OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY
THE UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

THE ETHERIOIDEA REVISITED: A PHYLOGENETIC ANALYSIS OF HYRIID RELATIONSHIPS (MOLLUSCA: BIVALVIA: PALEOHETERODONTA: UNIONOIDA)

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ABSTRACT. — *The Etherioidea revisited: a phylogenetic analysis of hyriid relationships (Mollusca: Bivalvia: Paleoheterodonta: Unionoida). Occ. Pap. Mus. Zool. Univ. Mich. 729: 1-21, 2 figs.* Almost all freshwater pearly mussels (Order Unionoida) have one of two types of parasitic larvae, either glochidia or lasidia. The most widely accepted hypothesis of freshwater mussel higher classification divides the order into two superfamilies, the Unionoidea and Etherioidea [= Muteloidea], based solely upon larval type. To test this hypothesis, specifically the relationships of the Hyriidae (which have glochidia), a morphological data set compiled from both larval and adult life history stages was analyzed phylogenetically using parsimony. Results indicate that hyriids, despite their development including a parasitic glochidium, share a more recent common ancestor with the Etherioidea than with any unionoidean. The Etherioidea, (Hyriidae, (Iridinidae, Etheriidae)), is diagnosed by at least three adult anatomical synapomorphies. The lasidium-type larva is hypothesized to be derived from glochidia. The bearing of these results on the biogeography, character evolution, and classification of the Unionoida is discussed.

Keywords: *freshwater pearly mussels, Hyriidae, Iridinidae, Etheriidae, Etherioidea, Gondwanaland, morphological phylogenetics, classification*

INTRODUCTION

Recently, there has been an increased awareness of the phylogenetic paradox created by disparity among evolutionary hypotheses derived from different semaphoronts. This is especially so among marine invertebrates (*e.g.*, Strathmann and Eernisse, 1994; Wray, 1996). Phylogenies recov-

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ered using adult morphology may not necessarily reflect the same evolutionary history suggested by comparisons of larval or juvenile characters (Wiley, 1980). Such is also the case among freshwater pearly mussels (Bivalvia: Unionoida). The order has been divided into two superfamilies based solely upon larval type— the Unionoidea have glochidia, the Etherioidea (= Muteloidea) have lasidia (Parodiz and Bonetto, 1963; Boss, 1982). The objective of this paper is to phylogenetically re-evaluate the monophyly of the Etherioidea, based upon both larval and adult characters. A study of these taxa is timely in light of the lack of phylogenetic testing afforded the etherioideans and the recent nomenclatural revision proposed by Kabat (1997).

The Order Unionoida is comprised of 6 nominal families, depending upon the authority (*e.g.*, Ortmann, 1912a, 1921; Haas, 1969a, 1969b; Heard and Guckert, 1971; Davis and Fuller, 1981; Boss, 1982): Margaritiferidae, Unionidae, Hyriidae, Iridinidae (= Mutelidae), Mycetopodidae, and Etheriidae (Table 1). This order is probably monophyletic, diagnosed by their restriction to freshwater, ovovivipary, and a parasitic larval stage that must infect an appropriate host to complete its metamorphosis (Boss, 1982). But, with the exceptions of the Margaritiferidae and Unionidae (Lydeard *et al.*, 1996; Graf and Ó Foighil, in press), the interrelationships of these families have not been tested phylogenetically.

Until the 1960's, the Margaritiferidae and Unionidae were considered to compose the Unionoidea, whereas the remaining families fell into the Etherioidea (Ortmann, 1912a, 1921; Thiele, 1934; McMichael and Hiscock, 1958). The Unionoidea was diagnosed by (1) presence of a supra-anal aperture dorsal to the excurrent aperture, (2) having inner demibranchs that connect to the visceral mass distant from the labial palps, (3) having a slightly incomplete diaphragm (*i.e.*, composed only of the demibranchs without pallial fusion) dividing the mantle cavity, and (4) use of the outer pair of demibranchs (or both pairs) as marsupia for brooding (Ortmann, 1912a). According to Ortmann (1921), the Etherioidea, *i.e.*, Hyriidae, Iridinidae, Mycetopodidae, and Etheriidae, was diagnosed by (1) pallial fusion between the incurrent and excurrent apertures (thus, a complete diaphragm), (2) having inner demibranchs with an anterior attachment adjacent to the labial palps, and (3) use of only the inner pair of demibranchs for brooding. Further enforcing this separation was the zoogeography of the two taxa— unionoideans on the northern continents, etherioideans with a Gondwana distribution (Ortmann, 1921).

