

**On becoming cemented: evolutionary relationships among the
genera in the freshwater bivalve family Etheriidae
(Bivalvia: Unionoida)**

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Abstract: A robust phylogeny for the Unionoida is emerging and presumed relationships of some major clades are being questioned. The Etheriidae or freshwater oysters has been a distinct family for over 160 years and currently contains three cemented genera: *Acostaea* (Columbia, South America), *Pseudomulleria* (India) and *Etheria* (Africa and Madagascar). Starobogatov (1970, *Nauka*, 1–372), Mansur and da Silva (1990, *Amazoniana*, 11(2), 147–166) and Bonetto (1997, *Biociências*, 5, 113–142) present conflicting testable hypotheses regarding the evolution of these taxa. Using cytochrome c oxidase subunit I DNA sequences the evolutionary relationships of these three genera has been examined, by comparing them to representatives of 30 other unionoid taxa from around the world. These analyses place *Acostaea* and *Etheria* within the Mycetopodidae while *Pseudomulleria* falls within the Unionidae. A monophyletic Etheriidae, composed of cemented freshwater bivalves, is not supported by the present analyses. Furthermore, the analyses indicate that cementation in the Unionoida has evolved at least twice.

In a paper which discusses the evolution of cementing bivalves, Yonge (1979) identified the variety, origin and problems of convergence in them, finding that over 20 families of bivalves have become cemented. This paper focuses on a group of bivalves which has become cemented in freshwater, namely, the freshwater oysters (Unionoida: Etheriidae).

Bivalves found in freshwater environments represent families from most of the major bivalve subclasses (Bogan 1993). The greatest diversity in freshwater bivalves is found in the radiation of the Unionoida. Currently this order is divided into two superfamilies, six families and, it is estimated here, approximately 180 genera. The two major modern unionoid radiations occurred in the southeastern United States (Bogan 1993, 1998; Williams *et al.* 1993) and China (Liu 1979). Our understanding of evolutionary relationships within the Unionoida is based primarily on comparative anatomy (e.g. Simpson 1900, 1914; Ortmann 1912; Parodiz & Bonetto 1963; Heard & Guckert 1970).

The family Etheriidae has been recognized as a distinct taxon for well over 160 years (e.g. Deshayes 1830; Tryon 1884; Fischer 1886; Thiele 1934; Starobogatov 1970) but the evolutionary relationships of this family to other unionoid families, and among its constituent genera, have

been debated (see Discussion). Most malacologists recognize three cemented genera in the Etheriidae: *Acostaea* (Columbia, South America), *Pseudomulleria* (India) and *Etheria* (Africa and Madagascar).

Prashad (1931) examined the convergence in the forms of the freshwater bivalve fauna of Southeast Asia and compared it with similar fauna from South America. At that time, he felt that the Unionoida was polyphyletic and the Mutelidae with a taxodont hinge was derived from the Arcidae. He suggested that the Etheriidae relationships were undoubtedly with the Unionidae and that they were not related to the Mutelidae. Prashad also noted the similarities of *Etheria*, *Acostaea* and *Pseudomulleria* but felt they all belonged to distinct genera with independent origins and observed that 'the Etheriidae present the most noteworthy examples of the parallel evolution of similar forms from distinct ancestral types, living under identical conditions in widely separated countries.' Prashad's ideas represent the multiple origins hypothesis for the evolution of cementation in the Unionoida.

In contrast, Yonge (1978, p. 446), in discussing *Acostaea* and the evolution of the Etheriidae, posited, 'Certainly *Acostaea* and *Pseudomulleria* must have arisen from a common dimyarian stock; the mode of growth and of assumption of the

monomyarian condition are too remarkable for convergence to be contemplated.' Yonge (1978) claimed that *Acostaea*, *Etheria* and *Pseudomulleria* were, in fact, each others closest relatives and so a monophyletic Etheriidae was supported. This is the single origin hypothesis for the genesis of cementation in the Unionoida.

