (character 20, state 2).

Node 9: *Tucetona*

» This genus is defined the presence of flattened commarginal lamellae (character 27) and by pigmentation of the posterior adductor muscle (character 78, state 1). This taxon also possesses tumescent spots on the mantle edge (character 95, state 1). The ctenidia are pigmented (character 107, state 1) and an anal process is present (character 127, state 1).

Node 10: Arcoidea *sensu* Newell, 1969

» Pallial line (character 6, state 0). [*Bathyarca*]

Absent in *Bathyarca*, see node 11 below.

» Inflation of the valves (character 14, state 0).

The relative distance between the two outer planes of the valves parallel to the ventral margin, is such that the bivalve appears inflated. Lateral compression, on the other hand, is found in the genera *Philobrya*, *Melaxinaea*, *Empleconia*, most *Limopsis* and *Stenocista* species.

» Umbonal arching (character 38, state 1)**.**

The umbones have a general tendency to arch, such that the face of the prodissoconch of each valve is directed towards the other.

» Hinge line (character 46, state 0).

A straight hinge line is generally present in the Arcoidea (sensu Newell, 1969). This straight hinge line was one of the defining characteristics of the superfamily (the Limopsoidea were described as having curved hinge lines). An exceptions to this state is seen in *Scaphula*, as well as a small number of arcid taxa.

» Orientation of the foot axis (character 63, state 0).

See Node 5.

» **Mantle flap or extension** (character 89, state 1). [*Bathyarca*]

The posterior inner mantle fold of *Bathyarca* is enlarged, such that when extended they ostensibly form 'siphons' of a sort. This character is unique to *Bathyarca*.

Node 11: Arcoidea sensu Newell, 1969 except *Bathyarca*

» The pallial line is present in all Arcoida except the Bathyarca species included in this analysis (character 6, state 1). In addition, the mantle flap or extension is absent, and is exclusively found in *Bathyarca* (character 89, state 0).

Node 12: *Scaphula* + Noetiidae

» The ventral edge of the valves of these bivalves make direct contact at the commissure plane such that the valves are of equal size (character 12, state 0). In addition, a posterior buttress is characteristic of the Noetiidae (character 42, state 1). Present in *Scaphula* also, this calcareous process aids in the attachment of the adductor muscle, and in inflated taxa, assists in reducing the effect of shearing on the adductor muscle (Kauffman, 1969).

Node 13: *Scaphula*

» The direction of prodissoconch coiling (character 34, state 2) in this taxon coils, such that it faces the posterior end of the organism. *Scaphula* possess a very strong, sharp keel (character 37, state 2), running from diagonally from the umbonal region of the hinge towards the posteroventral margin. This taxon is one of the few arcoidean taxa (*sensu* Amler, 1999), that possesses a curved hinge line (character 46, state 1). This form of hinge is more characteristic of limopsoidean taxa *sensu* Newell (1969). However, the

curvature of the hinge of *Scaphula* differs from that of the Glycymerididae for example, as the hinge line is straight for 2/3 of the hinge line and then it curves ventrally. A byssal ventral byssal gape is also present (character 67, state 1).

Node 14: Noetiidae

» The ligament found in the Noetiidae is similar to the duplivincular ligament found in other arcoid taxa, in that it is laid down in alternating bands of lamellar ligament that is embedded into sheets of the fibrous ligament. However, in the Noetiidae, the ligament differs in two respects: new elements of the lamellar ligament are laid down near the extremities of the hinge line (anteriorly and posteriorly) as opposed to medially, as in other arcoids (character 60, state 1); in addition, the striation of the ligament is vertical and the familiar chevron shaped grooves of a 'classic' duplivincular ligament are absent (character 61, state 1).

Node 15: Arcoidea except *Bathyarca* and *Scaphula*

» There are no characters or suite of characters that are not reversed within this clade that distinguish this clade from the other arcoids.

Node 16

» Prodissoconch coiling (character 34, state 1).

With few exceptions (*Arca noae* and *Litharca lithodomus)*, the bivalves in the remaining two large clades possess a prodissoconch that coils in an anterior direction, i.e. prosogyrous.

Node 17

» This clade is largely comprised of Anadarinae taxa, with the exception of *Bathyarca*, *Bentharca* and *Samacar* and the inclusion of the Cucullaeidae and *Trisidos* also. The presence of strong crenulations along the ventral margin of the shell defines this group (character 40, state 2) except in *Cucullaea alta* where it is restricted posteriorly and with the clade comprise of *Cucullaea labiata* and *Trisidos* where it is lacking. Within this clade, the taxa tend to lack an edentulous space between the anterior and posterior teeth (character 52, state 0); the only exception to this was with *Trisidos tortuosa*. With a few exceptions, the taxa included in this clade have rounded labial palps (character 112, state 1); exceptions include *Anadara geissei*, *Scapharca inaequivalvis* and *Scapharca rotundicostata* cf. that possess palps that are angled).

Node 18: *Trisidos*

» ***Twisting*** (character 15, state 1).

In this analysis, the twisting or rotation of the posterior part of the sagittal plane of the shell is a defining characteristic of this genus. However, as mentioned in the description of this character, this feature is also found in other bivalves not included in this analysis, including the extinct arcoid taxon *Ambrogia.*

» This taxon is also devoid of any pigmentation on the shell surface (character 29, state 4), lack umbonal separation (character 39, state 0), possess oblique furrows on the hinge teeth (character 54, state 1), the PPR and PAM are confluent (character 81, state 1), the posteroventral margin of the PAM is separate from the pallial line (character 82, state 1),

commarginal folds are lacking on the mantle edge (character 86, state 0) and osphradia are present (character 136, state 1). Because of the twisting of the shell, the ASO's are asymmetrical, such that the right ASO is much larger than the left (character 134, state 1).

Node 19: Arcinae except *Trisidos*

This clade is mostly comprised of Arcinae taxa, except Trisidos. There are no un-reversed synapomorphies, homoplastic or otherwise that define this node.

Node 20: *Litharca* + *Arca*

» Multiplication of mantle fold (character 83, state 2).

With the exception of *Arca ventricosa*, these organisms all exhibit triplication of the outer mantle folds (character 82), with a single fold in the inner mantle fold (character 84).

» Compound pallial eyes (character 139, state 1).

Ommatidium like eyes are found on the crest of the first outer fold of these organisms. They are especially large and numerous at the posterior region of the mantle.

Node 21: *Barbatia* (*Acar*) ?

» This clade, which ostensibly includes taxa that have been included in the arcid subgenus *Acar*, are defined here by the presence of a glabrous periostracum (character 9, state 0), possession of divided radial elements (character 21, state 1)—except for *Barbatia iota* where the radial sculpture is simple, having a strong umbonal carina (character 37, state 2), presence of elevated adductor muscle scars (character 44, state 1)

and possession of an anal papilla. *Barbatia candida*, which has been traditionally described within this genus, did not fall within this clade but placed towards the base of a larger *Barbatia* clade. However, as with many of the higher taxonomic groups in this order, the subgenus has been described on the basis of a composite of characters found in other taxa, i.e. 'mainly' opisthodetic ligament, posterior carina prominent, cardinal area narrow, adductor scars elevated. None of these characteristics are seen to optimize with clade in this analysis.

'Hard' Analysis

Node 22: Philobryidae

» This family is defined by the absence of a distinct pallial line (character 6, state 0), by inflation of the valves (character 14, state 0), by the presence of a D-shaped prodissoconch (character 31, state 0), by evidence for larval hinge teeth in the adult hinge (character 36, state 1) and by the absence of an external ligament (character 56, state 0).

DISCUSSION

The goal of this study is to elucidate the phylogenetic relationships of the Arcoida and to assess the relationships of the higher taxa in the group. To this end, 141 characters, taken from traditional shell characters and soft anatomical characters, were coded for 131 taxa. As is so often the case when dealing with descriptive features, there is sometimes subjectivity and ambiguity associated with the traditional descriptions of morphological characters and states. Therefore, in depth descriptions were provided for each character and state, many of these having associated figures or images. Many of these characters are newly described or delimited. In determining the characters and character states, an endeavor was made to move away from using character complexes—for example, rather than code for the presence or absence of a duplivincular ligament, this character complex was broken down into five separate characters—on the basis that these complexes make unwarranted statements about homology. Furthermore, the use of such character complexes reduces information. An example of this is seen in the general coding of the gills in bivalves, with grades of gills or gill types (e.g. filibranch, eulamellibranch, septibranch) often coded as character states. In his extensive examination of the structure of the gills of the Bivalvia, Ridewood (1903) found that a number of Arcidae did not conform to the usual form of the filibranch gill. Unlike their cohorts, these taxa also possess interlamellar, membranous connections between the ascending and descending lamellae of the ctenidia.

Two classes of characters are explored in this study. The first class represents those that have been generally utilized in both taxonomic and phylogenetic studies of Bivalvia and includes 'hard' or shell based characters. The second class of characters is taken from the soft anatomy of the organism, and include features that are explored in anatomical studies of the group, but are not generally employed in phylogenetic studies (except in the previously mentioned studies of Giribet and Wheeler (2002) and Carter et al. (2000)). The purpose of analyzing the 'hard' and 'soft' characters separately was to test their ability to recover monophyletic groups. This is more pertinent for the 'hard' than the 'soft' dataset, which have never been used in isolation to describe any bivalve group. The analysis of shell characters alone failed to recover most of the higher taxonomic units that they were traditionally used to prescribe. Given that all these taxa were initially described on the basis of shell characters only, this result would indicate the need for caution in the use of this suite of characters alone in the description of taxa. The analysis of soft anatomical characters only, surprisingly, provided little coherent phylogenetic signal. However, this is not to say that these characters should be omitted from future studies, but only illustrates the need to include all information to elucidate the relationships of the group. With the principle that all available cladistically scorable data must be employed to understand the phylogenetic relationships of a group, any changes to the classification of the order, should be based on *all* the information at hand.

Past discussions on the originations of the Arcoida (and generally of most other Mollusca, with the exception of perhaps the Cephalopoda and Aplacophora) are steeped in a paleontological perspective. This is hardly surprising, given the expansive fossil

record of the Mollusca and the heavy tendency to describe new species on the basis of shell characters only. It is not the purpose of this study, to postulate how this group evolved, but only to address the sister-group relationships within the taxa. As pointed out by De Pinna (1996), a major success of the cladistic approach was the recognition that ancestor-descendant relationships cannot be objectively proposed or tested. In phylogenetic studies, one can only assess the patterns, as evinced by the groupings of the terminal taxa at the tips of the tree (i.e. sister-group relationships); one cannot objectively assess the ascendant-descendent relationships without invoking *ad hoc* assumptions. The discussion that follows primarily deals with the sister-group relationships of the higher-level taxa of the order, as opposed to those of the individual species.

Despite the breadth of sampling in this study, it was not possible to fully resolve the relationships of the higher taxa within the group. Although this study is the largest of its kind for the order, it suffers from some limitations with respect to taxon and character sampling. It was not possible to include the type species of many of the genera (and especially subgenera) in the analysis; therefore any major taxonomic revision would necessitate their inclusion. Even though a broad range of taxa were included for some of the families, most notably the Arcidae with 62 representatives, the sampling of the Cucullaeidae and Parallelodontidae was limited, with two taxa included for each of these two families. This is in part due to limited representative of the Recent taxa of these families in malacological collections and also was largely due to the great number of fossil taxa described in both these families (the Cucullaeidae has a single Recent taxon, *Cucullaea* and the Parallelodontidae is represented by the Recent taxon, *Porterious dalli*

(this species is rare in collections and it was not possible to include it in this study). Such poor representation of these families in this study makes assessment of their monophyly and sister group relationships difficult.

The relationships of some of the taxa likely suffered due to an excess of missing character data, most notably the Philobryidae—for the 1724 cells coded for this family, 427 of these (~ 25%) were either coded as inapplicable '-' or missing '?'; this sampling problem was due largely to the fact that it was not possible to code some of the soft morphological characters, as the tissue preservation of these tiny creatures, was often so poor, such that the tissue was hardened or shriveled. A more comprehensive character sampling for this family is warranted.

In this study, the analysis of both shell and internal soft anatomical data suggest a monophyletic origin of the Arcoida. This result corroborates the findings of previous studies. Non-monophyly of the Arcoida has never been recovered in any published study. Prior establishment of the monophyly of the Arcoida has, with two exceptions, been based exclusively on the inclusion of arcoidean taxa (*sensu* Amler, 1999) only. Page and Linse's (2002) investigation of polar limid taxon *Limatula* (with six arcoid taxa included as outgroup taxa) and Matsumoto's (2003) examination of the Pteriomorphia are the only phylogenetic studies that have included taxa from the limopsoidean family Limopsidae. The Philobryidae have not, till now, been included in any phylogenetic study of this group. These other studies include the morphological analysis of extinct taxa by Carter et al. (2000), the molecular analyses of Campbell et al. (1998); Campbell (2000); Steiner and Hammer (2000); Hammer (2001); Giribet and Distel (2003), and the

combined analyses of both morphological and molecular data in the study of the Bivalvia by Giribet and Wheeler (2002). In the molecular analyses, the recovery of a monophyletic Arcoida was well supported with Bremer Support values ranging from 3-40 (Steiner and Hammer, 2000; Hammer, 2001) and equally high bootstrap values (Matsumoto, 2003). Although no morphological synapomorphy was reported for the group in Giribet and Wheeler (2002), the monophyly of the order was well supported and recovered under 11 different parameter sets. The monophyletic Arcoida of Carter et al. (2000) was supported by a number of synapomorphies, including "a stronger inflection in the posteroventral shell margin; posteroventral inclination of the anterior shell margin; reduction of the commissural shelf; secondarily equivalve shells; movement of the posterior adductor closer to the hinge; a more elliptical anterior adductor; increase in the number of anterior lateral or pseudolateral hinge teeth from two to three or more; and a change in the orientation of the pseudotaxondont subumbonal teeth from posteroventrally inclined to nearly vertical dorsally divergent." Virtually all these characters are subjective and highly relative and so for this reason, they were not included in the present analysis. Waller (1998) reported a number of synapomorphies for the group, including hinge teeth with an "arcoid plan", compound photoreceptors on the outer mantle fold, inner layers mainly consisting of crossed lamellar microstructure and shell tubules present throughout the area within the pallial line and penetrating the shell to the inner surface of the periostracum. However, it must be pointed out that the "recovery" of these synapomorphies was more inferential than explicit, given that the phylogeny an informal analysis with the characters simply mapped onto the tree.

Previous descriptions of the Arcoida have characterized these taxa as having a shell microstructure as comprised of aragonite, crossed lamellar and complex crossed lamellar structure, a filibranch gill, duplivincular ligament, and taxodont hinge. In this study, the monophyly of the order is supported by a single non-homoplastic synapomorphy—the presence of shell tubules across the entire area inside the pallial line or inside the area of apposition of the mantle to the inner shell surface, if a pallial line is lacking. Although present in some of the outgroup taxa, the composition of the shell microstructure, though homoplastic, also diagnoses the group. The characters pertaining to ligament, teeth and gills were not recovered as diagnoses of this clade. The other synapomorphies recovered for this clade include the absence of tentacles on the mantle margin. All other synapomorphies at this node (node 1) define the Philobryidae and are later reversed in the other arcoid taxa.

Questions relating to the relationships within the Arcoida have largely been restricted to the relationships of the higher taxa within the group, although some recent molecular studies have focused on arcoid species pairs (Marko and Moran, 2002; Marko, 2002). At the time of Newell's classification of the group in the *Treatise of Invertebrate Paleontology* (1969), there was some uncertainty as to the inclusion of the Cyrtodontoidea, Manzanellidae and Philobryidae. Since then, the taxonomy of these groups have been asserted—the Cyrtodontoidea are presently classified as an order, the Cyrtodontoida (Cope, 1996; Malchus, 2004a); the Manzanellidae were removed from the Arcoida and subsequently included in the Protobranchia (Allen and Sanders, 1969); and the Philobryidae's status as an arcoid was substantiated (Tevesz, 1977; Waller, 1978)—

the inclusion of the Philobryidae in the Arcoida, however, was not based on a phylogenetic study of the group, but on the basis of the shell microstructure and internal morphology being consistent with those of other arcoid families.

The higher taxonomy within the order remained largely unchanged, with seven nominal families in two superfamilies being included in the order. In Newell's classification scheme, the Glycymerididae were placed in the Limopsoidea, along with the Limopsidae and Philobryidae—their inclusion in this superfamily rested mainly on the basis of a similar shell form (ovate) and hinge line (curved) (see Table 2). At least superficially, the Glycymerididae appeared more similar to the Limopsidae and Philobryidae, than they did to the Arcoidea, which, are generally trapezoidal in shape and have a straight hinge line. While the shell form of the Limopsidae is highly convergent with those of the Glycymerididae, the Philobryidae differ from this family in their possession of an internal alivincular ligament and a D-shaped prodissoconch, which commonly has an associated prodissoconch rim. It is this classification that has gained the most acceptance within the malacological community. However, an alternate classification scheme proposed by Carter (1990a) and formally accepted by Amler (1999) placed the family in the Arcoidea, in the belief that the Glycymerididae's origination rested with the Cucullaeidae.

The results of previous studies have given no clear indication as to the relationships of the higher taxa in the group. In their analysis of the morphological data only Giribet and Wheeler (2002) found that the Arcoidea (represented by taxa from the Arcidae and Noetiidae) was polyphyletic with respect to the Limopsoidea (represented by *Glycymeris insubrica*). This representative taxon was nestled within the Arcidae and

Noetiidae. This result, however, is dependent on the chosen classification of the higher taxonomic groups—in this study the authors followed the classification of the Bivalvia in Beesley et al. (1998), which is akin to that of Newell (1969), wherein the Glycymerididae were included in the Limopsoidea. In the two studies that included a 'truly limopsoidean' taxon, Page and Linse (2002) and Matsumoto (2003), the two superfamilies were recovered. The Arcoidea (represented by the Arcidae and Glycymerididae) was paraphyletic with respect to the Limopsoidea (represented by two *Limopsis* species) in Page and Linse's (2002) study. Matsumoto (2003) recovered two large clades, however, these clades did not reflect traditional taxonomy, with one clade comprised largely of anadarine taxa and the other comprised of arcid, cucullaeid, glycymerid and limopsid taxa. In this clade, the Glycymerididae was polyphyletic, forming a sister group relationship with *Cucullaea* and the limopsid *Empleconia*.

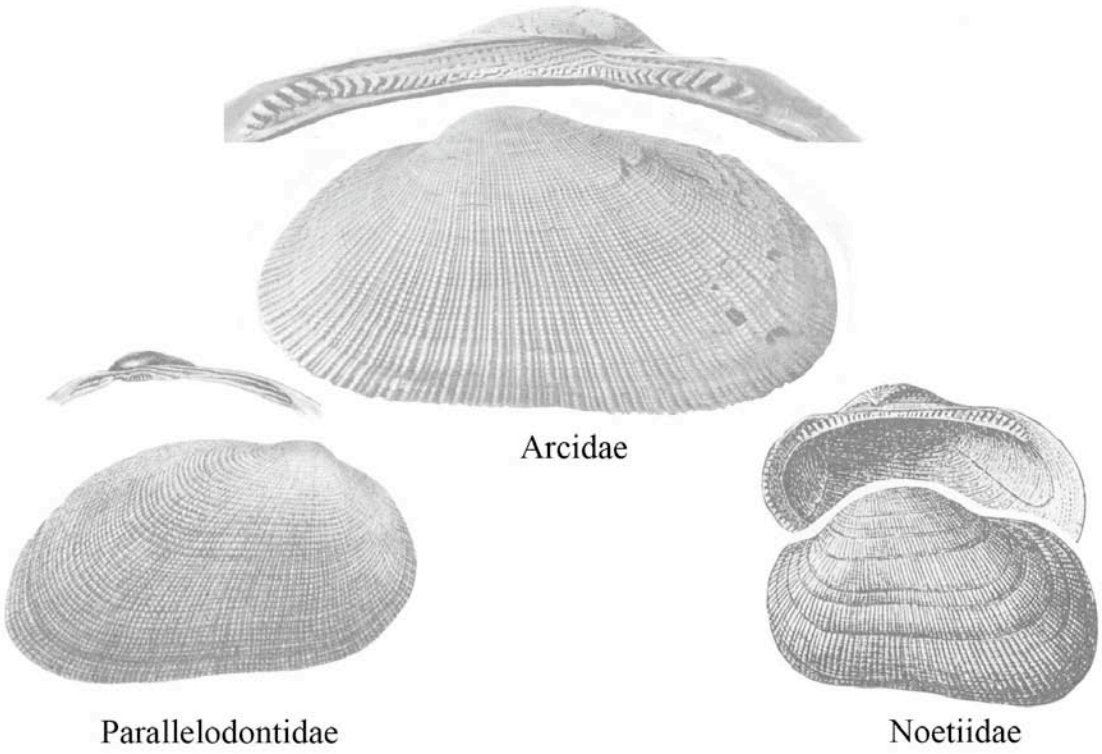
The results of the complete morphological analysis, give no clear indication as to the placement of the Glycymerididae in either the Arcoidea or Limopsoidea, as this family, along with other limopsid taxa, form a polytomy at the base of the larger Arcoidea (*sensu* Newell, 1969) clade. Moreover, there is no non-homoplastic, non-reversed synapomorphy that diagnosed their inclusion in the Arcoidea. When shell characters alone were analyzed, the Glycymerididae was seen to form a sister group with the Arcoidea of Newell (1969). Whilst there is some evidence that supports the Arcoidea (see the apomorphies for Node 10), whether this includes the Glycymerididae or not, there is no evidence that supports the validity of the Limopsoidea. In fact in the constrained analyses, in order to recover a phylogeny that mirrored the superfamily relationships of Newell (1969), this was achievable with 19 additional steps. Likewise, in

order to recover the classification of Amler (1999), this took an additional 18 steps. However, if one were to follow the creed that sister taxon are by necessity the same age and therefore must have the same taxonomic rank, this result would call for the abandonment of the rank of superfamily in the Arcoida.

The families of the Arcoida are defined by a constellation of characters, all of which are shell based. On the face of it, of all the Arcoida, the Noetiidae, Glycymerididae and Philobryidae would appear to be easily diagnosable, on the basis of either a single or complex of characters: a *transverse*, duplivincular ligament [Noetiidae]; an elongate, chevron-shaped, amphidetic ligament, curved hinge and renal concretions [Glycymerididae]; and an internal alivincular ligament with a D-shaped prodissoconch, often with an associated prodissoconch rim [Philobryidae]. The other families included in the order are not as easily diagnosed. The sole characteristic that would appear to distinguish the Parallelodontidae from the other families is the possession of longitudinal teeth that are proximal to the umbones. This character was seen to be homoplastic in the resulting phylogeny and did not recover a monophyletic Parallelodontidae. The cucullaeids are known for their strong myophoric flange and 'pseudolateral' teeth. In the first place, such a calcareous process is absent from many of the fossil cucullaeid taxa, and pseudolaterals, as they have been delimited in this study (see characters 50 and 51), are not unique to this family, but have been observed in some arcid taxa (e.g. *Bathyarca perversidens*). Moreover, other than their distinguished ligament, the Noetiidae are highly similar to the Arcidae in most other respects, virtually identical in some cases,

with many taxa converging in form. In addition, the external shell form of some Parallelodontidae also converges on those of the Arcidae (see Fig. 68).

FIGURE 68. Convergence of external shell form in the Arcidae (*Barbatia*), Parallelodontidae (*Cucullaria*) and Noetiidae (*Striarca*). [Images adapted from Newell, 1969.]



Convergence in some characters appears to be rife within the Arcoida; and its existence has been postulated by many authors (Heath, 1941; Stanley, 1977; Thomas et

al., 2000; Oliver and Holmes, 2002). Heath (1941), in his examination of a considerable number of arcoid taxa, observed that many bivalves with identical shells had different internal anatomies. Conversely, subspecies that were dissimilar in external form were almost identical anatomically. While the families and subfamilies occupy characteristic adaptive zones, there is considerable overlap in shell form both within and between higher taxa. As indicated by the character optimization on both the complete and shell only analyses, a considerable degree of homoplasy is found in the resulting trees and the majority of clades were defined by homoplastic synapomorphies only. Only five non-reversed, non-homoplastic synapomorphies were recovered. The fit statistics for the trees also reflect large amounts of homoplasy in the data, with a CI of 0.16 and RI of 0.66-0.67. This phenomenon may help to explain the recovery of a polyphyletic Arcidae, Cucullaeidae and Parallelodontidae.

Notwithstanding the inability of these characters to recover the monophyletic taxa that they were used to describe, the Glycymerididae was the only family that was consistently recovered in the analyses of both 'complete' and 'hard' datasets. Perhaps somewhat surprisingly, the Noetiidae where not recovered as monophyletic in the 'hard' dataset, where the two characters relating to their unique form of ligament (characters 59 and 60) were rendered homoplastic, but these characters diagnosed a monophyletic Noetiidae in the 'complete' dataset. This striking feature of the Noetiidae was thought to be one of the few unequivocal synapomorphies—a ligament comprised of vertical strips of lamellar bands that are embedded in grooves of the sheet of fibrous ligament, with a novel growth pattern—that defined a family-level clade (Thomas et al., 2000). A monophyletic Philobryidae was recovered in the 'hard' dataset, but not so in the

'complete' dataset. This is likely an artifact of character sample (with 21% of the characters missing for the family), but despite this absence, the Philobryidae must now be considered a grade. Likewise, with the Limopsidae, which was paraphyletic with respect to the Glycymerididae + Arcoidea (*sensu* Amler, 1999). As mentioned the Arcidae were rendered polyphyletic by the inclusion of the Cucullaeidae and Parallelodontidae. Both these families were represented by only two taxa, and *Cucullaea labiata* was the only Recent representative included. Because of this, many data, namely all the information pertaining to the 68 soft anatomical characters were missing for *Cucullaea alta* and the two fossil parallelodontid taxa. It is possible that this lack of data hindered the recovery of the phylogenetic relationships of the group.

In this study, none of the subfamilies of Newell (1969) were recovered as monophyletic (however, recall from Newell's classification (Table 3), that the Arcidae and Noetiidae are the only families that have Recent subfamilies. The Arcinae and Anadarinae (Arcidae) and the Noetiinae and Striarcinae (Noetiidae) were both polyphyletic in the resulting tree. The Arcinae are distinguished from the Anadarinae on the basis of habitat/lifestyle and characters associated with this. The Arcinae (*Arca*, *Barbatia*, *Litharca* and *Trisidos*) are defined as nestlers, employing a byssus that assists in attachment (hence they possess a byssal gape). These creatures also have a smooth ventral margin. The Anadarinae, which includes all other arcids, lack the byssal gape as the adults are either free or produce thin byssal strands. In addition, the umbones are prosogyrous. None of these characteristics (byssal gape, ventral margin crenulations, umbonal direction) recovered monophyletic arcid subfamilies. A polyphyletic Arcidae was found in the analysis of cytochrome *c* oxidase I of a number of arcoid taxa (Marko,

2002). The Arcidae were rendered polyphyletic by the inclusion of the Noetiidae among Arcinae taxa.

The caution taken in choosing representatives for generic taxa only and not to include those to represent subgenera was justified. This point is illustrated with the arcid subgenera *Acar* and *Fugleria* (both in the genus *Barbatia*). *Acar* is defined on the basis of a composite of characters relating to the cardinal area and ligament. The single unique character attributed to this subgenus is the presence of elevated adductor muscles. This character is seen to be homoplastic in both the complete and hard analyses, with *Barbatia* (*Acar*) *candida* being polyphyletic with respect to the other '*Acar'* taxa at node 21 (Fig. 65). '*Fugleria'* represented by *Barbatia illota* and *Barbatia tenera,* is defined by having an ovoid costellate shell, low carina with a cardinal area similar to *Acar* (Newell, 1969)—these taxa are also polyphyletic in both the complete and hard analyses.

OUTGROUP RELATIONSHIPS

On the basis of the analysis of all the morphological data, the Anomiidae taxon *Anomia simplex* was found to be the sister-taxon to the Arcoida. The Limidae was the sister taxon to the Anomiidae + Arcoida. A similar relationship has been recovered in a number of previous studies. Matsumoto (2003) found that the Arcoida was the closest sister taxon to a clade comprised of Limoidea, Anomioidea and Pectinoidea. Similarly, Steiner and Hammer (2000) and Giribet and Distel (2003) recovered a sister group relationship between the Arcoida and an anomiid and limid taxa (ostreid and pectinoid taxa were also in this clade). However, this assessment is based on restricted sampling as

a heterodont taxon, the purported sister group to the Pteriomorphia was not included (see Fig. 7). In order to truly assess the sister-group relationship of Arcoida with other pteriomorphian taxa, it would be necessary to include a non-pteriomorphian outgroup taxon.

CONCLUSIONS

The fundamental aim of this study was to ascertain the phylogenetic relationships of the Arcoida. This study is the first phylogenetic study of the Arcoida to include representatives from the seven nominal families. Furthermore, the gross and microscopic examination of anatomy of these organisms has resulted in the largest morphological dataset for the order. However, despite the fact that this study is the largest of its kind in terms of character determination and taxon sampling, the relationships are not fully resolved.

The translation of the resulting phylogeny into a new classification for the order, calls for the abandonment of the rank of superfamily in this group. Given that a monophyletic Limopsoidea, sister to a monophyletic Arcoidea, has *never* been recovered in any phylogenetic analysis that included representative taxa of these superfamilies, this abandonment of the superfamilial rank would seem justified. The new classification would also call for the abandonment of the majority of the familial ranks. Of the seven families, the Glycymerididae and Noetiidae are the only ones recovered as monophyletic taxa (although the Noetiidae is nestled within the Arcidae). The Philobryidae and

Limopsidae are both paraphyletic in this study. While the Parallelodontidae and Cucullaeidae may certainly have suffered from taxonomic sampling, the same cannot be said of the Arcidae. However, before abandoning all these family level taxa, the inclusion of additional Parallelodontidae and Cucullaeidae is needed, as their representation in this study is paltry in comparison with the other families. Moreover, the inclusion of more of these taxa will also expand the representation of fossil taxa in the study, which is highly desirable, given the long fossil record of this group.

Presently, the majority of phylogenetic analyses of bivalve taxa in some way invoke the classifications of either Newell (1969) or Amler (1999). In the case of the Arcoida, these schemes have been based on either superficial similarity—Newell (1969) classified the Glycymerididae with the Limopsidae and Philobryidae as these taxa are all somewhat ovoid, or on the assertion of one group evolving from another—Amler (1999) guided by Carter's (1990a) diagnosis of the order had grouped the Glycymerididae with the arcoidean taxa of Newell (1969) with the belief that this family was more closely related to the Cucullaeidae than to the Limopsidae. No phylogenetic study involving the Arcoida has ever recovered a phylogeny that reflected either of these two classification schemes. Moreover, very often the family level taxa are not recovered (e.g. Marko, 2002; Giribet and Wheeler, 2002). The results of this study highlight the need for a major taxonomic revision at all levels in the Arcoida. This may result in the redefinition of many of the family-level taxa, but would seem to call for the abandonment of taxa above this level.

CHAPTER 3

Phylogeny of the bivalve order Arcoida (Pteriomorphia: Mollusca) based on the combination of morphological and molecular data.

INTRODUCTION

Species in the bivalve order Arcoida Stoliczka, 1871 are for the most part distinguishable by their strong hinge of interlocking, taxodont teeth and a duplivincular ligament that stretches across all or part of the dorsal hinge plate. These organisms are also characterized by their possession of an aragonitic shell microstructure and simple, W-shaped filibranchiate gills. While some of these characteristics are also found in other bivalve taxa, it is the combination of these characters that is found in the Arcoida alone (Tevesz, 1977). It has been previously posited by Waller (1980) that the sole, unequivocal synapomorphy for the group was the possession of shell tubules, which are distributed across both shell layers inside the pallial line of the inner shell. This putative synapomorphy has been confirmed in this study (Chapter 2). A strong muscular foot, often with associated byssal threads, assists in the various life history strategies found in this group—epifaunal nestlers and free-living infaunal groups both utilize the foot for limited movement, attachment and stabilization in both hard and soft substrates.

The current diversity of this group is poorly known, with estimates ranging from 300 (Oliver and Holmes, 2006) to 1300 species for the Arcidae alone (Reinhart, 1935). These bivalves have a long fossil record, dating back to the early Ordovician (Newell, 1969) and the group encompasses an almost equal number of extant and extinct taxa. Familiar taxa in this group include the arks, blood cockles and bittersweets, the latter two being of great commercial importance in regions of Southeast Asia (FAO, 2008). Arcoids are common components of marine ecosystems, being especially abundant in tropical and subtropical regions (Lamprell & Healy 1998; OBIS, 2008) reaching their

highest diversity in these areas. This group is not, however, restricted in its distribution by salinity, water temperature or depth: taxa from this group are also found in fresh (*Scaphula*) and estuarine water (*Senilia* and *Anadara*); colder northern Atlantic (Oliver and Allen, 1980a, b; Morton, 1982; CLEMAM, 2008) and Antarctic waters (Burne, 1920; Nicol, 1967; Knudsen, 1970); and are common inhabitants of littoral zones, but can also be found at abyssal depths up to 5300 m (Knudsen, 1970).

The Arcoida is one of the five orders included in the bivalve subclass Pteriomorphia Beurlen, 1944. At the time of publication of the *Treatise of Invertebrate Paleontology* (Newell, 1969), the order was comprised of nine families in three superfamilies. The current classification (*sensu* Amler, 1999) recognizes seven nominal families: Arcidae Lamarck, 1809; Parallelodontidae Dall, 1898; Cucullaeidae Steward, 1930; Noetiidae Steward, 1930; Glycymerididae Newton, 1922; Limopsidae Dall, 1895; and Philobryidae Bernard, 1897. While there is broad agreement as to the familial-level taxa included in the group, there has been considerable disagreement as to the number of superfamilies—ranging from two (Carter, 1990a; Amler, 1999), three (Newell, 1969; Coal et al., 2000) to as many as seven (Scarlato and Starabogatov, 1979). The two most prevalent classification schemes recognize the Arcoidea Lamarck, 1809 and Limopsoidea Dall, 1895 (cf. Newell, 1969 and Amler, 1999). In addition, the placement of the Glycymerididae within these superfamilies is contentious; this family has been classified along with the Arcidae, Noetiidae, Cucullaeidae and Parallelodontidae in the Arcoidea (see Carter, 1990a; Amler, 1999; Giribet and Distel, 2003), or with the Limopsidae and Philobryidae in the Limopsoidea (see Newell, 1969, Boyd, 1998; Giribet and Wheeler, 2002).

The aim of this study is to establish a phylogenetic framework for the Arcoida using both morphological and molecular data. Because both these data types are vital to understanding and interpreting relationships among taxa, any inference about the relationships of the taxa in this group will be made from the phylogenetic hypothesis recovered from the analysis of the complete dataset (morphology and molecular).

PREVIOUS PHYLOGENETIC HYPOTHESES

Published studies of this group are few and have suffered from limited taxonomic sampling. While there has never been an explicit phylogenetic analysis of the group as a whole, arcoid taxa have been included in broader phylogenetic studies of the subclass Pteriomorphia (Hammer, 2001; Matsumoto, 2003), as well as larger studies of the class (Campbell, 2000; Carter et al., 2000; Steiner and Hammer, 2000; Giribet and Wheeler, 2002; Giribet and Distel, 2003). Matsumoto (2003), in his study of the Pteriomorphia, boasts one of the broadest studies of arcoid taxa in terms of familial representation, with 18 species from four families being included in the analysis (Noetiidae, Philobryidae[2] and Parallelodontidae were lacking). Matsumoto's study was the first to include a cucullaeid representative. In this analysis, the Arcidae was rendered paraphyletic with respect to the other three families he included in the analysis. Moreover, the Glycymerididae (represented by two taxa) was found to be polyphyletic, with the two glycymerids finding

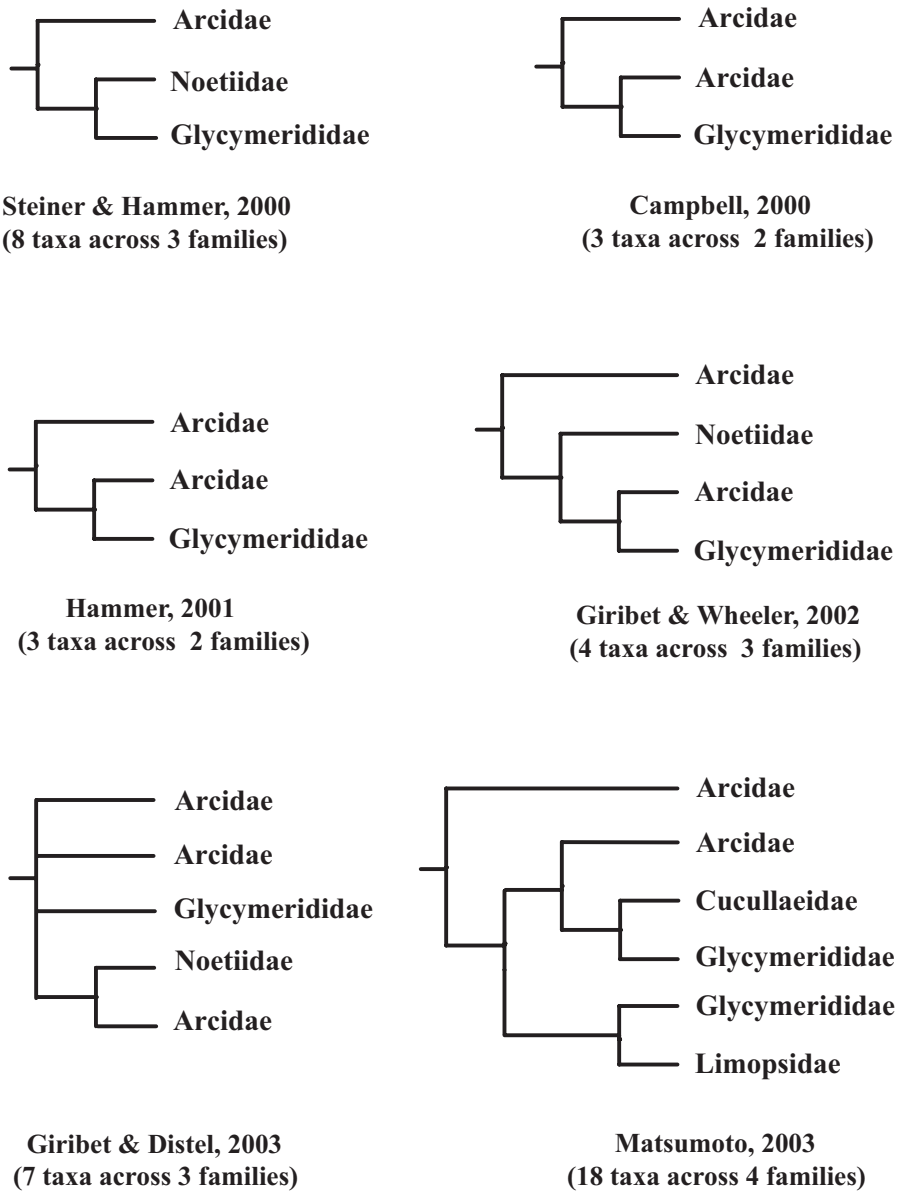
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[2] It is somewhat confusing as to the number of arcoid taxa included in this analysis. The author indicates that the philobryid taxon *Cosa waikikia* was examined for the study and indeed the COI gene was newly amplified, however, the taxon was not included in the final tree. The author gives no clear indication as to why this taxon was not included in the final analysis.

their sister taxon as either a limopsid or a cucullaeid. In all analyses where more than one representative of the Arcidae was included, the family was rendered either polyphyletic (Giribet and Distel, 2003) or paraphyletic (Steiner and Hammer, 2000; Matsumoto, 2003) in the recovered tree (Fig. 69). The Glycymerididae have been found nested within the Arcidae in the studies of Campbell (2000) and Giribet and Distel (2003). As only two arcids were included in the studies of Campbell (2000) and Hammer (2001), no statement can be made as to whether this taxon is paraphyletic or polyphyletic in these analyses.