Subsequent work by Parodiz and Bonetto (1963), however, emphasized the discordant distribution of larval types among these taxa. While non-parasitic life cycles have been reported for a small number of freshwater mussel genera (Howard, 1915; Parodiz and Bonetto, 1963; Kondo, 1990), most have larvae that are parasitic upon fish or, infrequently, am-

phibians (Watters, 1994b). Parasitic mussel larvae fall into two general types. Whereas the Unionoidea possess only glochidia, the Etherioidea *sensu* Ortmann had either glochidia or lasidia.

Glochidia are small (70-350 µm), composed of a single adductor muscle and mantle cells enclosed by a calcareous, bivalved shell. They attach to host tissue by clamping their valves over exposed gill or fin epithelium. The host tissue encysts the mussel larvae (Arey, 1921), and it is within this cyst that the glochidia undergo metamorphosis into juveniles (Kat, 1984; Graf, 1998). Glochidia generally belong to one of two morphological varieties: (1) sub-circular to sub-ovate and unhooked or (2) sub-triangular and hooked (Coker *et al.*, 1921), although there is variation within these types (*e.g.*, *Potamilus*; Roe and Lydeard, 1998). Lasidia are also small (85-150 µm, not including the 'larval thread') but are tri-lobed larvae with a univalve, uncalcified shell. Just as with the glochidia, they come in two forms: (1) lasidium-type and (2) haustorium-type (Bonetto and Ezcurra, 1965a). Although differing in morphology, the fundamental distinction between the two types is that whereas the former attaches to the host by forming cysts, the haustorium-type attaches via tubular appendages (Fryer, 1954, 1961; Parodiz and Bonetto, 1963).

Parodiz and Bonetto (1963: 185) argued that,

> "The two different types of larvae, i.e., glochidium and lasidium, cannot be considered to be derived one from the other or from any hypothetical direct ancestry."

They advocated the re-assignment of the Hyriidae (the only Etherioidea to have glochidia) to the Unionoidea, and this scheme has been largely followed in subsequence classifications (Table 1): Unionoidea = Margaritiferidae, Unionidae, and Hyriidae; and Etherioidea *sensu* Parodiz and Bonetto = Iridinidae, Mycetopodidae, Etheriidae.

The relatively recent consensus that classifications should be comprised of natural taxa reflecting their pattern of phylogeny requires that supraspecific groupings be monophyletic (*i.e.*, include all of the descendents of a common ancestor) and suggests that these should be diagnosable by shared, derived homologies (*i.e.*, synapomorphies) (Wiley, 1980). The systematic hypothesis of Parodiz and Bonetto (1963) suggests that the Unionoidea and Etherioidea are each monophyletic, as diagnosed by their larval type, but this has never been tested phylogenetically. Rather, classification has been largely authoritarian.

In order to test the monophyly of the Etherioidea *sensu* Parodiz and Bonetto (1963) and the placement of the Hyriidae among the Unionoidea, I coded 38 shell and soft-anatomy characters of 18 taxa for cladistic analysis under the optimality criterion of maximum parsimony. Results indi-

Table 1. Summary of the Parodiz and Bonetto (1963) suprageneric tax-
onomy of the Unionoida along with the genera included in the present
phylogenetic analysis. This scheme has been followed in most subse-
quent classifications (Haas, 1969a, 1969b; Heard and Guckert, 1971;
Boss, 1982; Vaught, 1989; Kabat, 1997), but it represents a shift from
the view before the work of Parodiz and Bonetto (1963) that the
Hyriidae should be placed among the Etherioidea (Ortmann, 1912a,
1921; Thiele, 1934; McMichael and Hiscock, 1958). Also provided
are the large-scale distributions of the genera analyzed (Brown and
Lomolino, 1998).