Development of a unionoid phylogeny

Recent work on the evolutionary relationships among unionoid higher taxa has progressed from the efforts of Parodiz & Bonetto (1963) and Heard & Guckert (1970) to the immunoelectrophoretic analyses of Davis & Fuller (1981). The cladistic analysis of 16S DNA and morphology data sets presented by Lydeard *et al.* (1996) has clarified phylogenetic relationships among a number of North American unionoid genera, but did not include potentially closely related taxa from other continents or a suitable outgroup taxon.

Hoeh *et al.* (1998b) examined the higher level relationships of the Unionoida based on cytochrome c oxidase subunit I (COI) sequences and supported the hypothesis that *Neotrigonia* (Trigonioida: Trigoniidae) is the sister group to a monophyletic Unionoida. These conclusions support the monophyly of the Palaeoheterodonta (Trigonioida + Unionoida) as proposed by Waller (1990, 1998). Hoeh *et al.* (1998a) presented a COI sequence-based phylogeny for the Unionoida including 30 taxa representing five families (excluding representatives of the Etheriidae). Their analyses suggest that the hyriids, not margaritiferae, are a product of the most basal cladogenic event within the Unionoida and that the glochidial larvae is the ancestral larval type. The margaritiferae, mycetopodids, iridinids and hyriids were all depicted as monophyletic groups, with the Unionidae being paraphyletic. Hoeh *et al.* (2001) have expanded on the data presented in Hoeh *et al.* (1998a) by adding a morphological data set of 28 characters and produced a total evidence-based phylogeny for the Unionoida. The total evidence analysis supported the earlier phylogeny and character evolution hypotheses of Hoeh *et al.* (1998a). If it is assumed that the tree based on the total evidence analysis is a reasonable estimate of unionoid evolutionary history, then morphological character evolution within the Unionoida was very homoplasious.

Etheriid genera

The Etheriidae as used today contains three cemented genera: *Acostaea*, *Etheria* and *Pseudomulleria*. *Acostaea rivoli* (Deshayes 1830)

was originally described in *Mulleria* Férussac, 1823 [non Leach 1814] and subsequently moved to *Acostaea* Orbigny, 1851. *Acostaea* is known from the Rio Magdalena in Columbia, South America. Arteaga Sogamoso (1994) discovered that the larvae of *Acostaea rivoli* is a lasidium which, from the diagnoses of the family Mycetopodidae, would argue that *Acostaea* belongs in this family.

The anatomy of *Etheria elliptica* Lamarck, 1807 has been reported, illustrated and discussed by Rang & Cailliaud (1834) and Anthony (1905, 1907). Heard & Vail (1976) examined the anatomy of *Etheria elliptica* and suggested that it belongs in the South American family Mycetopodidae. *Etheria elliptica* is widespread in Africa: the basins of the Nile, Lake Tanganyika and Lake Victoria; the basins of the Chad, Zaire, Niger and Senegal; part of the rivers in Angola and north Madagascar (Daget 1998); and it is known from the Miocene of northeast Zaire (Gautier 1965; Gautier & Van Damme 1973).

Specimens of *Pseudomulleria dalyi* (Smith 1898), from the Budra Drainage, Kadur district, State of Mysore, southern India, were initially placed in the genus *Mulleria* and in the family Etheriidae. Smith (1898) observed that *P. dalyi* was cemented by either the right or the left valves. Woodward (1898), in the same volume, carefully described the anatomy of *Pseudomulleria dalyi*, reported the monomyarian condition and noted that the rectum no longer passed through the heart. Woodward (1898) presented a cross-section diagram of the anatomy and figured the coiling of the intestine. The intestinal coiling, as figured by Woodward, appears very similar to the intestinal coiling of examined North American Unionidae (AEB, personal observations). Woodward (1898) concluded '... the details of the gills, the mantle lobes, and the kidney, *Mulleria* [= *Pseudomulleria*] approximates to the Unionidae.' However, Preston (1915) placed *Mulleria dalyi* in the Etheriidae and cited extensively from Woodward on the anatomy. The most recent coverage of the freshwater molluscan fauna of India by Subba Rao (1989) follows the taxonomy of the family put forward by Thiele (1934), recognizing *Pseudomulleria* as a subgenus of *Acostaea*.