Those studies that focused solely on the phylogenetic relationships of arcoid taxa have been restricted to an analysis of 15 glycymerid taxa (for 23 morphological characters) (Sanada and Matsukuma, 1996), Simone and Chickvarkhin's (2004) functional morphology paper which included an analysis of 6 arcid taxa (for 9 morphological characters) and investigations of geminate species pairs in the Arcidae and Noetiidae (Marko, 2002; Marko and Moran, 2002; Moran, 2004). In his investigation of geminate species pairs across the Panamanian isthmus, Marko (2002) analyzed cytochrome *c* oxidase subunit I and histone H3 for 27 arcoids from Arcidae, Noetiidae and Glycymerididae. This study focused mainly on arcid taxa (22 arcid taxa represented) with the sole glycymerid at the root of the tree. The Arcidae were rendered polyphyletic in this study, with a monophyletic Noetiidae nestled among arcid taxa at the base of the tree. A similar result was found in Marko and Moran (2002) and in Moran (2004), analyses that used many of the same taxa. In all these studies, the Arcoida have been recovered as a monophyletic group.

FIGURE 69. Phylogenetic hypotheses of higher-level arcoid relationships as recovered in previous studies. These studies include analyses of Bivalvia by Steiner and Hammer (2000), Campbell (2000), Giribet and Wheeler (2002) and Giribet and Distel (2003) and studies of the Pteriomorphia by Hammer (2001) and Matsumoto (2003) and that of *Limatula* by Page and Linse (2002). The number of species and familial representation are included.



SISTER-GROUP OF THE ARCOIDA

The increased interest in the study of bivalve phylogeny (Scarlato and Starobogatov, 1978, 1979; Waller, 1990; Starobogatov, 1992; Salvini-Plawen and Steiner, 1996; Cope, 1996; Morton, 1996; Carter, 1990; Campbell et al., 1998; Waller, 1998; Giribet and Wheeler, 2002; Giribet and Distel, 2003) has not helped to elucidate our understanding of the phylogenetic relationships within the Pteriomorphia. Despite the familiarity and commercial importance of many of the taxa in this group, e.g. scallops (Pectinidae), oysters (Ostreidae) and pearl oysters (Pterioidea), little attention has been paid to members of this subclass, leaving the sister-group relationships obscure (Steiner and Hammer, 2000; Hammer, 2001; Matsumoto, 2003). There is no clear indication in these studies as to the sister taxon of the Arcoida. Some studies suggest that the Mytiloidea are the sister-group to the Arcoida (Cope, 1996; Morton, 1996), but others have excluded the Mytiloidea from the Pteriomorphia entirely on the basis of shell microstructural and ligament data (Pojeta, 1978; Pojeta and Runnegar, 1985; Waller, 1990; Carter, 1990a). In a number of studies, the Arcoida was the sister-taxon to all other Pteriomorphia included in the analyses (Cope, 1996; Giribet and Distel, 2003). A number of different sister taxa have been proposed, including Mytiloidea (Morton, 1996), an Anomioidea + Plicatuloidea clade (Hammer, 2001), Limoidea (Waller, 1998), non-pectinoid pteriomorphs (Campbell et al., 1998); an Anomioidea + Limoidea + Pectinoidea clade (Matsumoto, 2003); as well the Arcoida being the sister taxon to non-mytiloid pteriomorphian bivalves (Giribet and Wheeler, 2002).

MATERIALS AND METHODS

TAXONOMIC SAMPLING

The majority of samples came from malacological collections of museums and institutions around the world, including: American Museum of Natural History, New York, USA (AMNH); Australian Museum, Sydney, Australia (AMS); The Natural History Museum, London, England (British Museum of Natural History) (BMNH); California Academy of Sciences, USA (CAS); Field Museum of Natural History, Chicago, USA (FMNH); Linnaean Society of London, London, England (LSL); Muséum national d'Histoire Naturelle, Paris, France (MNHN); University of Costa Rica: Instituto Nacional de Biodiversidad, Costa Rica (UCR-InBio); Smithsonian Institution, Washington, D.C., USA (United States National Museum) (USNM).

In addition to these museum specimens, fresh specimens were collected on a number of expeditions, including Costa Rica (January, 2003), Puerto Rico and Antigua (July, 2003) and the Great Barrier Reef, Australia (February - March, 2004). Specimens were obtained directly via snorkeling and SCUBA diving. Following initial relaxation in a solution of $MgCl_2$, the specimens were then fixed in either 5% buffered formalin (and subsequently transferred to 70% ethanol) for future dissection or were preserved in 95% ethanol to ensure proper preservation of the DNA. Voucher specimens are deposited in the malacology collection of the American Museum of Natural History.

Ingroup sampling—The classification scheme for the Arcoida adopted here largely follows that of the *Treatise of Invertebrate Paleontology* (Newell 1969: N248-N270), with subsequent adjustments by Allen & Sanders (1969), Cope (1996), Morton et al. (1998) and Tevesz (1977) (see Table 3 Chapter 2). Given that there has been no comprehensive taxonomic revision of the group, and the questionable validity of a number of subgenera, taxa were chosen to represent generic taxa only. Representatives from 33 extant genera, for a total of 128 ingroup taxa, were included in the analysis. For the first time, taxa from each of the seven nominal families are included in an analysis of both morphological and molecular data. The largely extinct family Parallelodontidae was represented by two fossil taxa only, *Parallelodon obsoletus* and *Grammatodon implicatus*. This family has a single extant representative, *Porterius dalli*; this taxon is extremely rare in collections and it was not possible to obtain specimens for this study. The Cucullaeidae is also represented by a fossil taxon, *Cucullaea alta,* along with the extant taxon *Cucullaea labiata*. These three fossil taxa were coded for shell characters only and no do not appear in the analysis of molecular data alone. When possible, the exemplars comprised the type species of each extant genus as well as at least one other congener (see Table 7). When a specimen of the type species was unavailable a similar congener was chosen. Nevertheless, as is often the case, the availability of specimens guided inclusion in the analysis.

TABLE 7. Systematic list of the arcoid taxa to be used in the analyses. [ŧ = extant type of genus; ¥ = extinct; ᴍ = Monotypic genus; є = non-type exemplar; X = amplified successfully; — = unable to amplify. For 18S: 1=1F-5R, 2=3F-Bi, 3=5F-9R/A2.0-9R. MORPH = morphology scored for taxon. Accession code for GenBank sequences used in analysis provided].

FAMILY/SPECIES	STATUS	18S	28S	H3	COI	MORPH
Arcidae						
Arca noae	ŧ	X	X	—	X	X
Arca navicularis	є	—	—	—	—	X
Arca zebra	є	X	X	X	—	X
Arca imbricata	є	AY654986	X	X	X	X
Arca avellana	є	1, 2	X	X	X	X
Arca mutabilis	є	X	X	X	AF253486	X
Arca bouvieri	є	X	X	X	X	X
Arca ventricosa	є	—	X	X	AB076935	X
Barbatia barbata	ŧ	X	X	—	AF120645	X
Barbatia sp. PR-01	є	X	X	—	—	X
Barbatia obliquata (flaky)	є	—	X	X	—	X
Barbatia obliquata (scaly)	є	—	—	—	—	X
Barbatia cancellaria	є	X	—	—	AF416820	X
Barbatia amygdalumtostum	є	X	X	X	AB050899	X
Barbatia terebrans	є	X	X	—	—	—

FAMILY/SPECIES	STATUS	18S	28S	H3	COI	MORPH
Barbatia lacerata	ϵ	X	X	X	AB076932	X
Barbatia setigera lacerata	ϵ	X	X	—	—	X
Barbatia virescens	ϵ	—	AB105356	—	—	—
Barbatia foliata	ϵ	X	X	X	X	X
Barbatia tenella	ϵ	X	X	—	X	X
Barbatia reeveana	ϵ	X	X	X	X	X
Barbatia metella	ϵ	—	—	—	—	X
Barbatia illota	ϵ	X	X	X	X	X
Barbatia tenera	ϵ	—	—	—	AF253490	X
Barbatia gradata	t	X	X	X	X	X
Barbatia dubia	ϵ	—	—	—	—	X
Barbatia botanica	ϵ	2, 3	—	—	—	X
Barbatia iota	ϵ	X	X	X	—	X
Barbatia rostae	ϵ	—	—	—	—	X
Barbatia candida	ϵ	X	X	X	X	X
Barbatia domingensis	ϵ	—	—	X	X	X
Barbatia bistrigata	ϵ	—	AB101604	—	AB076936	X
Litharca lithodomus	t M	—	—	—	—	X
Anadara antiquata	t	X	AB101601	X	X	X
Anadara trapezia	ϵ	X	X	X	X	X
Anadara notabilis	ϵ	X	X	X	AF416828	X

FAMILY/SPECIES	STATUS	18S	28S	H3	COI	MORPH
Anadara geissei	ϵ	X	X	X	X	X
Anadara floridana	ϵ	X	—	—	X	—
Anadara granosa	ϵ	X	X	—	EF583540	—
Anadara pilula	ϵ	—	X	—	—	X
Anadara rotundicostata	ϵ	—	—	—	—	X
Anadara grandis	ϵ	—	X	AF416841	AF345641	—
Larkinia sp. AMS C.434466	ϵ	—	—	X	—	X
Bathyarca perversidens	ϵ	—	X	X	—	X
Bathyarca corpulenta	ϵ	X	X	—	—	X
Bathyarca japonica	ϵ	—	—	X	—	X
Bathyarca freileyi	ϵ	—	X	X	—	X
Bathyarca sp. Brasil	ϵ	2	—	—	—	X
Bathyarca sp. A	ϵ	—	—	—	X	X
Bentharca asperula	ŧ	—	—	X	—	X
Bentharca nodulosa	ϵ	—	—	—	—	X
Bentharca xenophoricola	ϵ	—	—	—	—	X
Bentharca tenuis	ϵ	—	AB101607	—	—	X
Bentharca sp.	ϵ	—	—	—	AB076938	—
Samacar strabo	ŧ	1, 2	X	X	—	X
Scapharca inaequivalvis	ŧ	—	AB101596	—	AB076937	X
Scapharca ferruginea	ϵ	X	X	—	AB050896	X

FAMILY/SPECIES	STATUS	18S	28S	H3	COI	MORPH
Scapharca ovalis	є	X	X	X	AF416831	X
Scapharca transversa	є	—	—	X	X	X
Scapharca vellicata	є	—	—	—	—	X
Scapharca sp. PNM03	є	X	X	X	—	X
Scapharca sp. PNM07	є	X	X	—	—	X
Scaphula celox	ŧ	X	X	X	—	X
Scaphula pinna	є	—	—	—	—	X
Senilia senilis	ŧ	X	X	X	X	X
Trisidos tortuosa	ŧ	—	X	X	X	X
Trisidos semitorta	є	X	X	—	—	X
Cucullaeidae						
Cucullaea labiata	ŧ	X	AB101611	X	AB050892	X
Cucullaea alta	¥	—	—	—	—	X
Parallelodontidae						
Parallelodon obsoletus	¥	—	—	—	—	X
Grammatodon implicatus	¥	—	—	—	—	X
Noetiidae						
Noetia olssoni	є	—	—	AF416859	AF416830	X

FAMILY/SPECIES	STATUS	18S	28S	H3	COI	MORPH
Noetia ponderosa	ŧ	—	X	X	X	X
Sheldonella repenta	є	1, 3	X	X	—	X
Striarca sp. MNHN101	є	—	X	X	X	X
Striarca lactea	є	AF120531	AF120590	—	AF120646	X
Striarca interplicata	є	—	—	—	—	X
Arcopsis afra	є	X	X	X	X	X
Arcopsis adamsi	є	X	X	X	AF253481	X
Arcopsis solida	є	X	X	X	AF253477	X
Stenocista gambiensis	ŧ	—	—	—	—	X
Glycymerididae						
Axinactis inaequalis	ŧ	—	—	—	—	X
Glycymeris americana	є	—	—	—	—	X
Glycymeris glycymeris	ŧ	X	—	—	—	X
Glycymeris ovatus	є	X	—	—	X	X
Glycymeris striatularis	є	X	X	—	X	X
Glycymeris reevei	є	—	X	X	X	X
Glycymeris lividus	є	3	—	—	—	X
Glycymeris formosus	є	X	X	X	X	X
Glycymeris pilosa	є	—	X	—	—	X
Glycymeris scripta cf.	є	X	X	X	X	X

FAMILY/SPECIES	STATUS	18S	28S	H3	COI	MORPH
Glycymeris crebreliratus	ϵ	—	—	—	—	X
Glycymeris grayana	ϵ	—	—	X	X	X
Glycymeris holosericus	ϵ	—	—	X	—	X
Tucetona flabellata	ϵ	—	—	—	—	X
Tucetona gealei	ϵ	X	X	X	X	X
Tucetona pectinata	ϵ	—	—	—	X	X
Tucetona pectunculus	ϵ	—	X	X	—	X
Melaxinaea vitrea	ŧ	—	—	—	—	X
Limopsidae						
Limopsis diegensis	ϵ	—	—	—	—	X
Limopsis enderbyensis	ϵ	AJ422057	—	—	—	—
Limopsis woodwardi	ϵ	—	—	—	—	X
Limopsis aurita	ŧ	—	—	—	—	X
Limopsis tensioni	ϵ	—	—	—	—	X
Limopsis marionensis	ϵ	X	X	X	—	X
Limopsis soboles	ϵ	—	—	—	—	X
Limopsis forteradiata	ϵ	2, 3	—	—	—	X
Limopsis loringi	ϵ	—	—	—	—	X
Empleconia vaginatus	ŧ	X	—	—	—	X
Empleconia cumingii	ŧ	—	AB101610	—	AB076930	X

FAMILY/SPECIES	STATUS	18S	28S	H3	COI	MORPH
Philobryidae						
Adacnarca limopsoides	ϵ	X	—	—	—	X
Adacnarca nitens	ŧ	—	—	—	—	X
Aupouria parvula	ŧ	—	—	—	—	X
Cosa costata	ŧ	—	—	—	—	X
Cosa scabra	ϵ	3	—	—	—	X
Cosa waikikia	ϵ	—	AB101614	—	AB084107	X
Cosa parallelogramma	ϵ	X	X	—	—	X
Cratis cf. *ohasii*	ŧ	—	—	—	—	X
Lissarca rubrofusca	ŧ	—	—	X	—	X
Lissarca notorcadensis	ϵ	X	X	—	EF192477	X
Lissarca picta	ϵ	—	—	—	—	X
Micromytilus crenatulifera	ŧ	—	—	—	—	X
Neocardia sp. A	ϵ	—	—	—	—	X
Notomytilus rubra	ŧ	—	—	—	—	X
Philobrya setosa	ŧ	—	—	—	—	X
Philobrya sublaevis	ϵ	—	—	—	—	X
Philobrya sp. USNM07	ϵ	—	—	—	—	X
Philobrya munita	ϵ	—	—	—	—	X

Outgroup selection—No consistent pattern of sister-group relationship of the Arcoida with other pteriomorphian taxa has emerged in any previous study. In light of the fact that a sister-group relationship with each of the other pteriomorphian orders has been recovered in different analyses, taxa from each of these four orders were included here. The determination of the root for the tree is an important factor for purposes of polarity of the characters. Moreover, in cases such as this, where a number of different outgroup taxa are included, a well chosen taxon to root the tree will help to elucidate the sister-taxon to the ingroup taxon. Since a case could be made to root the tree on any of the representatives from each of the other pteriomorphian orders, it was deemed prudent to choose a representative from outside the Pteriomorphia. To this end, two protobranchian taxa—*Nucula sulcata* and *Solemya velum*—were included. GenBank sequences were available for each of the four genes for these taxa. Composite taxa were made for those outgroup taxa for which it was not possible to amplify certain genes, these taxa are named as 'sp.' in tree (see Table 8), e.g. *Pinna* sp. is represented by *Pinna carnea* for morphology, 18S rRNA, 28S rRNA and histone H3 and by *Pinna nobilis* for COI. For these composite taxa, the morphology is coded as for those outgroup taxa chosen in the morphological analysis (Chapter 2).

TABLE 8. List of the outgroup taxa used in the analyses. [X = gene amplified; — = unable to amplify; 18S: 1 = fragment 1F-5R, 2 = fragment 3F-Bi, 1-3 = complete 18S]. Morphology was scored for all taxa for which a specimen was available. For composite taxa, where additional sequences where obtained from GenBank, the morphology was not coded.

FAMILY	SPECIES	18S	28S	H3	COI	MORPH
Nuculidae	*Nucula sulcata*	AF120525	DQ279960	DQ280001	DQ280017	
Solemyidae	*Solemya velum*	AF120524	AY145421	AY070146	SVU56852	
Mytilidae	*Brachidontes domingensis*	1-3	X	X	X	X
	Mytilus edulis	L24489	Z29550	X	DQ917606	X
	Lithophaga aristata	1, 2	X	X	—	X
	Lithophaga curta	—	—	—	AB076944	
Pinnidae	*Pinna carnea*	1-3	X	X	—	X
	Pinna nobilis	—	—	—	EF536849	
	Atrina rigida	1-3	—	X	—	X
	Atrina pectinata japonica	—	DQ343846	—	—	
	Atrina pectinata	—	—	—	AB059424	
	Atrina fragilis	—	—	—	—	
Isognomonidae	*Isognomon alatus*	1-3	X	X	—	X
	Isognomon legumen	—	—	—	AB076950	

FAMILY	SPECIES	18S	28S	H3	COI	MORPH
Malleidae	*Malleus candeanus*	1-3	X	X	—	X
Pteriidae	*Pinctada mazatlantica*	1-3	X	X	X	X
	Pteria colymbus	1-3	X	X	X	X
	Pteria hirundo	—	—	—	—	
Limidae	*Lima lima*	AF120533	AF120594	X	AF120649	X
	Ctenoides scaber	—	X	X	—	X
	Ctenoides annulata	AJ389653	—	—	—	
Gryphaeidae	*Hyotissa hyotis*	1, 2	X	X	—	X
	Hyotissa imbricata	—	—	—	AB0769917	
Anomiidae	*Anomia simplex*	—	—	X	—	X
	Anomia sinensis	—	AB102739	—	—	
	Anomia ephippium	AF120535	—	—	—	

MORPHOLOGICAL DATA

Morphological characters were scored for each of the 123 ingroup and 13 outgroup taxa included in the analysis. Morphological data were not available for the protobranch taxa at the time of scoring. Detailed character descriptions and the final matrix appear in Chapter 2. In some cases, all the sequences for a particular taxon were taken exclusively from GenBank. In the case where a specimen was not on hand, morphological characters of a highly similar congener were attributed to this taxon. For example, in the case of *Empleconia cumingii*, sequences were available for 28S rRNA and COI. Given that this taxon is a congener of *Empleconia vaginatus* and with the exception of the dorsal cleft (see character 19, chapter 2), it is highly similar to this species. While not optimal, the purpose of this was to reduce the affect of missing data. This duplication was done for *Striarca* sp. MNHN101 coding for *Striarca lactea*; *Tucetona pectunculus* for *T. pectinata*; *Barbatia lacerata* for *B.* cf. *setigera*/*lacerata*; *Philobrya* sp. USNM07 for *Philobrya sublaevis*.

MOLECULAR DATA

Genes selected for a phylogenetic study need to contain information that reflects the phylogenetic history at the specific taxonomic level of interest. DNA sequence data were compiled for the mitochondrial cytochrome *c* oxidase subunit I (COI), as well as the two nuclear ribosomal genes 18S rRNA (18S) and 28S rRNA D1-D3 regions (28S) and the protein coding histone H3. Previous studies have demonstrated that these genes

provide different levels of variation that are informative for testing cladistic relationships during a time span that is relevant to this group.

The mitochondrial gene COI accumulates mutations more rapidly than the nuclear rRNA genes and therefore is widely used for comparison among closely related species. In fact, the primers for this gene were developed using, among others, molluscan taxa (Folmer et al., 1994). This gene has been used in previous phylogenetic studies of bivalve phylogenies at various taxonomic levels (e.g. Peek et al., 1997; Hoeh et al., 1998; Ó Foighil et al., 1998; Giribet and Distel, 2003; Matsumoto, 2003).

The complete sequence of the small nuclear ribosomal subunit (18S) has proven useful in previous studies on bivalve phylogeny (e.g. Campbell et al., 1998; Steiner and Hammer, 2000; Distel, 2000; Giribet and Wheeler, 2002). The D1-D3 domains of the large subunit nuclear rRNA gene have been successfully used to address phylogenetic questions spanning Tertiary to Devonian divergences in a variety of metazoan taxa (e.g. Littlewood, 1994; Park and Ó Foighil, 2000; Giribet and Distel, 2003; Giribet et al., 2006; Passamaneck and Halanych, 2006). The histone H3 gene has been used to examine divergence times of geminate species pairs of arcoid taxa (Marko, 2002).

MOLECULAR PROTOCOLS

DNA extraction, PCR amplification and DNA sequencing were accomplished with commercial kits including: Qiagen DNeasy Tissue Kit (Qiagen); Gentra Puregene Tissue Kit (Gentra Systems Inc. – now Qiagen); GenomiPhi (GE Healthcare); Ready-To-Go PCR beads (GE Healthcare); ABI PRISM BigDye™ Terminator Cycle Sequencing

Ready Reaction Kit (ABI); AMPure® and CleanSeq® (Agencourt) and generally followed the manufacturers instructions and standard protocols.

DNA Extraction **—** DNA was extracted from all tissue types found in collections and those collected, i.e. from those that were dried, formalin-fixed or ethanol-fixed. The protocols for formalin and dried tissue extraction call for a greater quantity of starting material, thus for smaller specimens, especially philobryids species which can be approximately no more than 1-5 mm in length, the entire animal was used.

DNA from formalin-fixed samples was extracted using a protocol by Dayton et al. (unpub. protocol), which employs a buffer developed by Shedlock et al. (1997) and PureGene solutions. 20 mg of tissue was diced and over a period of 72 hours, washed at room temperature in a rotary incubator at 60 rpm in 10 ml of GTE buffer (100 mM glycine, 10 mM Tris–HCl, and 1 mM EDTA, pH 8.0) to remove the formalin. The buffer was replaced at least three times. The washed tissue was then dried at 55°C. Following drying, each sample was placed in a cell lysis solution, along with proteinase K and DDT and incubated for 24 hours at 55°C. After this stage of digestion, a protein precipitation solution was added to the cell lysate. An isopropanol-ethanol precipitation followed wherein the now extracted DNA was rehydrated with DNA hydration solution (Gentra). If an orange pellet remained in the tube following precipitation, the protocol was repeated following the initial wash in GTE.

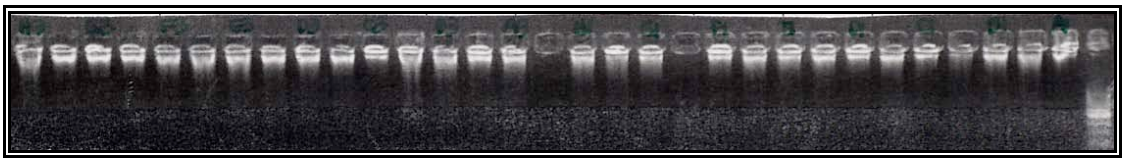
Dried tissue found within the enclosed valves was removed from the shell and cut into 20 mg pieces. The outside portion of the piece was sliced away so as to reduce the chance of contamination from fungi and bacteria, which are often found growing outside

the tissue. The tissue was then washed a number of times in ATL solution (Qiagen DNeasy Kit), vortexing the tube occasionally. Following the final wash, 25-50 μL of proteinase K were added to the tissue plus buffer solution and it was placed in an incubator for 24-48 hours at 55°C, or until such time that the tissue was completely lysed. The cell lysis solution subsequently followed the standard Qiagen protocol for extraction from ethanol-fixed, or fresh tissue.

DNA extraction for ethanol-fixed samples was accomplished with the Qiagen animal tissue extraction kit. A microliter of DNA was electrophoresed on a gel in order to assess the quality/quantity of DNA extracted from the samples. When a strong band was visualized, PCR amplification proceeded as usual, but in those cases where either a faint band or no band was visualized, an aliquot of the DNA in the sample was amplified using the methods described in the following section.

Genomic DNA amplification — Extracted genomic DNA (from dried and ethanol fixed samples) was subjected to a round of genomic amplification using GenomiPhi. GenomiPhi utilizes bacteriophage Phi29 DNA polymerase enzyme to exponentially amplify single- or double-stranded linear DNA templates by strand displacement amplification. The use of this product greatly increases the quantity of starting material for subsequent use in PCR amplification. It is possible to yield microgram quantities of DNA from nanograms of source material. This product is not optimized for short fragments of genomic DNA and therefore does not work well on tissue that was fixed in formalin, a fixative that has a tendency to shear DNA over time. An example of visualization of the genomic amplification is given in Fig. 70.

FIGURE 70. GenomiPhied samples of 70% ethanol-fixed and dried tissue samples: 5 µl of DNA was electrophoresed on an agarose gel with 1X TBE at 100 Volts for 2 hours. The fact that the DNA had not migrated from the well after this extended period of time indicates the high molecular weight of DNA.



PCR amplification — DNA amplification was carried out in a 25 µL volume reaction, using Ready-To-Go PCR beads. These beads contain approximately 2.5 units PuReTaq polymerase, 200 µM dNTP (dATP, dCTP, dGTP, dTTP), BSA, stabilizers and reaction buffer (10 mM Tris-HCl pH 9.0, 50 mM KCl, 1.5 mM $MgCl_2$). PCR reactions were set up by adding molecular grade dH_2O, specific primers and DNA template. Originally 1 µL of DNA with 0.5 µL of each primer (10 µM) was included, however, doubling the amount to 2 µL of DNA and 1 µL of each primer proved more satisfactory.

Universal and specifically designed primers were used for amplification. Fragments bounded by the overlapping primers for the nuclear 18S (1F-5R; 3F-bi; 5F-9R/A2.0-9R), 28S (A-Bout; D1F-D6R) and histone H3 (aF-aR) and the mitochondrial COI (LCO-HCO; HCOExA-HCOExB; LCO-HCOoutout; 179-871) were amplified and sequenced (see Table 9).

The PCR program consisted of an initial denaturing step at 94ºC for 60 seconds, 35 amplification cycles (94ºC for 15 sec, 50ºC for 15 sec, 72ºC for 15 sec), and a final step at 72ºC for 6 minutes. The annealing temperature for the protein-encoding genes was 46ºC, and for both mitochondrial genes was 48ºC.

TABLE 9. List of oligonucleotide primer sequences utilized in this study. The source for the first published appearance of the primer is also provided.

Gene	Primer	Sequence (5'-3')	Source
18S	1F	TACCTGGTTGATCCTGCCAGTAG	Giribet et al., 1996
	5R	CTTGGCAAATGCTTTCGC	Giribet et al., 1996
	3F	GTTCGATTCCGGAGAGGGA	Giribet et al., 1996
	bi	GAGTCTCGTTCGTTATCGGA	Whiting et al., 1997
	5F	GCGAAAGCATTTGCCAAGAA	Giribet et al., 1996
	9R	GATCCTTCCGCAGGTTCACCTAC	Giribet et al., 1996
	a2.0	ATGGTTGCAAAGCTGAAA	Whiting et al., 1997
28S	28SA	GACCCGTCTTGAAGCACG	Whiting, 2002
	Bout	CCCACAGCGCCAGTTCTGCTTACC	Prendini et al., 2005
	D1F	GGGACTACCCCCTGAATTTAAGCAT	Park & Ó Foighil, 2000
	D6R	CCAGCTATCCTGAGGGAAACTTCG	Park & Ó Foighil, 2000
H3	aF	ATGGCTCGTACCAAGCAGACVGC	Colgan et al., 1998
	aR	ATATCCTTRGGCATRATRGTGAC	Colgan et al., 1998
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al., 1994
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al., 1994
	COI179	ATDGGNGGVTTYGGNAAYTG	This study
	COI871	AARTANGCHCGNCTRTCNAC	This study
	HCOoutout	GTAAATATATGRTGDGCTC	AMNH laboratory fide Arango&Wheeler, 2007
	HCOExA	GAAGTTTATATTTTAATTTTACCTGG	AMNH laboratory fide Arango&Wheeler, 2007
	HCOExB	CCTATTGAWARAACATARTGAAAATG	AMNH laboratory fide Arango&Wheeler, 2007

PCR cleaning and sequencing — The generated PCR products were cleaned on a Beckman Coulter Laboratory Automation Workstation using magnetic bead technology (AMPure®). Double-stranded sequencing of the purified PCR products was conducted by the dideoxy termination method (Sanger et al., 1977) using an automated ABI Prism™ 3730xl DNA sequencer (Applied Biosystems). Cycle-sequencing of purified products

was achieved using dye-labelled terminators (ABI Prism™ BigDye™ v.1.1 or v.1.2. Terminator Cycle Sequencing Ready Reaction Kit) in a thermocycler. The cycle-sequencing reactions consisted of 1 µl Big Dye, 1 µl Big Dye Extender Buffer, 1 µl 3.2 µM primer, and 5 µl purified PCR-product (for a total of 8 µl). The cycle-sequencing program consists of 25 amplification cycles (96°C for 15 sec, 50°C for 15 sec, 60°C for 4 min). Tagged products were cleaned using CleanSEQ®. These cleaning techniques reduce the loss of PCR product often associated with the cleaning method of ethanol-isopropanol precipitation. Following cleaning, the tagged genes were sequenced using an ABI 3730 automated sequencing machine.

Sequence visualization and editing — The chromatograms of the sequences were assembled, visualized and editing using CodonCode Aligner (CodonCode Corporation). Primer sequences were removed from the 5' and 3' ends of the sequence fragment. The sequences were then checked for possible contaminants by performing a BLAST search (NCBI). Following BLASTing, the sequences were aligned in BioEdit (Hall, 2007). While it is not necessary to perform a multiple sequences alignment (MSA) prior to analyzing the sequences with dynamic homology (see below), it is desirable to perform a quick MSA for two reasons. A MSA is a useful 'tool' to visualize any potential problems with sequences; those sequences that have been reverse complemented during contig assembly are clearly evident in the MSA. In addition, the MSA facilitates the partitioning of the sequence data in fragments. The partitioning of sequences is commonly used technique for the analysis of molecular data under dynamic homology (see Giribet, 2002 and references therein). In cases such as these, the sequences are

partitioned so that two conserved regions flank a variable region, e.g. between primer regions (see Wheeler et al., 2006 for an in depth description on this method). The utility of this method is that the sequence optimization can proceed more rapidly and efficiently. In the case of complete data, the partition into smaller fragments is optional: this is not the case with incomplete datasets. The partitioning of sequences of unequal length (due to incomplete sequencing) is necessary in order to reduce the amount of ambiguity (IUPAC X or N coding) in these regions. These regions are subsequently treated as missing data in the analysis. These MSAs in no way constrained the subsequent analysis of the data under direct optimization (DO) (see below), given that gaps in the MSA are removed prior to analysis with DO.

PHYLOGENETIC ANALYSES

Homology and DNA sequence data — Molecular sequence data present a challenge in the determination of homologies across DNA sequences: morphological characters and states can be directly observed, DNA sequences cannot. With morphological data, the complexity of observed variation provides ample evidence to test hypothesized transformation series in isolation. The same cannot be said of DNA sequence data, where character-states are maximally reduced to the physico-chemical properties of the nucleotides and each of them is physically identical, so there is lower complexity from which, for instance, to infer which adenines are homologous, and which ones are not. For this reason, hypotheses of nucleotide homology can only be evaluated in reference to a topology (Wheeler 1994; Grant and Kluge, 2003).

Traditional analysis of sequence data involves a 'two-step' process wherein the sequences are aligned into a fixed alignment prior to cladogram searching (Giribet et al., 2001). These statements of homology are made ***a priori***. This MSA corresponds to the 'primary homology' *sensu* de Pinna (1991) or the 'topographic identity' *sensu* Brower and Schawaroch (1996). These resulting statements of homology are ***static***. When dealing with molecular sequences of unequal length it is necessary to insert gaps into the MSA, such that nucleotides of equal composition align. In this context, gaps represent insertion and deletion events (indels). These alignments can be performed either manually or with an automatic alignment program such as ClustalX (Thompson et al. 1997). Following the formation of this static 'primary' homology, cladogram searching is performed, wherein gaps are treated as a fifth state or missing data.

The separation of alignment and cladogram searching can lead to logical inconsistencies; unlike nucleotides, gaps cannot be observed, they are a representation of historical events (indels), and so they are not in reality a fifth state. Moreover, with this 'two-step' approach, the 'similarity' between sequence pairs is applied in the primary stage of alignment, which is then followed by an alternative optimality criterion during tree searching. Because gaps are treated as missing data in such analyses, very often 'gappy' areas in the MSA are deemed problematic and therefore excluded from the analysis. Nevertheless, gaps reflect historical information in a comparable manner as nucleotides changes, as they originate from particular biological events (mutation), and ignoring or excluding them may yield misleading topologies (Giribet and Wheeler 1999). Moreover, the treatment of gaps as missing data amount to the loss of information.

Dynamic homology is a concept of homology that seeks to circumvent this 'two-step' process (Wheeler, 2001), where potential character transformations are not restricted and homologies are inferred ***a posteriori*** as a result of the phylogenetic analysis. Within the framework of dynamic homology, the determination of nucleotide homology is treated as an optimization problem in which the preferred scheme of nucleotide homologies for a given topology is that which requires the fewest transformation events when optimized onto that topology and thereby providing the most parsimonious explanation of the observed diversity (Wheeler and Giribet, 2008). In this sense, the usual 'two-step' process of MSA followed by tree search, is streamlined to a one-step process with direct optimization (Giribet, 2003). With dynamic homology, indels do not appear as states but as transformations linking the ancestral and descendent nucleotide sequences (Giribet and Wheeler, 1999); gaps reflect a *process* (transformation) of evolution as opposed to reflecting a historical *pattern*. Under this scheme of analysis, the phylogeny (cladogram) and the homology correspondences (alignment) are searched simultaneously. Consequently, each cladogram has a potentially unique set of correspondences (Frost et al., 2000; Wheeler et al., 2006; Ramírez, 2007). Furthermore, given that each cladogram has a potentially unique set of correspondences, any change in the cladogram may change the correspondences. Because of this concurrent aspect, dynamic homology optimization allows the optimization of unaligned sequences, circumventing the need for MSA (Wheeler 1996). Moreover, the same optimality criterion, be that parsimony or likelihood, is employed for the discovery of both the primary homologies and optimal topology.

Heuristics and Tree-Alignment — In phylogenetics, exact solutions are impossible for any contemporary dataset, and heuristic algorithms are a necessity when searching for optimal alignments and topologies (see Giribet, 2007). Determining the optimal alignment for a given topology is an NP-complete problem (Wang and Jiang, 1994), which means that no polynomial time solution for the problem exists. To put in context the enormity of the problem, the number of possible alignments and topologies grows explosively with the addition of terminals: for *n* sequences of length *m*, the number of possible alignments of five sequences, each with five nucleotides is 1.05×10^{18} (Slowinski, 1998); moreover, the number of possible cladograms is solely a function of the number of terminals—for 10 terminal taxa, there are approximately 3.45×10^{7} possible directed cladograms. Given this problem, tree searching can be difficult for any kind of interesting, non-trivial dataset and therefore heuristic approximations must be applied.

Direct optimization and POY — Direct optimization (DO) is the heuristic method proposed by Wheeler (1996) that attempts to overcome the limitations of MSA and the necessity of creating gaps (placeholders in an alignment). Discussion of this feature of dynamic optimization in multiple sequence alignment dates back to Sankoff (1975). This algorithm, as implemented in the computer program POY (Varón et al., 2008), minimizes the number of hypotheses of state transformation dynamically, by examining heuristically a universe of possible alignments, choosing the tree(s) that imply the alignment(s) with fewer state transformations under the established costs of transformation. DO performs a one-step minimization of total changes on a trial topology, given a matrix of costs for

insertion–deletion events (indels) and nucleotide changes (transversions and transitions). Unlike MSA, DO combines alignment and tree-search into a single procedure. This is achieved by including insertions and deletions, in addition to transitions and transversions, as forms of character transformation during alignment and analysis. In this way, the search for optimal trees is not constrained by a single, potentially sub-optimal, alignment (Slowinski, 1998).

While POY avoids the formation of predetermined putative homologies (alignments), it can output an implied alignment (IA) (Wheeler 2003). The IA is visually similar to classic alignment, but can be quite 'gappy' in non-conserved regions of the alignment. This gappiness is one of the arguments frequently posed against the use of POY. However, the IA is derived from a totally different procedure to that used in alignment programs such as ClustalX (Thompson et al. 1997). ClustalX will align independent homoplastic insertions of the same nucleotide into the same 'column' in the alignment, POY will assign them to different columns because they are not homologous (Giribet 2005). The IA is a visualization of nucleotide transformation series and represents an optimal topology-specific homology hypothesis constructed through POY. All analyses in this study were performed using POY.

Optimality Criterion — All the datasets were analyzed with maximum parsimony (MP) only. Parsimony is a scientific approach that minimizes the cost of weighted transformation in order to explain the observed data. In phylogenetic systematics, the optimal tree is that which requires the minimum number of changes to explain the data. With the belief that any inference about the phylogenetic relationships of these organisms

can only be made on the totality of evidence, parsimony is the only optimality criterion that will allow the analysis of both morphological and molecular data, with realistic models of morphological change. This is especially pertinent for the inclusion of fossil taxa in the analysis.

Datasets — The molecular datasets were analyzed separately to assess the pattern of relationships from each. A number of datasets were analysed in this study; these include the analysis of each gene partition, a combined analysis of all the molecular data, as well as a complete analysis of all the available evidence (i.e. morphology plus molecular). A simultaneous analysis of all the available evidence was performed in the belief that this type of analysis will maximize explanatory power (Kluge, 1989; Nixon and Carpenter, 1996) and therefore all the conclusions will be based on the tree(s) resulting from this treatment of the data. These analyses were run on a parallel cluster computer of 128 processors, using the parallel version of POY version 4.1 (Varón et al., 2008). Each analysis was performed on 12-24 processors, therefore, a 12 hour timed search ostensibly equates to 144 analysis hours for a 12 hour search.

Analyses — Heuristics searches were performed in POY version 4.1.1.dev1 (Varón et al., 2008) using the timed search, which is a default search strategy that combines Wagner tree building with multiple rounds of TBR branch swapping, parsimony ratchet (Nixon, 1999) and tree fusing (Goloboff, 1996). The parsimony ratchet randomly reweights a fraction of the characters by an arbitrary factor, performs branch swapping, returns the weights to the original value and reswapping the trees again. The maximum time for this

timed search was set to 12 hours. Following the timed search the trees were subjected to additional rounds tree fusing and branch swapping [**fuse** (iterations: 250), **swap** (trees: 100))]. Between each round of refinement, all topologically unique trees were stored in memory [**select** (unique)], until the last round, when only topologically unique optimal trees were kept [**select** ()]. The advantage of selecting all the unique trees, whether they are optimal or not, following each iteration is that it assists in avoiding local optima. All trees were rooted on the protobranch bivalve *Nucula sulcata*. A strict consensus was reported from all the unique optimal trees in memory.