Taxon	Distribution
Unionoidea	
Unionidae	
Unio	Palearctic - Ethiopian
Elliptio	Nearctic
Lampsilis	Nearctic
Pyganodon	Nearctic
Parreysia	India
Grandidieria	Ethiopian
Margaritiferidae	
Margaritifera	Holarctic
Hyriidae	
Castalina	Neotropical
Diplodon	Neotropical
Hyridella	Australian
Velesunio	Australian
Etherioidea (= Muteloidea)	
Etheriidae	
Etheria	Ethiopian
Acostaea	Neotropical
Mycetopodidae	
Anodontites	Neotropical
Mycetopoda	Neotropical
Iridinidae (= Mutelidae)	
Mutela	Ethiopian
Iridina (= *Pleiodon*)	Ethiopian

cate that the Unionoidea is not monophyletic and that the Hyriidae is
part of a natural taxon when included among the Etherioidea. This has
implications not only for the classification of the Etherioidea, but also
the historical biogeography and character evolution of the freshwater
pearly mussels as a whole.

METHODS AND MATERIALS

Rather than limit the analysis to either adult or larval characters, a
combined evidence approach (Kluge, 1989) was applied that included

morphological and life history traits of both semaphoronts. One to six representatives of each of the six families where chosen for analysis (Table 1), with an emphasis on genera representing different infrafamilial taxa. Also included was the marine *Neotrigonia*, the solitary surviving genus of the once-diverse Trigonioida (Bivalvia: Paleoheterodonta). *Neotrigonia* is the presumed sister-group to all freshwater mussels (Thiele, 1934; Taylor *et al.*, 1969; Healy, 1989; Hoeh *et al.*, 1998; but see Newell and Boyd, 1975 and Morton, 1987).

Thirty-eight characters were coded from the literature and corroborated by personal examination of specimens deposited in the University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA. The specimens examined and accompanying literature references are listed in Appendix 1. The characters analyzed include those of the shell (1-11), gross soft-anatomy (12-22), brooding and life history (23-34), and larval (35-38), and these are principally the characters deemed significant by previous mussel systematists (*e.g.*, Ortmann, 1912a; Parodiz and Bonetto, 1963; Heard and Guckert, 1971). Character diagnoses are listed in Appendix 2.

Table 2 shows the matrix used in this analysis. Inapplicable characters (*e.g.*, marsupial characters in non-brooding taxa, hinge characters in edentulous taxa, *etc.*) were coded as dashes ('–'), and missing data with ques-

Table 2. Adult and larval unionoid morphology data matrix. *0* indicates the plesiomorphic condition of the Paleoheterodonta. Character diagnoses can be found in Appendix 2.

	1	2	3
	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8
Neotrigonia	0 0 1 0 0 0 0 0 0 –	0 0 0 0 0 0 0 0 – –	0 0 0 0 – – – 0 – – – – – – 0 – – –
Margaritifera	0 1 – 0 0 1 0 0 1 0	0 1 0 0 0 0 0 0 – –	0 0 1 1 0 – – 0 0 – 0 0 0 0 1 0 0 –
Pyganodon	0 1 – 2 – – 0 0 1 0	1 1 1 0 0 0 0 1 0 –	0 0 1 1 2 0 – 1 2 1 0 1 0 0 1 0 1 –
Lampsilis	0 0 0 0 0 0 0 0 1 0	1 1 1 1 0 0 0 1 0 –	0 1 1 1 2 1 – 1 2 0 0 1 1 1 1 0 0 –
Elliptio	0 0 0 0 1 1 0 0 1 0	1 1 1 0 0 0 0 1 1 –	0 0 1 1 2 0 – 1 2 0 0 – 0 0 0 1 0 0 –
Unio	0 0 0 0 0 0 0 0 1 0	1 1 1 0 0 0 0 1 0 –	0 0 1 1 2 0 – 1 1 0 0 0 0 0 1 0 1 –
Parreysia	0 0 0 1 0 0 0 0 1 1	1 1 1 1 0 0 0 1 0 –	0 0 1 1 0 – – 1 ? 0 0 0 0 0 1 0 0 –
Grandidieria	0 0 0 0 0 0 0 0 0 1	1 1 1 1 0 0 0 1 0 –	0 0 1 1 1 – 0 1 1 0 0 0 0 0 2 – – –
Hyridella	0 0 0 1 0 0 0 0 1 1	1 1 1 1 1 0 1 2 – 1	0 0 1 1 1 – 1 2 1 0 0 0 0 0 1 0 1 –
Velesunio	0 0 0 1 0 0 0 0 1 0	1 1 1 1 1 1 0 1 2 –	1 0 0 1 1 1 – 1 2 1 0 0 0 0 0 1 0 1 –
Diplodon	0 0 0 1 0 0 0 0 1 1	1 1 1 1 1 1 0 1 2 –	0 0 0 1 1 1 – 1 0 1 0 0 0 0 0 1 0 1 –
Castalina	0 0 1 0 1 1 0 0 1 1	1 1 1 1 1 1 1 1 2 –	0 0 0 1 1 1 – 1 0 1 0 0 0 0 0 1 0 1 –
Mutela	0 1 – 2 – – 0 0 1 0	1 1 1 1 1 1 1 2 – 0	0 0 1 1 1 – 0 1 2 0 1 0 0 0 1 1 – 0
Iridina	1 – – – – – 0 0 1 0	1 1 1 1 1 1 1 2 – 0	0 0 1 1 1 – 0 1 2 0 1 0 0 0 ? ? ? ?
Anodontites	0 1 – 2 – – 0 0 1 0	1 1 1 1 1 1 0 1 0 –	0 0 0 1 1 1 – 0 1 2 0 1 0 0 0 1 1 – 1
Mycetopoda	0 1 – 2 – – 0 0 1 0	1 1 1 1 1 1 0 1 0 –	0 0 0 1 1 1 – 0 1 2 0 1 0 0 0 1 1 – 1
Etheria	0 1 – 2 – – 1 0 – –	1 1 1 1 1 0 1 0 – 0	1 0 1 1 1 – 0 1 2 0 1 0 0 0 ? ? ? ?
Acostaea	0 1 – 2 – – 1 1 – –	1 1 1 1 1 0 1 0 – 0	1 0 1 1 1 – 0 1 2 0 1 0 0 0 1 1 – 1