Yonge (1953) recognized a single genus of monomyarian unionoid, *Acostaea*, with two subgenera, *Acostaea*, and *Pseudomullaria*. Both subgenera were monotypic and both species begin life as a young shell which is dimyarian and not cemented. Yonge (1953) noted no evidence for initial byssal attachment and observed that cementation takes place and growth continues at the anterior end of the shell with the subsequent loss of the anterior regions of the mantle, shell and the anterior adductor muscles.

Family level classification

Deshayes (1830) erected the family Etheriidae for *Etheria* Lamarck, 1807 and for many years it contained only *Etheria*. Lamarck (1819) placed the group close to the Chamidae and thought the group was marine, which confused the placement of this family (Fischer 1886). Swainson (1835) recognized the genera *Etheria* and *Mulleria* but placed them not within the Unionidae but rather within his *Ostredea* (*sic*), or oysters. Swainson (1840) recognized the family Etheriidae and included *Etheria* and *Mulleria*, and placed the family between the Unionidae and Ostreidae completing his circle of related families.

Tryon (1884) and Fischer (1886) placed the Etheriidae next to the Unionidae and included three genera: *Etheria*, *Mulleria* (+ *Acostaea*) and *Bartlettia*. Simpson (1896, 1900, 1914) did not mention the Etheriidae in any of his treatments of the unionoid bivalves.

Germain (1907) placed *Etheria* in the Etheriinae, which he considered a subfamily of the Unionidae because the juvenile *Etheria* looked like an *Anodonta*. Later, Dautzenberg & Germain (1914) recognized *Etheria* as belonging to a separate family, Etheriidae, but did not comment on this change of rank.

Thiele (1934) recognized the superfamily Unionacea and included Margaritiferidae, Unionidae, Mutelidae and Etheriidae [*Bartlettia*, *Etheria*, *Acostaea* (*Acostaea*) and *A. Pseudomulleria*]. Modell (1942, 1949) developed an alternative classification for the Unionoida. He placed *Acostaea* and *Bartlettia* in a subfamily Bartlettiinae, and *Etheria* and *Pseudomulleria* in the Etheriinae, both subfamilies in his inclusive Mutelidae. He later (Modell 1964) modified his ideas on the cemented bivalve placement, including only *Etheria* in the Etheriinae and including *Pseudomulleria* as a subgenus under *Acostaea*, which he moved to the Bartlettiinae.

Mandahl-Barth (1954) listed *Etheria* in the Etheriinae within the Mutelidae and subsequently (1988) decided that the group should have familial status. Pain & Woodward (1961) reviewed the family Etheriidae and included *Etheria*, *Bartlettia*, *Acostaea* and *Pseudomulleria*. They elevated *Pseudomulleria* from subgeneric to generic rank based on the disparate distribution of *Acostaea* in South America and *Pseudomulleria* in India.

Newell (1965) provided a complete classification of the Bivalvia and placed all of the living families of unionoid bivalves in the single superfamily Unionacea, recognizing four families: Unionidae, Mutelidae, Etheriidae and Margaritiferidae. Haas (1969a, b) recognized the families Etheriidae, Margaritiferidae, Mutelidae and Unionidae, all

within a single superfamily, the Unionacea. He included *Etheria*, *Bartlettia* and *Acostaea* with two subgenera, *Acostaea* and *Pseudomulleria*, in the Etheriidae.

Starobogatov (1970) split what others had lumped as the Etheriidae, placing the three genera into distinct families: *Acostaea* in the Mulleriidae, along with the Mycetopodidae, forming the Mullerioidea; *Etheria* remained in Etheriidae; and *Pseudomulleria* in Pseudomulleriidae, both families placed in the Etherioidea.