Sensitivity Analysis — An exploration of different parameter costs (e.g. different gap opening, insertion/deletion (indel) and different transition/transversion costs) was undertaken. In the context of phylogenetic analyses, sensitivity analysis (Wheeler, 1995) explores the effects of parameter variation (in this case different costs associated with the different types of transformation) on the phylogenetic results. Three indel cost ratios (1, 2, 4) and 3 transversion/transition (tv/ts) cost ratios (1, 2, 4) were used. In each case, the morphological transformations were weighed equal to the cost of the indels.

In exploring the data using this approach, it is necessary to test for character congruence among the various partitions. The parameter set that minimized the incongruence among the partitions is considered optimal. One of the most commonly used congruence measures is the incongruence length difference (ILD) (Mickevich and Farris, 1981; Farris et al., 1995). The ILD compares the number of extra steps required in analyzing the different partitions together as opposed to separately. A rescaled variation of the ILD, the RILD (Wheeler and Hayashi, 1998) scales the number of extra steps as a

fraction of the maximum number of possible extra steps that could be obtained from the combination of the data partitions. The Meta Retention Index (MRI) (Wheeler et al,. 2006) is an extension of Farris' (1989) Retention Index and corresponds to the RI applied to the fragments of the sequence data as opposed to the individual nucleotides. In direct optimization, the sequence fragment is the character as opposed to the individual nucleotides, therefore, character congruence among the various partitions was subsequently measured using the MRI (Wheeler et al., 2006), was considered optimal.

Support — Measures of support were calculated for all the resulting trees. Some of the more commonly used measures in phylogenetic analysis include the bootstrap (Felsenstein, 1985), parsimony jackknife (Farris et al., 1996) and Bremer (Goodman et al., 1982; Bremer, 1994) support values. Both jackknife and bootstrap support techniques are based on the resampling of characters from the original character matrix; Bremer support values are optimality-based measures of support.

Bootstrapping is one of the most popular measures of support currently employed in phylogenetic studies. Bootstrapping has its foundation in statistical inference (Effron, 1979). Applied to cladistic data, the bootstrap randomly samples characters from the original dataset, forming a pseudoreplicate dataset of the same dimensions as the original, *with* character replacement following each iteration. There are fundamental problems associated with this method. One of the assumptions of bootstrapping is that characters are independent and that the sampled characters are a representative sample from the overall character data. DNA sequence data is not independent or devoid of sampling bias (Wheeler and Honeycutt, 1988; DeSalle et al., 1994). Given the random nature of the

resampling, some characters will be over-represented in the pseudoreplicate dataset (more than two times) and some will not appear at all. Moreover, autapomorphic and symplesiomorphic characters will reduce the bootstrap values, as these characters do not increase support for clades in a phylogenetic tree, but instead to the terminals. For this reason, bootstrap values will not be calculated as a measure of support in this study.

Jackknifing methods date back to Quenouille (1949) and Tukey (1958) where they were employed for statistical purposes. Applied to phylogenetic systematics, the character jackknife or the parsimony jackknife involves the random resampling of the character matrix to form a 'pseudoreplicate' dataset and from this a search for the optimal tree is performed. This original character matrix is resampled iteratively *without* replacing the characters following each iteration, such that each character has the probability of $1 - e^{-1}$ of occurrence. The majority-rule consensus tree of all the nodes with a frequency ≥ 0.50 is then reported. In the context of dynamic homology, it is the entire sequence fragment that is being sampled during the formation of the pseudoreplicates and not the actual nucleotides themselves. For this reason, jackknife values calculated for dynamic characters are not directly comparable to those calculated on static characters (the same is true for bootstrap values). It is feasible to calculate jackknife values for the 'dynamically treated' molecular datasets—it is possible to output a phastwinclad file (Hennig86) from POY, which amounts to a static representation of the implied alignment. From this static IA, jackknife values can be calculated. These values, though likely inflated, were calculated in this study.

Bremer support values are optimality-based measures of support as opposed to those that based on pseudoreplicates. This method involves the calculation of the length

of the optimal tree with, versus without, a node; more simply it is the number of extra steps required before a clade is lost from the optimal tree. Because Bremer supports are optimality-based, their calculation is more appropriate for dynamic characters, and so these values were calculated for all analyses. In POY, one of the ways to calculate Bremer support values, is to generate a tree file (e.g. by performing a timed search), saving the visited trees to a temporary tree file (**search** (max_time:0:12:0, visited: 'TmpTree1.txt')) and to subsequently calculate the Bremer values from this pool of trees. In order to guarantee that all clades have adequate estimates of Bremer support values, the search strategy employed in POY ensures that a large number of trees are visited. Bremer calculations are upper-bound values, and are therefore dependent on the size of the tree file generated—a smaller pool of visited trees may inflate Bremer values relative to those generated by a more exhaustive search. These values were calculated for the analysis of all the morphological data, the shell characters only and the total evidence tree.

In this study, support values were calculated for the total evidence tree only.

RESULTS

Molecular loci used in this study — Cytochrome *c* oxidase subunit I was amplified for 65 taxa included in this study. Using a combination of four primer pairs, it was possible to amplify 1077 bps. This sequence was divided into 6 fragments, the longest being 238 bps in length. This gene displayed the highest degree of dissimilarity among the ingroup taxa, with pairwise similarity ranging between ~60 and 82%.

The 28S rRNA gene was amplified with two overlapping primer pairs. The combination of these regions yielded a DNA sequence of length 1295 bps. This region of the 28S rRNA gene was amplified for 63 taxa. The minimum length of sequence included was 323 bps. In addition to these fragments, 14 complete or nearly complete 28S sequences, ranging between 2767 and 3574 bps, were included from GenBank. This complete gene was divided into nine fragments, the longest being 1581 bps in length. This gene exhibited a high rate of similarity, ranging between ~92 and 99% similarity across the ingroup taxa.

The 18S rRNA gene was amplified with three overlapping primer pairs for 73 taxa included in this study. The total length of the amplified sequence ranged between 489 and 1747 bps. The complete 18S rRNA gene was amplified for 56 taxa, the remaining taxa either amplified for only one or two of the primer sets. The entire sequence was divided into seven fragments according to primer regions and to highly conserved regions that minimized the effects of missing data (as discussed previously);

the longest fragment was 469 bps long. This gene was highly conserved across all taxa, with ~95-99% similarity among the ingroup taxa.

The protein coding histone H3 was amplified for 64 taxa. Due to the inability to amplify the 3' region of this gene for some taxa using the aR primer, it was necessary to divide this relatively short sequence into two fragments of 198 and 140 bps in length. The complete sequence was amplified for 63 taxa. This gene showed between ~80 and 99% similarity among ingroup taxa.

In total, approximately 300 Kb were included in the analysis. Each of the six families (with extant taxa) has representation for the four molecular markers included in this study.

Phylogenetic Results — Discussion of the results from both the partitioned and combined datasets follow below. Included are the results from the analysis of each gene ('18S', '28S', 'H3' and 'COI'), as well as from the combination of all molecular partitions ('MOL') and from the total evidence analysis of both the morphology and molecular data ('TOTAL'). The notation for the parameter sets follow such that 041 equals initial gap opening 0, the cost of indels are set to 4 and substitution ratios equal 1. Tree lengths and MRI values for all the analyses are shown in Table 10. For all of these analyses, the additional cost for opening a gap was set to 0. As can be seen from this table, the parameter set with gaps receiving four times as much weight as the transition/transversion ratio and morphological characters receiving a weight of 4, minimizes character incongruence for the total evidence analysis ('TOTAL'). The parameter set that minimizes incongruence between the morphological and molecular

characters (MORPH-MOL') is the parameter set where gaps, tv/ts and morphology are equally weighted to 1. Among the molecular datasets ('MOL'), the parameter set with gaps half the weight of the tv/ts ratio and morphology weighted to 8, minimizes incongruence among these data partitions (i.e. 024).

Because any conclusions should be based on all the available evidence, the trees (mpt or strict consensus) from the analysis under the weighting scheme 041 are discussed in greater depth. For comparative purposes, the strict consensus of the trees analyzed under the equally weighted parameter set 011 (gaps = tv/ts = 1) and the strict consensus of all the trees obtained under all analyzed parameter sets are also presented. Needless to say, where only one tree was recovered, this tree, as opposed to a strict consensus, is presented. Terminology for group inclusion (i.e. monophyly, paraphyly and polyphyly) follows Farris, 1974.

TABLE. 10. Tree statistics for the sensitivity analysis for the different parameter set values (gap and transition/transversions ratio costs). Tree costs/lengths for each analysis are provided; the number of mpts recovered from each analysis are shown [ ]. The MRI values for the analyses of the combined datasets are also reported—the parameter set that minimizes incongruence among the partitions is highlighted in bold. The morphology was applied a weight equal to that of the gap times the tv/ts ratio for the total analysis.

GAP	Tv/Ts	MRI TOTAL	MRI MORPH-MOL	MRI MOL	MORPH	TOTAL	MOL	18S	28S	COI	H3
1	1	0.06159	**0.02690**	0.04526	1287 [49]	14107 [2]	12593 [3]	1054 [31]	3230 [17]	7154 [5]	843 [60]
1	2	0.06276	0.03205	0.04256	2574	22052 [2]	19025 [6]	1603 [4]	4976 [11]	10823 [1]	1160 [155]
1	4	0.06344	0.03439	0.04212	5148	37439 [1]	31423 [5]	2671 [5]	8349 [6]	17854 [1]	1766 [14]
2	1	0.06419	0.03576	0.04390	2574	16631 [1]	13664 [3]	1210 [66]	4043 [42]	7234 [3]	843 [193]
2	2	0.06477	0.03837	0.04384	5148	26966 [1]	21076 [2]	1906 [41]	6513 [17]	10951 [1]	1160 [9]
2	4	0.06524	0.04143	**0.04170**	10296	47261 [1]	35480 [3]	3272 [22]	11394 [5]	18135 [1]	1766 [48]
4	1	**0.05967**	0.03696	0.04349	5148	21243 [1]	15509 [1]	1485 [44]	5506 [22]	7292 [1]	843 [242]
4	2	0.06226	0.04011	0.04603	10296	36151 [1]	24687 [1]	2442 [35]	9339 [9]	11058 [3]	1160 [9]
4	4	0.06173	0.03999	0.04790	20592	65384 [2]	42588 [2]	4291 [9]	16914 [13]	18340 [3]	1766 [35]

Results from the individual gene partitions — As is evident from the trees presented (Figs. 71-87), there is substantial variation in the results from the different gene sequences. Discussion of the combined analyses follows those of the individual partitions.

COI —Analysis of the mitochondrial cytochrome *c* subunit I yields a single most parsimonious tree of length 7292 under the parameter set 041 (Fig. 71). The Philobryidae, represented by the taxa *Cosa waikikia* and *Lissarca notorcadensis*, is the only family recovered as monophyletic. The Limopsidae and Cucullaeidae are represented by a single taxon and so no statement can be made as to the monophyly of these families, except to comment on their sister group relationships: the limopsid *Empleconia cumingii* is sister to the Philobryidae and *Cucullaea labiata* to a noetiid clade comprised of *Arcopsis afra* and *Striarca lactea*. The Glycymerididae, Arcidae and Noetiidae are polyphyletic. Within the Arcidae, a large clade comprised of anadarine taxa is recovered (although the genera within this clade, *Anadara* and *Scapharca* are not monophyletic). Henceforth, this clade shall be referred to as the anadarine clade (although not all Anadarinae taxa are included in this clade, e.g. *Bathyarca* and *Bentharca*).

Under the parameter costs 011, five most parsimonious trees of length 7154 are found. These trees differ only in the placement of taxa in the large anadarine clade. The strict consensus of these trees (Fig. 72) is similar in structure to that of 041, in that the component taxa of the major clades are highly similar. As with 041, the Philobryidae are monophyletic and all other families are recovered as polyphyletic.

The strict consensus of all the trees obtained under all analyzed parameter sets (Fig. 73) indicates that a number of clades are recovered under all conditions. Among arcid taxa these include three clades comprised of *Barbatia* taxa, one with *Bentharca* sp. + *Bathyarca* sp. + *Barbatia fusca*, a clade comprised of *Arca* species and the large anadarine clade of *Anadara* + *Senilia* + *Scapharca* species. The taxa *Barbatia tenera* and *Barbatia illota* have been considered as *Barbatia* (*Fugleria*) by some authors (Oliver and Holmes, 2006). The Noetiidae is consistently rendered polyphyletic, with *Arcopsis afra* and *Striarca lactea* forming a sister-group relationship with *Cucullaea labiata* and all other noetiids forming a separate clade. The glycymerids are recovered in two clades, each with two taxa, and the others falling in a comb at the base of the tree. The limopsid *Empleconia cumingii* is sister to the philobryid species *Cosa waikikia* and *Lissarca notorcadensis*.

In all the analyses of COI data, limid taxon *Lima lima* is the sister taxon to the monophyletic Arcoida.

FIGURE 71. Relationships of the Arcoida and outgroup taxa based on the analysis of cytochrome *c* oxidase subunit I under the parameter set 041. A single most parsimonious tree of cost 7292 is recovered.

FIGURE 72. Relationships of the Arcoida and outgroup taxa based on the analysis of cytochrome *c* oxidase subunit I under the parameter set 011. The strict consensus of 5 equally most parsimonious trees of length 7154 is shown.

FIGURE 73. Strict consensus of the 19 trees recovered from the analysis of cytochrome *c* oxidase subunit I under the 9 different cost parameter conditions.

FIGURE 71: COI – 041

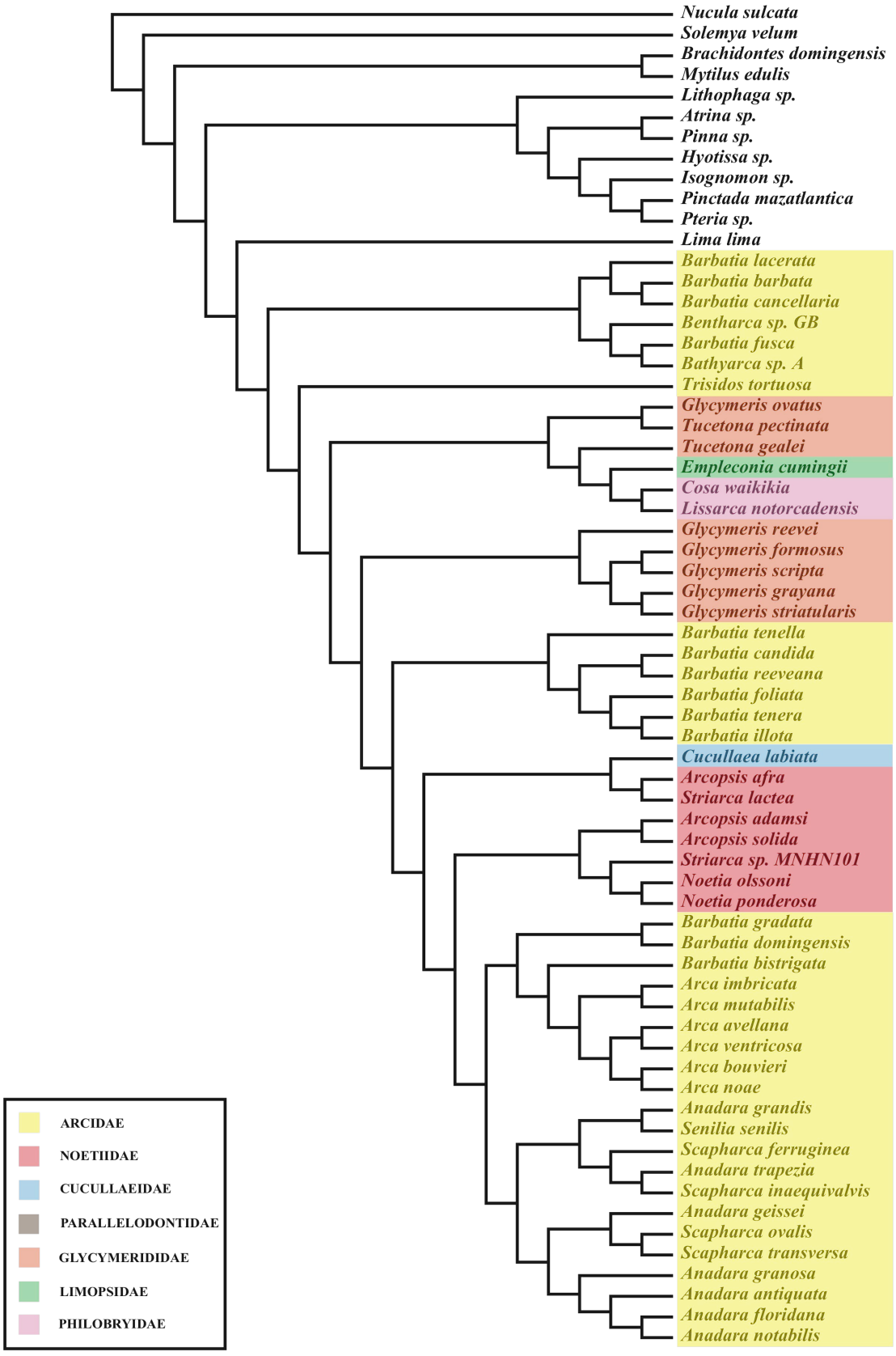
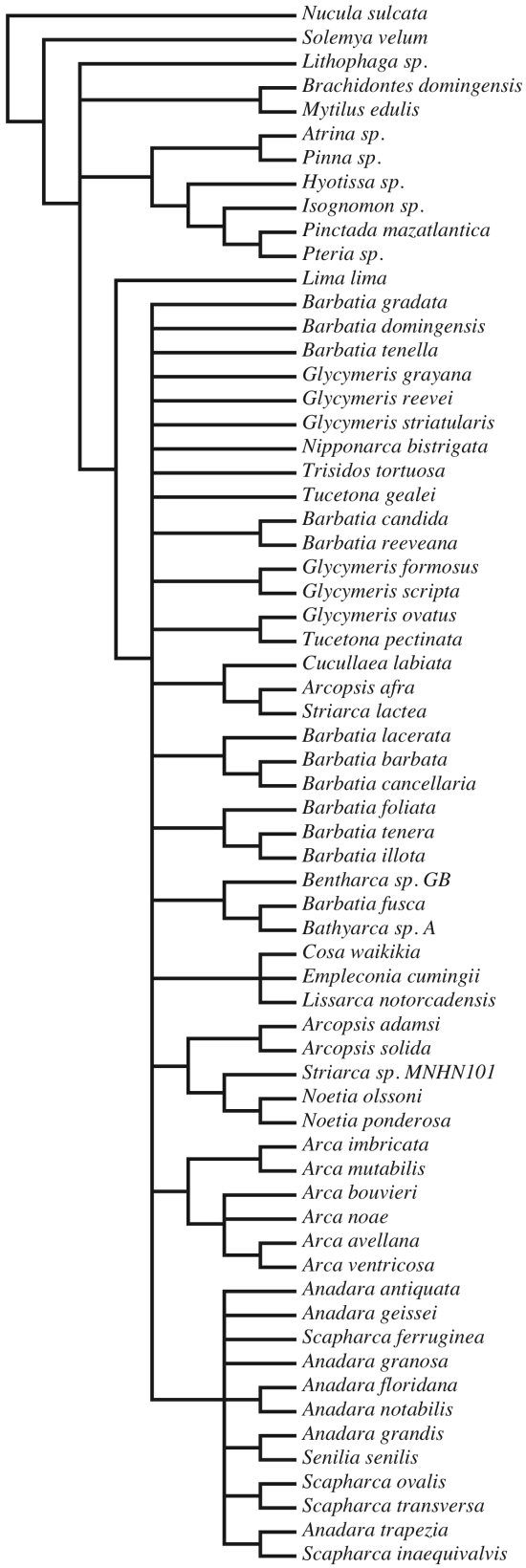


FIGURE 72: COI – 011



FIGURE 73: COI
– Strict Consensus of Sensitivity Analysis



28S — The analysis of the nuclear ribosomal 28S rRNA sequence under the optimal weighting regime (041) recovered 22 equally parsimonious trees of cost 5506. The basic structure of these trees is consistent across all the mpts, only the sister-group relationships within these clades change. The strict consensus of these trees is illustrated in Fig. 74. The analysis of this gene under this weighting scheme recovered a monophyletic Glycymerididae, Noetiidae and Limopsidae. The Philobryidae are polyphyletic with *Cosa waikikia* and *Lissarca notorcadensis* falling within a clade among *Arca* species. *Cosa parallelogramma* places with other arcid taxa at the opposite end of the tree. This taxon has a distinct deletion of 28 bps in the 28S fragment amplified. *Cucullaea labiata* is sister to the arcid *Bathyarca corpulenta*. A similar relationship is recovered in the analysis of morphological characters in Chapter 2, with *C. labiata* forming a clade with another *Bathyarca* taxon, *B. japonica*. These taxa are recovered in a large clade with a monophyletic Glycymerididae and Limopsidae. As with COI, a large clade of anadarine taxa is recovered, with the addition of *Barbatia bistrigata*. No consistent pattern is seen with the other arcid taxa analyzed for this gene, with *Barbatia* placing in different clades across the tree.

Seventeen trees of equal length 3230 are recovered from the analysis under the parameter set 011. As with the other gene partitions, the overall structure remained the same throughout the mpts. As with 041, the Glycymerididae and Noetiidae are monophyletic, however the Limopsidae are paraphyletic with respect to a philobryid clade (Fig. 75). Again, *Cosa parallelogramma* places with arcid taxa and *C. labiata* and *B. corpulenta* form a clade, which is sister to the monophyletic Glycymerididae. Similar arcid clades are recovered as in 041, such as *Arca* and the large anadarine + *Barbatia*

bistrigata clade. Under both parameter sets, a large clade comprised of all the outgroup taxa, with the exception of the root *Nucula sulcata*, is the sister taxon to the Arcoida.

In the strict consensus of the 142 trees recovered from the different parameter sets (Fig. 76), the Arcoida are not recovered as monophyletic—under the parameter sets 041 and 044, all the outgroup taxa, with the exception of the *Nucula sulcata* and the mytiloid outgroups, place far from the base of the tree. However, the arcoid clades that are consistently recovered include, the Glycymerididae, Noetiidae, *Arca*, two clades comprised of *Barbatia* species and the anadarine clade.

FIGURE 74. Relationships of the Arcoida and outgroup taxa based on the analysis of 28S rDNA sequences under the parameter set 041. A strict consensus of 22 trees of cost 5506 is presented.

FIGURE 75. Relationships of the Arcoida and outgroup taxa based on the analysis of 28S rDNA sequences under the parameter set 011. The strict consensus of 17 equally most parsimonious trees of length 3230 is shown.

FIGURE 76. Strict consensus of the 142 trees recovered from the analysis of 28S rDNA sequences under the 9 different cost parameter conditions.

FIGURE 74: 28S – 041

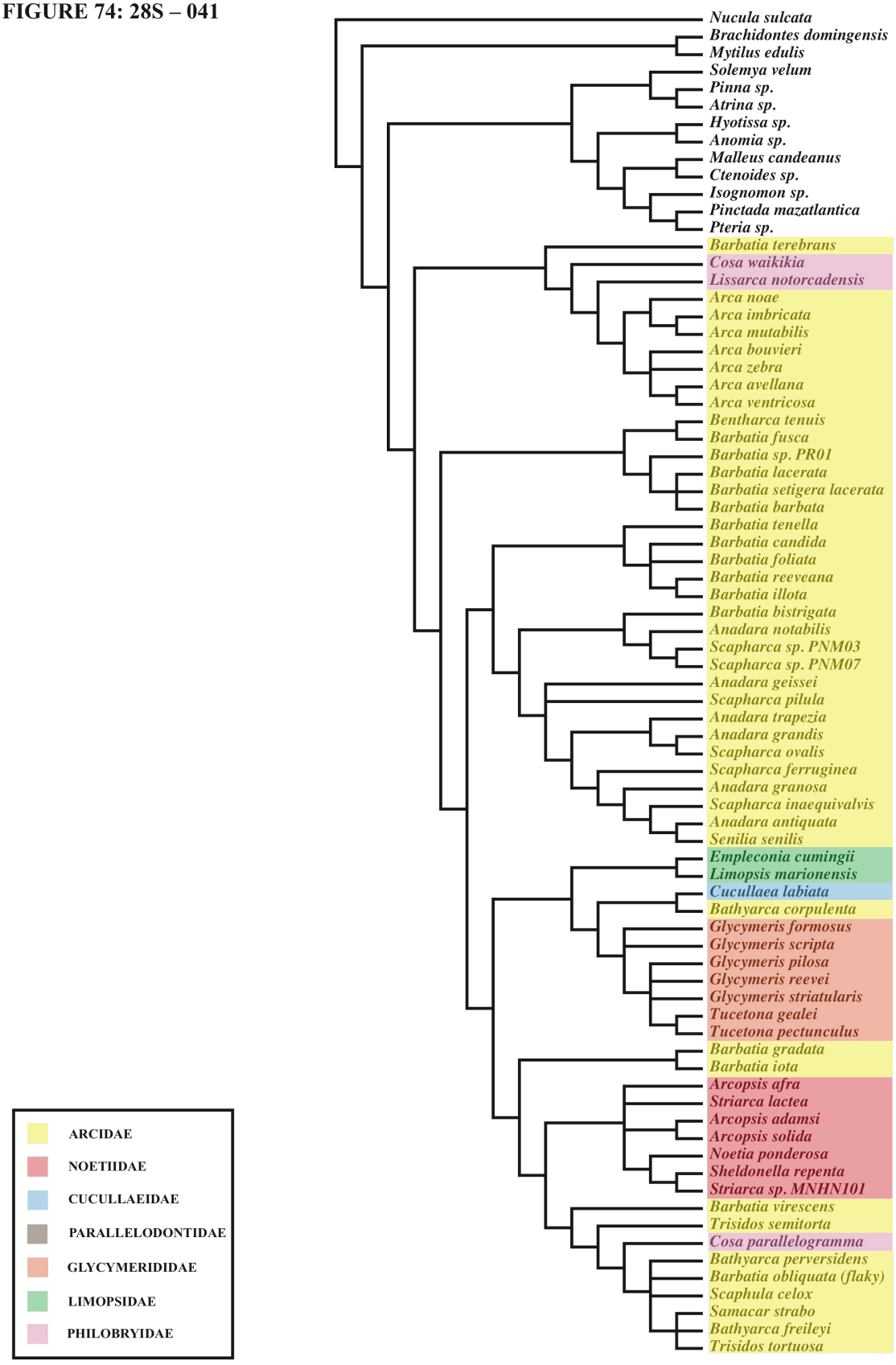


FIGURE 75: 28S – 011

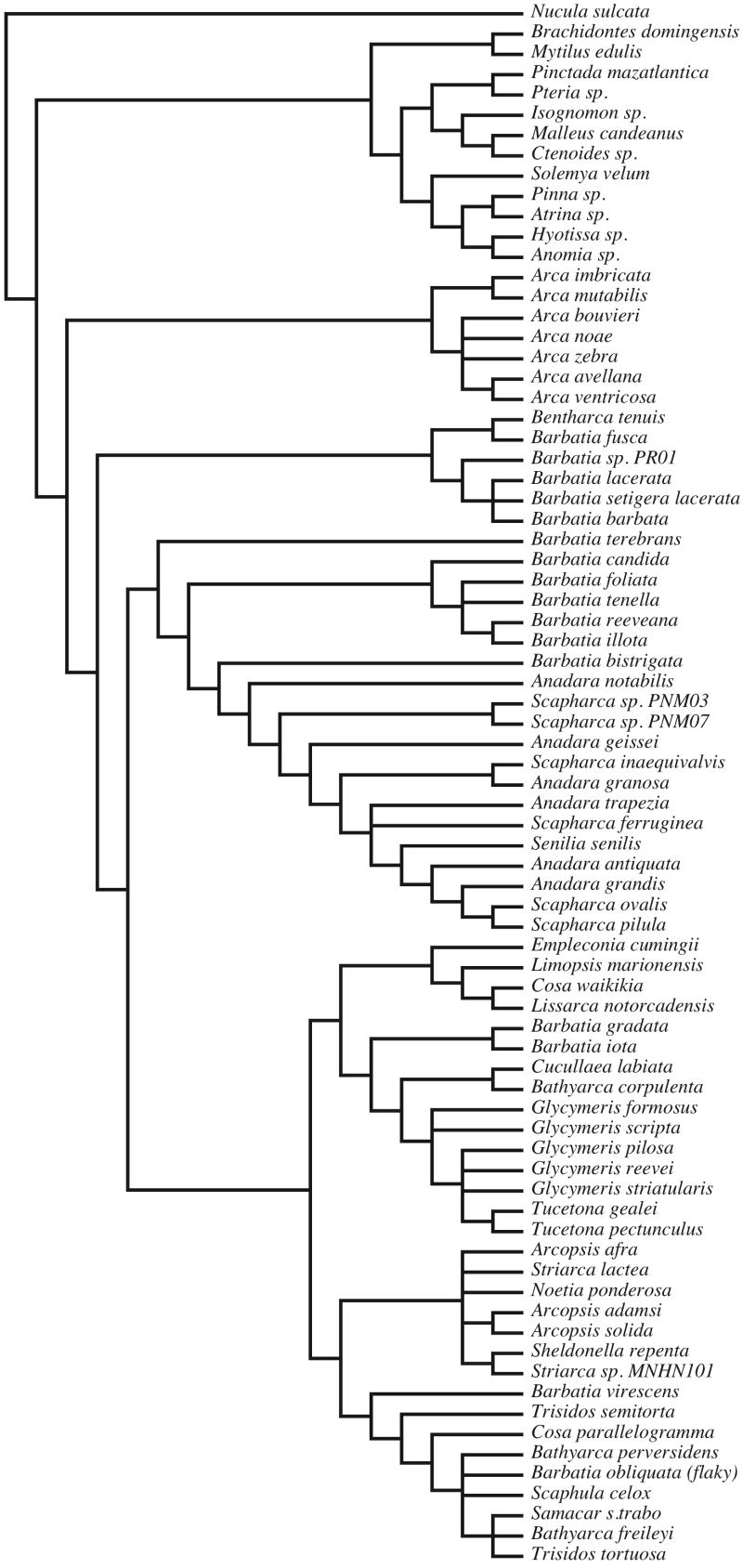
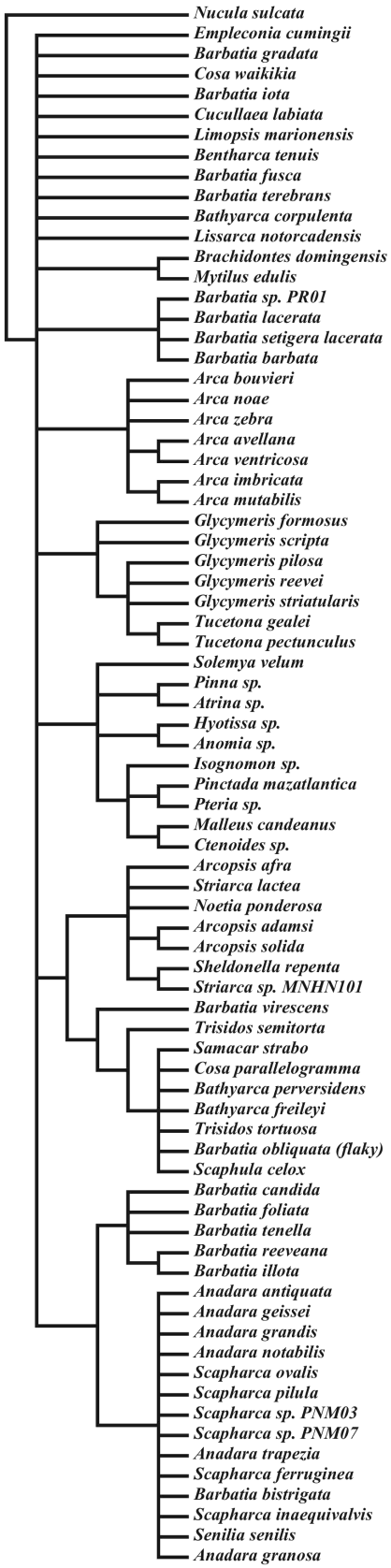


FIGURE 76: 28S
– Strict Consensus of Sensitivity Analysis



18S — The analysis of the small subunit ribosomal sequence under the parameter set 041 resulted in 44 most parsimonious trees of cost 1485. The strict consensus of these trees is illustrated in Fig. 77. No clear pattern emerges from the analysis of this DNA sequence. Of the six arcoid families included, only the Glycymerididae are recovered as monophyletic. As in the other analyses, a monophyletic *Arca* is recovered. This gene is the most conserved across all the ingroup taxa and so perhaps the polytomy structure of the tree is not unexpected.

Under the parameter set 011, 31 mpts of length 1054 are recovered. The strict consensus of these trees (Fig. 78) is similar to the 041, in terms of the comb-like structure of the tree, none of the clades recovered in the strict consensus tree of the 041 analyses are recovered in the strict consensus of the 011 analyses. In this analysis, none of the families are recovered as monophyletic. With the exception of *Anadara antiquata*, a large anadarine clade is recovered. *Arca* has split into two smaller clades. The Noetiidae are rendered non-monophyletic by the exclusion of *Sheldonella repenta*, as is the Limopsidae, with *Limopsis forteradiata* falling within the 'comb'. In both of these analyses, a large clade comprised of non-mytiloid, non-protobranch taxa is sister to the monophyletic Arcoida.

Little can be said of the phylogenetic relationships of the Arcoida as seen from the strict consensus of the 257 trees recovered from the different parameter sets (Fig. 79). As with the large subunit ribosomal sequence, the Arcoida are not recovered as monophyletic—in the 044 analysis, a clade of *Arca* taxa fall within the outgroup taxa, being sister to *Ctenoides* sp.

FIGURE 77. Relationships of the Arcoida and outgroup taxa based on the analysis of 18S rDNA sequence fragments under the parameter set 041. A strict consensus of 44 trees of equal cost 1485 is presented.

FIGURE 78. Relationships of the Arcoida and outgroup taxa based on the analysis of 18S rDNA sequences under the parameter set 011. The strict consensus of 31 equally most parsimonious trees of length 1054 is illustrated.

FIGURE 79. Strict consensus of the 257 trees recovered from the analysis of 18S sequences under the 9 different cost parameter conditions.

FIGURE 77: 18S – 041



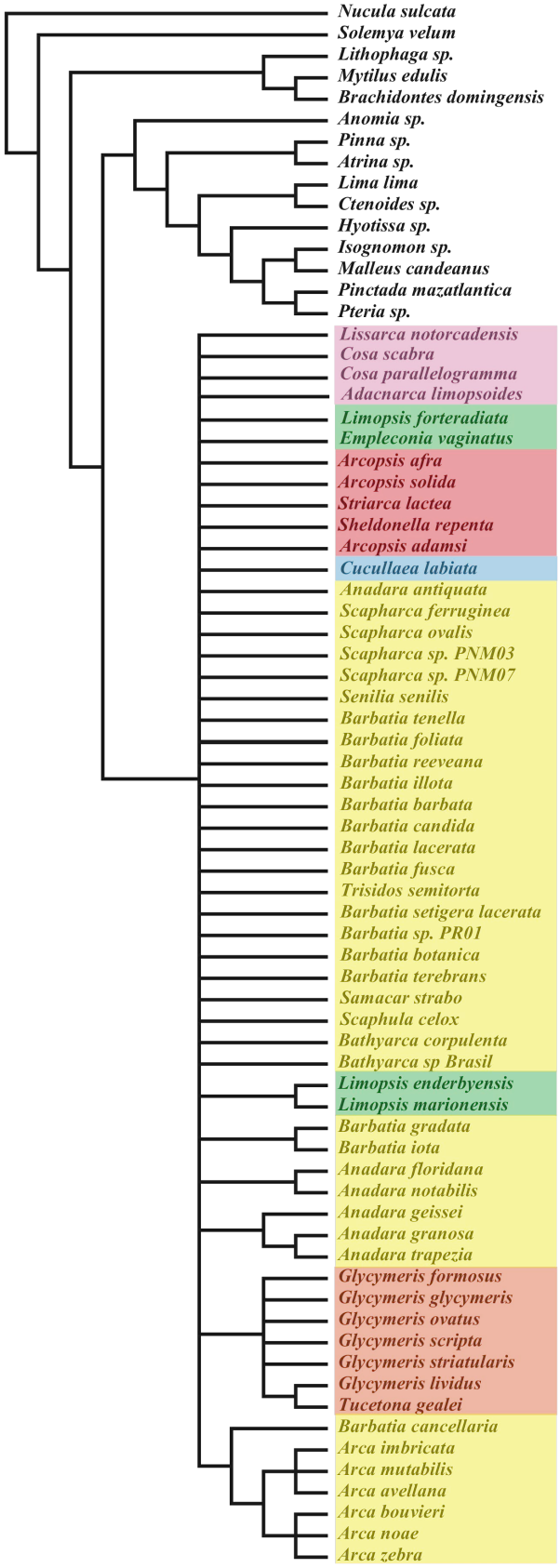


FIGURE 78: 18S – 011

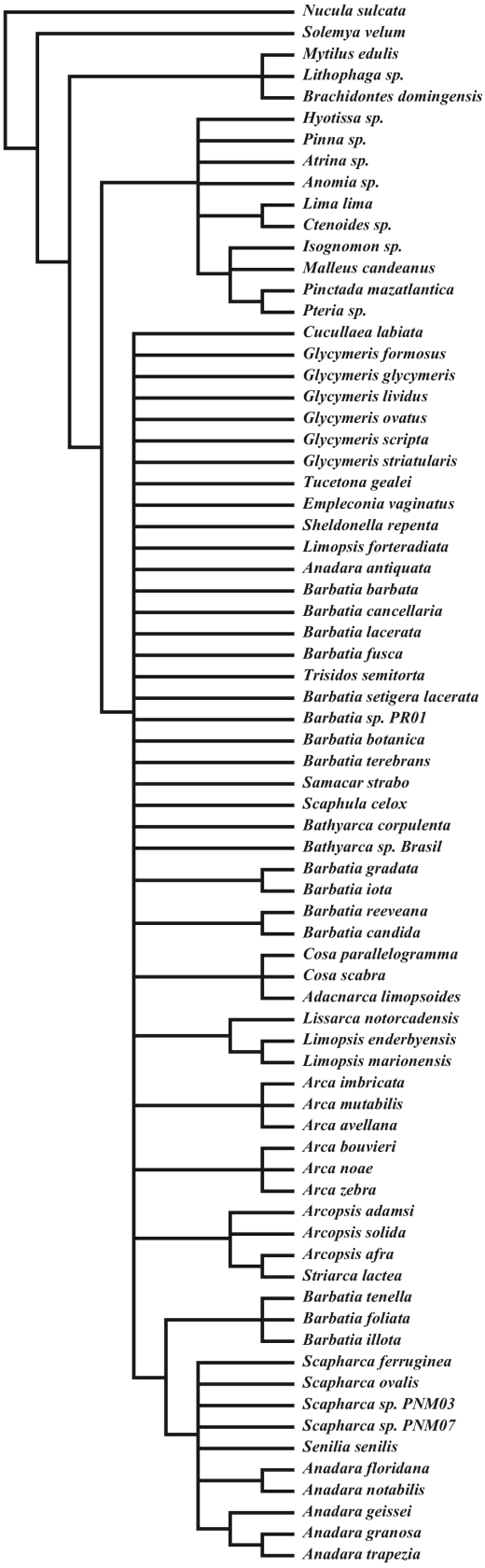
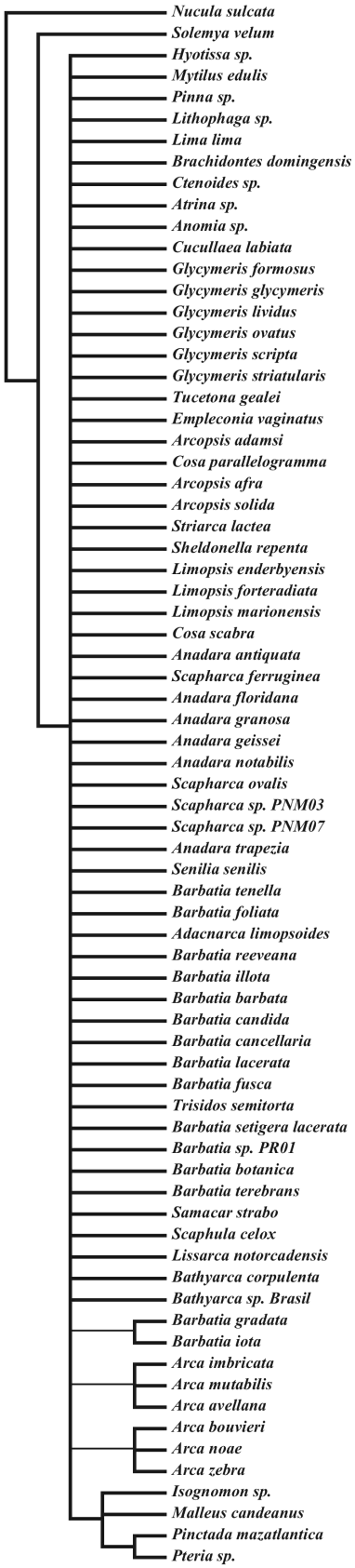


FIGURE 79: 18S
– Strict Consensus of Sensitivity Analysis



H3 — The strict consensus trees from the analyses of the protein coding histone H3 under the parameter sets 041 and 011 are topologically identical (Fig. 80). 242 equally parsimonious trees of cost 843 are recovered from the analysis under the weighting scheme 041, and 60 from the analysis under the parameter set 011. Despite the large number of mpts recovered from these analyses, the strict consensus trees are somewhat resolved. However, none of the families are recovered as monophyletic. The taxon sampling is somewhat imbalanced in this dataset, with the majority of included taxa being from the Arcidae, and the Limopsidae, Cucullaeidae and Philobryidae being represented by a single taxon. The ostreid taxon *Anomia* sp. is the proposed sister taxon from these analyses. The strict consensus of 765 trees recovered from the different parameter sets is similar is structure to that of 011 and 041, except that some clades are less resolved (Fig. 81). Furthermore, the proposed sister taxon to the monophyletic Arcoida is unclear, with the outgroup taxa forming a polytomy towards the base of the tree.