tion marks ('?'). When a particular character varied intragenerically, the character state of the type species was given precedence, rather than assuming monophyly of the genus and coding the character as polymorphic. Phylogenetic analysis (branch-and-bound) was performed with PAUP* (Swofford, 1998). Dashes were treated as missing data rather than as a new state. *Neotrigonia* was designated as the outgroup, and the ingroup was constrained to be monophyletic in order to root the phylogeny. Character transformation series were traced using MacClade 3.07 (Maddison and Maddison, 1997) and PAUP*. To gauge the 'robustness' of each node, Bremer Support-Decay (Bremer, 1995) values were calculated using TreeRot (Sorenson, 1996), and a bootstrap analysis (200 replicates, heuristic searches with 10 random sequence additions each) was performed using PAUP*.

RESULTS

Parsimony analysis recovered a single, most-parsimonious tree 62 steps long (25 parsimony informative characters, CI = 0.625, RC = 0.561) (Fig. 1). The Margaritiferidae (= *Margaritifera*) is sister to the remaining Unionoida. The other families are recovered as monophyletic with the exceptions of the "Unionidae" and the "Mycetopodidae" (= Etheriidae; see below). The Hyriidae are sister to the Etherioidea *sensu* Parodiz and Bonetto (1963), not the "Unionoidea." Thus, parsimony analysis of the characters traditionally employed to diagnose unionoid taxa rejects the hypothesis that glochidia diagnose a monophyletic clade composed of the Margaritiferidae, Unionidae, and Hyriidae. The bootstrap 50% consensus tree (not shown) differs from Fig. 1 in that the unionids collapse into a polytomy. The (Hyriidae, (Iridinidae, Etheriidae)) clade, however, is resolved by the bootstrap analysis. Fig. 2 illustrates all character transformations, and these are also described in Appendix 3.

The recovered phylogeny finds no support for a monophyletic "Mycetopodidae" (Fig. 1). Heard and Vail (1976a), finding no soft-anatomical synapomorphies to distinguish *Etheria* from mycetopodids, synonymized Etheriidae with Mycetopodidae. Kabat (1997) demonstrated that, of the two, Etheriidae has priority. Parodiz and Bonetto (1963) recognized several subfamilies within the "Mycetopodidae," but the monophyly of these has not been tested.