Van Damme (1984) summarized the freshwater molluscs of northern Africa and used the family Etheriidae. Kabat (1997) provided an examination of the dates and priority of the various family group names for the Etherioidea: Etheriidae Deshayes, 1830, Iridinidae Swainson, 1840(+ Mutelidae Gray 1847) and Mycetopodidae Gray, 1840, with these being the oldest available names.

Mansur & da Silva (1990) recently supported a monophyletic view of the Etheriidae, including *Bartlettia*, based on anatomical analyses. However, Bonetto (1997) has placed *Acostaea* in the Acostaecinae in the Mycetopodidae, *Etheria* in the Etheriinae and *Pseudomulleria* in the Pseudomulleriinae, with both subfamilies placed in the Mutelidae.

Recently, Daget (1998) has produced a complete catalogue of the freshwater bivalves of Africa and has recognized a single genus within the Etheriidae, *Etheria*, with a single species *Etheria elliptica* Lamarck, 1807. This volume contains a very detailed listing of four generic synonyms, 20 specific synonyms and a listing of citations using the various names and combinations.

Good (1998), in discussing the Late Triassic freshwater bivalve fauna of the North American southwest, placed the Etheriidae within the Unionoida but without further comment. He observed that the Etheriidae originated on Gondwanaland but erroneously included Australia as part of their modern range.

Other cemented freshwater bivalves

Recently, Bogan & Bouchet (1999) described *Posostrea*, a cemented corbiculid from Lake Poso, Sulawesi, Indonesia. This is the first record of cementation in the Corbiculidae and represents the only known cemented freshwater bivalve outside of the Unionoida.

Fossil record

The fossil record for the three etheriid genera examined here is restricted to *Etheria*, which occurs in the Miocene (Gautier 1965; Gautier & Van Damme 1973) of East Africa. Nothing is

known of the fossil record regarding *Acostaea* and *Pseudomulleria*.

The works of Starobogatov (1970) and Bonetto (1997), as well as that of other authors, contradict the monophyletic nature of the Etheriidae, which has been supported most recently by Mansur & da Silva (1990), by suggesting that the Etheriidae is a polyphyletic assemblage. The conflicting views on the evolutionary relationships surrounding the Etheriidae hinder the development of a basic understanding of the circumstances involved in the evolution of the cemented habit in freshwater bivalves. Phylogenetic analyses of COI DNA sequences will be used herein to evaluate the taxonomic status of the Etheriidae, i.e. is the Etheriidae a monophyletic assemblage? These analyses will enable the following fundamental evolutionary questions to be addressed: did the cemented habit in unionoids evolve once (or multiple times); from which non-cemented ancestral taxon (or taxa) did it evolve?

Materials and methods

Organisms

The 34 bivalve species examined in this study are listed in Table 1 with their GenBank accession numbers for the COI sequences. The COI sequences representing the three etheriid genera are the only new sequences added in this paper. The other COI sequences have been analysed previously in Hoeh *et al.* (1996, 1998a, b, 2001). The names for the North American taxa follow Turgeon *et al.* (1998).

Methods

Total DNA was isolated from somatic (mantle) tissues from individuals representing *Acostaea*, *Etheria* and *Pseudomulleria*. Male gonadal tissues were specifically avoided to prevent comparisons of non-orthologous sequences due to the actual or potential presence of doubly uniparental inheritance of mitochondrial (mt)DNA in some bivalve taxa (e.g. see Skibinski *et al.* 1994; Zouros *et al.* 1994; Hoeh *et al.* 1996, 1997). Subsequently, a 710 base pair (bp) fragment of COI was polymerase chain reaction (PCR) amplified and cycle sequenced for each of the three taxa as described elsewhere (Folmer *et al.* 1994). Both strands of the COI fragment were sequenced from each of two individuals to guard against PCR-based contamination artifacts. The resulting sequences were readily aligned by eye, using MacClade (Maddison & Maddison 1997), with the one trigonioid and 30 unionoid COI sequences analysed previously (Hoeh *et al.* 1998a). Of the 34 total

Table 1. List of specimens used in this analysis and their associated GenBank accession numbers