FIGURE 80. Relationships of the Arcoida and outgroup taxa based on the analysis of histone H3 sequences under the parameter set 041 and 011.

FIGURE 81. Strict consensus of the 765 trees recovered from the analysis of histone H3 sequences under the 9 different cost parameter conditions.

FIGURE 80: H3 – 041 and 011

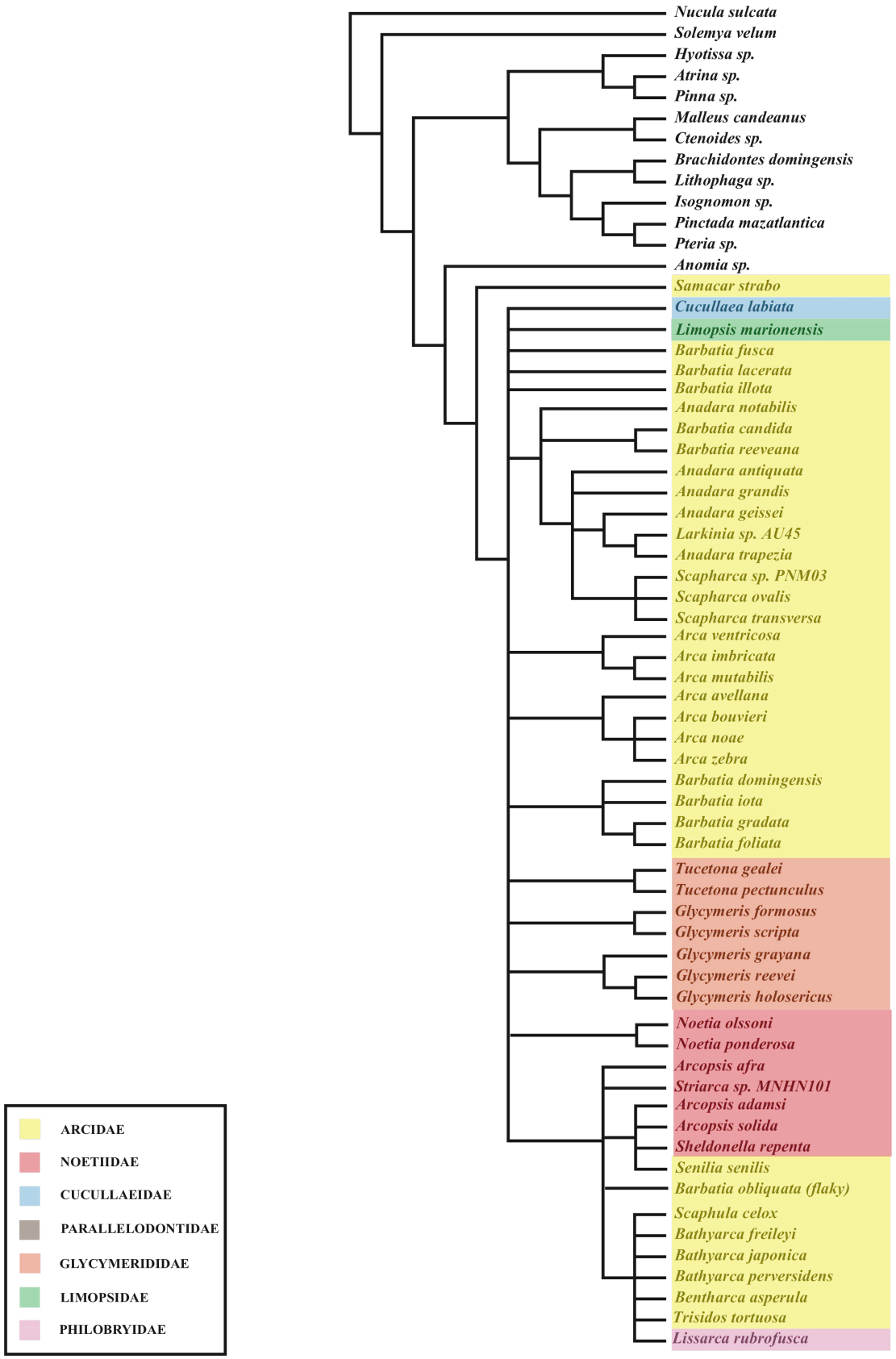
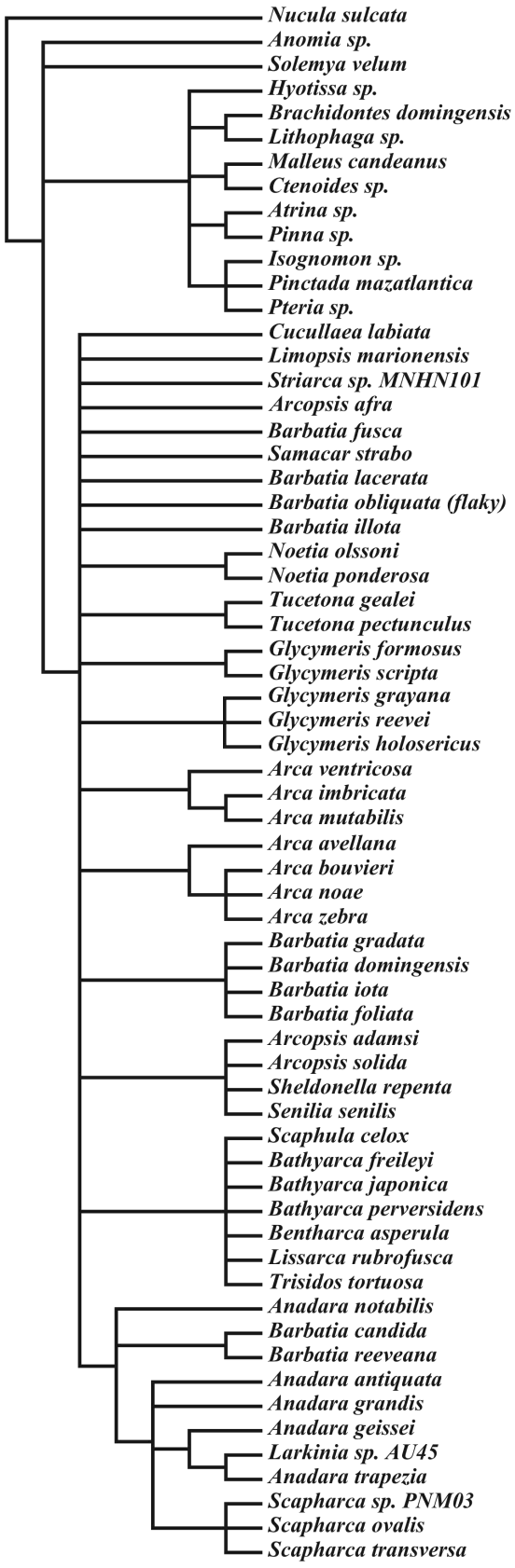


FIGURE 81: H3
– Strict Consensus of Sensitivity Analysis



MOL — A monophyletic Arcoida is recovered from the analysis of all four molecular markers with the parameter set 041 (Fig. 82). Under this weighting scheme a single most parsimonious tree of cost 15509 is recovered. In this analysis of 89 ingroup and 15 outgroup taxa, the Glycymerididae and Noetiidae are monophyletic. The Philobryidae are polyphyletic and form a clade with limopsid or arcid taxa. Similarly, the Limopsidae place in three different parts of the tree. Many of the arcid clades proposed in the analyses of the individual partitions are recovered in this combined analysis, including *Arca*, anadarine + *Barbatia bistrigata,* as well as many of the smaller *Barbatia* clades. The Limidae are the proposed sister taxon to the Arcoida from the analysis of the molecular data under this weighting scheme.

When equal weights are applied to the transformations, many of the same relationships as those recovered from 041 are found. Three mpts of equal cost 12593 are found. While the overall topology of the strict consensus cladogram differs from that of 041, the constituent taxa of the smaller clades remain the same (Fig. 83). The same cannot be said the strict consensus of the 26 trees recovered from all the analyses under the different parameter sets (Fig. 84). In this tree, we see a monophyletic Noetiidae, anadarine + *B*. *bistrigata*, *Arca* as well as two clades comprised of *B*. *illota* + *B*. *tenera* and *B*. *reeveana* + *B*. candida. *Tucetona pectinata* + *G*. *ovatus* is also proposed. There is no clear indication as to the sister taxon of the Arcoida as the outgroups form a polytomy at the base of the tree.

FIGURE 82. Relationships of the Arcoida and outgroup taxa based on the analysis of all the molecular data (18S rRNA, 28S rRNA, histone H3 and cytochrome *c* oxidase subunit 1) under the parameter set 041. A single most parsimonious tree of cost 15509 is found.

FIGURE 83. Relationships of the Arcoida and outgroup taxa based on the analysis of the four molecular markers under the parameter set 011. The strict consensus of 3 equally parsimonious trees of length 12593 is shown.

FIGURE 84. Strict consensus of the 26 trees recovered from the analysis of all the molecular sequence data under the 9 different cost parameter conditions.

FIGURE 82: MOL – 041

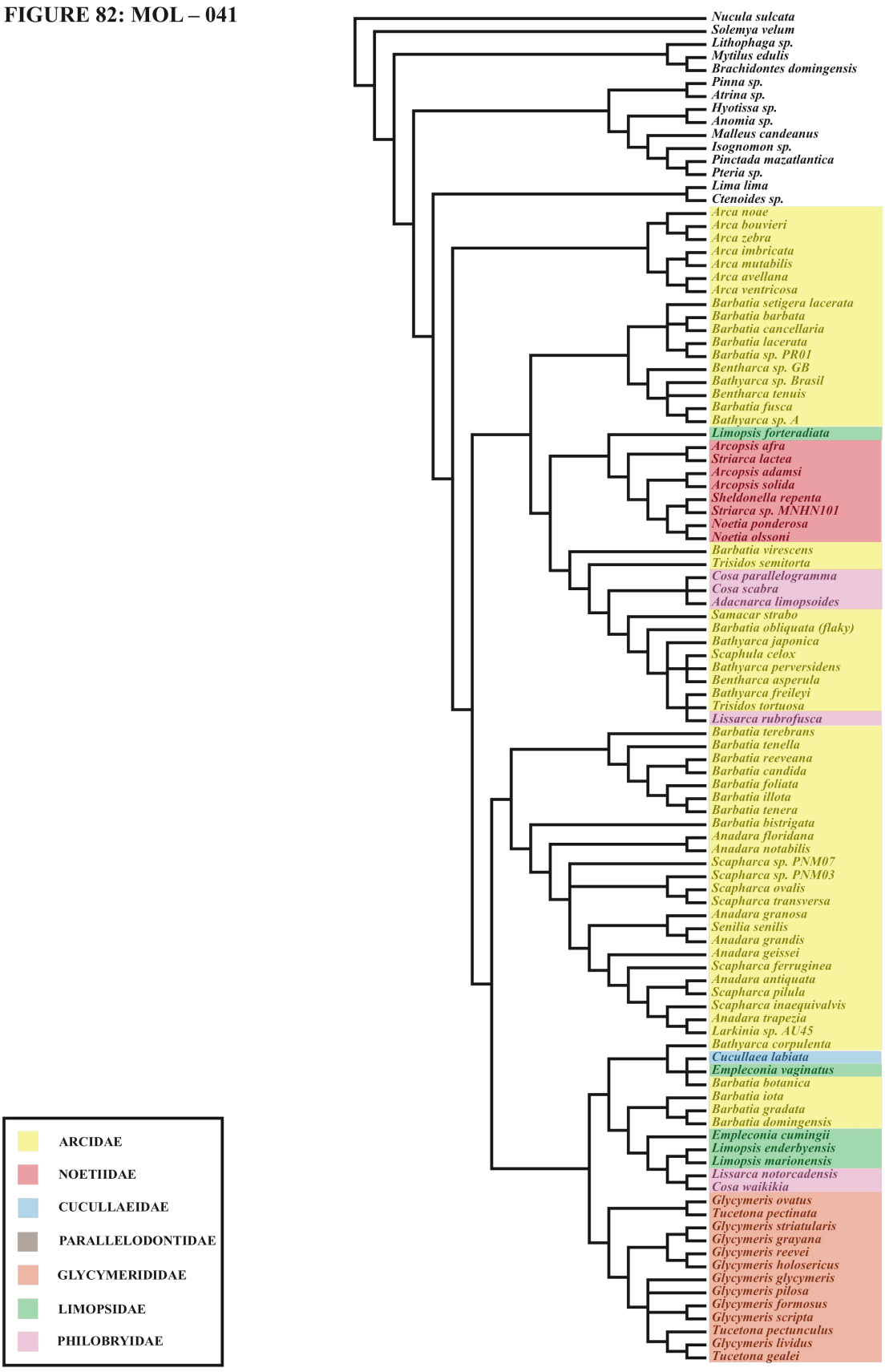


FIGURE 83: MOL – 011

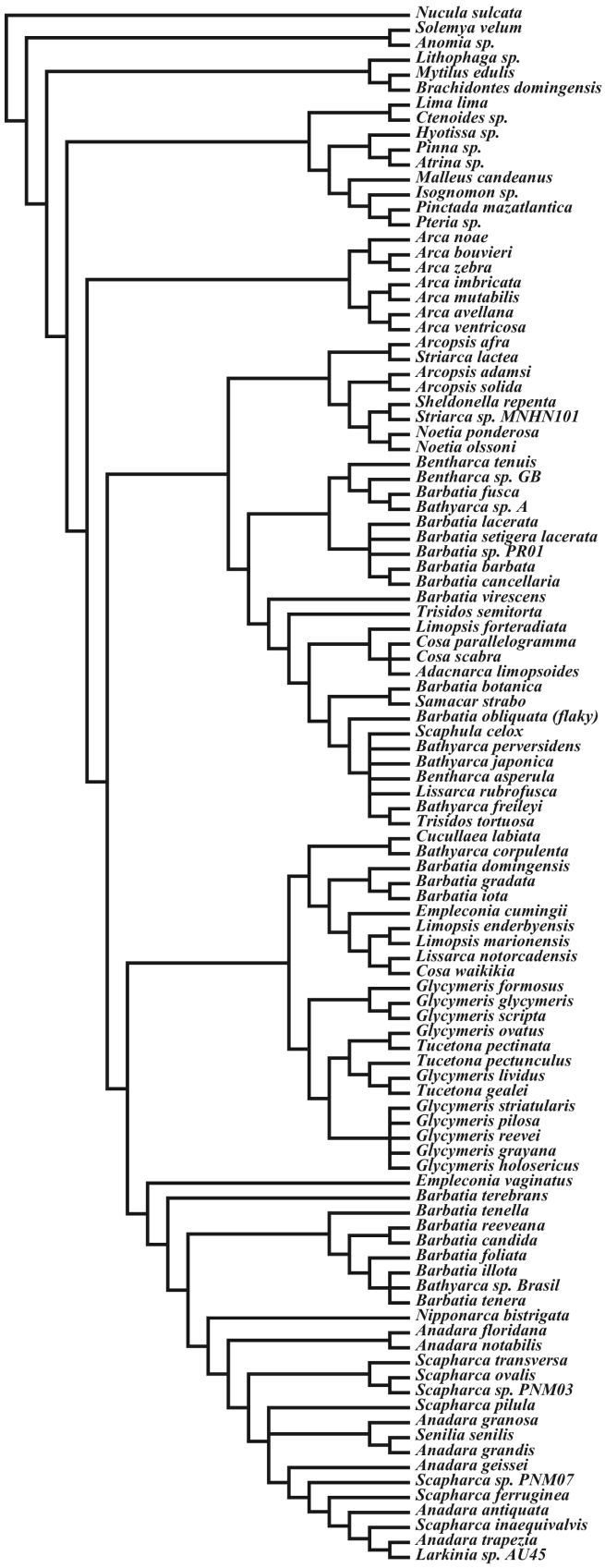
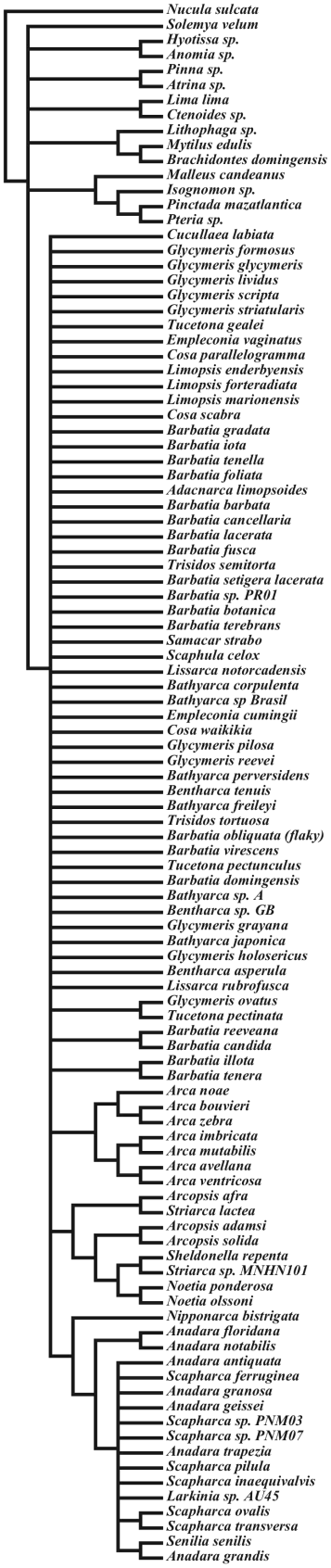


FIGURE 84: MOL
– Strict Consensus of Sensitivity Analysis



TOTAL — The analysis of both morphological and molecular data largely agrees with the analysis of morphological data only (Chapter 2). The analysis under the parameter set that minimizes incongruence across all the data (041), resulted in a single mpt of cost 21243 (Fig. 85a, b). In this analysis, the Arcoida is recovered as monophyletic, with a large clade comprised of limid, mytiloid, pinnid and pterioid taxa proposed as the sister taxon. Of the seven arcoidan families, only the Glycymerididae and Noetiidae are recovered as monophyletic. As in the analysis of morphological data alone, the Limopsidae are paraphyletic with respect to the Arcoidea sensu Amler (1999), although this clade is not strictly the Arcoidea of Amler (1999), as a philobryid clade is nested within the Arcidae. One significant difference between these two analyses arises with the Philobryidae, recovered as polyphyletic in this analysis, but proposed as a paraphyletic grade in the analysis of morphological data only. No consistent pattern is seen in these two polyphyletic groups, as *Cosa* and *Lissarca* are found in both. As seen previously, the Cucullaeidae and Parallelodontidae do not form monophyletic groups in this analysis. The parallelodontid taxa, *Grammatodon implicatus* and *Parallelodon obsoletus*, while not each other's closest relative, are both found within a clade comprised of *Barbatia* and *Bentharca* taxa. The Cucullaeidae placed at different regions of the tree, with the Mesozoic taxon *Cucullaea alta* falling within the anadarine clade and *Cucullaea labiata* placing with *Barbatia terebrans*. The Arcidae are rendered non-monophyletic with the inclusion of the Noetiidae, Parallelodontidae and Cucullaeidae.

In the total evidence analysis under the parameter set 011, the Arcoida are not recovered as monophyletic (Fig. 86). In one of two mpts recovered, a number of Philobryidae fall with the outgroup taxa. It is worth noting that these taxa do not have

any molecular data associated with them. A similar result is found under the parameter set 022. However, as with 041, the Noetiidae and Glycymerididae are monophyletic. Not surprisingly, the strict consensus of all the trees recovered from the analyses under the different parameter sets, did not find the Arcoida to be monophyletic (Fig. 87). However, under all parameter set conditions, a monophyletic Glycymerididae is recovered.

FIGURE 85a, b. Relationships of the Arcoida and outgroup taxa based on the analysis of both morphological and molecular data (18S rRNA, 28S rRNA, Histone 3 and COI) under the parameter set 041. A single most parsimonious tree of cost 21243 is found. The tree continues on the following page. Jackknife values between 50-74 are indicated by blue box on the branch and between 75-100 are indicated by a red box. The tree continues on the following page. Bremer support values are in green font above the branches.

FIGURE 86. Relationships of the Arcoida and outgroup taxa based on the analysis of both morphology and four molecular markers under the parameter set 011. The strict consensus of 2 equally parsimonious trees of length 14107 is shown.

FIGURE 87. Strict consensus of the 12 trees recovered from the analysis of all the data under the 9 different cost parameter conditions.

FIGURE 85a: TOTAL - 041

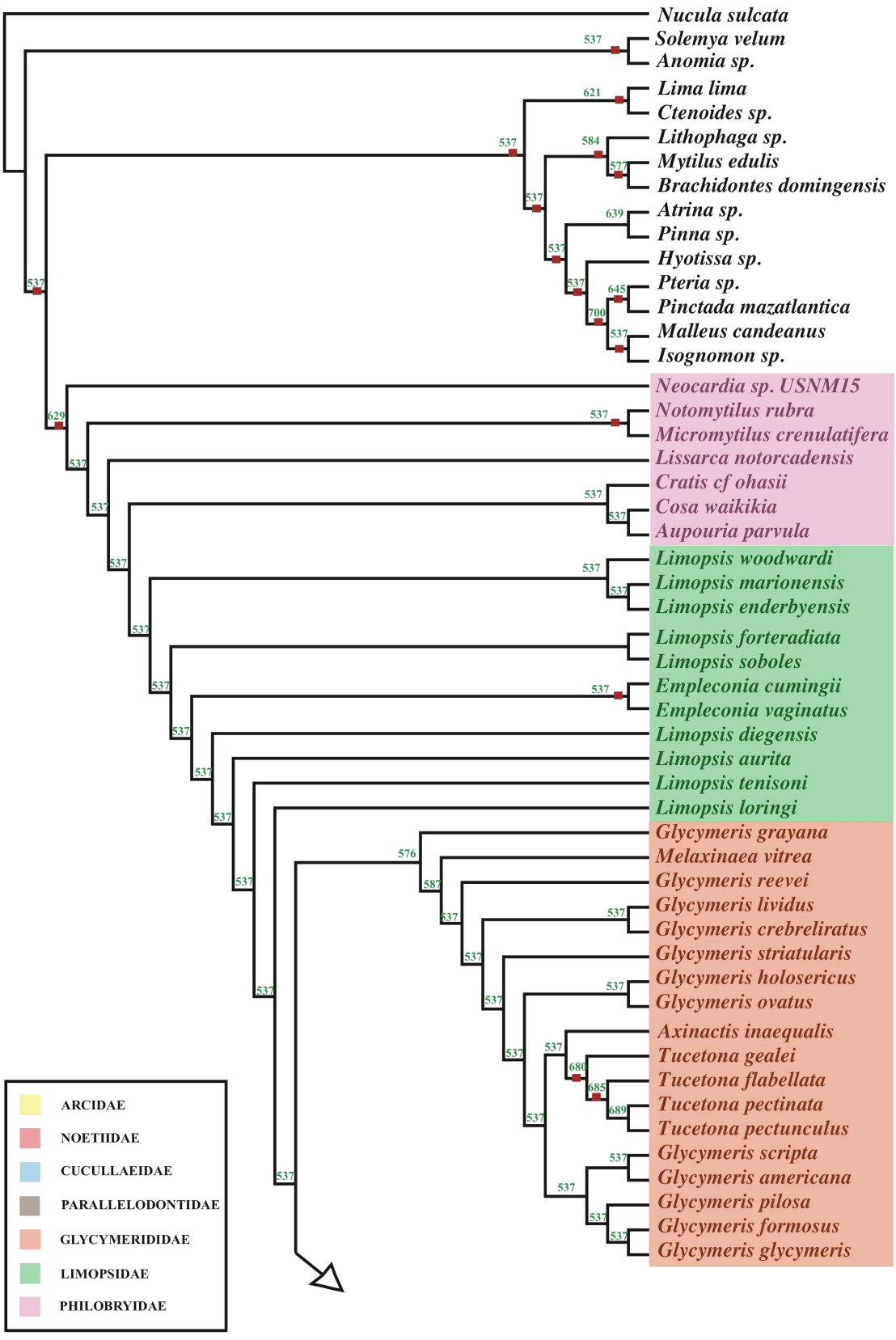


FIGURE 85b: TOTAL - 041

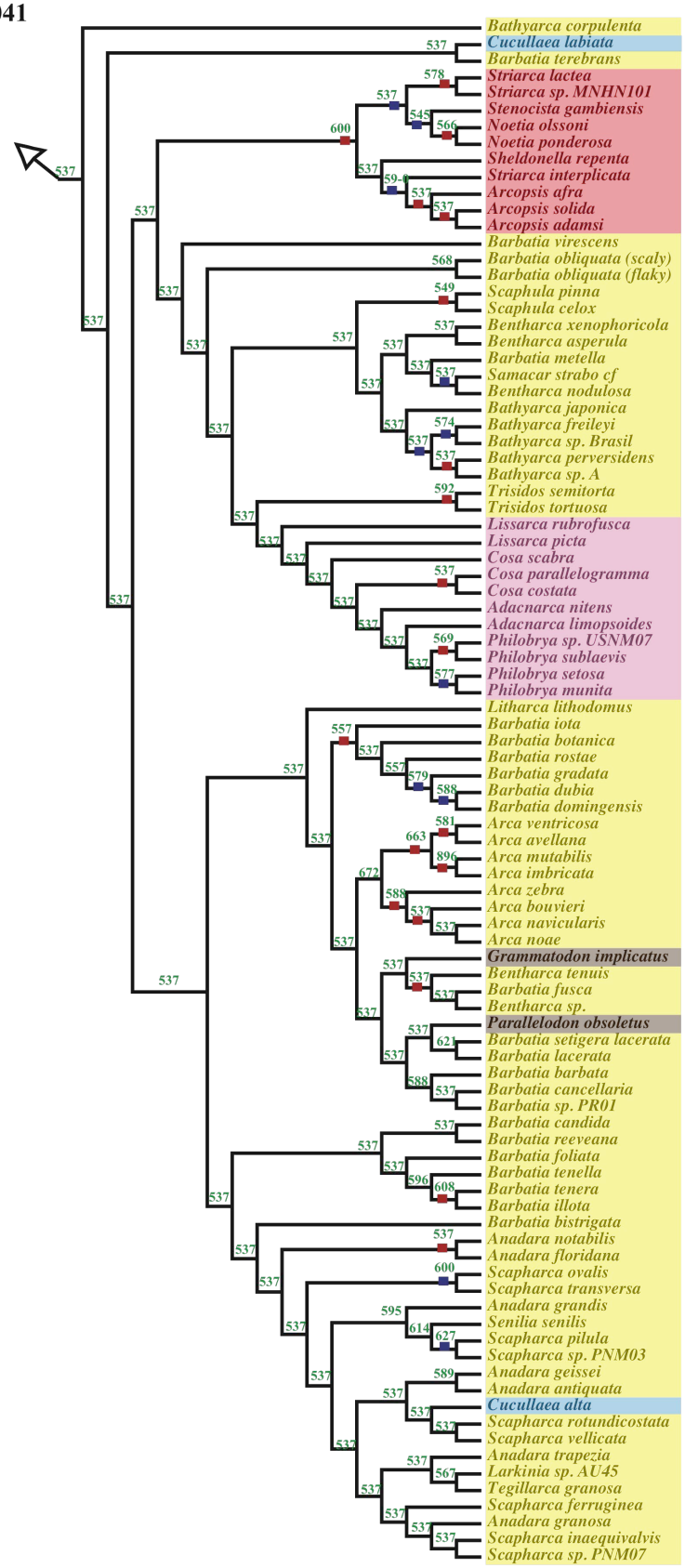


FIGURE 86: TOT - 011

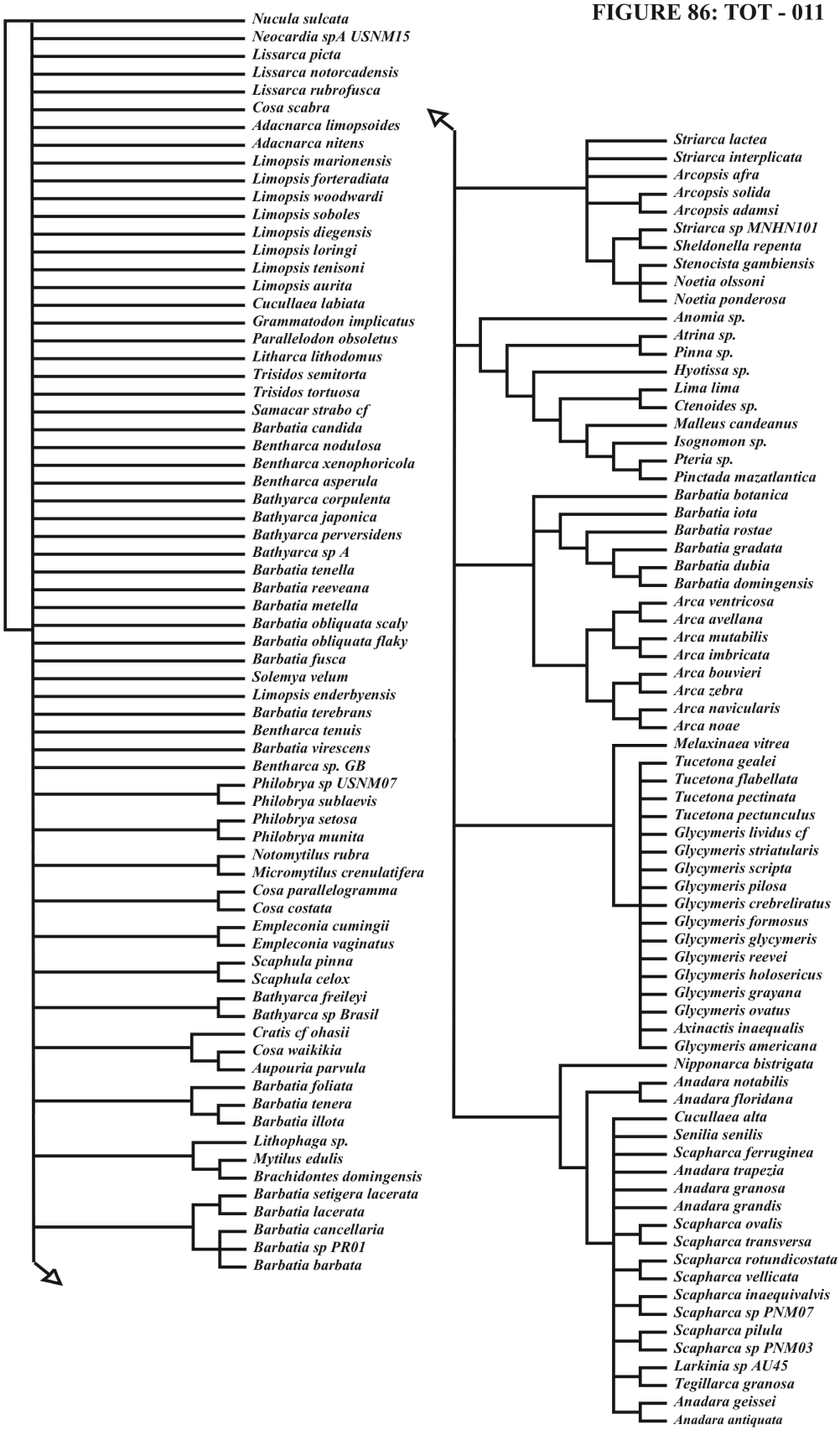
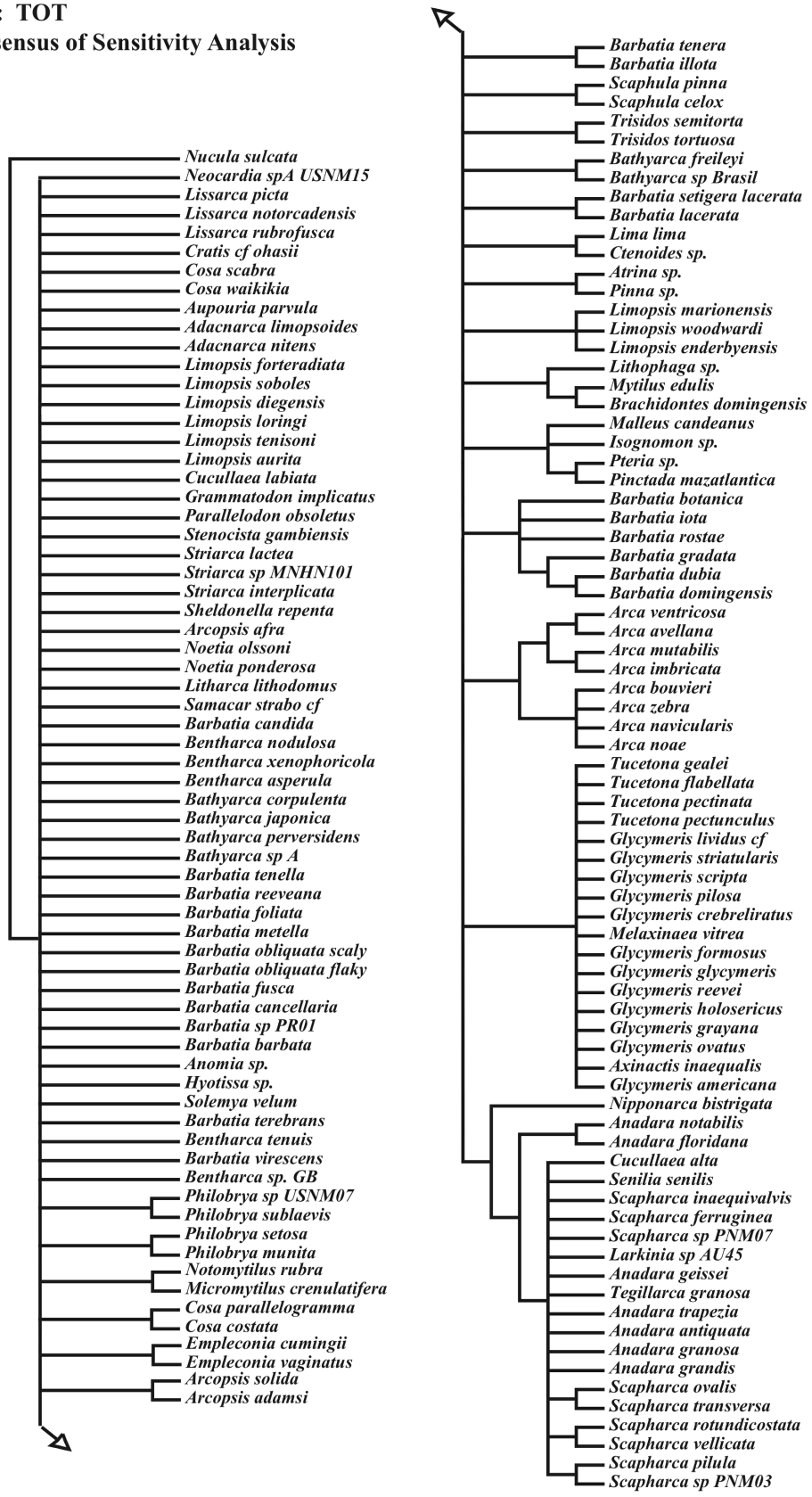


FIGURE 87: TOT
- Strict Consensus of Sensitivity Analysis



DISCUSSION

This study represents the largest analysis for the Arcoida in terms of both taxon representation and character sampling. There is no previous analysis of this kind with which to compare the results of this study. Any conclusions as to the phylogenetic relationships of this group and its constituent taxa will be based on the results of the total evidence analysis of the morphological and molecular data under the parameter set that minimized the incongruence among the different data partitions (041).

HIGHER RELATIONSHIPS OF THE ARCOIDA

Arcidae — Except in studies where a single arcid has been included, this family has never been recovered as a monophyletic clade. It has been recovered as a paraphyletic grade with respect to other arcoids (Steiner and Hammer, 2000; Page and Linse, 2002; Giribet & Wheeler, 2002; Giribet & Distel, 2003; Matsumoto, 2003).

In this study, a polyphyletic Arcidae is recovered in the analysis of each data partition, including the analysis of morphological data alone, as well in the combined analysis of all the molecular data and in the total evidence analysis of all the data. However, despite the polyphyletic nature of this large family, some of the traditional genera are recovered, including *Trisidos*, *Scaphula* and *Arca.* A clade of *Bathyarca* taxa is recovered, however, the exclusion of *B*. *corpulenta* from this clade, renders this genus polyphyletic. *Barbatia* shows the highest degree of polyphyly, with multiple clades

found across the tree. A large number of subgenera have been proposed for this taxon, with seven in the *Treatise of Invertebrate Zoology* (Newell, 1969) to 23 valid subgeneric names in Voke's (1980) catalogue of generic names of Bivalvia. Three of these subgenera have been recovered in this analysis: *Acar*, with the taxa *Barbatia iota*, *B. botanica*, *B. rostae*, *B. gradata*, *B. dubia* and *B. domingensis*; *Cucullaearca* with the proposed taxa *Barbatia candida* and *Barbatia reeveana*; and *Fugleria* with *Barbatia illota* and *Barbatia tenera*.