DISCUSSION

The phylogenetic reconstruction of Parodiz and Bonetto (1963; also Haas, 1969a, 1969b; Heard and Guckert, 1971) divided the Unionoida into two "clades" based on larval type. That hypothesis is rejected by the
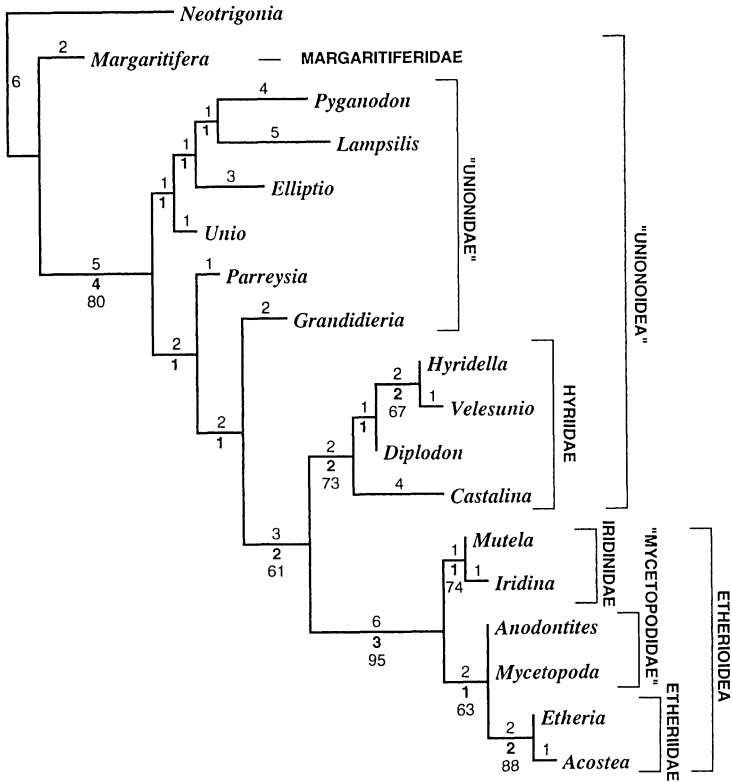
Fig. 1. Single tree recovered by parsimony analysis (62 steps, *CI* = 0.625, *RC* = 0.561). Taxonomy reflects the classification listed in Table 1. The "Unionidae," "Mycetopodidae," and "Unionoidea" are shown not to be monophyletic. The revised taxonomy of the Etherioidea is listed in Table 3 and depicted in Fig. 2. Numbers above the branches indicate branch lengths, those below are Bremer-Decay and bootstrap values, respectively.

present analysis of the characters that have been considered important by past mussel systematists. In the most parsimonious reconstruction, glochidium-type parasitic larvae are considered synapomorphic at the ordinal level — a glochidium is the primitive state among the Unionoida. In the lineage leading to the (Iridinidae, Etheriidae) clade (= Etherioidea *sensu* Parodiz and Bonetto), the glochidium was modified into a lasidium (Fig. 2). This is in direct contradiction to Parodiz and Bonetto (1963) who could not imagine one larval type being derived from the other (see quote above). The definition of the Etherioidea should be expanded to include the Hyriidae.

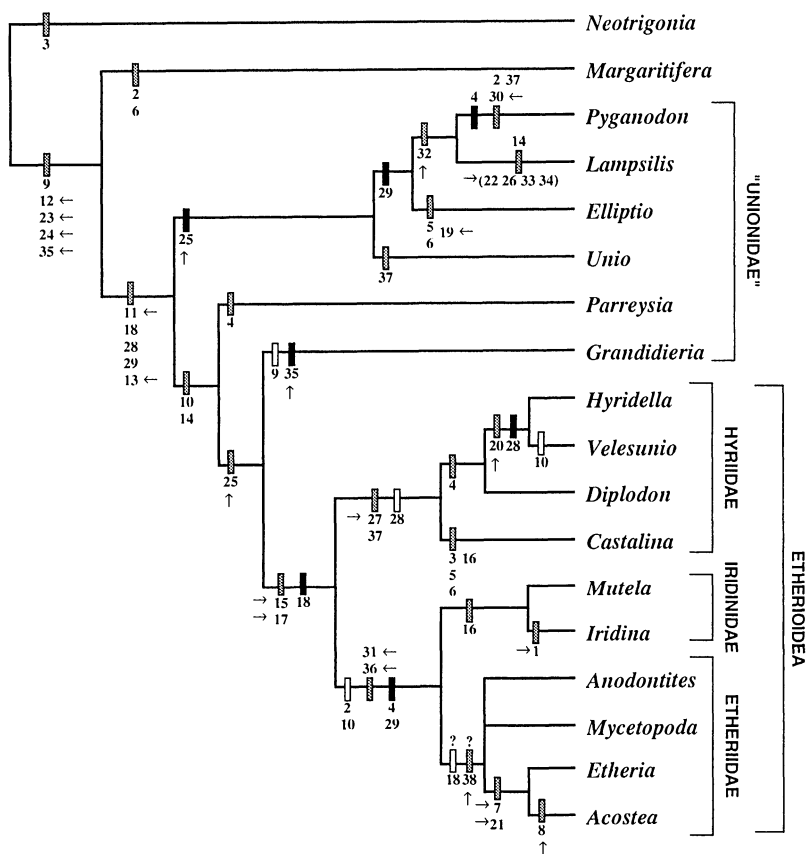The Etherioidea, *i.e.*, (Hyriidae, (Iridinidae, Etheriidae)), is synony-