Taxa	GenBank numbers
In-group, Order Unionoida	
Superfamily Etherioidea, Family Etheriidae	
<i>Etheria elliptica</i> Lamarck, 1807	AF231742
<i>Acostaea rivoli</i> (Deshayes, 1827)	AF231739
<i>Pseudomulleria dalyi</i> (Smith, 1898)	AF231750
Family Iridinidae	
<i>Mutela dubia</i> (Gmelin, 1791)	AF231737
<i>Mutela rostrata</i> (Rang, 1835)	U56849
Family Mycetopodidae	
<i>Anodontites guanarensis</i> Marshall, 1927	AF231741
<i>Anodontites trigonus</i> (Spix, 1827)	AF231738
<i>Monocondylaea minuana</i> (d'Orbigny, 1835)	AF231745
Superfamily Unionoidea, Family Hyriidae	
<i>Castalia stevensi</i> (H. B. Baker, 1930)	AF231736
<i>Diplodon deceptus</i> (Simpson, 1914)	AF231744
<i>Hyridella menziesi</i> (Gray, 1843)	AF231747
<i>Lortietta rugata</i> (Sowerby, 1868)	AF231746
<i>Velesunio angasi</i> (Sowerby, 1867)	AF231743
Family Margaritiferidae	
<i>Cumberlandia monodonta</i> (Say, 1829)	AF231753
<i>Margaritifera margaritifera</i> (Linnaeus, 1758)	U56847
Family Unionidae	
<i>Actinonaias ligamentina</i> (Lamarck, 1819)	AF231730
<i>Amblyma plicata</i> (Say, 1817)	U56841
<i>Anodonta cygnea</i> (Linnaeus, 1758)	U56842
<i>Coelatura aegyptiaca</i> (Cailliaud, 1827)	AF231735
<i>Cyrtonaias tampicoensis</i> (Lea, 1838)	AF231749
<i>Elliptio dilatata</i> (Rafinesque, 1820)	AF231751
<i>Fusconaia flava</i> (Rafinesque, 1820)	AF231733
<i>Glebula rotundata</i> (Lamarck, 1819)	AF231729
<i>Gonidea angulata</i> (Lea, 1838)	AF231755
<i>Ligumia recta</i> (Lamarck, 1819)	AF231748
<i>Pleurobema clava</i> (Lamarck, 1819)	AF231754
<i>Potamilus alatus</i> (Say, 1817)	AF231752
<i>Pyganodon grandis</i> (Say, 1829)	AF231734
<i>Quadrula quadrula</i> (Rafinesque, 1820)	AF231757
<i>Strophitus undulatus</i> (Say, 1817)	AF231740
<i>Toxolasma lividus</i> (Rafinesque, 1831)	AF231756
<i>Unio pictorum</i> (Linnaeus, 1758)	AF231731
<i>Unio tumidus</i> (Retzius, 1788; 2)	AF231732
Outgroup, Order Trigonioida	
<i>Neotrigonia margaritacea</i> (Lamarck, 1804).	U56850

aligned COI sequences, 33 were of identical length (= 630bp) while that of *Acostaea* had a single inferred codon deletion (= 627bp). The autapomorphic nature of the inferred single codon deletion in *Acostaea* (i.e. it is not shared with any other taxon) excludes this mutation from playing a role in the subsequent phylogenetic analyses.