Except for the inclusion of *Cucullaea alta*, a large anadarine clade, comprised of *Anadara*, *Scapharca*, *Larkinia* and *Senilia* is recovered. These taxa are highly similar in shell form, with a heavy shell and strong radial ribs. One of the key diagnostic differences between *Anadara* and *Scapharca* is the discordance between the valves in *Scapharca*, with the left valve being larger than the right (inequivalve). Given that these taxa do not form monophyletic clades and that this character is not group defining in this analysis, this would suggest that *Scapharca* should be subsumed within *Anadara* (both of these taxa were described by Gray in 1847).

In the *Treatise of Invertebrate Zoology* (Newell, 1969), this family is further classified into the subfamilies, Arcidae (*Arca*, *Barbatia*, *Litharca* and *Trisidos*) and Anadarinae (*Anadara*, *Bathyarca*, *Bentharca*, *Larkinia*, *Samacar*, *Scapharca*, *Scaphula* and *Senilia*). The results from this study do not support the validity of this taxonomic rank, as neither of these two traditional subfamilies is recovered in any of the analyses.

Cucullaeidae — Members of the Cucullaeidae are distinguishable by the presence of a large myophoric flange (a calcareous process that supports the large posterior adductor

muscle of these taxa) and lateral teeth on the dorsal hinge line (see note on hinge dentition below). The Cucullaeidae have a rich fossil record, being abundant in the Jurassic and Cretaceous. The extant diversity of this group is not well understood, with estimates ranging from one species with four local forms (Habe, 1964) to three valid species (Oliver and Holmes, 2006).

In this study, the family is represented by the Mesozoic *Cucullaea alta* and the Recent taxon *Cucullaea labiata*. In the total analysis of all the data, the Cucullaeidae is polyphyletic with *Cucullaea alta* falling within a clade of anadarine taxa and *C. labiata* being sister to *Barbatia terebrans* at the opposite end of the tree. Molecular data were available for *C. labiata* only. This taxon has only been included once in a phylogenetic analysis of bivalves; Matsumoto's (2003) study of the Pteriomorphia. In Matsumoto's study, the Cucullaeidae is sister to a polyphyletic Glycymerididae. There have been many proposals as to the origin of this family, including their derivation from the Parallelodontidae (Newell, 1954; Cox, 1959). Many authors hold to the belief that all modern arcoids can be traced to cucullaeid origins (Nicol, 1950, 1954; Tevesz, 1977; Thomas, 1978; Oliver, 1981; Carter, 1990). This supposition is founded on the form of hinge dentition and largely on the basis of age.

Parallelodontidae — The earliest fossil record of the Arcoida is attributable to a member of this family (*Parallelodon*) in the Lower Ordovician. Only one known extant species (*Porterius dalli*) has been described for this family. As it was not possible to obtain *P. dalli* for this study, a representative from each of the two subfamilies (Parallelodontinae and Grammatodontinae) was included. Members of this family are very similar

morphologically to the Arcidae, in terms of shell shape and form. However, they differ in their formation of teeth along the dorsal hinge, which have been described as 'pseudolaterals' in all earlier descriptions of the group (see note below).

As with the Cucullaeidae, this family is shown to be polyphyletic, with both of these taxa falling within a clade comprised of *Barbatia* and *Bentharca* species. This is the first phylogenetic study of this family, in which other extant members of the Arcoida are included. The only other phylogenetic study of this group comes from Carter et al.'s (2000) study of the evolution of 'early' bivalves and focused on extinct taxa only. However, as no representatives from the other six arcoid families were included in this cladistic analysis, is it difficult to ascertain the arcoid sister taxon to this group.

In this study a polyphyletic Parallelodontidae is recovered, with the two representatives, *Grammatodon implicatus* and *Parallelodon obsoletus*, falling within a clade comprised of the arcid taxa *Barbatia* and *Bentharca*. In the analysis of morphological data only, the Parallelodontidae is also polyphyletic and also falls among *Barbatia* species.

A note on hinge dentition: In general, descriptions of the teeth of this bivalve order center on the simple nature of the taxodont teeth that are characteristic of the group. As mentioned previously, the dentition is usually comprised of a row of simple or bifid teeth along the dorsal hinge. However, coding for the presence or absence of taxodont teeth does not take into account the orientation of these teeth, which can be vertical, oblique or lateral. In fact, it is possible to find hinges with all three teeth orientations in the same organism. In examining the shell morphology across the Arcoida, it was clear to the

author that the coding for the presence or absence of laterals and pseudolaterals (see characters 50 and 51: Chapter 2) would introduce unwarranted inferences about dental homologies. Recall that lateral teeth are those where the proximal end of 'lateral' teeth is well separated from the umbonal region and the proximal end of pseudolaterals extends to the cardinal region beneath the umbones. The presence of teeth with a lateral, or a longitudinal orientation is not restricted to cucullaeid or parallelodontid taxa; teeth of this orientation are also found in species of *Bathyarca*, *Bentharca* and *Samacar* (although not all the taxa in these genera possess lateral teeth). Thus, the teeth were redefined in terms of orientation and proximity to the umbonal region.

Noetiidae — The Noetiidae is recovered as a monophyletic group in the analysis of the morphological and molecular data, as well as in the combined analyses of these datasets. This family is united on the basis of their unique form of ligament—vertical strips of fibrous bands embedded in lamellar elements that are laid down at the extremities of the hinge.

Noetiids have been included in phylogenetic studies on five previous occasions (Steiner and Hammer, 2000; Giribet and Wheeler, 2002; Marko, 2002; Marko and Moran, 2002; Giribet and Distel, 2003). However, in three of these studies, those involving large-scale analyses of Bivalvia, a single taxon, *Striarca lactea* was included. In the studies involving geminate species (Marko, 2002; Marko and Moran, 2002), two to four noetiid taxa were included. In these two latter studies, the Noetiidae were seen to nest with the Arcidae.

The noetiids are also similar in form to that of the Arcidae. In fact, these taxa are often mistakenly identified as Arcidae in museum collections (pers. obs.). The classification of Newell (1969) identifies two subfamilies in this group, the Noetiinae (*Noetia, Stenocista* and *Sheldonella*) and Striarcinae (*Striarca* and *Arcopsis*). The phylogenetic relationship of the family recovered in this study does not support the validity of these subfamilies.

Glycymerididae — Members of this family have been included in each of the phylogenetic studies in which arcoid taxa have been included (Steiner and Hammer, 2000; Giribet and Wheeler, 2002; Marko, 2002; Marko and Moran, 2002; Page and Linse, 2002; Giribet and Distel, 2003). A monophyletic Glycymerididae was recovered in all of these studies, except in the case of Matsummoto (2003), where it was found to be polyphyletic. Despite the sampling effort in Sanada and Matsukuma's (1996) study on the phylogenetic relationships of the Glycymerididae (15 taxa, 23 morphological characters) did not improve our understanding of the relationship of this family with other arcoids, as the cladogram was rooted on a glycymerid taxon.

In this study, the family is recovered as monophyletic in the analysis of morphology, 18S and 28S as well as in the combined analysis of all the data. The COI and H3 datasets recovered two polyphyletic clades in each of these analyses. In addition to the Noetiidae, the Glycymerididae is the only other family that is defined by an unequivocal, unreversed synapomorphy, renal concretions beneath the ctenidial suspensory membrane. Representatives from genera were included in this analysis, with *Melaxinaea* and *Axinactis* being represented by a single taxon. In the total evidence

analysis, *Tucetona* is recovered as monophyletic, having *Axinactis* as its sister, and *Glycymeris* is rendered polyphyletic by the inclusion of this *Axinactis* + *Tucetona* clade.

Limopsidae — Limopsid taxa have been included in two previous phylogenetic analyses: Matsumoto (2003) included a single limopsid, *Empleconia cumingii,* in his investigation of the phylogenetic relationships of the Pteriomorphia; and Page and Linse (2002), in their investigation of the phylogenetic relationships of the Antarctic limids, chose to include a large number of pteriomorphian taxa in their analysis, including six arcoid taxa, of which two were limopsid taxa. Given the paucity of sampling of this family in these studies, it is difficult to infer anything about their phylogenetic relationships from these studies. In both of these molecular studies, the Limopsidae were sister to the Glycymerididae.

Members of the Limopsidae are characterized by their ovate form, alivincular ligament and generally curved hinge. As none of these characteristics are unique to this group, it is not surprising that they are recovered as paraphyletic with respect to a clade largely comprised of arcoidean taxa (sensu Amler, 1999) as well as the philobryid clade that is nested within the Arcidae. Two extant genera are attributed to this family, *Empleconia* and *Limopsis*. The former was recovered as a monophyletic clade in the total evidence analysis, but Limopsis was rendered polyphyletic by the inclusion of *Empleconia*.

Philobryidae — These miniscule taxa are the least 'arcoid-like' in form, generally lacking teeth and possessing an *internal* ligament of the alivincular type. The D-shaped

prodissoconch, which is often bounded by a raised rim, is believed to be associated with brooding. Every recent description of this family reports a viviparous reproductive strategy for this group. However, this categorical characterization of the reproductive strategy of the group was not been observed in all taxa and so was only scored in taxa for which brooded young were directly observed. (*Note*: brooded young have also been observed in the arcid *Barbatia bailyi* by Moran (2004a) and in *Barbatia dubia* and *Barbatia botanica* (this study)). These three taxa have been attributed to the *Barbatia* subgenus *Acar*. However, given that brooded young were not observed in the other taxa prescribed to this subgenus (i.e. *Barbatia iota*, *B*. *rostae*, *B*. *gradata* and *B*. *domingensis*) no conclusions can be made as to whether this is a synapomorphy[3] for the group).

This is the first time that a philobryid has been included in a phylogenetic study. In the analysis of morphological characters only, the Philobryidae are found to be paraphyletic with respect to all other arcoids, with a paraphyletic Limopsidae being its closest sister taxon. The sampling of molecular characters for this group was also limited and amplification of the chosen markers was hampered by poor preservation of the samples. In the total evidence analysis, the Philobryidae are polyphyletic, with a paraphyletic grade falling at the base of the arcoid clade and another clade falling within the Arcidae. It is unclear as to why this happens, given that *Cosa* and *Lissarca* are found in both groups. A possible explanation might be due to the sampling of molecular data for these taxa—no philobryid had complete coverage for all genes and some are represented by a single gene.

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[3] Given that reproductive cycles are seasonal, it cannot be concluded whether the lack of evidence of brooded young relates to the absence of this character in some of the taxa in this subgenus or whether this is due to collection bias.

CONCLUSIONS

The monophyly of the Arcoida has never been questioned, with a single origin of this group being recovered in all the previously discussed phylogenetic studies. This has been confirmed in this study.

The relationships of the Arcoida to other pteriomorphian taxa remain poorly understood. Given that a heterodont taxon was not included in this study, it is difficult to assess the sister-group relationship between Arcoida and other pteriomorphian taxa. However, various sister-group relationships have been suggested including one with Mytiloidea (Cope, 1996; Morton, 1996), Anomioidea + Plicatuloidea (Hammer, 2001), other pteriomorphian taxa (Campbell et al., 1998; Giribet and Distel, 2003), Anomioidea + Pectinoidea + Limioidea (Matsumoto, 2003), as well the Arcoida being the sister taxon to non-mytiloid pteriomorphian bivalves (Giribet and Wheeler, 2002). A number of different sister-group relationships are proposed by the various parameter sets utilized in this study including one with *Lima lima* (COI), *Anomia* sp. (H3; morphology), Limidae (MOL), and a large clade comprised of non-protobranch + non-*Anomia* sp. taxa.

An often-posed question relating to the systematics of these bivalves has centered on the taxonomy and classification of the higher-level taxa in this group; the number of superfamilies and their constituent taxa. As discuss previously, some of the conflict in the classification of this group lay in the placement of the Glycymerididae in either the Arcoidea (along with the Arcidae, Noetiidae, Cucullaeidae and Parallelodontidae) or in the Limopsoidea (with the Limopsidae and Philobryidae). Recent studies have appeared

to settle on the treatment of this family as an arcoidean taxon, with the Limopsidae and Philobryidae being classified in the Limopsoidea (both these families possess an alivincular ligament). Since only one previous study, that of Matsumoto (2003) has included a limopsid and philobryids are lacking from these analyses, no comment can be made as to the recovery of these superfamilies in previous works. However, the proposed phylogenetic from the present analysis sees no justification for these taxonomic ranks. At best a paraphyletic Limopsoidea is recovered in some of the analyses (e.g. morphology). The inclusion of a philobryid clade among the Arcidae, in fact renders it polyphyletic.

Of the seven families included in this study, only two are recovered as monophyletic. The monophyly of the Glycymerididae and Noetiidae are well established on the basis of morphological and molecular data in this study. This implication of a single origin for both of these families is founded on the basis on unequivocal, non-reversed, non-homoplastic synapomorphies. The renal concretions of the Glycymerididae were first described by Pelseneer (1911). However, till now, this character has never been discussed as a synapomorphy for the group. This is because the majority of studies of this family have focused either on shell characters or molecular data. Extensive work on the ligaments of Noetiidae was undertaken by Thomas et al. (2000). Using modeling techniques, the authors were able to show that the 'novel' ligament of this group can be achieved by one or two simple changes in the regulation of development of the arcoid duplivincular ligament. However, Thomas and coauthors do not believe that 'noetiid' ligaments are monophyletic, as extreme variants in species of *Limopsis* were observed to develop a ligament that was similar in form to that of the noetiid ligament.

All other families are recovered as paraphyletic (Limopsidae) or polyphyletic (Philobryidae, Cucullaeidae, Parallelodontidae and Arcidae). The inclusion of fossil taxa in an analysis of extant species is often deemed to be problematic, especially in cases where molecular characters are included. In cases such as this, their inclusion introduces a great deal of missing data. One could use this as an excuse to explain the polyphyletic recovery of both the Parallelodontidae and Cucullaeidae, both of which were represented by fossil taxa. However, recall that in the analysis of shell characters only, both of these families are polyphyletic, thus, this *ad hoc* explanation cannot be employed. The convergence in shell form of the Parallelodontidae with the Arcidae has been discussed previously. In order to incorporate the diversity of form and orientation of the teeth found in the Arcoida, it was necessary to redefine the 'taxodont' teeth of Arcoida into a series of binary characters as opposed to character complexes ('taxodont', 'laterals', 'pseudolaterals'). This introduced a lot of homoplasy in these characters and reduced the phylogenetic significance of the 'holy grail' of teeth (refer to the six higher-level taxonomic ranks that have been erected on the basis of hinge teeth; Chapter 2, Table 1).

The results of this study highlight the need for a major taxonomic revision at all levels in the Arcoida. This may result in the redefinition of many of the family-level taxa, but would seem to call for the abandonment of the superfamilial ranks of the Arcoidea and Limopsoidea as well as the subfamily ranks in the Arcidae and Noetiidae.

APPENDIX 1. List of specimens and types examined and used for character coding. Sources of literatures relating to the anatomy of a taxon, when utilized, are also provided. AMNH TBD indicates a specimen that will be accessioned to the AMNH malacology collection.

INGROUP TAXA

ARCIDAE

Anadara antiquata (Linnaeus, 1758)

Type material examined: Holotype — *Arca antiquata* Linnaeus, 1758 one valve, LSL no, 144.

Additional material examined: Japan, Okinawa, Kue (four pairs dried shells AMNH 249/85/- Madagascar, Nossi Bé, figured specimen Treatise Invertebrate Paleontology (6): fig. C5, 5a (one pair, no tissue AMNH 158948); Madagascar, Tuléar Port, SE of the main port, sand and herbiers, 0-3 m (three specimens with tissue MNHN uncatalogued); Philippines, Negros Oriental Province, Negros Island, Bais, Sanlagan, 09º38.000'N, 127º07.000'E, Stn. 1-305 (tissue only USNM 802329); Australia, Queensland, Great Barrier Reef, Swain Reefs, Mystery Reef, 21º23.000'S, 152º01.000'E, 3-8 m (four pairs with tissue, AMS C.161815); Madagascar, Ile. Ste. Marie, from harbor breakwater south to Ilot Madame, Stn. FM-32, R.W. Foster! 1961 (three pairs dried tissue AMNH 175410); Federal States of Micronesia, Not Point, Pohnpei, 1-6 ft, under coral heads, shallow reef

(three pairs, dried tissue AMNH 283963); Madagascar, Ambodifototra, Ile. Ste. Marie, from harbor breakwater south to Ilot Madame, Stn. FM-32, R.W. Foster! 1961 (two pairs dried tissue USNM 709422); Marlcet, B/C 1661 (one pair with tissue MNHN uncatalogued); New Caledonia, Secteur de Nouméa, Stn. 250, 22º19.000'S, 166º26.000'E (two pairs dried tissue, MNHN uncatalogued).

Anadara floridana (Conrad, 1869)

USA, Florida, Ustichke! (AMNH 133990); USA, Florida, from scallop dump, dredged from St. Joseph's Bay at ~ 100ft, Boyko & Sage! (AMNH 266762).

Anadara geissei (Dunker, 1891)

Senegal (one pair with tissue CV-01 AMNH TBD).

Anadara granosa Linnaeus, 1758

Philippines, Vicinity of Cebu City, Cebu Island, du Point-Academy Expedition, 1958 (four pairs, five left valves, five right valves USNM 631586); Indonesia, Java, Teluk Djakarta (Bay), 06º05.000'S, 106º48.000'E, 2-3 m, sandy mud (three pairs dried shells, AMS C.118855); Malaysia, Upper Sungai Selinsing, Matang Est., 7 yr *Rhizophora* (four pairs with tissue, BMNH 20050265); New Guinea, 300 miles west of Alexishafen, north of Madang, 5º05.400'S, 145º49.200'E, mudflats (seven pairs with tissue AMS C.070645); Australia, Queensland, Gulf of Carpentaria, Karumba, Pilot Station, 17º29.000'S, 140º50.000'E, mudflats (six pairs with tissue AMS C.434465).

Anadara grandis (Broderip and Sowerby, 1829)

No data (one pair with tissue USNM 803482).

Anadara notabilis (Röding, 1798)

Antigua, Maid Island, on sand bottom (one pairs, one left valve and one right valve AMNH TBD); Puerto Rico, Mouth of Phosphorescent Bay, 17º58.162'N, 067º00.928'W, on shore (one left valve, one right valve AMNH TBD); Puerto Rico, Media Luna Bay, 17º56.350'N, 067º03.036'W, on sand bottom (one pair, one right valve AMNH TBD); Puerto Rico, Puerto de Culebra, Culebra, on sand bottom (one left valve, four right valves AMNH TBD); Puerto Rico, Combate, 17º58.772'N, 067º12.788'W, on beach (five left valves, five right valves AMNH TBD); Brasil, Arraial do Cabo, Rio de Janeiro State, 10-20 m (two pairs with tissue AMNH TBD); Florida, Florida Keys, Monroe County, just west of Everglades National Park border, bayside, IMBW-FK-649, 24º54.075'N, 080º56.24'W, *Thalassia*/*Syringodeum* seagrass, 0.1-0.9 m (one pair with tissue AMNH 305147); Haiti, Port-au-Prince (two pairs no tissue AMNH 179530).

Anadara pilula (Reeve, 1843)

Type material examined: *Arca pilula* Reeve, 1843 — syntypes, three pairs BMNH 1969161, Philippines, Island of Burias, figured specimen in Reeve, 1844, Conch. Icon. Vol. 2, sp. 8; 1844, Proc. Zool. Soc.: 39; *Potiarca pilula saccula* Irelade, 1939 — syntypes one valve AMS C.79067 Australia, Queensland, Port Curtis 23º55'S, 151º23'E; *Potiarca pilula saccula* Irelade, 1939 — syntypes three valves AMS C.79065 Australia, Queensland, Cooktown 15º28'S, 145º15'E; *Potiarca pilula saccula* Irelade, 1939 —

syntype 50+ valves AMC C.77146 Australia, Queensland, Townsville, 19º16’S, 146º49’E.

Additional material examined: Australia, Queensland, Keppel Bay, Zilzie Point, ca. 9 miles south of Yeppoon, 23º17.000’S, 150º50.000’E, on sheltered mudflats (ten pairs with tissue AMS C.432779); Australia, Queensland, Bargara, near Bundaberg, 24º49.000’S, 152º28.000’E, pre 1970 (two pairs dried tissue AMS C.074165); Thailand, ‘Siam’, Lem Sing, beach, June 1926 (eight left valves, twelve right valves, no tissue USNM 367428); New Caledonia, Secteur de Touho, Anse de Tiouandé, 20º43.400’S, 165º02.000’E, 2-4 m, fine sand, Montrouzier Expedition Sep 1993, Stn. 1267 (one pair with tissue MNHN uncatalogued).

Anadara rotundicostata (Reeve, 1844)

Australia, Queensland, Separation Point, junction of Mary and Susan Rivers, 25º25.802’S, 152º54.611’E, mudflats, sandy mud and mud (one pair broken AMS C.433842); Australia, Queensland, Gulf of Carpentaria, west of Edward River, 14º46.000’S, 141º09.100’E, trawled, Stn. 11.7, I. Loch! (one pair with tissue AMS C.440804); Australia, Queensland, Clairview, north of St. Lawrence, 22º11.000’S, 149º3.000’E, N. & V. Gomersall! (one pair with tissue AMS C.440808); Australia, Queensland, Gulf of Carpentaria, west of Nassau River, 15º53.500’S, 140º42.100’E, 25.6 m, Stn. 7.7, I. Loch! (one pair with tissue AMS C.440805).

Principal literature source: Sullivan, 1961.

Anadara trapezia (Deshayes, 1840)

Australia, Queensland, Keppel Bay, 4 miles east of Yeppoon, 23º07.000’S, 150º48.000’E, 10-11 m, shelly sediment, dredged, B.W. Jenkins! (two pairs with tissue AMS C.440802); Australia, New South Wales, Sydney, Port Hacking, Gunnamatta Bay, 34º04.010’S, 151º08.650’E, east side (six pairs with tissue AMS C.315622).

Arca avellana Lamarck, 1819

Type material examined: *Arca avellana* Lamarck, 1819 — syntypes MNHN uncatalogued.

Additional material examined: Australia, Queensland, Great Barrier Reef, Lizard Island, btw. Bird and South Ids., 14º41'06.4"S, 145º27'52.6"E (two pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Whitsunday Passage, Lindeman Island, 20º27.000’S, 149º021.000’E (three pairs dried tissue AMS C.058917); Australia, Queensland, Great Barrier Reef, Port Clinton, beach to the south of Holtness Point, 22º32.511’S, 150º45.348’E, cobbles on sheltered sandy mud, low tide, Loch, Beechey, Miller! (three pairs dried tissue AMS C.433839); Australia, Queensland, Great Barrier Reef, Horse Shoe Reef, (five pairs dried tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Stn. 2 02/18/04, (one pair dried tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Horseshoe Reef 03/01/04, (eight pairs dried tissue AMNH TBD; Australia, Queensland, Great Barrier Reef, Dive 8 Coconut Reef, 02/28/04, (one pair dried tissue AMNH TBD); S12-BC-933 (one pair with tissue MNNH-112); dive 7 off Palfrey 2/28/04 (three pairs with tissue AMNH TBD).

Arca bouvieri (P. Fischer, 1874)

Senegal, Dakar, Baie de Goree, rocks, Stn. IKSE-013 (six pairs with tissue, FMNH 306490).

Principal literature source: Heath, 1941.

Arca imbricata Bruguière, 1789

Antigua, Maid Island, on sandy bottom (one pair, one left valve, dried shells AMNH TBD); Puerto Rico, Crashboat Beach, on sandy bottom (one pair, one right valve, dried shells AMNH TBD); Puerto Rico, Mouth of Phosphorescent Bay, dead on shore 17º58.162'N, 067º00.928'W (two pairs, one left valve, one right valve, dried shells AMNH TBD); Puerto Rico, Cayo Enrique, in corals or rocks 17º57.033'N, 067º03.192'W (one pair with tissue AMNH TBD); Puerto Rico, Crashboat Beach, growing in coral on jetty pilings (six pairs with tissue AMNH TBD). Puerto Rico, Mouth of Phosphorescent Bay 17º58.162'N, 067º00.928'W, in coral/rocks, 2-4 ft (17 pairs with tissue AMNH TBD).

Arca mutabilis Sowerby, 1833

Costa Rica, Puntarenas, no protegida, Isla Mogos, 08º43'59.6890"N, 83º22'24.8910"W, Avila! (one pair with tissue UCR-INBIO 0001486347); Costa Rica, Puntarenas, P.N. Marino Ballena, Punta Utiva, 09º08'50.9650"N, 83º45'47.1900"W, 0-1 m, Valdés! (five pairs with tissue UCR-INBIO 0003572355); Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, Bajo del Diablo, 08º42'53.9107"N, 83º54'07.3237"W, 22 m, Gosliner! (one pair with tissue UCR-INBIO 0003572333); Costa Rica, Puntarenas, no protegida, Lado

NE de la Isla Cabuya, 09º35’53.0600”N, 85º04’54.7200”W, 2 m, Mena! (one pair with tissue UCR-INBIO 0001482918).

Arca navicularis Bruguière, 1789

Australia, Queensland, Off Burnett Heads 24º46.500’S, 152º26.000’E, (two pairs with dried tissue AMS C.074149); Australia, Queensland, Moreton Bay, Peel Island, off south side, 27º31.000’S, 153º21.000’E, 3-4.6 m (seven pairs with tissue AMS C.158394); Australia, Queensland, Islands Head Creek, 22º21.640’S, 1503º38.610’E, 20-29 m, dredged (one pair with tissue AMS C.433625).

Arca noae Linnaeus, 1758

Croatia, Kastela Bay, Adriatic Sea, M. Peharda! (six pairs with tissue AMNH TBD); Mediterranean Sea, figured specimen Treatise Invertebrate Paleontology (6) fig. C2, 3a (one pair, dried shells AMNH 28415); Morocco, Melilla (two pairs, dried shells AMNH 294978); Morocco, Melilla (two pairs, dried shells AMNH 199482).

Principal literature source: Heath, 1941; Morton and Peharda, 2007.

Arca ventricosa Lamarck, 1819

New Guinea, Off Madang, north end of Kranket Island, 05º11.000’S, 145º51.000’E, intertidal, inlet (one pair with with tissue AMS C.440823); Mariana Islands, lagoon west of Saipan, dead coral/algal rock taken from anchor (ten pairs, dried shells USNM 595469), Hawaii, Kauai, Koloa Landing, 30 ft, M. Harrison! (one pair with tissue AMNH TBD).

Arca zebra Swainson, 1833

Antigua, Maid Island, on sandy bottom (left valve AMNH TBD); Antigua, Buccaneer Cove, on sandy bottom, 0-4 m (three right valves, one left valve AMNH TBD); Antigua, Buccaneer Cove, in coral/rocks (one pair with tissue AMNH TBD); Puerto Rico, Mouth of Phosphorescent Bay, dead on shore 17º58.162'N, 067º00.928'W (two left valves, three right valves AMNH TBD); Puerto Rico, Combate, dead on shore, 17º58.722'N, 067º12.788'W (eight left valves, four right valves AMNH TBD); Florida (two pairs with tissue AMNH TBD).

Principal literature source: Heath, 1941.

Barbatia amygdalumtostum (Röding, 1798)

Australia, Queensland, Torres Strait, Thursday Island, 10º35.000'S, 142º13.000'E, M. Ward! (seven pairs with tissue AMS C.440801); Australia, Queensland, Great Barrier Reef, Coconut Reef 02/29/04, (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Coconut Reef dive 10, (two pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, btw. Bird and South Ids., 14º41'06.4"S, 145º27'52.6"E (two pairs with tissue AMNH TBD); Western Samoa, Savaii Island, Mataatu Harbor, EasterN Reef, 8 ft, in crevices of coral, Second Templ. Crocker "Zaca" Expedition (seven pairs with tissue AMNH 181303); Australia, Great Barrier Reef, attached to coral (four pairs dried shells FMNH 35847); Australia, Western Australia, Broome, just south of Gantheaume Point Light, L. Price & C. Christensen! (one pair with tissue FMNH 210223/1); Australia, Northern Territory, Melville Island,

Cape Keith, 11º37.000’S, 131º28.000’E, M. Ward! (one pair, dried shells AMS C.433851).

Barbatia barbata Linnaeus, 1758

Mediterranean Sea, including figured specimen Treatise Invertebrate Paleontology (6): figs. C2, 6a, b (five pairs plus figured specimen, dried shells AMNH 28550); Principal literature source: Heath, 1941

Barbatia bistrigata (Dunker, 1866)

India, Bombay (four pairs, dried shells AMNH 28645); Guinea, Villa Ratoma, Ratoma, Conakry II, D. Simard! (three pairs with tissue FMNH 195553/3).

Barbatia botanica (Hedley, 1917)

Australia, New South Wales, Ballina Coast, 28º53’S, 153º34.5’E, open coast under stones, Ponder! (14 pairs, one lv, dried tissue AMS C.364432 D/W); Australia, Tasmania, Tomahawk Island, 40º52.000’S, 147º46.000’E, D. Wolfe! (15 pairs with tissue AMS C.440830 D/W).

Barbatia cancellaria (Lamarck, 1819)

Martinique (>20 pairs, dried shells AMNH 100540); Belize (nine pairs with tissue AMNH uncatalogued Blz-06); U.S.A., Florida, Florida Keys, Monroe County, east end of Rodriguez Key, 25º03.130’N, 80º26.490’W, Stn. FK-206, 1-2 m, sand/seagrass/rubble (12 pairs with tissue AMNH 298078).

Principal literature source: Simone & Chichvarkhin, 2004.

Barbatia candida (Heibling, 1779)

Puerto Rico, Crashboat Beach, growing in coral on jetty pilings, Crowley & Harrison! (two pairs with tissue, 3 rv, 7 lv AMNH TBD); U.S.A., Florida, Florida Keys, Monroe County, wreck of the Thunderbolt, ~6 nmi. east of Marathon Key, 24º39.68'N, 80º57.82'W, Stn. FK-650, steel wreck with fouling organisms, 34.1 m (one pair with tissue AMNH 305160); U.S.A., Florida, Florida Keys, Monroe County, American Shoals, 24º31.54'N, 81º31.26'W, *Thalassia* seagrass with large coral rubble, 2.7-3.3 m, (one pair with tissue AMNH 298975); Mexico, Vera Cruz, Isla de Media, pilings (two pairs with tissue AMNH 142238); Antigua, Maid Island, on sandy bottom (one rv AMNH TBD); U.S.A., off North Carolina, 33º32.36'N, 077º25.24'W, C-V dredge (one rv with tissue USNM 847848); Panama, Kappner! (four pairs with tissue AMNH TBD); Panama, Kappner! (one pair with tissue AMNH TBD); Spondyler Oil Platform (one pair with tissue AMNH 315587).

Principal literature source: Heath, 1941; Simone & Chichvarkhin, 2004.

Barbatia domingensis (Lamarck, 1819)

U.S.A., Florida, Monroe County, off Key Colony Beach, MM 54, FK-112, 24º41.4'N., 81º01.5'W, SCUBA on coral heads/gorgonians, *Thalassia*/sand areas, 5.5 m (one pair with tissue AMNH 298098); U.S.A., Florida, Monroe County, SCUBA in channel, Key Vaca, MM 52, FK-117, 24º44.19"N., 81º02.92'W, <4.6 m (one pair with tissue AMNH 298099); U.S.A., Florida, Monroe County, Coffins Patch, Grassy Key, FK-236,

24º41’05”N., 80º57’28”W, <16 ft (six pairs with tissue AMNH 298094); U.S.A., Florida, Monroe County, French Reef, FK-206, 25º02.15’N., 80º21.08’W, spur and groove reef, rubble sand plains, 28 ft (one pair with tissue AMNH 298095); U.S.A., Florida, Monroe County, Ramrod Key, FK-047, 24º35.80’N., 81º27.24’W, rubble and patch reef,15 ft (three pairs with tissue AMNH 298097); U.S.A., Florida, Monroe County, East Washerwoman Shoal, off Key Colony Beach MM-54, FK-115, 24º40’N., 81º04.3’W, rubble and patch reef, 2.7 m (two pairs with tissue AMNH 298096); U.S.A., Florida, Monroe County, Marquesas Rock, FK-608, 24º27.547’N., 82º12.339’W, hard bottom with gorgonians, coral heads overhanging leading in sand plain, 2.7 m (two pairs with tissue AMNH 298096); U.S.A., Gulf of Mexico, Florida, Bay County, St. Andrews State Park (one pair with tissue AMNH 267675); U.S.A., off North Carolina, 34º24’06”N., 076º35’48”W (one pair with tissue USNM 849372); U.S.A., off North Carolina, 34º24’06”N., 076º35’48”W (one pair with tissue, juvenile USNM 849371).

Barbatia dubia Baird, 1873

Norfolk Island, 29º02’S, 167º57’E, R. Bell & T. Irelade! (16 pairs, dried tissue AMS C.059880).

Principal literature source: Iredale, 1939.

Barbatia gradata (Broderip & Sowerby, 1829)

Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, 800 m east and 150 m from the beach, 08º43’01.2868”N, 083º52’42.2685”W, (one pair with tissue UCR-INBIO 0003572322); Costa Rica, Puntarenas, San Pedrillo, 500 m S. del puesto, hacia Llorona,

08º37’45.7229”N, 083º43’58.7649”W, 1-6 m (seven pairs with tissue UCR-INBIO 0003572341); Panama, Cebaco Island, 5-6 ft. (two pairs with tissue AMNH 312373); Mexico, Acapulco (four pairs dried shells AMNH 250278); Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, Bajo del Diablo, 08º42’53.9107”N, 083º54’07.3237”W, 22 m, Gosliner! (four pairs with tissue UCR-INBIO 0003572334); Costa Rica, Puntarenas, P.N. Marino Ballena, Punta Utiva, 09º08’50.9650”N, 083º45’47.1900”W, 22 m, Valdés! (one pair with tissue UCR-INBIO 0003572351); Costa Rica, Puntarenas, Playa San Josecito, 08º39’39.6653”N, 083º43’09.7200”W, 1-6 m, Camacho! (three pairs with tissue UCR-INBIO 0003572338); Costa Rica, Puntarenas, no protegida, San Pedrillo, 500 m sud del puesto, hacia Llorona, 08º37’45.7229”N, 083º43’58.7649”W, 1-6 m, F. González! (two pairs with tissue UCR-INBIO 0003572340); Costa Rica, Puntarenas, P.N. Marino Ballena, Punta Utiva, 09º08’50.9650”N, 083º45’47.1900”W, 0-1 m, Valdés! (one pair with tissue UCR-INBIO 0003572352); Costa Rica, Puntarenas, no protegida, Playa San Josecito, 08º39’39.6653”N, 083º43’09.7200”W, 1-6 m, Camacho! (three pairs with tissue UCR-INBIO 0003572337); Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, Bajo del Diablo, 08º42’53.9107”N, 83º54’07.3237”W, 22 m, Gosliner! (one pair with tissue UCR-INBIO 0003572332); Costa Rica, Puntarenas, P.N. Marino Ballena, 09º06’14.7466”N, 083º43’32.8761”W, <7 m, F. González! (three pairs with tissue UCR-INBIO 0003572359); Ecuador, Punta Ancon (one pair, dried tissue AMNH 285223).

Barbatia foliata (Forsskål, 1775)

Australia, Queensland, Great Barrier Reef, Heron Island, Harry's Bombie (three pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Heron Island,

Harry's Bombie (two pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Harry's Bombie, Heron Is. (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Heron Island, Harry's Bombie (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, btw. Bird and South Ids., 14º41'06.4"S, 145º27'52.6"E (two pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, btw. Bird and South Ids., 14º41'06.4" S, 145º27'52.6" E (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, btw. Bird and South Ids., (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, btw. Bird and South Ids., (three pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, Coconut Beach (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, Coconut Beach (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, Coconut Beach (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, Coconut Beach (three pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, Coconut Beach (two pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, Pidgin Pt., (two pairs with tissue AMNH TBD); Australia, Lizard Island, Pidgin Pt., (two pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Heron Island, The Canyons (three pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Heron Island, The Canyons (three pairs with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Heron Island, Coral Gardens (one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Lizard Island, Horseshoe, 14º41'06.4"S, 145º26'35.3"E

(one pair with tissue AMNH TBD); Australia, Queensland, Great Barrier Reef, Heron Island, North Wistari Reef (one pair with tissue AMNH TBD); Australia, Lizard Island, Off Palfrey Is. (one pair with tissue AMNH TBD); Thailand, Phuket, reef flat in front of Phuket Marine Biological Center (one pair with tissue AMNH TBD); No data, Stn. R43/BC 909 (one pair with tissue MNHN uncatalogued).

Barbatia illota (Sowerby, 1833)

Costa Rica, Puntarenas, Isla del Caño, Isla del Cao, 800 m east del puesto y 150 m fuera de la playa, 08º43'01.2868"N, 83º52'42.2685"W, 5-10 m, Avila! (one pair with tissue UCR-INBIO0003572323); Panama, Perlas (two pairs dried shells AMNH 250301); Mexico, Nayarit, Banderas Bay (four pairs dried shells AMNH 246584); Mexico, Puertecitos, Baja California (four pairs dried shells AMNH 246585); Mexico, Sonora, Adair Bay, Cholla Bay, under rocks intertidal (two pairs dried shells AMNH 175776); Mexico, Sonora, Punta Peñasco (six pairs dried shells AMNH 88908); Panama, Vera Cruz. Camaron (two pairs dried shells AMNH 292469).

Barbatia iota (Iredale, 1939)

No data B21/BC 1812 (one pair with tissue MNHN uncatalogued MNHN 94).

Principal literature source: Iredale, 1939.

Barbatia metella (Hedley, 1917)

Australia, New South Wales, Sydney, off Cronulla, 34º04.000'S, 151º28.000'E, 180 m, McIntyre! (22 pairs with tissue, three pairs, one lv AMS C.440828 D/W); Australia, New

South Wales, east of Port Jackson, 33º48.000’S, 151º44.000’E, 183-165 m, ‘Derwent Hunter’, dredged, Stn. 34 (25 pairs with tissue, one pair, one rv AMS C.432957).

Barbatia sp. PR-01

Puerto Rico, Mouth of Phosphorescent Bay 17º58.162’N, 067º00.928’W, in coral/rocks, 2-4 ft (12 pairs with tissue PR-01 E/F AMNH accesssion); Puerto Rico, Cayo Enrique, 17º57.478’N, 067º02.525’W, in coral/rocks, 2-4 ft (18 pairs with tissue PR-02 E/F accesssion); Puerto Rico, Isla Cueva, 17º57.51’N, 067º04.50’W, in coral/rocks, ~3 m (16 pairs with tissue PR-03 E/F AMNH accesssion); Puerto Rico, Playa Buye, 18º02.799’N, 067º11.932’W, in coral/rocks, 0-3 m (two pairs with tissue PR-08 AMNH accesssion); Puerto Rico, Punta Solera, Culebra, 18º16.816’N, 065º17.279’W, in coral/rocks (two pairs with tissue PR-09 AMNH accesssion); Puerto Rico, Media Luna Bay, 17º56.350’N, 067º03.036’W, in coral/rocks, (two pairs with tissue PR-10 AMNH accesssion).

Barbatia obliquata cf (Scaly)

South Africa, Transkei, Coffee Bay, 31º59.230’S, 29º09.230’E, in pools below LWN, R. E. Stobbs! (one pair with tissue AMS C. 440871); South Africa, Zululand, 11 km south of Sudwana (Sordwana) Bay, Six Mile Reef, 27º26.000’S, 32º47.000’E, 0-2 m, reef pool, R. E. Stobbs! (one pair with tissue AMS C.440872); India, Madras, S. Arcot District, Tranquebar, A. Kohn! (one pair with tissue FMNH 297580); Hong Kong, Kowloon Peninsula (four pairs with dried tissue AMNH 101505); South Africa, Durban (four pairs, dried shells AMNH 292461); South Africa, East London, Fullers Bay, low tide mark (one

pair, dried shell AMNH 232394); South Africa, Cape Province, Haga Haga, fresh on beach two miles north (seven pairs, dried shells AMNH 295000).