Fig. 2. Cladogram depicting character transformations and the revised taxonomy of the Etherioidea. Character numbers refer to those listed in Appendices 2 and 3. Shaded boxes indicate character acquisition (gray and black for states *1* and *2*, respectively), white boxes identify character losses (character state *0*). Unambiguous character transformations ($CI = 1.0$) are marked by an arrow ('$\rightarrow$').

mous with the Mutelidae of Ortmann (1912a, 1921), Thiele (1934), and McMichael and Hiscock (1958). That clade is diagnosed by at least three morphological synapomorphies: pallial closure above the excurrent aperture [character 18, see Appendices 2 and 3], attachment of the inner demibranchs to the visceral mass near to or in contact with the labial palps [15], and pallial fusion between the incurrent and excurrent apertures creating a complete diaphragm [17] (Fig. 2). Within the Etherioidea, the tendency for complete fusion of the inner demibranchs to the visceral mass [14] and parasitism via a glochidium [35, 36] are plesiomorphic;

they define natural taxa with levels of universality higher than the Etherioidea.

Endobranchy (the use of only the inner demibranchs for brooding) is also plesiomorphic among the Etherioidea, according to the present analysis (Fig. 2, character 25). This result, however, hinges on the position of *Grandidieria* and the apparent paraphyly of the Unionidae (Fig. 1). While parsimony analysis of this data set weakly supports the paraphyly of the Unionoidea, more extensive molecular phylogenetic analyses support the monophyly of (Margaritiferidae, Unionidae) (*e.g.*, Graf and Ó Foighil, in press). Presuming the Unionidae are monophyletic, the endobranchous condition of *Grandidieria*, as well as certain other unionids (*e.g.*, *Moncetia*; Kondo, 1984), should not be considered homologous with that of the Etherioidea. Thus, endobranchy may be a fourth synapomorphy diagnosing the (Hyriidae, (Iridinidae, Etheriidae)) clade.

The inclusion of the Hyriidae among the Etherioidea is circumstantially supported by the biogeography of the clade. The Unionoida is an ancient group, the extant families extending perhaps as far back as the Triassic (Henderson, 1935; Haas, 1969b). It is expected that the evolution of an ancient, continental taxon would reflect the break up of Pangaea. This expectation is born out in the phylogeny recovered here. While there is evidence for Mesozoic etherioideans in North America (Pilsbry *in* Wanner, 1921; Morris and Williamson, 1988), the present-day Etherioidea are limited to the southern Gondwana continents. Unionoideans occur almost exclusively on the northern continents (Table 1). Etherioideans and unionoideans are sympatric only in areas of secondary contact: Central America, Africa, and Southeast Asia.

The results of this analysis bear directly upon the taxonomy of the Unionoida. A revised system of the Etherioidea, based on this and other studies as well as Kabat's (1997) nomenclatural revisions, is presented in Table 3. An important aspect of this classification — equally as important as the hierarchical arrangement of taxa within it — is its rejectability. It is based upon explicit statements of character homology (Appendix 2) and the single, best corroborated pattern of nested synapomorphies (Fig. 1). However, further testing is necessary. Preliminary results (Rosenberg *et al.*, 1994, 1997; Lydeard *et al.*, 1996; Hoeh *et al.*, 1998; Graf and Ó Foighil, in press) demonstrate the suitability of molecular characters to test hypotheses of freshwater mussel phylogeny and morphological character evolution with a large, independent data set. Future combined-matrices of DNA sequences and anatomical data from all life history stages coupled with global taxon sampling will further refine these hypotheses of the pattern of evolution among the Etherioidea.