The suitability of the COI data set for

phylogenetic analyses at this hierarchical level was evaluated by plotting the substitution pattern of transitions and transversions for each codon position (e.g. see Hoeh *et al.* 1998b). Furthermore, the degree of phylogenetic signal within the COI data set was evaluated using the g_1 statistic of a random tree distribution (from 10 000 000 random trees; e.g. see Hillis 1991; Hillis & Huelsenbeck 1992) and the permutation tail probability (PTP) test (Faith & Cranston 1991) as implemented in PAUP* (Swofford 1998). Phylogenetic analyses were carried out on the COI nucleotide sequences using the maximum parsimony (MP) algorithm contained in PAUP* (Swofford 1998). Based on previous morphological (e.g. see Atkins 1937; Taylor *et al.* 1969, 1973; Tevesz 1975; Popham 1979; Tevesz & Carter 1980; Smith 1986; Healy 1989; Waller 1990) and molecular (Hoeh *et al.* 1998b) systematic analyses that indicated the Trigonioidea is the sister taxon to a monophyletic Unionoidea, *Neotrigonia margaritacea* was used to root the resulting topologies. One thousand random terminal taxon addition order runs, combined with global branch rearrangement options, were employed to generate topologies from the MP analysis (all substitutions received equal weight). These options increased the probability of finding the best topology under the parsimony criterion (e.g. see Maddison 1991). The robustness of the resulting topologies was evaluated by bootstrap (10 000 replicates) and jackknife (50% deletion for 1000 replicates) analyses. In addition, character mapping, using MacClade (Maddison & Maddison 1997), was performed on the COI-based topologies to investigate their implications for the evolution of cementation within the Unionoidea.

Results

Scatter plots of the relationship between the number of transitional and transversal substitutions, and the percentage of total uncorrected sequence divergence at each of the three codon positions for the COI sequences, revealed that only transitional substitutions at the third codon position had reached saturation (plots not shown). Since saturated categories of substitution can contribute to erroneous estimates of evolutionary history (e.g. see Swofford *et al.* 1996), all first and second position substitutions, together with only transversions at the third codon position, were included in the phylogenetic analyses. Of the 630 nucleotide positions in the transformed COI data matrix, 383 were constant while 194 were parsimony informative. Analysis of the tree length distribution of 10 000 000 randomly generated trees, using all 34 sequences, suggested that there is a significant amount of hierarchical structure within the

transformed COI data set ($g_1 = -0.487$; with 247 variable sites, $p < 0.01$; Hillis & Huelsenbeck 1992). A PTP test on the transformed matrix also indicated significant hierarchical structure ($P = 0.001$). The findings from the plots of substitution pattern, g_1 statistics and the PTP test are consistent with the hypothesis that significant phylogenetic signal exists in the transformed COI nucleotide data matrix and validates its use in this particular phylogenetic context (e.g. see Swofford *et al.* 1996).

The strict consensus tree, derived from ten equally parsimonious trees (each of 879 steps; retention index = 0.5551) and produced by MP analysis of the transformed COI nucleotide matrix, is presented in Fig. 1, along with bootstrap (above branches, 10 000 replicates) and jackknife (below branches, 1000 replicates) percentages (only percentages > 50% are shown).

Discussion

Evolutionary relationships within the Unionoidea

All ten equally parsimonious trees resulting from analyses of the transformed COI nucleotide matrix supported the monophyly of the Hyriidae, Margaritiferidae, Iridinidae, Mycetopodidae and Etherioidea (Mycetopodidae, Iridinidae and Etheriidae) (e.g. Fig. 1). However, the Unionoidea (Unionidae, Margaritiferidae, Hyriidae) was found paraphyletic since the etherioids are more closely related to the unionids than are the hyriids. These higher level phylogenetic relationships within the Unionoidea are congruent with the results of Hoeh *et al.* (1998a, 2001).

The concept of the Etheriidae as a monophyletic bivalve family containing all of the cemented unionoid genera is rejected by the COI sequence analyses herein. Rather, the Etheriidae is shown to be a polyphyletic concept because two of the 'etheriid' genera are closely related to mycetopodids (*Acostaea* and *Etheria*) while another (*Pseudomulleria*) is a unionid. Constraining the parsimony analysis to produce a monophyletic Etheriidae produced three equally parsimonious trees of 900 steps each. These trees are 21 steps (2.4%) longer than the unconstrained trees. Therefore, the analysis of COI nucleotides contained herein rejects the notion of a monophyletic Etheriidae. Furthermore, these results suggest that cementation evolved at least twice (three times if Deltran character optimization is used) within the Unionoidea, and that it arose from both etherioid and unionid ancestors (Fig. 1).