Barbatia obliquata cf (Flaky)

Western Australia, Dampier, next to baths 20º39.000’S, 116º43.000’E, on rocks, M-LTL, B. W. Jenkins! (13 pairs with tissue AMS C.440869); Australia, Queensland, Mourilyan Harbour, near Innisfail, 17º36.000’S, 146º07.350’E, R. Turner and J. Marshall! (one pair with tissue AMS C.440870); Western Australia, Roebourne, low tide at Pt. Samson, N. of Wickham, Stn. WA-34, A. Solem & L. Price! (one pair with tissue FMNH 182567/1); China, Hong Kong, Wah Fu, 22º15.000’N, 114º08.000’E, on exposed rocks, W. Ponder! (four pairs with tissue AMS C.440873).

Barbatia reeveana (Orbigny, 1846)

Costa Rica, Puntarenas, Isla del Caño, Isla del Cao, 800 m east del puesto y 150 m fuera de la playa, 08º43’01.2868”N, 83º52’42.2685”W, 5-10 m, Avila! (one pair with tissue UCR-INBIO0003572321); Costa Rica, Puntarenas, Isla del Caño, Isla del Cao, 800 m east del puesto y 150 m fuera de la playa, 08º43’01.2868”N, 83º52’42.2685”W, 5-10 m, Avila! (one rv with tissue UCR-INBIO0003572324); Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, Bajo del Diablo, 08º42’53.9107”N, 83º54’07.3237”W, 22 m, Gosliner! (one pair with tissue UCR-INBIO 0003572336); Panama, Isla Vendo, Gonsalves-Jackson! (three pairs with tissue AMNH 301783).

Barbatia rostae Berry, 1954

Costa Rica, Puntarenas, P.N. Marino Ballena, 09º08’50.9650”N, 083º45’47.1900”W, 0-1 m, Valdés! (one pair with tissue UCR-INBIO 0003572353); West Colombia = Panama, figured specimen Treatise Invertebrate Paleontology (6): fig. C2, 4a-b, Steward Collection [misidentified as Barbatia (Acar) gradata (one lv AMNH 28649); U.S.A., California, Gulf of California, San Lucas (six pairs, dried shells AMNH 78095); Ecuador, La Plata Island, Askoy Expedition 1941 (one pair, dried shell AMNH 73559); Hawaii (one rv AMNH 46260); Mexico, Tangola Bay, Tangola, “Zaca” Expedition 1937 (eight pairs with tissue AMNH 73897).

Barbatia tenella (Reeve, 1844)

Type material examined: *Arca tenella* Reeve, 1844 — syntypes, three pairs BMNH 1969184, Philippines, Island of Burias, figured specimen in Reeve, 1844, Conch. Icon. Vol. 2, pl. IV, sp. 91.

Additional material examined: Australia, Queensland, Great Barrier Reef, northeast end of Michaelmas Reef, 16º33.000’S, 146º03.000’E, attached under rocks on reef crest & platform (four pairs with tissue AMS C.440795); Australia, Queensland, Great Barrier Reef, Capricorn Group, Wilson Is., eastside, 23º18.000’S, 151º57.000’E, under coral boulders on dead littoral reef (four pairs with tissue AMS C.440794); Thailand, Phuket, reef flat in front of Phuket Marine Biological Center (one pair with tissue AMNH TBD); No data, Stn. P1/BC 2862 (one pair with tissue MNHN uncatalogued); Australia, Queensland, Murray Is, Torres Strait, 09º56’S, 144º04’E (one pair dried shells AMS C.047191); Philippines (two pairs dried shells AMNH 28637); Philippines (one left valve

AMNH 28602); U.S.A., Hawaii, Makena, Maui, E. A. Dunlap! (three pairs dried tissue AMNH 247741); U.S.A., Hawaii, Oahu, D. Shasky! (one pair juvenile dried tissue AMNH 285645); Federal States of Micronesia, Caroline Islands, Ponape (one pair, dried tissue AMNH 283981); Federal States of Micronesia, Caroline Islands, Ponape (one pair, dried shell AMNH 283982); Federal States of Micronesia, Caroline Islands, Ponape (one pair, dried tissue AMNH 283983).

Barbatia tenera (C. B. Adams, 1845)

U.S.A., Florida, Monroe County, Florida Keys, Sand Island, 25º01.116'N, 80º22.046'W, FK-696, max 22 ft, patch reef with rubble (four pairs with tissue AMNH 310444); U.S.A., Florida, Monroe County, Florida Keys, Marquesas Rock, 24º27.547'N, 82º12.339'W, FK-608, 9.7 m, hard bottom with gorgonians, coral heads leading into sandy plain (five pairs with tissue AMNH 305075); U.S.A., Florida, Florida Keys, Monroe County, American Shoals, 24º31.41'N, 81º31.14'W, FK-358, reef/patch reef/gorgonians/rubble, rocks, 5.5 m (two pairs with tissue AMNH 298980); U.S.A., Florida, Monroe County, Channel marker 50A off Ramrod Key, Oceanside, FK-047, 24º35.80'N., 81º27.24'W, rubble and patch reef, 15 ft (three pairs with tissue AMNH 298091).

Bathyarca perversidens Hedley, 1902

Australia, Queensland, off Moreton Bay, 27º27.370'S, 153º39.000'E, 77 m, HMAS 'Kimbla', Stn. 2 (>ten pairs with tissue AMS C.432989 D/W).

Bathyarca corpulenta (Smith, 1885)

New Caledonia, 20º19’S 167º18’E, N.O. “Jean-Charcot” BIOCAL, Stn. CP13, 3690-3740 m, Bouchet, Métivier & Richer! (five pairs with tissue, one rv MNHN uncatalogued).

Principal literature source: Oliver & Allen, 1980.

Bathyarca freileyi

Norwegian Sea, ‘Norbi’ DS04, 65º23’N, 00º02.5’E, 301 m (> 100 pairs with tissue MNHN uncatalogued).

Bathyarca japonica Habe, 1977

Indonesia, Iles Kai, N.O. “Baruna Jaya 1” KARUBAR, Stn. CP12, 05º23’S, 132º37’E, 413-436 m, Bouchet, Kastoro & Métivier! (six pairs with tissue MNHN uncatalogued); Philippines, 13º31’N, 121º24’E, Stn. CP36, 569-595 m (one pair with tissue MNHN uncatalogued).

Bathyarca sp. A

Australia, Queensland, E. of Lady Musgrave Is., 23º33.700’S, 152º37.000’E, 348-339 m, HMAS ‘Kimbla’, Stn. 3 (one pair with tissue AMS C.440833 D/W); No data, T9/BC949 (one pair with tissue MNHN uncatalogued); No data, T36/BC2665 (two pairs with tissue MNHN uncatalogued); No data, P1/BC2018 (one pair with tissue MNHN uncatalogued); No data, T18/BC1396 (one pair with tissue MNHN uncatalogued).

Bathyarca sp. Brasil

Brazil, N.O. “Marion-Defresne”, 23º47’S 42º10’W, MD55, Stn. CB105, 610 m, Bouchet, Leal & Métivier (one pair with tissue, one rv MNHN uncatalogued); Brazil, N.O. “Marion-Defresne”, 18º59’S 37º50’W, MD55, Stn. CB76, 637 m, Bouchet, Leal & Métivier (fourteen pairs with tissue MNHN uncatalogued); Brazil, N.O. “Marion-Defresne”, 21º34’S 40º08’W, MD55, Stn. CB97, 600 m, Bouchet, Leal & Métivier (two pairs with tissue MNHN uncatalogued).

Bentharca asperula Dall, 1881

Type material examined: *Macrodon asperula* Dall, 1881 — lectotype, one left valve USNM 63174, Mexico, Gulf of Yucatan, 24º01’00”N, 088º58’00”W, 1568 fms.

Additional material examined:

Principal literature source: Oliver & Allen, 1980.

Bentharca nodulosa O.F.Müller, 1766

Rech Lacaze-Dutheirs (Banyuls), Gulf of Lion, 42º35.2’N, 03º24.3’E, 300 m, among *Madrepora* and *Pycnodonte* (83 pairs with tissue, three pairs no tissue, 1 lv MNHN uncatalogued); Azores, south of Graciosa N.O. “Jean Charcot” BIAÇORES, Stn. DG88, 32º02’N, 28º06’W, 400-450 m, B. Métivier! (17 pairs with tissue, one right valve MNHN uncatalogued).

Principal literature source: Oliver &Allen, 1980. check paper w/ matrix

Bentharca xenophoricola Kuroda, 1930

Japan, Tosa, 70 fms (one pair, dried shell USNM 622798); Japan, Tosa (three pairs, dried shell FMNH 152086); Japan, Tosa (one pair, dried shell FMNH 70131); Japan, Tosa (one pair, dried shell FMNH 152095); No Data (>1000 pairs, dried shells USNM 246276).

Larkinia sp.

Malaysia, Palau Langkawi, Country Club, 6 18.000'N, 99 52.000'E, sand and mud flats, I. Loch! (one pair with tissue AMS C.434466).

Litharca lithodomus Sowerby, 1833

Type material examined: *Byssoarca lithodomus* — syntypes, three pairs BMNH 1969230, Ecuador, Manta Bay, Manta, Manabi Province, figured specimen in Reeve, 1844, Conch. Icon. Vol. 2, pl. IV, sp. 76.

Additional material examined: Ecuador, Manta (two pairs dried shells FMNH 69058). Ecuador, Manta Bay, Manta, Manabi Province, figured specimen Mollusks of the Tropical Eastern Pacific, Olsson, 1967: 77-79, pl. 5, figs 1a-f (three pairs no tissue, five pairs with tissue USNM 635321).

There appears to be some confusion as to the general form of this species. This is an elongate cuneiform species with one extremity very short and inflated, close to the umbones and truncated with a bristly keel that extends to the margin. The other extremity is elongate, thin, narrow and rotundately acuminate. While these points are consistent is all descriptions of this taxon, the confusion lies is which end of the bivalve is anterior and which is posterior. Reeve (1844) describes the shortened end as the

anterior and the extended flattened end as the posterior, while most other authors vice versa. Reeve's estimation is correct. Sowerby also describes it as Reeve with 'latere antico breviore, obliquè truncato, postico elongato, declivi, rotundato-acuminato'. Principal literature sources: Frizzell, 1946; Olsson, 1961; Nicol, 1986.

Samacar strabo (Hedley, 1915)

Indonesia, Iles Kai, N.O. "Baruna Jaya 1" KARUBAR, Stn. DW14, 05º18'S, 132º38'E, 245-246 m, Bouchet, Kastoro & Métivier! (>100 pairs with tissue MNHN uncatalogued); Indonesia, Iles Tanimbar, N.O. "Baruna Jaya 1" KARUBAR, Stn. CP45, 07º54'S, 132º47'E, 302-305 m, Bouchet, Kastoro & Métivier! (>100 pairs with tissue MNHN uncatalogued); New Caledonia, Iles Loyaute, Lifou, Baie du Santal, Plage de Ngoni, 20º46.5'S, 167º02.9'E, Stn. 1404, intertidal rock face (one pair with tissue MNHN uncatalogued); Indonesia, Iles Tanimbar, N.O. "Baruna Jaya 1" KARUBAR, Stn. DW50, 07º59'S, 133º02'E, 184-186 m, Bouchet, Kastoro & Métivier! (11 pairs with tissue MNHN uncatalogued); Indonesia, Iles Kai, N.O. "Baruna Jaya 1" KARUBAR, Stn. CP16, 05º17'S, 132º50'E, 315-349 m, Bouchet, Kastoro & Métivier! (one pair with tissue MNHN uncatalogued); Australia, New South Wales, Off Broken Bay 32º52.000'S, 152º32.000'E, FRV 'Kapala', dredged. Stn. K78-26-07, 145 m, Graham, Rudman & Colman! (2 pairs with tissue AMS C.432984 D/W).

Scaphula deltae Blanford, 1867

Unknown locality. W. T. Blanford Coll^{n}. Acc. 1944. Journal Asiatic Society of Bengal, 36: pl. III (= pl. XIV), figs. 7-8 (two pairs, dried mantle tissue BMNH 20050258).

Principal literature source: Blanford, 1867.

[This is likely a mixed lot, with *Scaphula deltae* and *S. pinna* (even though it's from the Blanford collection). The larger redder specimen is identical (except in size) to BMNH 20050259.]

Scaphula celox Benson, 1834

India, Calcutta (two pairs, dried shells MNHN uncatalogued); India, Ganges (four pairs, dried shells MNHN uncatalogued); Burrampooler (two pairs, dried shells USNM 715633); India, Calcutta (two pairs, dried shells AMNH 28746).

Principal literature source: Benson, 1856.

Scaphula pinna Benson, 1856

Burma, Tenasserim, V. W. MacAndrew Coll[n] (two pairs, no tissue BMNH 20050259).

Principal literature source: Benson, 1856.

Scapharca ferruginea (Reeve, 1844)

Type material examined: *Arca ferruginea* Reeve, 1844 — possible syntypes, three pairs BMNH 1969178, China Seas, figured specimen in Reeve, 1844, Conch. Icon. Vol. 2, pl. IV, sp. 39; 1844, Proc. Zool. Soc.: 43.

Additional material examined: Fiji, Viti Levu lagon Ouest, N/O "Alis" campagne SUVA 2, Stn. CP 57, 17º43.400'S, 177º22.800'E, 17 m (four pairs with tissue, MNHN uncatalogued); New Guinea, mid-west of Bougainville Island, Buka Passage, Torokina Harbour, 6º14.500'S, 155º01.750'E, mudflats (eight pairs with tissue AMS C.99860).

Scapharca inaequivalvis (Bruguière, 1789)

Madras, India, dredged. R. Winckwirth Coll[n] (nine pairs, dried tissue BMNH 1953.1.26.70-77).

Scapharca ovalis (Bruguière, 1789)

U.S.A., Gulf of Mexico, Louisiana, Bay Marchand Lease Area, 2000 m north of platform, 29º02’50”N, 090º00’46”W, Stn. O2P (three pairs with tissue USNM 803534); U.S.A., Florida, St. Lucy Inlet, Seminole Shoales, sand flats, grass beds (three pairs with tissue USNM 836642); U.S.A., Louisiana, Chauvin (fours pairs, dried shells AMNH 87107).

Scapharca sp. PNM03

Panama, I. Kappner! (ten pairs with tissue AMNH TBD); Panama, I. Kappner! (12 pairs with tissue AMNH TBD).

Scapharca sp. PNM07

Panama, I. Kappner! (15pairs with tissue AMNH TBD); Panama, I. Kappner! (8 pairs with tissue AMNH TBD).

Scapharca transversa (Say, 1822)

USA, Florida, Panama City, Bay Co., C. Boyko and W. Sage! (four pairs with tissue AMNH 266964); USA, Florida, Tamp Bay Benthic Stn., 95-LTB-08, Karlen! (ten pairs

with tissue AMNH 312804); USA, Florida, St. Andrew's Bay, Franklin Co., C. Boyko and W. Sage! (two pairs with tissue AMNH 266910).

Scapharca vellicata (Reeve, 1844)

Tanzania, west coast of Zanzibar, 1.5 mi northwest of Ras Shangani, 06º08.500'S, 039º10.000'E, 11-15 m, sand and shell (one pair dried tissue AMS C.070314); Australia, Queensland, off North Keppel Island, off Yeppoon, 23º02.000'S, 151º20.000'E, 51 m, T. Nielsen! (one pair with tissue AMS C.440809); Australia, Queensland, Magnetic Island, Horseshoe Bay, 19º08.800'S, 146º51.800'E, in sand muddy fringe reef, I. Loch! (one pair with tissue AMS C.440813).

Senilia senilis (Linnaeus, 1758)

Senegal, Dakar, Saloum, in mud (five pairs with tissue, FMNH 306491); Belgian Congo, Banana, Lang & Chapin! July 1915 (one pair with tissue, AMNH 162396); Senegal, Saloum River Estuary (four pairs no tissue AMNH 266379); Angola, Lobito, Lang & Boulton! (two pairs with tissue, AMNH 3244); Senegal, figured specimen Treatise Invertebrate Paleontology (6): 255, fig. 8a, Storer Collection (one pair, no tissue AMNH 158947); West Africa, French Congo, Cap Lopez, Gabon (eight pairs, one valve, no tissue AMNH 232508).

Principal literature source: Yoloye (1975).

Trisidos semitorta (Lamarck, 1819)

No data (two pairs with tissue BMNH 20050269); Western Australia, Dampier Archepelago, Woodside Dampier Expedition 2, 20º37.74-71'S, 116º31.57-05'E, 10.5-11 m (three pairs with tissue, three pairs dried shell, juveniles BMNH 20013287); Western Australia, Off Carnarvon, 24º52.000'S, 113º36.000'E, 24 m (one pair with tissue AMS C.434062); Philippines, no data (two pairs dried shells AMNH 46719); Philippines, Mindanao Sea, Mactan, Cebu (one pair dried shell AMNH 278801); Australia, Queensland, Brampton Reef, Bowen (five pairs dried shells AMNH 110236); No data MNHN Stn.S48/BC2499 (two pairs with tissue, juveniles MNHN uncatalogued); Western Australia, Causeway Beach, Dampier, 20º40.500'S, 116º41.500'E (one pair with tissue AMS C.434061).

Principal literature source: Morton, 1983.

Trisidos tortuosa (Linnaeus, 1758)

Philippines figured specimen Treatise Invertebrate Paleontology (6): fig. C3, 3a-c (one pair, dried shell AMNH 28737); India, Madras, Bay of Bengal (one pair, dried shell AMNH 278800); Australia, Port Albert, Victoria (one pair dried shell AMNH 173531); Australia, Queensland, S. Moreton Bay, dredged 6.5 m (one pair, tissue sample only AMNH TBD); Australia, Queensland, Joskeleigh Beach (twelve pairs, dried shells AMNH 295014); Australia, Queensland, Calliope River mouth of Gladstone Power Station, 23º50.500'S, 151º13.500'E, (three pairs with tissue, juveniles AMS C.440790); Australia, Queensland, Townsville, Rowes Bay, rocky muddy spit, 19º14.000'S, 146º48.000'E (one pair with tissue AMS C.440787; Australia, Queensland, Townsville,

Kissing Point, intertidal sand, 19º14.000’S, 146º48.000’E (one pair with tissue AMS C.440782); Western Australia, Exmouth Gulf, SE or Exmouth Homestead, muddy sandflats with mangroves on upper shore, Australia, Queensland, Townsville, Rowes Bay, rocky muddy spit, 22º24.000’S, 114º08.000’E (two pairs with tissue AMS C.432764).

CUCULLAEIDAE

Cucullaea labiata (Lightfoot, 1786)

Australia, Queensland, Gulf of Carpentaria, 14º46.00’S, 141º9.10’E, 25.5 m (one pair with tissue AMS C.434063); Queensland, Great Barrier Reef, off Bowen, 19º44.00’S, 148º14.00’E, 40 m (one pair with tissue AMS C.119541); Queensland, Gulf of Carpentaria, W. of Horoyd River, 14º10.00’S, 141º13.00’E, 24 m (one pair plus one valve, both with tissue AMS C.109307); Queensland, off Abbot Point, N. of Bowen, 19º53.00’S, 148º5.00’E, 10 m (one pair with tissue AMS C.313603); Queensland, Great Barrier Reef, E. of Sarina, 21º27.50’S, 150º8.00’E., 42 m (two pairs with tissue AMS C.119598, juveniles); Western Australia, Dampier Archipelago, 20º33.58-88’S, 116º36.87-25’E, 13 m (one pair with tissue BMNH 200112660); Thailand, Phuket Island, collected in sand in deep water (one pair AMNH 278803).

Principal literature source: Morton 1981.

Cucullaea alta Sowerby, 1846

Argentina, Patagonia, Lower Miocene, Santa Cruz Rover, Barnum & Brown! (one specimen AMNH 11601).

PARALLELODONTIDAE

Parallelodon obsoletus (Meek, 1871)

Texas, Upper Pennsylvanian, "Jacksboro" (one pair AMNH N. Newell Colln).

NOETIIDAE

Noetia ponderosa (Say, 1822)

U.S.A., Florida, Sanibel (five pairs with tissue AMNH TBD); U.S.A., Florida, St. Lucy Inlet, Seminole Shoales, sand flats/grass beds (one pair with tissue USNM 836640); U.S.A., Florida, Sebastian (three pairs and one valve dried shells USNM 703247); U.S.A., Florida, Panama City, Bay County, Gulf of Mexico (one pair with tissue AMNH 266967); U.S.A., Florida, St. Andrews Bay, Bay County, Gulf of Mexico (two pairs with tissue AMNH 267615); U.S.A., Georgia, St. Catherine's Island, Liberty County (one pair with tissue AMNH 278906); U.S.A., Florida, 70 feet from Bell Buoy # 26, 10 miles south of Alligator Point, Franklin County (eight pairs with tissue AMNH 147691).

Noetia olssoni (Sheldon and Maury, 1922)

Mexico, Mazatlan, Sinaloa, L. Hettick! (four right valves, three left valves CAS 56606).

Principal literature source: MacNeil, 1938.

Arcopsis adamsi (Dall, 1886)

Antigua, Hawksbill, 0-2 m (six pairs with tissue AMNH TBD); Antigua, Buccaneer Cove, 0-4 m (five pairs with tissue AMNH TBD); U.S.A., Florida, Missouri-Ohio Key, Monroe County, MM39.5, FK-111, 24º40’29”N., 81º14’21”W, subtidal rocks, rock washing and by hand (19 pairs with tissue AMNH 298055); U.S.A., Florida, West Summerland Key (Spanish Harbor Keys), Monroe County, “The Horseshoe site”, south arm, MM35, 24º39’19”N., 81º18’13”W, to 1.5 m (30 pairs with tissue AMNH 298950); U.S.A., Florida, Craig Key, between housing developments in the Florida Keys, Monroe County, MM72.3, FK-167, with *Caulerpa*, 0-1 m (11 pairs with tissue AMNH 298053); U.S.A., Florida, Missouri-Ohio Key, Missouri-Ohio Key bridge, Monroe County, MM39.5, FK-111, 24º40.22”N., 81º14.31”W, subtidal rocks, >1 m (two pairs with tissue AMNH 298065); U.S.A., Florida, West Summerland Key, Monroe County, “The Horseshoe site”, MM35, IMBW-FK-629, 24º39’19”N., 81º18’13”W, by rocks at ca. 1 m (11 pairs with tissue AMNH 305127); U.S.A., Florida, West Summerland Key Monroe County, “The Horseshoe site”, south arm, MM35-FK-245, 24º39’19”N., 81º18’13”W, 0.5-2 ft along outer shore of western arm (ten pairs with tissue AMNH 298057); U.S.A., Florida, channel west of Stirrup Key, Key Vaca, Monroe County, MM52-FK-117, 24º44.19”N., 81º02.92’W, <4.6 m by *Thalassia* (14 pairs with tissue AMNH 298060); U.S.A., Florida, channel west of Stirrup Key, Key Vaca, Monroe County, MM52-FK-118, 24º44.19”N., 81º02.92’W, <4.6 m by *Thalassia* (ten pairs with tissue AMNH 298056); U.S.A., Florida, Indian Key Fill, Monroe County, MM52-FK-118,

24º53’25”N., 80º40’28”’W, *Thalassia* seagrass bed (one pair with tissue AMNH 298061); U.S.A., Florida, West Summerland Key Monroe County, “The Horseshoe site”, south arm, MM35-FK-245, 24º39’19”N., 81º18’13”W, 0.5-2 ft along outer shore of western arm (ten pairs with tissue AMNH 298057); U.S.A., Florida, West Summerland Key Monroe County, “The Horseshoe site”, outermost end of western ar
m, MM35-FK-2475, 24º39’19”N., 81º18’13”W (three pairs with tissue AMNH 298054). Principal literature source: Heath, 1941.

Arcopsis afra (Gmelin, 1791)

Australia, Queensland, Keppel Bay, Humpy Is., 23º13.00’S, 150º58.00’E, T.A. Garrard! (22 pairs with dried tissue AMS C.418783); New Caledonia, Secteur de Koumac, Pointe Pandop, 20º35.00’S, 164º15.50’E, mare, fonds durs, herbiers, Stn. 1279 (seven pairs with tissue MNHN uncatalogued); Australia, Queensland, NE side of Cape Capricorn, Hummocky Is., north side of adjacent to anchorage, 23º23.905’S, 151º09.311’E, sheltered rocky shore, low tide, under and on rocks, Stn. M2002/20, Loch, Beechey, Miller! (seven pairs with tissue AMS C.433841); Australia, Queensland, Great Barrier Reef, Port Clinton, beach to the south of Holtness Point, 22º32.511’S, 150º45.348’E, cobbles on sheltered sandy mud, low tide, Loch, Beechey, Miller! (one pair with tissue AMS C.433840); Strait of Gibraltar. CEUTA NORD, Punta Almina, 35º54. 1’S, 05º16.5’W, 25-40 m, Bouchet, Gofas, Lozouet! (three pairs with tissue MNHN uncatalogued); Thailand, Phuket, reef flat in front of Phuket Marine Biological Center (one pair with tissue AMNH TBD).

Arcopsis solida (Sowerby, 1833)

Panama, Isla Venado (four pairs with tissue AMNH 301785); Costa Rica, Puntarenas, no protegida, Isla Golfo de san Lucas, Playa Manzanillo, 09º56'03.4990"N, 084º54'52.7660"W, <2 m, M. Calderon! (ten pairs with tissue UCR-INBIO 0001497272); Panama, Panama City, Paitilla Beach, east side of Paitilla Point, Stn. 25, rocky intertidal with pools and sand gutters (three pairs with tissue USNM 733210). Principal literature source: Heath, 1941.

Sheldonella repenta (Iredale, 1939)

Type material examined: *Didimacar repenta* Iredale, 1939 — Holotype one pair AMS C60310.

Additional material examined: Australia, Queensland, Keppel Bay, Yeppoon, 28º08.00'S, 150º44.00'E (two pairs dried shells AMS C.433589); Australia, Northern Territory. Darwin, Lee point, 12º20.00'S, 130º54.00'E, semi-exposed to semi-sheltered rocky reef (11 pairs with tissue AMS C.440826).

Striarca interplicata (Grabau & King, 1928)

Japan, off Hondo, south coast, Sta. 3723, 12-15 fms (one pair with dried tissue USNM 204544).

Striarca sp. MNHN101

No data (one pair with dried tissue MNHN uncatalogued).

Stenocista gambiensis (Reeve, 1844)

Senegal, S-Casamance, au Sud du Cap Skirring, 3-5 m, fine sand (45 pairs with dried tissue, one figured specimen in Oliver and von Cosel, 1992, Bull. Mus. natl. Hist. nat., Paris, vol. 14, 655-691, MNHN uncatalogued).

Principal literature source: Oliver and von Cosel, 1992.

GLYCYMERIDIDAE

Axinactis inaequalis (Sowerby, 1833)

Type material examined: *Pectunculus inaequalis* Sowerby, 1833 — Syntypes one pair BMNH 1953.4.20.17/1, Bay of Panama, figured specimen in Reeve, 1844, Conch. Icon. Vol. 1, pl. IV, sp. 16.

Additional material examined: Locality unknown (three pairs, dried shells AMNH 51503); West Colombia (five pairs, shells only AMNH 28760); Ecuador, Guayaquil (three pairs, shells only AMNH 28761); Ecuador, Guayaquil Province, Santa Elena Peninsula, Colombia University Expedition (rv AMNH 136892).

Glycymeris americana (DeFrance, 1829)

U.S.A., off North Carolina, 33º32.12’N, 077º24.30’W, Sta. MS04, C-V dredge, 29 m (one pair with tissue USNM 847902); U.S.A., Gulf of Mexico, off Florida, 26º45.42’N, 084º00.08’W, Sta. 05, Unseld Spade Corer, 89.8 m (one pair with tissue, juvenile USNM 855308).

Principal literature source: Heath, 1941.

Glycymeris crebreliratus (Sowerby, 1889)

Australia, Queensland, Mackay, 21º07.000’S, 149º14.000’E, 11 m (one pair with dried tissue AMS C.433587); Australia, Queensland, Moreton Bay, between Yellow Beacon and Pat’s Pt., 27º33.000’S, 153º20.000’E, 10 m (seven pairs with tissue AMS C.169087).

Glycymeris formosus (Reeve, 1843)

Cape Verde Islands, São Vincente, São Pedro (two valves with tissue AMNH TBD); Cape Verde Ids., São Vincente, São Pedro, bycatch of fishermen dredging with “rocega” for *Strombus* IKCV-036 (two valves with tissue FMNH 306486); Cape Verde Ids., São Vincente, Mindelo, Mindelo Bay, 16º53.00’N, 25º000.00’W (two valves with tissue FMNH 306485).

Glycymeris glycymeris (Linnaeus, 1758)

No data, Granville dans les drapes des pêchours (3 pairs, dried shells MNHN uncatalogued); English Channel, South of Îles Chausey, 48º46.7’N, 01º46.7’W, 20 m (six pairs with tissue BMNH 20050270); ‘Presumably from North Sea’, served live in French restaurant in Brussels, Belgium (one pair with tissue USNM 794960).

Glycymeris grayana (Reeve, 1843)

Australia, New South Wales, Off Newcastle, 32º52-50.00’S, 151º53-57.00’E, trawled 29-33 m (three pairs with tissue, AMS C.433453).

Glycymeris holosericus (Reeve, 1843)

Australia, New South Wales, Off Newcastle, 32º54-56.00’S, 151º54-56.00’E, trawled 40-49 m (five pairs with tissue, AMS C.430762); Australia, New South Wales, Off Newcastle, 32º50-52.00’S, 151º53-57.00’E, trawled 29-33 m (four pairs with tissue, AMS C.433454).

Glycymeris lividus (Reeve, 1843)

Réunion, MD32 Stn. DC124 (seven pairs with tissue, FMNH 70129).

Glycymeris ovatus (Broderip, 1832)

Chile, Captured during a cruise of Comite Oceanografico Nacional de la Armada De Chile, 36º43’S, 73º09’W, 34 m (six pairs with tissue AMNH TBD).

Glycymeris pilosa (Linnaeus, 1758)

Red Sea (two pairs dried shells, FMNH 70129).

Glycymeris reevei (Mayer, 1868)

New Caledonia, Secteur de Koumac, Chenal de l’Infernet, Stn. 1305, 20º36.20’S, 164º11.00’E, 12-15 m (four pairs with tissue MNHN uncatalogued); New Caledonia, Lagon d’Ouvéa, Stn. 1305, 20º32.00’S, 136º24.00’E, 31 m (six pairs with tissue MNHN uncatalogued MNHN50); No data, MNHN R31/BC1485 (one pair with tissue MNHN uncatalogued, juvenile); Indonesia, West Irian, Padaido Islands, Pulau Nukori (Noekori), south side, 1º16.00’S, 136º40.00’E (three pairs with dried tissue AMS C.114509);

Philippines, Dipalian Island, Calamianes Group, Palawan (one pair, shell AMNH 107528).

Glycymeris scripta (Born, 1778)

Senegal, Dakar, left of Oceanaium, rocky littoral, Sta. IKSE-001, I. KAPPNER! (two pairs with tissue FMNH 306488).

Glycymeris striatularis (Lamarck, 1819)

Australia, New South Wales, Twofold Bay, 37º05.00'S, 149º56-56.00'E (one pair dried shell, AMS C.069137); Australia, New South Wales, E of Harrington, 31º52.29'S, 152º41.25'E, 30-40 m, regurgitated by sand flathead, *Platycephalus* (one pair with tissue, AMS C.399746).

Melaxinaea vitrea (Lamarck, 1819)

Western Australia, Dampier Archipelago, 20º31.38-72'S, 116º44.24-116º43.80'E, 16-17 m (five pairs with tissue, one pair dried BMNH 20013123); Queensland, Great Barrier Reef, Penguin Channel, 16º15.00'S, 145º31.00'E, 18-28.5 m (one pair with dried tissue AMS C.062563).

Principal literature source: Matsukuma 1980.

Tucetona flabellata (Tennison-Woods, 1877)

Southern Australia, Cape Donnington, 34º45.50'S, 135º59.00'E, 15 m (seven pairs with tissue AMS C.434467).

Principal literature source: Tschudin 2001.

Tucetona pectunculus (Linnaeus, 1758)

Australia, Queensland, Great Barrier Reef, Michaelmas Cay, 16º36.00'S, 145º59.00'E, intertidal (one pair with tissue AMS C. 434509); Queensland, Great Barrier Reef, off Lizard Is., 14º40.00'S, 145º26.00'E, 9 m (one pair with tissue AMS C.434510); Queensland, Great Barrier Reef, off Lizard Is., 14º39.00'S, 145º29.00'E, 6-17m (two pairs with tissue AMS C.434511); Queensland, Great Barrier Reef, Swain Reefs, 21º47.00'S, 152º24.00'E, 6 m (one pair with tissue AMS C.380679).

Tucetona gealei (Angas, 1873)

No data, R42/BC916 (one pair with dried tissue MNHN uncatalogued).

LIMOPSIDAE

Empleconia vaginatus (Dall, 1891)

Type material examined: ?Type — Limopsis vaginatus, Dall, 1891, USNM 122547, 1 pair, U.S.A., Alaska, N. of Unalaska, mud, sta. 3330, 351 fms.

Additional material examined: U.S.A., Off Davidson Bank stn. 3337-280 (seven pairs, one valve, dried tissue USNM 173006); Alaska, Bering Sea, off Unalashka Island, Aleutian Islands (FMNH 149986); U.S.A., Gulf of Alaska, Alaska, 53º37.00'N, -165º98.00'W, F/V "Gladiator", V.G. Smith! 466 m (one pair with tissue CAS 173006); U.S.A., Gulf of Alaska, Alaska, 53º10.00'N, -166º89.00'W, F/V "Gladiator", benthic,

V.G. Smith! (three pairs with tissue CAS 172925); U.S.A., Alaska, Aleutian Islands, Fox Islands, Sanak Bank, 54º09.00'N, -161º70.00'W, F/V "Gladiator", V.G. Smith! 249 m (one pair, one right valve with tissue CAS 172907); U.S.A., Alaska, vicinity of Aleutian Islands, 53º07.02'N, -166º59.12'W, F/V "Vesteraalen", 249 m (one pair with tissue CAS 119152).

Limopsis aurita (Brocchi, 1814)

Celtic Sea, 50º45.500'N, 07º43.100'W, 106 m, dredged small agassiz trawl stn. 75 sea area S40 (three pairs dried tissue BMNH 20031463); Norwegian Fjords, Sogne Fjords, R.V. Sarsia Cruise to the Norwegian Fjords No. NS4 (nine pairs with tissue BMNH 20050264).

Principal literature source: Oliver and Allen, 1980; Oliver, 1981.

Limopsis diegensis (Dall, 1814)

Type material examined: ?Type — Limopsis diegenis, Dall, 1814, USNM 122585, 3 pairs, Off San Diego, California.

Additional material examined: U.S.A., California, off San Diego, stn. 2923, 822 fms, in mud (36 pairs dried tissue USNM 111422); U.S.A., California, off San Diego, 80 fms (3 pairs dried tissue FMNH 149970).

Principal literature source: Oliver, 1981

Limopsis forteradiata Cotton, 1930

Australia, southern Australia, 50 miles south of Cape Wiles 35º39’S, 136º40-50’E (one pair dried tissue AMS C.304567); Australia, southern Australia, Nuyts Archipelago between St. Francis and Smooth Ids, 32º29.500’S, 133º19.000’E, 20-30 m, dredged (two pairs with tissue AMS C.102096).

Limopsis loringi (Angas, 1873)

Australia, New South Wales, off Tweed Heads, 28º17.000’S, 153º44.000’E, 73 m coarse sand and ‘beach rock’, HMAS ‘Kimbla’ (nine pairs with tissue AMS C.117642); Australia, New South Wales, off Hastings Point, 28º20.400’S, 153º47.100’E, 82 m, MV ‘San Pedro Strait’ dredged (one pair with tissue AMS C.433626); Australia, New South Wales, 18 km east of Ballina, 28º49.800’S, 153º47.800’E, 92 m MV ‘San Pedro Strait’ dredged (one pair with tissue AMS C.433627); Australia, Queensland, off Moreton Bay, 27º31.000’S, 153º40.000’E, 75-80 m, HMAS ‘Kimbla’ (one pair with tissue AMS C.393130).

Limopsis marionensis (Smith, 1885)

Antarctic Ocean, Scotia Sea, S.E. of South Orkney Islands (Stn. 121), 61º47”00’S, 043º40”00’W, 616-642 m, blake trawl (five pairs with tissue USNM 881700); Antarctic Ocean, South Shetland Islands, 60º59-57”00’S, 055º55-45”00’W, 214-219 m, bottom trawl (one pair with tissue USNM 901812); Antarctic Ocean, South Shetland Islands, Aspland Island, N.W. of Island, 61º17-10”00’S, 056º26-285”00’W, 421-462 m, bongo

net/bottom trawl (one pair with tissue USNM 901818); Chile, Fiordas sur de Chile, (Stn. 6), 44º01' S., 73º23' W, 230 m, Agassiz trawl (two pairs with AMNH TBD).

Principal literature source: Burne, 1920; Oliver, 1981.

Limopsis soboles (Iredale, 1931)

Australia, New South Wales, Sydney, N.E. of Port Hacking, Gunnamatta Bay, 34º02.500’S, 151º20.000’E, 128 m ‘Derwent Hunter’, trawled (one pair dried tissue AMS C.124194); Australia, New South Wales, Off Coffs Harbour, 30º36-39.000’S, 153º18-19.000’E, FRV ‘Kapala’, trawled (with tissue AMS C.393755).

Limopsis tenisoni (Tenison-Woods, 1879)

Australia, southern Australia, St. Francis Island, 32º29.000’S, 133º18.000’E, 20 m dredged (four pairs with tissue AMS C.440874); Australia, southern Australia, 32º18.000’S, 133º50.000’E, 40 m dredged (one pair dried tissue AMS C.433588).

Limopsis woodwardi A. Adams, 1863

Australia, Queensland, Off Tin Can Bay, 25º49.000’S, 153º13.000’E, 46 m, trawled (one pair dried shell AMS C.418471); Indonesia, Iles Tanimbar, N.O. ‘Baruna Jaya’ Karubar, Stn. CP87, 1017-1024 m (seven pairs with tissue, two pairs MNHN uncatalogued MN32.).

PHILOBRYIDAE

Adacnarca limopsoides (Thiele, 1912)

Antarctica, Antarctic Peninsula, South Shetland Islands, Deception Island, 62º56.9'S, 060º50.10'W, Stn. 465, RV 'Hero', 154 m (one pair with tissue USNM 886828); Antarctica, Antarctic Peninsula, northeast of Joinville Island, 62º40'S, 054º45'W, Stn. 465, RV 'Eltanin', 210-220 m (one pair with tissue USNM 886431).