Table 3. Revised taxonomy of the Etherioidea (Mollusca: Bivalvia: Paleoheterodonta: Unionoida) as compiled from the results of this study as well as various syntheses. Although *Leila* was not included in the present analysis, what is known of its anatomy suggests that it may belong among the Iridinidae (Parodiz and Bonetto, 1963; Bonetto, 1963). This analysis does not support a monophyletic Hyriinae. However, the data, thus far, are insufficient to revise the taxonomy of the Hyriidae.

Etherioidea Deshayes, 1830
  Etheriidae *s.s.*
      Etheriinae *s.s.* — *Etheria* Lamarck, 1807; *Acostaea* d'Orbigny, 1851; *Pseudomulleria* Anthony, 1907. (Heard and Vail, 1976a; Yonge, 1978)
      Mycetopodinae Gray, 1840 — *Mycetopoda* d'Orbigny 1835; *Mycetopodella* Marshall, 1927. (Parodiz and Bonetto, 1963)
      Monocondylaeinae Modell, 1942 — *Monocondylaea* d'Orbigny, 1835; *Haasica* Stans, 1932; *Fossula* Lea, 1870; *Tamsiella* Haas, 1931. (Parodiz and Bonetto, 1963)
      Anodontitinae Modell, 1942 — *Anodontites* Bruguière, 1792.
  Iridinidae Swainson, 1840
      Iridininae *s.s.* — *Mutela* Scopoli, 1777; *Aspatharia* Bourguignat, 1885 [= *Spathopsis* Simpson, 1900]; *Iridina* Lamarck, 1819 [= *Pleiodon* Conrad, 1834]. (Haas, 1969b)
      ?? Leilinae Morretes, 1949 — *Leila* Gray, 1840.
  Hyriidae Swainson, 1840
      Hyriinae *s.s.* (Parodiz and Bonetto, 1963)
          Hyriini *s.s.* — *Prisodon* Schumacher, 1817 [= *Hyria* Lamarck, 1819]; *Paxyodon* Schumacher, 1817.
          Castaliini Parodiz and Bonetto, 1963 — *Castalia* Lamarck , 1819; *Castalina* von Ihering, 1891; *Callonaia* Simpson, 1900; *Castaliella* Simpson, 1900.
          Diplodontini Parodiz and Bonetto, 1963 — *Diplodon* Spix, 1827; *Diplodontites* Marshall, 1922.
      Velesunioninae Iredale, 1934 — *Velesunio* Iredale, 1934; *Microdontia* Tapparone-Canefri, 1883; *Alathyria* Iredale, 1934; *Westralunio* Iredale, 1934. (McMichael and Hiscock, 1958)
      Lortiellinae Iredale, 1934 — *Lortiella* Iredale, 1934.
      Hyridellinae Iredale, 1934 — *Hyridella* Swainson, 1840.
      Cucumerunioninae Iredale, 1934 — *Cucumerunio* Iredale, 1934; *Virgus* Simpson, 1900.

ACKNOWLEDGMENTS

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APPENDIX 1: MATERIAL EXAMINED

The following is a catalog of the general analyzed, the specimen lots examined, and relevant literature references to anatomical descriptions of larvae and/or adults. Genera are listed alphabetically. All specimens are deposited in the University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Michigan. An asterisk ('*') identifies the type species of each genus.