Figure 1 clearly shows that, as currently recognized, the Etheriidae is polyphyletic. However, the

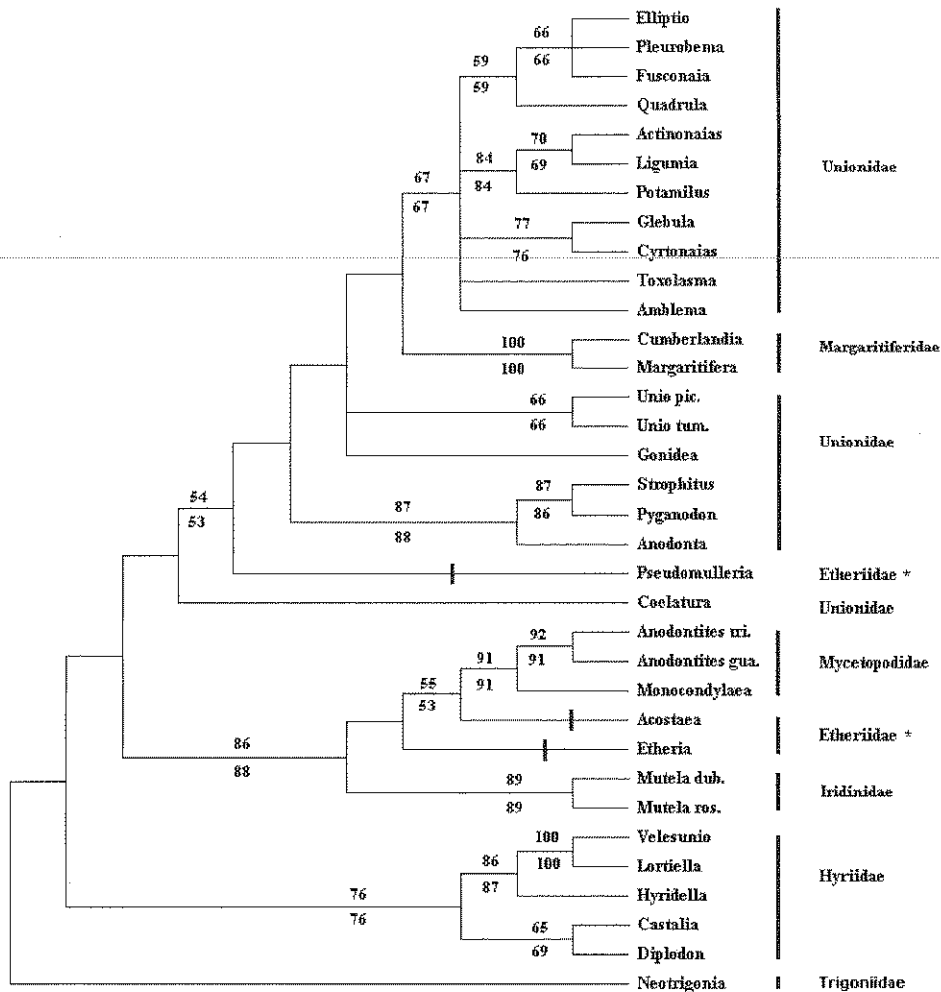


Fig. 1. Strict consensus tree of ten equally parsimonious trees. Tree length: 879 steps; retention index = 0.5551. Numbers above the branches are parsimony bootstrap percentages based on 10 000 replicates and those numbers below the line are parsimony jackknife percentages based on 1000 replicates. Current family names are listed on the right-hand side of the tree. *Neotrigonia* belongs to the Trigonidae, Trigonioidea, and is used as the outgroup (Hoeh *et al.* 1998b). The three independent origins of cementation, which are indicated by Deltran character optimization, are mapped onto the topology with hash marks.

present analyses used representatives of only 27 out of about 180 recognized unionoid genera. The topologies of the trees and evolutionary relationships of major clades may continue to change as more taxa are added. Furthermore, due to the incongruence between the trees generated from COI and anatomical data sets (Hoeh *et al.* 2001), and the relatively weak support for most basal nodes (Fig. 1), it is very premature to reassign higher taxa based on the clades produced herein.