Adacnarca nitens (Pelseneer, 1903)

Antarctica, Discovery Expedition, Stn. 1660, OTL net, 351 m (seven pairs with tissue BMNH 196599W); Antarctica, Discovery Expedition, Stn. 123, OTL net, 230-250 m (four pairs with tissue, one valve BMNH 196585W); Antarctica, Discovery Expedition, Stn. 1658, DRR net, 230-250 m (five pairs with tissue BMNH 196597W); South Atlantic Ocean, South Georgia Islands, 54º28'S, 037º24'W, Stn. 44, trawled, 152-162 m (six pairs with tissue USNM 882523); Antarctica, Long Peninsula Bulatnaya Bay entrance north of Davis 68º28.000'S, 078º10.000'E, 15 m, rock and silt (16 pairs with tissue AMS C.440835); Antarctica, Antarctic Peninsula, Palmer Archipelago, Anvers Island, Ryswyck Point, 64º37'00"S, 062º51'36"W, trawled, 640-670 m (>12 pairs with tissue USNM 899419).

Principal literature source: Burne, 1920.

Aupouria parvula Powell, 1937

New Zealand, off Three Kings Islands, 34º00'S, 171º55'E, HMN25 'Tui', 440 fms (one pair, dried shell USNM 655447).

Cosa costata (Bernard, 1896)

Type material examined: *Hochstetteria costata* Bernard, 1896 — Syntypes MNHN uncatalogued, New Zealand, Stewart Island.

Additional material examined: New Zealand, Bay of Plenty, off Mayor Island, 46-82 fm (25 pairs, dried tissue USNM 602646).

Principal literature sources: Bernard, 1896; Tevesz, 1977.

Cosa parallelogramma (Hedley, 1906)

New Zealand, South Island, south of Oamaru, 45º37'S, 170º58'E, Stn. 1431, otter trawl, RV 'Eltanin' (20+ pairs with tissue USNM 886489).

Cosa scabra (Hedley, 1906)

Australia, Queensland, Flat Rock, off North Stradbroke Island, 27º23.500'S, 153º33.000'E, 21-27 m, algae (two pairs with tissue AMS C.441070); Australia, Queensland, Flat Rock, off North Stradbroke Island, 27º23.500'S, 153º33.000'E, 24-30 m, algae (46 pairs with tissue AMS C.145238 D/W).

Cosa waikikia (Dall, Bartsch & Rehder, 1938)

Type material examined: *Limopsis waikikia* Dall, Bartsch & Rehder, 1938 — type? USNM 484219, Hawai'i, Oahu, off Waikiki, 25-50 fm.

Principal literature source: Dall, Bartsch & Rehder, 1938.

Cratis ohasii cf Hayami & Kase, 1993

New Caledonia, St. DW164, 255 m, N.O. 'Vauban", Musorstom 4 (two pairs with tissue MNHN uncatalogued); New Caledonia, 18º33'S, 163º13'W., St. DW164, 255 m, N.O. 'Vauban", Musorstom 4 (six pairs with tissue MNHN uncatalogued).

Lissarca notorcadensis Melville & Standen, 1907

South Atlantic Ocean, Scotia Sea, Georgia Island, 53º58'S, 038º25'W, Stn. 22, 136-142 m, trawled (45+ pairs with tissue USNM 897783); South Atlantic Ocean, Scotia Sea, Georgia Island, 53º47'S, 038º47'W, Stn. 117, 246-260 m, trawled (38+ pairs with tissue USNM 897785).

Principal literature source: Burne, 1920.

Lissarca picta (Hedley, 1899)

Australia, New South Wales, Sydney, Sydney Harbour (fours pairs, dried shells USNM 162148); Australia, New South Wales, Port Stephens, 32º42'S, 152º05'E (20+ pairs dried shells AMS C.047111); Australia, New South Wales, Sydney, 5 km east of Long Reef (Long Pt.), 33º45.000'S, 152º19.000'E, 39 m, rocky bottom (one pair with tissue AMS

C.433629); Australia, New South Wales, Sydney, Clovelly, 33º55.000’S, 151º15.000’E, 10 m, algae on rocky reef terrace, N. Coleman! (20+ pairs with tissue AMS C.441063).

Lissarca rubrofusca (Smith, 1877)

Antarctic, Melchior Archipelago, British Graham Land Expedition (31 pairs with tissue BMNH 1938.5.19.57-76); Indian Ocean, Stn. 5042, RV ‘Eltanin’, 210-234 m (four pairs with tissue USNM 886657).

Micromytilus crenulatifera (Tate, 1892)

Australia, Victoria, moonlight Beach, W. of Cape Otway, 38º44.000’S, 143º12.000’E, on rock platforms (~ten pairs with tissue AMS C.441075 D/W); Australia, South Australia, Middle Point, 600 m offshore, near Cape Northumberland, 38º3.000’S, 140º37.000’E, on algae (~ ten pairs with tissue AMS C.441071 D/W); Australia, South Australia, Kangaroo Island, 36º02.000’S, 136º51.000’E, on *Caulerpa* in rock pool on exposed rock platform (two pairs with tissue AMS C.441072).

Neocardia sp. A

New Zealand, Campbell Island, mouth of small cove east of Limestone Pt., Northwest Bay, 52º33.000’S, 169º04.000’E, 8 m (four pairs with tissue AMS C.441068); Argentina, Tierra Del Fuego, Isla del los Estados, west side Bahia Buen Suceso, RV ‘Hero’, 54º47’48”S, 065º16’E, Stn. 71-2-8 (25+ pairs with tissue USNM 88111); Argentina, Tierra Del Fuego, Isla del los Estados, Bahia Crossley, RV ‘Hero’, 54º46’12”S, 064º42’42”E, Stn. 71-2-16 (10+ pairs with tissue USNM 88101); Argentina, Tierra Del

Fuego, Isla del los Estados, two miles west of Puerto Basil Hall, RV ‘Hero’, 54º43’05”S, 064º13’36”E, Stn. 71-2-41 (25+ pairs with tissue USNM 88111).

Notomytilus rubra (Hedley, 1904)

Australia, Tasmania, Bruny Island, Fluted Cape, 43º22.000’S, 147º22.000’E, 13-15 m, algae under *Macrocystis* at base of cliff (>20 pairs with tissue AMS C.441067).

Philobrya munita (Finlay, 1930)

New Zealand, Hauraki Gulf, Tiritiri Matang Island (16 pairs with tissue USNM 679933). Principal literature source: Morton, 1978.

Philobrya sp. USNM

South Atlantic Ocean, Scotia Sea, South Georgia Islands, 54º39’S, 035º49’W, (one pair with tissue (USNM 881314).

Philobrya sublaevis (Pelseneer, 1903)

South Atlantic Ocean, Scotia Sea, South Georgia Islands, 53º57’S, 036º06’W, (one pair with tissue (USNM 882492).

Philobrya setosa (Carpenter, 1865)

Type material examined: *Bryophila setosa* Carpenter, 1865 — Syntypes (#) USNM 16187, Mexico, Baja California, Cape St. Lucas.

Additional material examined: U.S.A., California, Channel Islands, Catalina Island, 33º25’70’N, 118º30’70”W, mid-intertidal (one pair with tissue USNM 802720); U.S.A., California, Channel Islands, Catalina Island, North Point Fisherman’s Cove, 33º26’47’N, 118º29’04”W, mid-intertidal (two pairs with tissue USNM 802648).

OUTGROUP TAXA

MYTILIDAE

Brachidontes domingensis (Lamarck, 1819)

Puerto Rico, Phosphorescent Bay, 17º58.162’N, 067º00.928’W, attached to mangrove roots, 2-4 ft, Crowley! (six pairs with tissue AMNH accession PR-28); Puerto Rico, Isla Cueva, 17º57.51’N, 067º04.50’W, attached to coral/rocks, ~3 m, Crowley! (five pairs with tissue PR-27E/F AMNH accession); Puerto Rico, Cayo Enrique, 17º57.478’N, 067º02.525’W, in sand, 2-4 ft, Crowley! (two pairs with tissue PR-26 accession).

Lithophaga aristata

Costa Rica, Puntarenas, Marino Ballena, Punta Utiva, intertidal, Crowley! (one pair with tissue INBIO 0003572364 incorrect label); U.S.A., Texas, 66 mi. south of Freeport, on oil platform #480, at 160 ft contour, 28º13’N, 94º40’W, 80-90 ft (four pairs with tissue AMNH 315590); Angola, West Africa, Lobito Bay (> ten pairs with tissue AMNH 3269).

Principal literature source: Morton, 1993.

Mytilus edulis Linnaeus, 1758

U.S.A., New York, Queens County, three miles off Rockaway Beach, R/V "Atlantic Twin" (one pair with tissue AMNH 269978); U.S.A, Connecticut, New Haven (nine pairs with tissue AMNH 269658).

Principal literature source: Trueman, 1950.

PINNIDAE

Atrina rigida (Lightfoot, 1786)

U.S.A., Florida, Florida Keys, Monroe County, Lower Matecombe Key, 24º51' 24"N, 80º43'40"W, FK-179, The Billboard site, oceanside, MM 74.5, beach, huge *Thalassia* seagrass droves, 1 - 3 ft., washed ashore Mikkelsen! (one pair with tissue AMNH 298908).

Principal literature source: Grave, 1911

Pinna carnea Gmelin, 1791

U.S.A., Florida, Florida Keys, Monroe County, American Shoals, NW of lighthouse, 24º31' 54"N, 81º31'26"W, *Thalassia* seagrass with large coral, 2.7-3.3 m, Mikkelsen! (four pairs with tissue AMNH 298969); Puerto Rico, Cayo Enrique, 17º57.478'N, 067º02.525'W, in sand, 2-4 ft, Crowley! (one pair with tissue PR-25 accession); Puerto Rico, La Parguera, in sand, 2-4 ft (two pairs with tissue PR-24 accession).

Principal literature source: Yonge, 1953.

ISOGNOMONIDAE

Isognomon alatus (Gmelin, 1791)

Puerto Rico, Mouth of Phosphorescent Bay 17º58.162'N, 067º00.928'W, attached to red mangrove roots, 2-4 ft (six pairs with tissue PR-44 AMNH accession); Puerto Rico, Mouth of Phosphorescent Bay 17º58.162'N, 067º00.928'W, attached to rocks, 2-4 ft (13 pairs with tissue PR-34 AMNH accession); U.S.A., Florida, Monroe County, off Key Colony Beach, MM 54, FK-120, seawall at rental house, 24º44.6'N., 81º01.0'W, Mikkelsen & Bieler! (six pairs and one valve with tissue AMNH 298026).

Principal literature sources: Yonge, 1968; Tëmkin, 2006.

MALLEIDAE

Malleus candeanus (d'Orbigny, 1842)

U.S.A., Florida, Monroe County, off Key Vaca, outer patches south of Hawk Channel, oceanside, MM-50, FK-131, 24º39.30'N, 81º01.30'W, 6.4 m rubble/gorgonians/sponges, (one pair with tissue AMNH 298035); Puerto Rico, Cayo Enrique, 17º57.033'N, 067º03.192'W, in coral/rocks, 2-4 ft (seven pairs with tissue PR-31 AMNH accession); Puerto Rico, Culebra, Puerto de Culebra, attached to coral/rocks (two pairs with tissue PR-32 AMNH accession).

Principal literature source: Yonge, 1968.

PTERIIDAE

Pinctada mazatlantica (Linnaeus, 1758)

Costa Rica, Puntarenas, P.N. Marino Ballena, Punta Utiva, 09º08’50.9650”N, 083º45’47.1900”W, 0-1 m, Valdés! (one pair with tissue INBIO 0003572347); Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, Bajo del Diablo, 08º42’53.9107”N, 83º54’07.3237”W, 22 m, Gosliner! (one pair with tissue INBIO 0003572328); Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, Bajo del Diablo, 08º42’53.9107”N, 83º54’07.3237”W, 22 m, Gosliner! (one pair, dried shell INBIO 0003572325); Costa Rica, Puntarenas, P.N. Marino Ballena, Punta Utiva, 09º08’50.9650”N, 083º45’47.1900”W, 0-1 m, Valdés! (one pair with tissue INBIO 0003572357.

Principal literature source: Tëmkin, 2006.

Pteria colymbus Röding, 1798

Puerto Rico, Mata la Gata, 17º57.642’N, 067º02.366’W, 2-3 ft, Crowley! (one pair with tissue, juvenile AMNH accession PR-37); U.S.A., Florida, Monroe County, FK-601 (one pair with tissue AMNH 305038); Haiti, Port-au-Prince, southwest side of Grand Banc, on Gorgonians, 2-5 ft (three pairs with tissue AMNH 177642).

Principal literature source: Tëmkin, 2006.

LIMIDAE

Lima lima (Linnaeus, 1758)

Spain, Girona, Tossa de Mar, under stones, 9 m, Giribet! (one pair with tissue AMNH 232694); Spain, Girona, Roses, under stones, 8 m, Giribet! (three pair with tissue AMNH –01 accession).

Principal literature source: Stuardo, 1968.

Ctenoides scaber (Born, 1778)

U.S.A., Florida, Monroe County, Channel marker 50A off Ramrod Key, Oceanside, FK-047, 24º35.80'N., 81º27.24'W, rubble and patch reef, 15 ft (four pairs with tissue AMNH 232699); U.S.A., Florida, Monroe County, Channel marker 50A off Ramrod Key, Oceanside, FK-069, 24º35.80'N., 81º27.24'W, rubble and patch reef, 5.5 m (five pairs with tissue AMNH 232697); Puerto Rico, Isla Cueva, 17º57.51'N, 067º04.50'W, in coral/rocks, ~3 m (one pair with tissue PR-18 AMNH accession).

Principal literature source: Stuardo, 1968.

GRYPHAEIDAE

Hyotissa hyotis (Linnaeus, 1758)

Hong Kong, Lamma Island, Sham Wam, underside of rock ledge, 12 ft (three pairs with tissue AMNH 315862); Costa Rica, Puntarenas, R.B. Isla del Caño, Isla del Cao, Bajo del Diablo, 08º42'53.9107"N, 83º54'07.3237"W, 22 m, Gosliner! (one pair with tissue INBIO 0003572329); Japan, Amami Islands (one pair, dried shell AMNH 222283); Kenya, Shimoni (one pair, dried shell AMNH 249991).

ANOMIIDAE

Anomia simplex d'Orbigny, 1842

U.S.A., New York, Suffolk County, on beach at Morton State Park, Hampton Bays, Long Island (> 50 pairs AMNH 175691); U.S.A., Florida, Bay County, Gulf of Mexico, Panama City, Boyko & Sage! (six pairs with tissue AMNH 266966).

Principal literature source: Yonge, 1977.

APPENDIX 2. Data matrix of morphological characters scored for each of the taxa used in this analysis. Characters used in the shell only' analysis are highlighted in a blue bold font. The characters have been divided into blocks of 10 for ease of reading.

Hyotissa hyotis	**1 1 0 0 0 1 0 0 0 -**	**- 0 0 0 0 1 0 0 0 2**	**0 0 0 0 0 0 1 0 3 1**	**? 0 0 ? 1 0 0 0 1 0**	**0 0 - 0 0 0 - 2 2 3**
	- - - - - 0 1 1 0 2 0	**-** 2 - - - - - - - - -	- - - 0 **2 0 0 1 - 0**	**0 1** 0 1 0 1 1 1 0 1	0 1 1 0 0 1 0 - 1 1
	0 1 0 1 0 0 1 ? 0 ?	1 1 0 0 1 1 0 0 0 0	0 0 1 2 0 0 0 0 0 0	0 1 0 2 ? ? 0 0 0 ?	?
Lithophaga aristata	**1 0 0 0 0 0 1 1 0 -**	**- 0 0 0 0 1 0 0 0 0**	**- - 0 0 0 0 0 0 0 0**	**1 0 0 1 0 0 0 0 0 0**	**0 0 0 0 1 1 - 2 2 3**
	- - - - - 1 1 0 0 0 2	**-** 0 1 0 **1 0 0 0** 0 1	0 0 0 0 **1 0 0 0 1 0**	**1 1** 0 2 0 1 0 0 0 2	0 1 0 0 0 0 1 0 0 1
	1 1 0 0 - - 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 1 1 0 0 0 0 0	0 1 1 0 0 1 0 0 0 1	0
Brachidontes domingensis	**0 1 0 0 0 1 1 1 0 -**	**- 0 0 0 0 1 0 0 0 1**	**1 0 0 0 1 0 0 0 3 0**	**1 0 0 1 0 0 0 1 0 1**	**0 0 0 0 1 1 - 2 2 3**
	- - - - - 1 1 0 0 0 2	**-** 0 1 0 **1 0 0 1** 0 1	0 0 1 0 **1 0 0 0 1 0**	**1 0** 0 1 0 1 0 2 0 1	0 1 0 0 0 0 1 0 0 1
	1 1 0 1 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 0 1 1 1 0 0 0 0 0	0 1 1 0 0 1 1 0 0 1	0
Mytilus edulis	**1 1 0 0 0 1 1 1 0 -**	**- 0 0 0 0 1 0 0 0 0**	**- - 0 0 0 0 0 0 0 0**	**1 0 0 1 0 0 0 0 0 0**	**0 0 0 0 1 1 - 2 2 3**
	- - - - - 1 1 0 0 0 2	**-** 0 1 0 **1 0 0 1** 0 1	0 0 0 0 **1 0 0 0 1 0**	**1 0** 2 0 0 1 2 - 0 1	0 1 0 0 0 0 1 0 0 2
	1 1 0 0 - - 0 1 0 0	0 0 0 0 0 1 0 0 0 0	0 0 1 1 1 0 0 0 0 0	0 1 0 0 0 1 1 0 0 1	0
Pinna carnea	**1 1 0 0 0 0 0 1 0 -**	**- 0 0 1 0 1 0 0 0 2**	**0 0 0 0 0 0 0 0 0 1**	**1 0 0 2 0 0 2 0 0 0**	**0 0 0 0 1 0 - 2 2 3**
	- - - - - 0 1 0 0 0 2	**-** 0 0 0 **1 0 0 1** 0 1	0 1 0 1 **1 0 1 0 1 0**	**1 -** 0 1 0 0 0 1 0 0	1 1 1 0 0 2 0 - 1 2
	0 1 0 0 - - 0 1 0 1	2 0 0 0 1 1 0 1 0 1	0 1 1 1 0 0 1 1 0 0	0 1 1 1 1 0 0 0 1 1	0
Atrina rigida	**1 1 0 0 0 0 0 1 0 -**	**- 0 0 1 0 1 0 0 0 2**	**0 0 0 0 0 0 0 0 0 1**	**1 0 0 2 0 0 0 0 0 0**	**0 0 0 0 1 0 - 2 2 3**
	- - - - - 0 1 0 0 0 2	**-** 0 0 0 **1 0 0 1** 0 1	0 1 0 1 **1 0 1 0 1 0**	**1 -** 0 1 0 1 0 0 0 0	1 1 1 0 0 2 0 - 1 2
	0 1 0 0 - - 0 1 0 1	2 0 0 0 1 1 1 1 0 1	0 1 1 4 0 0 1 0 0 0	0 1 1 1 1 0 0 0 0 1	0
Isognomon alatus	**1 0 0 0 0 1 1 1 0 -**	**- 1 0 1 0 1 0 0 0 0**	**- - 0 0 0 0 1 0 3 0**	**1 0 0 1 0 0 0 0 0 0**	**0 0 - 0 0 0 - 1 1 3**
	- - - - - 0 1 1 1 0 0	**-** 0 1 0 **1 0 0 1** 0 1	0 0 0 0 **2 0 1 0 -** 0	**0 1** 1 1 0 0 1 1 0 0	0 0 1 1 0 0 1 1 0 3
	1 0 0 1 0 0 1 ? 0 1	1 0 0 0 1 1 0 0 0 0	0 1 1 2 1 0 1 1 0 0	0 1 1 1 1 ? 1 0 0 1	0
Malleus candeanus	**1 1 0 0 0 0 0 1 0 -**	**- 1 0 1 0 1 0 0 0 0**	**- - 0 0 0 0 1 0 3 0**	**1 0 0 2 1 0 0 0 0 0**	**0 0 - 0 0 0 - 2 1 3**
	- - - - - 0 1 1 0 2 0	**-** 1 2 1 **1 0 2 1** 0 1	0 0 0 0 **2 0 1 0 -** 0	**1 1** 1 1 0 0 1 1 0 0	0 1 1 1 0 0 1 1 0 4
	0 0 0 1 0 0 1 2 0 1	1 0 0 0 ? 1 0 0 0 0	0 1 0 1 1 0 1 1 0 0	0 1 1 1 0 0 1 1 0 1	0
Pinctada mazatlantica	**1 0 0 0 0 1 1 1 0 -**	**- 1 1 1 0 1 0 0 0 0**	**- - 0 0 0 0 1 0 3 0**	**1 0 0 1 0 0 0 0 0 0**	**0 0 - 0 0 0 - 2 2 3**
	- - - - - 0 1 1 0 0 0	**-** 0 1 0 **1 0 0 1** 0 1	1 1 0 0 **2 0 1 0 -** 0	**1 1** 0 1 0 1 2 2 0 0	0 1 1 0 0 1 1 1 1 4
	0 1 0 1 0 0 1 ? 0 1	1 1 0 0 1 1 0 0 0 0	0 0 1 $ 1 0 1 1 0 0	2 1 1 1 0 ? 0 0 0 1	0
Pteria colymbus	**1 0 0 0 0 1 1 1 0 -**	**- 1 0 1 0 1 0 0 0 0**	**- - 0 0 0 0 1 0 $ 0**	**1 0 0 1 1 0 0 0 0 0**	**0 0 - 0 0 0 - 1 1 3**
	- - - - - 0 1 1 0 0 0	**-** 0 1 1 **1 1 2 1** 0 1	1 1 0 0 **2 0 0 0 -** 0	**1 1** 1 1 0 1 1 2 0 0	0 1 1 0 0 1 0 0 1 4
	0 1 0 1 0 0 1 ? 0 1	1 0 0 0 1 1 0 0 0 0	0 0 1 3 1 0 1 1 0 0	0 1 0 1 0 ? 1 0 0 1	0

Anomia simplex	1 0 1 1 0 1 0 0 0 -	- 1 0 1 0 1 0 0 0 0	- - 0 0 0 0 0 0 $ 0	1 0 0 1 1 0 0 0 0 0	0 0 - 0 0 1 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 2 0 1 2 2 1 1 1	- 1 0 0 2 0 0 0 - 0	0 1 0 1 0 0 1 0 0 0	0 0 * 0 0 0 0 - 0 0
	1 0 0 0 - - * 0 1 1	2 1 0 0 1 1 0 1 0 0	0 0 1 0 0 0 1 0 0 0	1 1 ? ? ? ? 1 0 0 1	0
Ctenoides scaber	1 0 1 1 0 1 0 0 0 -	- 0 0 1 0 1 0 0 0 1	0 0 1 0 1 0 0 0 0 0	0 0 0 1 1 0 0 0 1 0	0 0 - 0 0 0 1 2 2 0
	1 1 0 0 0 1 1 0 2 0	- 0 1 0 1 0 0 1 0 0	0 0 0 0 2 0 0 0 - 1	0 1 1 1 0 0 0 1 0 0	0 0 0 0 0 2 0 - 1 1
	1 0 0 1 0 0 0 ? 0 1	1 1 0 0 0 1 0 2 0 0	0 0 2 6 0 0 0 0 0 1	1 1 1 0 0 ? 0 0 0 1	0
Lima lima	1 0 1 1 0 1 0 0 0 -	- 0 0 0 0 1 0 0 0 2	0 0 0 0 0 0 0 0 4 1	1 0 0 0 1 0 0 0 1 0	0 0 - 0 0 0 1 2 2 0
	1 1 0 0 0 1 1 0 2 0	- 0 1 0 1 0 0 1 0 1	0 0 0 0 0 0 0 0 - 1	1 1 1 1 0 0 1 0 0 0	0 0 0 0 0 2 0 - 1 1
	1 0 0 1 0 0 0 ? 0 1	0 0 0 0 0 1 0 0 0 0	? 0 2 6 0 0 1 0 0 1	0 1 1 0 0 ? 0 0 0 1	0
Arca noae	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 0 1 0 2	1 1 1 0 1 0 1 0 1 0	1 0 0 $ 1 0 2 2 1 1	0 0 0 0 0 0 1 0 0 3
	- 0 1 1 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 1 1 0	0 1 2 0 0 1 0 0 0 0	0 1 1 1 0 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 0 0 0	0 0 1 1 1 0 0 1 0 2	- 1 0 0 0 0 0 0 1 1	0
Arca navicularis	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 1 0 2	0 0 1 0 1 0 1 0 1 0	1 0 0 1 1 0 2 2 1 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 * 1 0	0 1 2 0 0 1 0 0 0 0	0 1 1 1 0 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 2 0 0	0 0 1 5 1 0 0 1 0 2	- 1 0 0 0 0 0 0 1 0	0
Arca zebra	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 1 0 2	0 0 1 0 1 0 1 0 1 0	1 0 0 1 1 0 2 1 1 1	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 * 1 0	0 1 2 0 0 1 0 0 0 0	0 1 1 1 0 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 2 0 0	0 0 1 5 0 0 1 0 0 2	- 1 0 0 0 0 0 0 1 0	0
Arca imbricata	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 1 0 1	0 0 1 0 1 0 1 0 3 0	1 0 0 1 1 0 2 1 1 2	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 1 1 0	0 1 2 0 0 1 0 0 0 0	0 0 1 1 0 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 0 0 0	0 0 1 1 0 0 1 0 0 2	- 1 0 0 0 0 1 0 1 1	0
Arca avellana	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 1 0 1	0 1 0 0 1 0 1 0 3 0	1 0 0 1 1 0 2 2 1 2	0 0 1 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 1 1 2 1 0 1	0 1 1 0 1 0 0 1 1 0	0 1 2 0 0 1 0 0 0 0	0 0 1 1 0 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 0 0 0	0 0 1 1 0 0 1 1 0 2	- 1 0 0 0 0 0 0 1 1	0
Arca mutabilis	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 0 0 0 1	0 0 1 0 1 0 1 0 3 0	1 0 0 1 1 0 2 1 1 2	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 1 1 2 1 0 1	0 1 0 0 1 0 0 * 1 1	0 1 2 0 0 1 0 0 0 0	0 1 0 0 0 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 0 0 0	0 0 1 1 1 0 1 0 0 2	- 1 1 0 0 0 1 1 1 1	0
Arca bouveiri	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 1 0 2	0 0 1 0 1 0 1 0 1 0	1 0 0 1 1 0 2 1 1 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 1 1 0	0 1 2 0 0 1 0 0 0 0	0 0 1 1 0 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 2 0 0	0 0 1 5 1 0 1 0 0 2	- 1 0 0 0 0 1 0 1 1	0
Arca ventricosa	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 1 0 1	0 1 0 0 1 0 1 0 3 0	1 0 0 1 1 0 2 1 1 2	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 1 1 0	0 1 1 0 0 1 0 0 0 0	0 1 1 0 0 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 1 0 1 1 0 2 0 1	0 0 1 5 0 0 1 0 0 2	- 1 1 0 0 0 0 0 1 1	0

Barbatia barbata	0 1 1 1 1 1 0 0 1 2	2 0 1 0 0 1 0 0 0 1	1 1 0 0 1 0 1 0 3 0	1 0 0 1 1 0 1 1 1 0	0 0 1 0 0 0 0 0 0 3
	- - 1 0 0 1 0 0 1 0	0 0 0 ? ? ? ? 1 0 1	0 ? ? 0 1 0 0 1 1 0	0 1 ? ? ? ? 0 0 0 0	0 ? ? ? ? 0 1 ? 0 ?
	1 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	0 ? 1 ? ? ? ? ? 0 ?	? 1 1 0 0 ? ? ? ? ?	0
Barbatia sp PR01	0 1 1 1 1 1 0 0 2 0	1 0 1 0 0 1 0 0 0 1	0 1 0 0 1 1 0 0 3 0	1 0 0 1 1 0 1 1 1 0	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 0 1 0	0 0 1 1 1 1 0 0 0 0	0 0 1 1 0 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 0 0 0	0 0 1 1 0 0 1 1 0 1	2 1 1 0 0 0 1 1 1 1	0
Barbatia cancellaria	0 1 1 1 1 1 0 0 2 0	1 0 1 0 0 1 0 0 0 1	0 1 0 0 1 1 0 0 3 0	1 0 0 1 1 0 1 1 1 0	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 0 1 0	1 1 1 1 1 1 0 0 0 0	0 1 1 1 0 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 2 0 0	0 0 1 2 0 0 1 1 0 1	1 1 1 0 0 0 0 1 1 1	0
Barbatia amygdalumtostum	0 1 1 1 1 1 0 0 2 2	1 0 1 0 0 1 0 0 0 1	1 1 0 0 1 1 0 0 2 0	1 0 0 1 1 0 1 1 1 0	0 0 1 0 0 1 1 0 0 3
	- 0 1 1 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 1 1 0	0 0 1 1 0 1 0 0 0 0	0 1 0 0 1 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 1 0 2 0 1	0 0 1 1 0 0 1 1 0 1	1 1 1 1 1 0 0 0 1 1	0
Barbatia obliquata flaky	0 1 1 1 1 1 0 0 1 0	2 0 1 0 0 1 0 0 0 1	0 0 0 0 1 0 1 0 0 0	1 0 0 1 1 0 1 1 1 0	0 0 1 0 0 0 0 0 0 3
	- - 1 0 0 1 0 0 1 0	0 0 0 0 1 1 2 1 0 1	0 1 1 0 1 0 0 0 1 0	0 1 1 1 0 1 0 0 0 0	0 1 1 1 0 0 1 0 1 0
	1 0 0 1 0 0 1 0 1 1	2 1 0 0 1 0 0 2 0 0	0 0 1 1 1 0 0 0 0 1	0 1 1 0 0 0 0 1 0 1	0
Barbatia obliquata scaly	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 0 0 0 1	0 0 0 0 1 1 0 0 0 0	1 0 0 1 1 0 1 1 0 0	0 0 0 0 0 1 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 1 1 0 1 0 1	0 1 0 0 1 0 0 * 1 0	1 1 1 1 0 1 0 0 0 0	0 1 1 1 0 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 0 0 0 0 0 0	0 0 1 1 1 0 0 1 0 1	0 1 1 0 0 0 0 1 0 1	0
Barbatia metella	0 1 1 1 1 1 0 0 2 1	1 1 1 0 0 1 1 0 0 1	1 1 0 0 1 1 0 0 0 0	1 0 0 1 1 0 1 1 1 0	0 0 0 0 0 0 1 0 0 3
	- 1 1 0 0 1 0 0 0 0	0 0 0 0 1 1 1 1 0 1	0 1 0 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 0 0 1 0 2 0 0	0 0 1 1 0 0 0 0 0 ?	? 1 1 0 0 1 0 0 0 0	0
Barbatia foliata	0 1 1 1 1 1 0 0 2 1	2 0 1 0 0 1 0 0 0 1	0 1 0 0 1 0 0 0 0 0	1 0 0 1 1 0 1 1 0 0	0 0 1 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 2 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 0 1 0	0 1 1 0 0 1 0 0 0 0	0 1 1 1 0 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 1 1 1 0 2 0 0	0 0 1 2 1 0 1 1 0 1	0 1 1 0 0 0 0 1 0 0	0
Barbatia reeveana	0 1 1 1 1 1 0 0 2 1	2 0 1 0 0 1 0 0 0 1	0 1 0 0 1 0 0 0 0 0	1 0 0 1 1 0 1 1 1 3	0 0 1 0 0 0 0 0 0 3
	- 0 1 0 0 1 0 0 2 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 0 1 0	0 1 1 0 0 1 0 0 0 0	0 1 1 1 0 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 1 0 0 2 0 0	0 1 1 2 1 0 1 0 0 1	0 1 1 0 0 0 1 1 0 1	0
Barbatia lacerata	0 1 1 1 1 1 0 0 2 0	1 0 1 0 0 1 1 0 0 1	0 0 0 0 1 1 0 0 2 0	1 0 0 1 1 0 1 1 0 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 0 0	0 0 0 1 1 ? ? 1 0 1	0 1 1 0 1 0 0 * 1 0	0 1 1 1 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 1 1 1 0 0 0 0	0 0 1 5 0 0 1 1 0 1	0 1 1 0 0 1 ? 1 0 1	0
Barbatia tenella	0 1 1 1 1 1 0 0 2 1	1 0 1 0 0 1 1 0 0 1	1 0 0 0 0 0 0 1 0 0	1 0 1 1 1 0 1 1 1 2	0 0 1 0 0 0 1 0 0 3
	- 1 1 0 0 1 0 0 0 0	0 0 0 0 0 - - 1 0 1	0 1 1 0 1 0 0 0 1 0	0 0 2 0 0 1 0 0 0 0	0 1 0 0 0 0 1 0 0 0
	1 0 0 1 1 0 0 0 1 1	2 0 0 0 1 1 0 0 0 0	0 0 1 5 1 0 1 0 0 1	0 1 1 0 0 1 0 0 0 1	0

Barbatia cf tenella	0 1 1 1 1 1 0 0 2 2	1 0 1 0 0 1 0 0 0 1	0 1 0 0 0 1 0 0 4 0	1 0 0 1 1 0 1 1 1 0	0 0 0 0 0 0 1 0 0 3
	- 1 1 0 0 1 0 0 0 0	0 0 0 0 1 1 2 1 0 1	0 1 0 0 1 0 0 0 1 0	0 0 1 1 0 1 0 0 0 0	0 0 1 0 1 0 1 1 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 1 0 1 0 2 0 0	0 0 1 1 0 0 1 1 0 1	0 1 1 0 0 0 1 1 1 0	0
Anadara antiquata	0 1 1 1 1 1 0 0 1 1	2 0 1 0 0 1 0 0 0 2	1 0 0 0 0 0 1 0 3 0	1 0 0 1 1 0 1 2 1 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 1 1 1 0 0 1	1 1 1 0 1 0 0 0 1 0	0 0 1 0 1 1 0 0 0 0	0 0 0 0 1 0 1 0 0 0
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Anadara trapezia	0 1 1 1 1 1 0 0 1 0	2 0 0 0 0 1 0 0 0 2	0 1 0 0 0 0 1 0 0 0	1 0 0 1 1 0 1 2 1 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 1 1 0 0 0 0 1	1 1 1 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 1 1 0 0 0 1 0 0 0
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Anadara granosa ss	0 1 1 1 1 1 0 0 0 -	- 0 1 0 0 1 0 0 0 2	0 1 0 0 0 0 0 0 0 0	1 0 0 1 1 0 1 1 1 3	0 0 1 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 0 - - 0 0 0	0 0 1 0 1 0 0 0 0 0	0 0 1 1 0 1 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 1 0 0 0 1 1 2 0 0	0 0 1 5 1 1 0 1 0 1	0 1 0 0 0 0 0 1 0 1	0
Anadara notabilis	0 1 1 1 1 1 0 0 2 1	1 0 1 0 0 1 0 1 0 2	0 1 0 0 0 0 1 0 0 0	1 0 0 1 1 0 1 2 1 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 0 - - 0 0 1	1 1 1 0 1 0 0 0 1 0	1 0 1 0 1 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
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Anadara geissei	0 1 1 1 1 1 0 0 2 1	1 0 1 0 0 1 1 0 0 2	1 0 0 0 0 0 0 0 0 0	1 0 0 1 1 0 1 1 0 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 1 1 0 0 0 1	0 1 1 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 1 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 0 0 1 0 $ 0 0	0 0 1 2 1 0 1 1 0 1	0 1 1 0 0 0 0 1 0 1	0
Larkinia sp AU45	0 1 1 1 1 1 0 0 0 -	- 0 1 0 0 1 0 0 0 2	0 1 0 0 0 0 0 0 0 0	1 0 0 1 1 0 2 2 1 3	0 0 1 0 0 0 1 0 0 3
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	1 0 0 1 0 0 0 0 1 1	2 1 0 0 1 1 1 2 0 0	0 0 1 5 1 1 0 1 0 1	0 1 0 0 0 0 0 0 0 1	0
Scapharca sp PNM03	0 1 1 1 1 1 0 0 2 1	1 1 0 1 0 1 0 0 0 1	0 1 0 0 0 0 0 0 0 0	1 0 0 1 1 0 1 2 1 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 0 - - 0 0 0	1 0 0 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 1 0 0 1 0 1 0 0 0
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	1 0 0 1 0 0 0 0 1 1	2 1 0 0 0 1 1 2 0 1	0 0 1 2 1 0 0 1 0 1	0 1 1 0 0 1 0 0 0 0	0
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	- 0 1 0 0 1 0 0 0 0	0 0 0 0 1 1 0 0 0 1	0 1 0 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 1 0 0 0 0 1 0 0 0
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Scapharca vellicata	0 1 1 1 1 1 0 0 1 1	2 1 1 0 0 1 1 0 0 2	1 0 0 0 0 0 1 0 0 0	1 0 0 1 1 0 2 1 1 3	0 0 1 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 0 - - 0 0 1	1 1 1 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 1 0 0 1 0 1 2 0 1	0 1 1 5 1 1 0 1 0 1	0 1 0 0 0 0 0 1 0 0	0
Scapharca inaequivalvis	0 1 1 1 1 1 0 0 2 1	1 1 1 0 0 1 1 0 0 1	0 0 0 0 0 0 0 0 0 0	1 0 0 1 1 0 1 1 0 3	0 0 0 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 0 0	0 0 0 ? 1 0 0 0 0 ?	1 ? 0 0 1 0 0 0 1 0	0 1 1 0 0 ? 0 0 0 0	0 0 0 ? 0 0 1 ? 0 ?
	1 0 ? 1 0 0 0 0 1 1	2 0 ? ? ? ? ? ? ? ?	? ? 1 ? 1 0 ? ? 0 ?	? 1 ? ? ? ? ? 0 0 ?	0
Scapharca rotundicostata cf	0 1 1 1 1 1 0 0 1 1	1 1 1 0 0 1 0 0 0 2	0 1 0 0 0 0 1 0 0 0	1 0 0 1 1 0 2 2 1 3	0 0 1 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 1 0	0 0 0 0 1 1 0 0 0 1	1 1 0 0 1 0 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 0 1 1 0 2 0 1	0 1 1 5 1 1 0 1 0 1	0 1 0 0 0 1 0 1 0 0	0
Scapharca transversa	0 1 1 1 1 1 0 0 2 1	1 1 1 0 0 1 1 0 0 1	0 1 0 0 0 0 1 0 $ 0	1 0 0 1 1 0 1 1 0 3	0 0 1 0 0 0 1 0 0 3
	- 0 1 0 0 1 0 0 0 0	0 0 0 0 0 - - 0 0 1	1 1 0 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 0 1 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 1 0 0 0 0 0 0 0 0	0 0 1 2 1 0 0 1 0 1	0 1 0 0 0 0 0 1 0 0	0
Scapharca ovalis	0 1 1 1 1 1 0 0 1 1	1 1 0 0 0 1 0 0 0 2	1 0 0 0 0 0 1 0 0 0	1 0 0 1 1 0 0 1 0 3	0 0 0 0 0 1 1 0 0 3
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Bathyarca sp A	0 1 1 1 1 0 0 0 1 0	2 1 0 0 0 1 0 0 0 0	- - 1 0 0 0 0 1 4 0	1 0 0 1 1 1 0 1 0 0	0 1 1 0 0 0 1 0 0 0
	1 1 1 0 0 1 0 0 0 0	0 0 0 0 1 0 0 1 0 1	1 1 0 0 1 0 0 0 1 0	0 - 1 0 0 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0
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	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 ? 1 0 1 0 0 0	0 1 0 0 0 1 0 0 0 0	0
Bathyarca sp Brasil	0 1 1 1 1 0 0 0 2 1	1 1 0 0 0 1 0 0 0 0	- - 0 1 0 0 0 1 4 0	1 0 0 1 1 0 0 1 1 0	0 0 0 0 0 0 1 0 0 0
	- 0 1 0 0 1 0 0 $ 0	0 0 0 0 1 0 0 0 0 1	1 0 0 0 1 0 0 0 1 0	0 - 1 0 0 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0
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Bathyarca japonica	0 1 1 1 1 0 0 0 1 1	2 1 1 0 0 1 0 0 0 1	0 0 0 0 1 1 0 0 3 0	1 0 0 1 1 0 1 2 1 0	0 0 0 0 0 0 0 0 0 3
	- - 1 0 0 1 0 0 $ 0	0 0 0 0 1 0 0 0 0 0	1 0 0 0 1 0 0 0 1 0	0 - 1 0 0 0 0 0 1 0	0 0 1 1 0 0 1 1 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 0 0 0 0 2 0 0	0 0 1 1 0 0 0 0 0 0	0 1 1 0 0 1 0 0 0 0	0
Bathyarca corpulenta	0 1 1 1 1 0 0 0 1 1	1 1 0 0 0 1 0 0 0 0	- - 0 1 0 0 0 1 4 0	1 0 0 1 1 0 0 2 0 0	0 0 0 0 0 0 1 0 0 3
	- * 1 0 0 1 0 0 0 0	0 0 0 0 1 0 0 0 0 0	1 0 1 0 1 0 0 0 ? 0	1 - 1 0 0 0 0 0 1 0	0 0 0 0 0 0 1 0 0 0
	1 0 ? 1 0 0 0 0 1 1	2 0 0 1 0 0 1 2 0 0	0 0 1 1 0 0 0 0 0 0	0 1 1 0 0 1 0 0 0 0	0
Bathyarca freilei	0 1 1 1 1 0 0 0 1 1	1 1 0 0 0 1 0 0 0 0	- - 0 1 0 0 0 1 4 0	1 0 0 1 1 0 0 1 1 0	0 0 0 0 0 0 1 0 0 1
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Bentharca asperula	0 1 1 1 1 1 0 0 2 1	1 1 1 0 0 1 1 0 0 0	- - 0 1 0 0 1 0 4 0	1 0 0 0 1 0 1 1 1 0	0 0 * 0 0 0 1 0 0 1
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	1 0 0 1 0 0 0 0 1 1	2 0 0 0 0 0 0 2 0 0	0 0 1 ? 0 0 0 0 0 1	0 1 1 0 0 1 0 0 0 0	0
Bentharca xenophoricola	0 1 1 1 1 1 0 0 2 2	2 1 1 0 0 1 1 0 0 1	1 0 0 0 0 1 0 0 4 0	1 0 0 0 1 0 1 1 1 0	0 0 1 0 0 0 1 0 0 3
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	1 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	? ? 1 ? ? ? ? ? 0 ?	? 1 ? ? ? ? ? ? ? ?	0
Bentharca nodulosa	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 0 0 0	- 1 0 0 0 0 1 0 3 0	1 0 0 1 1 0 1 0 1 0	0 0 1 0 0 0 1 0 0 3
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	- - 1 0 0 1 0 0 1 0	0 0 0 1 1 1 2 1 0 1	0 1 1 0 1 0 0 0 1 0	0 1 2 0 0 1 0 0 0 0	0 1 1 0 0 0 1 ? 0 1
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Barbatia iota	0 1 1 1 1 1 0 0 0 -	- 0 1 0 0 1 0 0 0 2	0 0 1 0 0 0 1 0 2 0	1 0 1 1 1 0 2 1 0 3	0 0 0 1 0 0 1 0 0 3
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Samacar strabo cf	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 1 0 0 0	- - 0 0 0 0 1 0 4 0	1 0 0 1 1 0 1 1 0 0	0 0 0 0 0 0 1 0 0 3
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Nipponarca bistrigata	0 1 1 1 1 1 0 0 2 0 - 0 1 0 0 1 0 0 1 0 1 0 0 1 0 0 0 0 1 1	2 0 1 0 0 1 1 0 0 2 0 0 0 0 1 1 2 1 0 1 2 1 0 0 1 1 0 2 0 0	1 1 0 0 0 1 0 0 0 0 1 1 0 0 1 0 0 0 1 0 0 0 1 5 1 1 1 0 0 1	1 0 0 1 1 0 1 1 1 3 0 0 1 0 0 1 0 0 0 0 0 1 0 0 0 1 0 1 0 0	0 0 1 0 0 0 1 0 0 3 0 1 1 0 0 0 1 0 0 0 0
Trisidos tortuosa	0 1 1 1 1 1 0 0 2 0 - 1 1 1 0 1 0 0 1 0 1 0 0 1 0 0 0 0 1 1	2 1 1 0 1 1 0 0 0 1 0 0 0 0 1 1 1 0 0 1 2 1 0 0 0 ? 0 2 0 0	0 0 0 0 1 0 1 0 4 0 1 1 0 0 1 0 0 0 1 0 0 0 1 2 1 0 0 1 0 1	1 0 0 1 1 0 2 0 0 0 1 1 1 0 0 0 0 0 0 0 0 1 1 1 0 1 0 0 0 0	0 0 1 0 0 0 1 0 0 3 0 1 0 0 0 0 1 0 0 0 0
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Scaphula celox	0 1 1 1 1 1 0 0 1 0 - 1 1 0 0 1 0 0 1 0 1 0 ? 1 ? 0 ? 0 1 1	2 0 1 0 0 1 0 0 0 0 0 0 0 ? 1 0 0 1 0 ? 2 1 ? ? ? ? ? ? ? ?	- - 0 1 0 0 0 1 0 0 1 ? ? 0 1 0 0 0 1 0 0 ? 1 ? 0 ? ? ? 0 1	1 0 0 2 1 0 2 1 1 0 0 0 ? ? 0 ? 0 0 0 0 2 1 ? ? ? 0 ? ? ? ?	0 1 1 0 0 1 1 0 0 3 0 ? ? ? ? 0 1 0 0 1 0
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Litharca lithodomus	0 1 1 1 1 1 0 0 2 0 - 0 1 0 0 1 0 0 3 0 1 0 0 1 1 0 1 0 1 1	2 0 0 0 0 1 0 0 0 1 0 0 0 0 1 0 2 1 0 1 2 1 0 0 0 0 1 2 0 0	0 0 1 0 0 0 1 0 0 0 0 1 1 0 1 0 0 0 1 0 0 0 1 1 1 0 0 1 0 1	1 0 0 2 0 0 1 1 1 0 0 1 2 0 0 1 0 0 0 0 0 1 1 0 0 0 0 1 1 1	0 0 0 0 0 0 1 0 0 3 0 1 1 0 0 0 1 0 0 0 0
Barbatia illota	0 1 1 1 1 1 0 0 2 0 - 1 1 0 0 1 0 0 0 0 1 0 0 1 1 0 0 0 1 1	2 0 1 0 0 1 1 0 0 1 0 0 0 0 1 1 2 1 0 1 2 0 0 0 1 0 0 2 0 0	0 1 0 0 1 1 0 0 4 0 1 1 1 0 1 0 0 0 1 0 0 0 1 2 ? 0 ? ? 0 1	1 0 0 1 1 0 1 1 1 0 0 0 2 1 0 1 0 0 0 0 0 1 ? ? ? ? 0 0 0 ?	0 0 0 0 0 0 1 0 0 3 0 1 0 0 0 0 1 0 0 0 0
Barbatia tenera	0 1 1 1 1 1 0 0 2 0 - 1 1 0 0 1 0 0 0 0 1 0 0 1 0 0 0 0 1 1	1 0 1 0 0 1 1 0 0 1 0 0 0 0 1 1 2 1 0 1 2 0 0 0 1 0 0 2 0 0	1 1 0 0 1 0 0 0 4 0 0 1 0 0 1 0 0 0 1 0 0 0 1 5 1 0 1 0 0 1	1 0 0 1 1 0 1 1 1 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 0 1	0 0 1 0 0 0 1 0 0 3 0 1 0 0 0 0 1 0 0 0 0
Noetia ponderosa	0 1 1 1 1 1 0 0 1 2 - - 1 0 0 1 0 0 1 1 1 0 0 1 0 0 0 0 1 1	2 0 1 0 0 1 0 0 0 2 1 0 0 0 1 1 1 0 0 0 2 1 0 0 0 0 0 0 2 0 0	1 0 0 0 0 0 1 0 0 0 1 1 0 0 1 0 0 0 1 0 0 0 1 5 1 0 0 1 0 1	1 0 0 2 1 0 2 2 1 3 0 0 1 0 0 1 0 0 0 0 1 1 1 0 0 1 0 0 0 0	0 1 0 0 0 0 0 0 0 3 0 1 1 0 0 0 1 0 0 1 0
Noetia olssoni	0 1 1 1 1 1 0 0 ? 2 - 0 1 0 0 1 0 0 1 1 ? 0 ? 1 ? ? ? 0 1 1	2 ? 1 0 0 1 0 1 0 2 1 0 0 ? ? ? ? ? 0 ? ? ? ? ? ? ? ? ? ? ?	1 1 0 0 1 0 1 0 0 0 ? ? ? ? ? ? 0 0 1 0 ? ? 1 ? ? ? ? ? 0 ?	1 0 0 2 1 0 2 1 1 1 1 0 ? ? ? ? 0 0 ? 0 ? 1 ? ? ? ? ? ? ? ?	0 1 1 0 0 0 1 0 0 3 0 ? ? ? ? 0 1 ? 0 ? 0

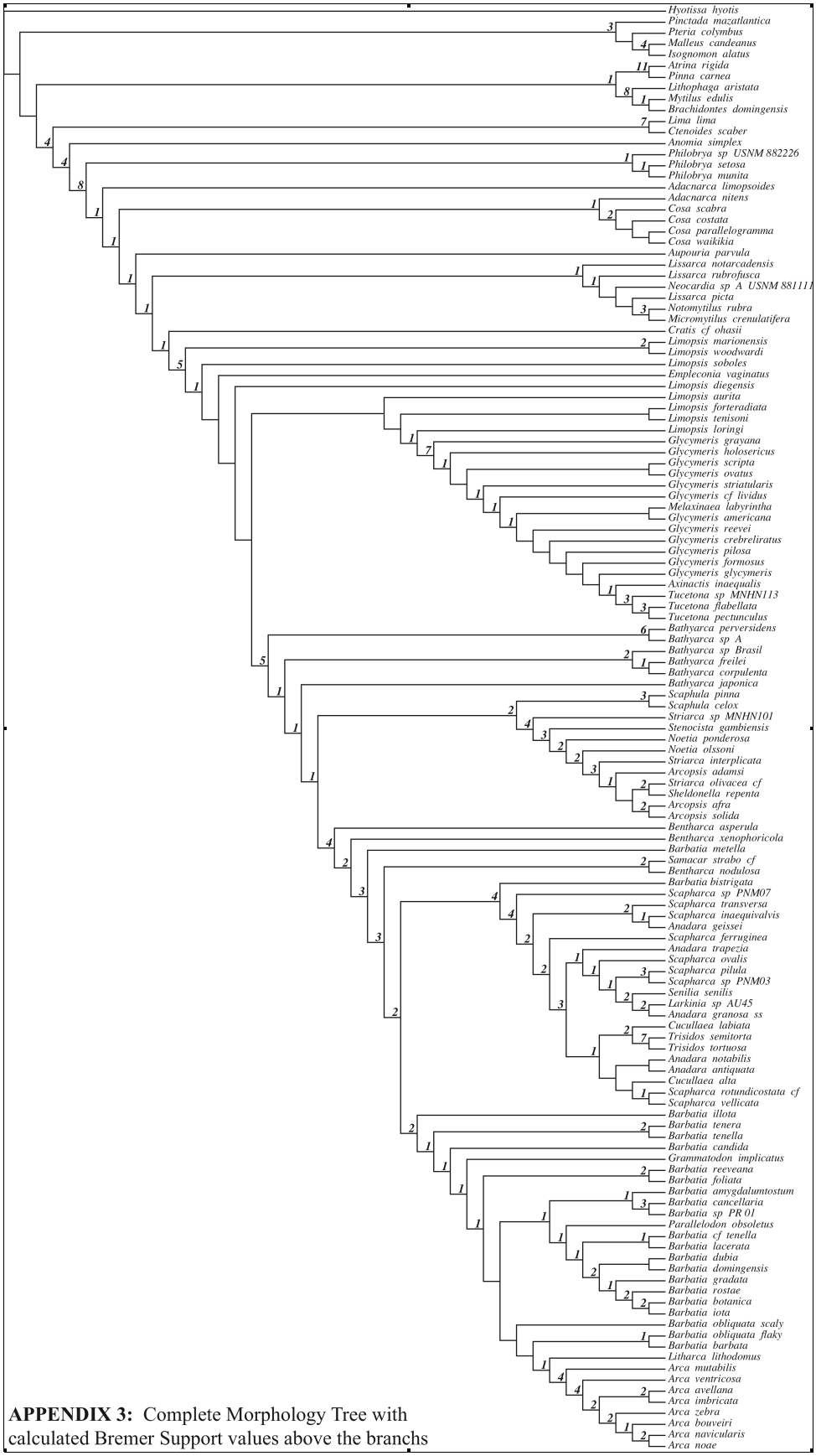
Arcopsis adamsi	0 1 1 1 1 1 0 0 1 0	2 0 1 0 0 1 0 0 0 1	0 1 0 0 1 0 1 0 0 0	1 0 0 1 1 0 2 1 1 0	0 1 1 0 0 0 1 0 0 3
	- 1 1 0 0 1 0 0 2 1	1 0 0 0 1 0 0 0 0 0	0 1 0 0 1 0 0 0 1 0	0 0 1 1 0 1 0 0 0 0	0 1 0 0 0 0 1 0 0 0
	1 0 1 1 0 0 0 0 1 1	2 1 0 0 0 0 0 0 0 0	0 0 1 5 1 0 0 0 0 1	1 1 1 0 0 1 1 1 0 1	0
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Arcopsis afra	0 1 1 1 1 1 0 0 2 0	2 0 1 0 0 1 0 0 0 1	0 1 0 0 1 1 0 0 0 0	1 0 0 1 1 0 2 1 1 0	0 1 1 0 0 0 0 0 0 3
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Sheldonella repenta	0 1 1 1 1 1 0 0 1 1	2 0 1 0 0 1 0 0 0 1	0 0 1 0 1 0 1 0 0 0	1 0 0 1 1 0 1 1 1 0	0 1 1 0 0 0 0 0 0 3
	- - 1 0 0 1 0 0 0 1	1 0 0 0 1 1 1 1 0 0 1	0 1 0 0 1 0 0 0 1 0	0 0 1 1 0 1 0 0 0 0	0 1 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 1 0 0 0 0 0 0 0 0	0 0 1 5 1 0 0 0 0 1	0 1 0 0 0 1 0 1 0 1	0
Striarca olivacea cf	0 1 1 1 1 1 0 0 1 0	2 0 1 0 0 1 0 0 0 1	0 1 0 0 1 0 1 0 0 0	1 0 0 1 1 0 1 1 1 0	0 1 1 0 0 0 0 0 0 3
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Striarca interplicata	0 1 1 1 1 1 0 0 1 0	2 0 1 0 0 1 0 0 0 1	0 1 0 0 1 0 1 0 0 0	1 0 0 0 1 0 1 1 1 3	0 1 1 0 0 0 0 0 0 3
	- - 1 0 0 1 0 0 1 1	1 0 0 0 1 1 ? 0 0 ?	? ? ? 0 1 0 0 0 1 0	0 0 1 1 0 1 0 0 0 0	0 1 0 0 0 0 1 ? 0 ?
	1 0 ? 1 0 0 0 0 1 1	2 1 0 0 ? ? 1 ? ? ?	? ? 1 ? 1 ? ? ? 0 ?	? 1 1 0 0 ? ? 1 0 ?	0
Striarca sp MNHN101	0 1 1 1 1 0 0 0 1 1	1 0 1 0 0 1 0 0 0 0	- - 0 1 0 0 1 1 0 0	1 0 0 0 1 0 1 1 1 0	0 1 0 0 0 0 0 0 0 3
	- - 1 1 0 1 0 0 1 1	1 0 0 0 0 - - 0 0 0	0 0 1 0 0 0 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 1
	1 0 0 1 0 0 0 0 1 1	2 1 0 0 0 1 0 0 0 0	0 ? 1 1 ? ? ? ? 0 1	0 1 ? ? ? ? 0 1 0 ?	0
Stenocista gambiensis	0 1 1 1 1 1 0 0 2 2	2 0 1 1 0 1 0 0 0 2	1 0 0 0 0 0 0 0 0 0	1 0 0 0 1 0 1 1 1 3	0 0 0 0 0 0 0 0 0 3
	- - 1 0 0 1 0 0 1 1	1 0 0 0 1 0 0 0 0 ?	0 0 0 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 ? 0 ? 0 0 1 ? 0 ?
	1 0 ? 1 0 0 0 0 1 1	2 1 0 0 ? ? 0 0 ? ?	0 ? 1 ? 1 ? 0 0 0 1	1 1 1 0 0 ? ? 0 0 1	0
Parallelodon obsoletus	0 1 1 1 1 1 0 0 ? ?	? 0 1 0 0 1 1 0 0 1	0 1 0 0 1 1 0 0 0 0	1 0 ? 1 1 0 1 1 1 0	0 ? ? 0 0 0 0 0 0 0
	0 - 1 0 0 1 0 0 0 0	0 0 0 ? 1 ? ? 1 ? ?	? ? ? 0 1 0 0 ? 1 ?	? ? ? ? ? ? ? ? ? ?	0 ? ? ? ? ? ? ? ? ?
	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	0
Grammatodon implicatus	0 1 1 ? 1 1 0 0 ? ?	? 0 1 0 0 1 0 1 0 1	1 ? ? 0 1 1 0 0 0 0	1 0 ? 1 1 0 1 1 0 0	0 0 0 0 0 0 1 0 0 1
	0 1 1 0 0 1 0 0 1 0	0 0 0 ? ? ? ? 0 ? ?	? ? ? 0 1 0 0 ? 1 ?	? ? ? ? ? ? ? ? ? ?	0 ? ? ? ? ? ? ? ? ?
	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	0
Cucullaea labiata	0 1 1 1 ? 1 0 0 1 1	1 1 1 0 0 1 0 0 0 1	1 0 0 0 1 0 0 1 3 0	1 0 0 1 1 0 2 2 1 0	0 2 0 0 0 0 1 0 0 0
	1 0 1 0 0 1 0 0 1 0	0 0 0 0 1 0 0 0 0 0	0 1 1 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 1 1 0 0 0 1 0 0 0
	1 0 1 1 0 0 0 0 1 1	2 1 1 1 0 1 0 2 0 1	0 1 1 2 1 0 0 1 0 1	0 1 1 0 0 0 0 0 1 0	0

Cucullaea alta	0 1 1 1 ? 1 0 0 1 ?	? 0 1 0 0 1 0 0 0 2	0 0 0 0 0 0 1 0 0 0	1 0 ? 1 1 0 1 2 1 1	0 2 1 0 0 0 ? 0 0 0
	1 ? 1 0 0 1 0 0 1 0	0 0 0 ? ? ? ? 0 ? ?	? ? ? 0 1 0 0 ? 1 ?	? ? ? ? ? ? ? ? ? ?	0 ? ? ? ? ? ? ? ? ?
	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	0
Limopsis aurita	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 0	- - 0 0 0 0 0 1 4 0	1 0 0 0 1 0 0 0 0 0	0 0 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 1 0 0 0 0 1	1 0 0 0 1 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 1 2 0 0	0 0 1 1 0 0 0 0 0 0	0 1 0 0 0 1 0 0 0 1	0
Limopsis tenisoni	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 1	0 0 0 0 1 0 1 0 4 0	1 0 0 2 1 0 0 0 0 0	0 1 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 2 - - 0 0 1	1 0 0 0 1 0 0 0 1 0	0 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 1 2 0 0	0 0 1 6 0 0 0 0 0 0	0 1 0 1 0 1 0 0 0 1	0
Empleconia vaginatus	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 1 0	- - 0 0 0 1 0 1 4 0	1 0 0 0 1 0 0 0 0 0	0 0 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 1 0 0 0 0 1	1 0 0 0 1 0 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 0 0 1 1 0 0 0	0 0 1 0 0 0 0 0 0 1	1 1 1 0 0 1 0 0 0 0	0
Limopsis loringi	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 0	- - 0 1 0 0 0 1 0 0	1 0 0 0 1 0 0 0 0 0	0 1 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 2 - - 0 0 0	1 0 0 0 1 0 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 0 0 0	0 0 1 1 0 0 0 0 0 0	0 1 0 1 0 1 0 0 0 0	0
Limopsis diegensis	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 0	- - 0 1 0 0 0 1 4 0	1 0 0 0 1 0 0 0 0 3	0 0 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 1 0 0 0 0 ?	1 0 0 0 1 0 0 0 1 0	0 0 1 0 0 ? 0 0 0 0	0 ? 0 ? 0 0 1 ? 0 ?
	1 0 ? 1 0 0 ? 0 1 1	2 0 0 1 0 0 ? ? ? ?	? ? 1 ? 0 ? 0 ? 0 0	0 1 1 0 0 ? ? 0 0 0	0
Limopsis soboles	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 1	0 0 0 0 1 1 0 0 0 0	1 0 0 0 1 0 0 0 0 0	0 0 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 0 - - 0 0 0	1 0 0 0 1 0 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 0 0 0	0 0 1 0 0 0 0 0 0 1	0 1 1 0 0 1 0 0 0 0	0
Limopsis woodwardi	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 0	- - 0 0 0 0 1 0 0 0	1 0 0 0 1 0 0 0 0 0	0 0 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 0 - - 0 0 ?	1 0 0 0 1 0 0 0 1 0	1 0 1 0 0 1 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 0 0 0	0 0 1 6 0 0 0 0 0 1	0 1 1 0 0 1 0 0 0 0	0
Limopsis forteradiata	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 1	0 0 0 0 1 0 1 0 4 0	1 0 0 0 1 0 0 0 0 0	0 1 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 2 0	- 0 1 0 0 - - 0 0 1	1 0 0 0 1 0 0 0 ? 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 ? ? ?	? ? 1 ? ? ? ? ? 0 ?	? 1 ? ? ? ? 0 0 0 0	0
Limopsis marionensis	0 1 1 1 1 1 0 0 2 1	2 0 0 1 0 1 0 0 0 0	- - 0 0 0 0 1 0 4 0	1 0 0 0 1 0 0 0 0 0	0 0 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 1 0 1 0	- 0 1 0 2 - - 0 0 1	1 0 0 0 1 0 0 0 1 0	1 0 1 1 0 1 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 1 0 * 0 1 1	2 0 0 1 0 0 0 0 0 0	0 0 1 6 0 0 0 0 0 1	0 1 1 0 0 1 0 0 0 0	0
Glycymeris americana	0 1 1 1 1 1 0 0 1 1	1 0 0 0 0 0 0 0 0 1	0 0 0 0 1 0 0 1 1 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 0 0 0 3
	- - 1 1 0 1 0 0 1 0	0 0 0 1 2 - - 0 0 0	0 0 1 0 0 1 0 0 0 0	1 0 2 0 0 0 0 0 0 0	0 1 1 0 1 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 1 0 0 0 0 1 0	0 1 1 1 1 1 0 1 1 0	0

Axinactis inaequalis	0 1 1 1 1 1 0 0 0 -	- 0 0 0 0 1 0 0 0 2	1 0 0 1 0 0 0 1 1 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 0 1 1 0 1 0 0 1 0	0 0 0 ? 2 - - 0 0 ?	? ? ? 0 0 1 0 0 ? 0	? 0 ? ? ? ? 0 0 0 0	0 ? ? ? ? 0 1 ? 0 ?
	1 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	? ? 1 ? ? ? ? ? ? ?	? 1 ? ? ? ? ? ? ? ?	0
Glycymeris ovatus	0 1 1 1 1 1 0 0 1 1	2 0 0 0 0 1 0 0 0 0	- - 0 1 0 0 0 0 0 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 0 0 0 1 0 0 1 0	0 0 2 0 0 0 0 0 0 0	0 1 1 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 1 1 0 0 0 1 0	0 1 1 1 0 1 0 1 1 0	0
Glycymeris grayana	0 1 1 1 1 1 0 0 0 -	- 0 0 0 0 0 0 0 0 0	- - 0 0 0 0 0 0 3 0	1 0 0 0 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 0 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 1 0 1 0 0 0 1 0	0 0 2 0 0 0 0 0 0 0	0 1 1 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 0 0 0	0 0 1 5 1 0 0 1 1 0	0 1 0 1 0 1 0 1 0 0	0
Glycymeris holosericus	0 1 1 1 1 1 0 0 1 1	2 0 0 0 0 0 0 0 0 0	- - 0 1 0 0 0 0 0 0	1 0 0 0 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 0 0 0 0 0 0 1 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 1 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 4 0 0 0 0 1 0	0 1 1 1 0 0 0 1 1 0	0
Glycymeris reevei	0 1 1 1 1 1 0 0 1 1	1 0 1 0 0 1 0 0 0 1	0 0 0 0 1 0 0 1 3 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 0 0 0 3
	- - 1 1 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 1 0 0 0 0 0 1 0	0 0 2 1 0 1 0 0 0 0	0 0 1 0 0 0 1 0 0 0
	1 0 1 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 1 0 0 0 0 1 0	0 1 1 1 0 1 0 1 1 0	0
Glycymeris glycymeris	0 1 1 1 1 1 0 0 1 1	2 0 0 0 0 1 0 0 0 0	- - 0 1 0 0 0 1 1 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 1 2 - - 0 0 0	0 0 1 0 0 0 0 1 0 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 1 1 0 0 0 0 1 1	2 0 0 1 0 ? 0 2 0 0	0 0 1 1 0 0 0 1 1 1	0 1 1 1 0 1 0 1 1 0	0
Glycymeris formosus	0 1 1 1 1 1 0 0 1 1	2 0 0 0 0 1 0 0 0 0	- - 0 1 0 0 0 0 3 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 0 0 0 3
	- - 1 1 0 1 0 0 1 0	0 0 0 1 2 - - 0 0 0	0 0 1 0 0 1 0 1 1 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 1 0 0 0 1 1 1	0 1 0 1 0 1 0 1 1 0	0
Melaxinaea labyrintha	0 1 1 1 1 1 0 0 0 -	- 0 0 1 0 0 0 0 0 1	1 1 0 0 1 0 0 1 1 0	1 0 0 0 1 0 0 0 0 3	0 1 0 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 1 2 - - 0 0 0	0 0 1 0 1 0 0 0 1 0	0 0 1 0 0 0 0 0 0 0	0 0 1 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 1 0 0 0 1 1 0	0 1 1 1 0 1 0 0 1 0	0
Glycymeris crebreliratus	0 1 1 1 1 1 0 0 1 1	1 0 0 0 0 1 0 0 0 1	0 1 0 0 1 0 0 1 3 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 0 1 1 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 0 0 0 1 0 1 1 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 1 0 1 0 0 0 2 0 0	0 0 1 1 0 0 0 1 1 1	0 1 0 1 0 1 0 1 1 0	0
Glycymeris pilosa	0 1 1 1 1 1 0 0 1 1	2 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 1 0 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 ? 2 - - 0 0 ?	? ? ? 0 0 1 0 1 ? 0	0 0 ? ? ? ? 0 0 ? 0	0 ? ? ? ? 0 1 ? 0 ?
	1 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	? ? 1 ? ? ? ? ? ? ?	? 1 ? ? ? ? ? ? ? ?	0
Glycymeris scripta	0 1 1 1 1 1 0 0 1 1	2 0 0 0 0 0 0 0 0 0	- - 0 0 0 0 0 0 1 0	1 0 0 0 1 0 0 0 0 3	0 1 0 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 1 0 0 1 0 0 1 0	1 0 2 1 0 1 0 0 0 0	0 1 1 0 0 0 1 0 0 0
	1 0 1 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 1 0 0 0 0 1 0	0 1 1 1 1 1 0 1 1 0	0

Glycymeris striatularis	0 1 1 1 1 1 0 0 1 1	2 0 0 0 0 0 0 0 0 1	0 0 0 0 1 0 0 0 0 0	1 0 * 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 0 0 0 1 0 * 1 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 ? 0 0 0 ? 1 ?	? 1 ? ? ? ? 0 1 1 ?	0
Glycymeris cf lividus	0 1 1 1 1 1 0 0 1 1	1 0 0 0 0 0 0 0 0 1	0 0 0 0 1 0 0 1 3 0	1 0 0 0 1 0 0 0 0 3	0 ? ? 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 * 2 - - 0 0 0	0 0 0 0 0 1 0 0 1 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 0 0 1 0 0 0 2 0 0	0 0 1 5 0 0 0 0 1 0	0 1 1 1 0 0 0 1 1 0	0
Tucetona pectunculus	0 1 1 1 1 1 0 0 0 -	- 0 0 0 0 0 0 0 0 2	0 1 0 0 0 0 1 0 1 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 1 2 - - 0 0 0	0 0 1 0 0 1 0 1 0 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 1 0 1 0 0 0 0 0 0	0 0 1 1 0 0 1 0 1 0	0 1 0 1 0 0 0 1 1 0	0
Tucetona flabellata	0 1 1 1 1 1 0 0 0 -	- 0 0 0 0 0 0 0 0 2	0 0 0 0 0 0 1 0 3 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 0 2 - - 0 0 0	0 0 1 0 0 1 0 1 1 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 0 0 0
	1 0 0 1 0 0 1 0 1 1	2 1 0 1 0 0 0 0 0 0	0 0 1 1 0 0 1 0 1 0	0 1 0 1 0 0 0 1 1 0	0
Tucetona sp MNHN113	0 1 1 1 1 1 0 0 0 -	- 0 0 0 0 0 0 0 0 2	1 1 0 0 0 0 1 0 1 0	1 0 0 2 1 0 0 0 0 3	0 1 1 0 0 1 1 0 0 3
	- 1 1 1 0 1 0 0 1 0	0 0 0 1 2 - - 0 0 0	0 0 1 0 0 1 0 1 0 0	0 0 2 0 0 1 0 0 0 0	0 0 1 0 1 0 1 1 0 0
	1 0 1 1 0 0 1 0 1 1	2 0 0 1 0 0 0 2 0 1	0 0 1 1 0 0 1 1 1 0	0 1 1 1 0 1 0 1 1 0	0
Adacnarca nitens	0 1 1 1 1 0 0 0 0 -	- 0 0 0 0 1 0 0 0 0	- - 0 1 0 0 0 1 4 0	0 1 0 0 1 1 0 0 0 3	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 1 0 1 0 0 0 0 1	1 0 0 0 2 0 0 0 1 0	0 - 1 1 0 0 0 0 0 0	0 0 0 0 0 0 1 1 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 0 0 1 0 2 0 0	1 0 1 0 0 0 1 0 0 0	2 1 0 0 0 1 1 0 0 1	1
Adacnarca limopsoides	0 1 1 1 1 0 0 0 1 1	1 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 4 0	0 1 0 0 1 1 0 0 0 1	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 1 0 1 0 0 0 0 1	1 0 0 0 2 0 0 0 1 0	1 - 2 0 1 0 0 0 0 0	0 0 0 0 ? 0 1 ? 0 ?
	1 0 0 ? 0 0 0 0 1 1	2 0 0 0 ? 1 0 0 ? 0	1 0 1 ? 0 ? 1 ? 0 ?	? 1 1 0 0 0 1 0 0 1	1
Aupouria parvula	0 1 1 1 1 1 0 0 0 -	- 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 4 0	0 1 0 0 1 1 0 0 0 0	0 0 1 0 0 0 - 0 - 2
	0 - 1 0 0 0 1 0 2 0	- 0 1 ? ? ? ? 0 ? ?	? ? ? 0 0 1 0 0 ? 0	? 1 ? ? ? ? 0 0 0 0	0 ? ? ? ? 0 1 ? 0 ?
	1 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	? ? 1 ? ? ? ? ? 0 ?	? 1 ? ? ? ? ? ? ? ?	?
Cosa waikikia	0 1 1 1 1 0 0 0 2 0	2 0 1 0 0 1 0 0 0 1	0 0 0 0 0 0 1 0 4 0	0 1 0 0 1 1 1 0 0 2	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 1 ? ? ? ? 0 ? ?	? ? ? 0 2 0 0 0 ? 0	? - ? ? ? ? 0 0 0 0	0 ? ? ? ? 0 1 ? 0 ?
	? 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	? ? 1 ? ? ? ? ? 0 ?	? 1 ? ? ? ? ? ? ? ?	1
Cosa costata	0 1 1 1 1 0 0 0 ? ?	? 0 1 0 0 1 0 0 0 1	0 0 1 0 0 1 0 0 0 0	0 1 0 0 0 1 0 0 0 3	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 1 ? ? ? ? 0 ? ?	? ? ? 0 2 0 0 0 ? 0	? - ? ? ? ? 0 0 0 0	0 0 0 ? ? 0 1 ? 0 ?
	1 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	? ? 1 ? ? ? ? ? 0 ?	? 1 ? ? ? ? 1 1 0 ?	1
Cosa parallelogramma	0 1 1 1 1 0 0 0 0 -	- 0 1 0 0 1 0 0 0 1	0 0 1 0 0 0 1 0 4 0	0 1 0 0 1 1 0 0 0 3	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 1 0 1 0 0 0 0 0	1 1 0 0 2 0 0 0 1 0	1 - 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 ? 1 0 0 0 0 1 1	2 0 0 ? ? ? ? ? ? ?	? ? 1 ? 1 0 0 0 0 0	0 1 0 0 0 1 1 1 0 1	1

Cosa scabra	0 1 1 1 1 0 0 0 0 -	- 0 1 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0 $ 0	0 1 0 0 1 1 0 0 0 1	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 1 0 1 ? ? 0 ? ?	? ? ? 0 2 0 0 0 ? 0	? - ? ? ? ? 0 0 0 0	0 0 0 ? ? 0 1 ? 0 ?
	1 0 ? 1 ? ? ? 0 1 1	2 ? ? ? ? ? ? ? ? ?	? ? 1 ? 1 ? ? ? 0 ?	? 1 ? 0 0 0 1 1 0 ?	?
Cratis cf ohasii	0 1 1 1 1 0 0 0 2 1	2 0 0 0 0 1 0 0 0 0	- - 0 0 0 1 0 0 4 0	0 1 0 0 0 1 0 0 0 0	1 0 - 0 0 1 1 0 0 1
	0 1 1 0 0 0 1 0 2 0	- 0 1 0 1 0 0 0 0 0	1 0 0 0 2 0 0 0 1 0	1 - 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 0 0 0 0 0 0 0	? 0 1 ? 0 0 0 0 0 1	0 1 1 2 - 1 1 0 1 0	?
Philobrya munita	0 1 1 1 1 0 0 0 1 1	2 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 4 0	0 1 0 0 0 0 0 0 0 0	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 0 0	- 0 1 0 1 0 1 1 0 ?	1 ? ? 0 2 0 0 0 1 0	1 - 2 1 0 0 0 0 0 0	0 0 1 ? ? 0 0 0 0 ?
	1 0 ? 0 - - 1 0 1 1	2 1 0 0 ? ? 0 0 0 0	1 0 1 6 0 0 1 ? 0 0	0 1 1 0 0 ? 1 1 0 1	1
Lissarca rubrofusca	0 1 1 1 1 1 0 0 0 -	- 0 1 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 0 0	0 0 0 0 1 1 1 0 0 1	0 0 - 0 0 1 1 0 0 3
	- 1 0 0 0 0 1 0 2 0	- 0 1 0 1 1 1 1 0 0 1	1 1 0 0 2 0 0 0 1 0	1 0 1 0 0 0 0 0 0 0	0 1 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 1 0 1 0 0 0 0 0 0	1 0 1 0 1 0 0 0 0 1	1 1 1 0 0 1 1 1 0 1	1
Lissarca notarcadensis	0 1 1 1 1 0 0 0 0 -	- 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 4 0	0 0 0 0 1 1 0 0 0 3	0 0 - 0 0 1 1 0 0 3
	- 1 0 0 0 0 1 0 2 0	- 0 1 0 1 0 0 0 0 1	1 1 0 0 2 0 0 0 1 0	1 - 1 0 0 0 0 0 0 0	0 0 0 0 0 0 1 0 0 0
	1 0 0 1 0 0 0 0 1 1	2 0 0 0 0 0 0 0 0 0	1 0 1 ? 1 0 0 0 0 0	1 1 1 0 0 1 1 0 0 1	1
Lissarca picta	0 1 1 1 1 0 0 0 0 -	- 0 1 0 0 1 0 0 0 0	- - 0 0 0 0 0 1 $ 0	0 0 0 0 1 1 1 0 0 1	0 1 - 0 0 1 1 0 0 3
	- 1 1 0 0 0 1 0 2 0	- 0 1 0 0 - - 0 0 1	1 1 0 0 2 0 0 0 1 0	1 - 1 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
	0 0 0 0 - - 0 0 1 1	2 0 0 0 0 0 0 2 0 0	1 0 1 ? 1 0 0 0 0 0	1 1 0 0 0 1 1 1 0 1	1
Micromytilus crenulatifera	0 1 1 1 1 0 0 0 0 -	- 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 3 0	0 0 1 0 1 1 0 0 0 ?	1 0 - 0 0 1 - 2 2 3
	- - - - 0 0 1 0 2 0	- 0 1 0 0 - - 0 0 0	1 0 0 0 2 0 0 0 1 0	1 - 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
	0 0 ? 0 - - 0 0 1 1	2 0 0 0 0 0 0 2 0 0	? 0 1 ? 1 0 0 0 0 ?	? 1 0 0 0 1 1 0 0 1	?
Neocardia sp A USNM15	0 1 1 1 1 0 0 0 0 -	- 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 0 0	0 1 0 0 0 1 0 0 0 0	0 0 - 0 0 1 1 1 0 1
	1 1 0 0 0 0 1 0 1 0	- 0 1 0 1 1 0 0 1 0 1	1 1 0 0 2 0 0 0 1 0	1 - 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
	1 0 0 0 - - 0 0 1 1	2 1 0 2 ? ? 0 0 0 0	? 0 1 ? 1 0 0 0 0 ?	? 1 1 0 0 1 1 0 0 1	1
Notomytilus rubra	0 1 1 1 1 0 0 0 0 -	- 0 0 0 0 1 0 0 0 0	- - 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	1 0 - 0 0 1 - 2 2 3
	- - - - 0 0 1 0 0 0	- 0 1 0 0 - - 0 0 0	1 0 0 0 2 0 0 0 ? 0	1 - 1 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
	1 0 0 0 - - 0 0 1 1	2 0 0 0 0 0 0 0 0 0	? 0 1 ? 1 0 0 0 0 ?	? 1 0 0 0 1 1 0 0 1	1
Philobrya setosa	0 1 1 1 1 0 0 0 1 0	2 0 0 1 0 1 0 0 0 0	- - 0 0 0 0 0 0 0 0	0 1 0 0 0 1 0 0 0 0	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 0 0	- 0 1 0 1 0 0 ? 0 0	1 1 0 0 2 0 0 0 1 0	1 - 1 0 0 1 0 0 0 0	0 0 1 0 0 0 0 0 0 0
	1 0 0 0 0 0 1 0 1 1	2 1 0 0 0 0 0 0 0 0	1 0 1 ? 1 0 1 0 0 ?	? 1 1 0 0 1 1 0 1 1	1
Philobrya sp USNM07	0 1 1 1 1 0 0 0 2 1	2 0 0 1 0 1 0 0 0 0	- - 0 0 0 0 0 0 4 0	0 1 0 0 0 0 0 0 0 3	0 0 - 0 0 0 - 2 2 3
	- - - - 0 0 1 0 0 0	- 0 1 0 1 0 0 0 0 1	1 1 0 0 2 0 0 0 1 0	1 - 2 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0
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APPENDIX 3: Complete Morphology Tree with calculated Bremer Support values above the branchs

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