The COI analysis implies that *Pseudomulleria*

falls within the 'unionid' clade. The *Pseudomulleria* placement on the tree (Fig. 1) suggests that the larval structure, when discovered, will be a glochidium. Morrison (1973) separated this genus from *Acostaea* because the nacre was different. He felt that *Pseudomulleria* belonged within his Unionacea.

Acostaea appears closely related to the Mycetopodidae (Fig. 1). Morrison (1973) placed the Acostaecidae close to the Mycetopodidae in the Mutelacea as then recognized. Arteaga Sogamoso

(1994) confirmed that the *Acostaea* larval form was the lasidium.

Etheria also appears closely related to the Mycetopodidae but there is very weak support for this placement (Fig. 1). The placement of *Etheria* with the Mycetopodidae herein corroborates the hypothesis of Heard & Vail (1976). Heard & Vail (1976) suggested that the split of the South American and African 'Mutelids' into Mycetopodidae and Iridinidae based on geography needs to be re-examined, and that some South American genera such as *Leila* actually belong to the Iridinidae and not the Mycetopodidae.

Cementation in freshwater bivalves: hypotheses

Freshwater cemented bivalves have a tropical/subtropical distribution while the areas of highest unionoid diversity occur in more temperate zones. What has influenced the biogeography of cemented freshwater bivalves? Harper (1991) suggested a driving force in the evolution of cementation in marine bivalves is predation by such groups as crabs (Crustacea) and starfish (Echinoderms). Harper (1991) performed a test of the predation hypothesis on byssally attached v. cemented bivalves and found a significantly higher level of predation on those animals attached with a byssus. She suggests that cementation, as recorded in the fossil record, may be due to the concurrent development of crustacean and echinoderm bivalve predators and notes their co-occurrence in the fossil record.

Harper's (1991) idea of predation as a driving force in the origin of cementation of marine bivalves can be extended to freshwater. In this case, the freshwater crayfish and crabs may substitute for their marine relatives and the echinoderms. A problem with this hypothesis arises in North America with the world's greatest diversity of Unionoidea (Williams *et al.* 1993) and an equally diverse freshwater crayfish fauna but no freshwater crabs (Hobbs 1989; Taylor *et al.* 1996). There are no cemented freshwater bivalves in North America. The same holds for Europe and northern Asia (Liu 1979) where there are crayfish but no cemented bivalves or freshwater crabs. The tropics of Southeast Asia are home to *Modellnaia*, a crevasse-dwelling unionoid (Brandt 1974), and *Posostrea*, a cemented corbiculid. Both of these species apparently live with freshwater crabs. South America has a variety of freshwater bivalves, which includes the cemented *Acostaea* and the crevasse-dwelling unionoid *Bartlettia*, as well as a variety of freshwater crabs. The same picture holds for Africa with *Etheria*, and is assumed to be true

for India with *Pseudomulleria*. Is the occurrence of cemented freshwater bivalves a reaction to predation by crabs? If this is the case, why is the number of cemented species so low?

An alternative hypothesis would be that the cemented freshwater bivalves represent a relatively recent opportunistic movement of species into high-energy environments and the evolution of local species into crevasse dwellers, such as *Bartlettia* in South America and *Modellnaia* in Thailand. This scenario of local species evolving to fill the cemented oyster niche in freshwater would explain why the different cemented bivalves are from different families. This might be the reason for the development of *Posostrea* in the absence of unionoids in ancient Lake Poso. In the case of *Etheria*, *Acostaea* and *Pseudomulleria*, they became fully cemented as opposed to crevasse dwellers. *Acostaea* and *Pseudomulleria* both begin life as a dimyarian shell and later became wedged in the substrate and developed into cemented freshwater oysters. These two species take the oyster habit to the extreme in becoming secondarily monomyarian as adults (see Yonge 1979). However, this ecological niche hypothesis fails to explain the lack of cemented bivalves in the highly diverse areas of the southeastern United States and China.

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