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Anodontites Bruguière, 1792. — **A. crispata* (Brug., 1792) UMMZ 112391 upper Daule River, Ecuador. *A. trapesialis* (Lam., 1819) UMMZ 112429 Rio Grande do Sul, Brazil. — Ortmann (1921), Bonetto and Ezcurra (1962, 1965b).
Castalina von Ihering, 1891. — **C. martensi* (von Ihering, 1891) UMMZ 110907 Rio Grande do Sul, Brazil. *C. undosa* (von Martens, 1885) UMMZ 110905 Sao Paulo, Brazil. — Ortmann (1911a, 1921), Bonetto (1961b).
Diplodon Spix, 1827. — **D. ellipticum* (Spix, 1827) none examined. *D. paranensis* (Lea, 1834) UMMZ 248835 Buenos Aires, Argentina. *D. fontainianus* (d'Orbigny, 1835) UMMZ 111280 Rio Grande do Sul, Brazil. — Ortmann (1921), Bonetto (1951, 1961a, 1962a).
Elliptio Rafinesque, 1819. — **E. crassidens* (Lam., 1819) UMMZ 129451 Mississippi River, Wabasha Co., Minnesota, USA. *E. dilatata* (Rafinesque, 1820) UMMZ 205584 Kalamazoo River, Jackson Co., Michigan, USA. — Ortmann (1912a), Baker (1928).
Etheria Lamarck, 1807. — **E. elliptica* (Lam., 1807) UMMZ 43223 White Nile River, Africa. — Yonge (1962), Heard and Vail (1976a).
Grandidieria Bourguignat, 1885. — **G. burtoni* (Woodward, 1859) UMMZ 248778 Lake Tanganyika, Zambia; UMMZ 110105 Lake Tanganyika, Zaire. — Bloomer (1933), Kondo (1990).
Hyridella Swainson, 1840. — **H. australis* (Lam., 1819) UMMZ 111296 Australia. *H. depressa* (Lam., 1819) UMMZ 111827 Paramalta River, New South Wales, Australia. — McMichael and Hiscock (1958), Jones et al. (1986), Jupiter and Byrne (1997).
Iridina Lamarck, 1819 [= *Pleiodon* Conrad, 1834]. — **I. exotica* Lam., 1819 UMMZ 111973 Africa. *I. ovatus* Swainson, 1823 UMMZ 112006 Senegal. — Heard and Dougherty (1980).
Lampsilis Rafinesque, 1820. — **L. ovata* (Say, 1817) [= *L. cardium* Raf., 1820] UMMZ 50637 St. Joseph River, Berrien Co., Michigan, USA; UMMZ 130005 Mississippi River, Wabasha Co., Minnesota, USA. — Ortmann (1912a), Baker (1928), Kraemer (1970).
Margaritifera Schumacher, 1816. — **M. margaritifera* (Linn., 1758) UMMZ 4338 St. Lawrence River, New York, USA. *M. hembeli* (Conrad, 1838) UMMZ 107633 Alexandria, Rapides Parish, Louisiana, USA. — Ortmann (1911b, 1912a), Smith (1979).
Mutela Scopoli, 1777. — **M. dubia* (Gmelin, 1793) UMMZ 111979 Nile River, Africa. *M. nilotica* (Cailliaud, 1823) UMMZ 111984 Mahmoudich, Egypt. — Bloomer (1932), Fryer (1954, 1961).

Mycetopoda d'Orbigny, 1835. — **M. soleniformis* d'Orbigny, 1835 none examined.
    M. siliquosa (Spix, 1827) UMMZ 112645 Marañon, Peru. — Ortmann (1921),
    Bonetto (1962b), Bonetto and Ezcurra (1965b).
Neotrigonia Cossmann, 1912. — **N. pectinata* (Lam., 1819) none examined. *N.
    margaritacea* (Lam., 1804) UMMZ 253004 Tasmania. — Tevesz (1975), Morton
    (1987), Darragh (1998), Ó Foighil and Graf (in press).
Parreysia Conrad, 1853. — **P. corrugata* (Müller, 1774) UMMZ 110263 Sri Lanka.
    — Ortmann (1910b, 1911a), Pilsbry and Bequaert (1927).
Pyganodon Crosse and Fischer, 1894. — **P. grandis* (Say, 1829) UMMZ 205535
    Portage Creek, Kalamazoo Co., Michigan, USA. *P. cataracta* (Say, 1817) UMMZ
    101840 Framingham, Middlesex Co., Massachusetts, USA. — Ortmann
    (1912a), Baker (1928).
Unio Philipsson, 1788. — **U. pictorum* (Linn., 1758) UMMZ 79230 Birmingham,
    England; UMMZ 79213 River Saale, Jena, Germany. *U. caffer* Krauss, 1848
    UMMZ 60409 Irene, Transvaal, South Africa; UMMZ 234710 Lundi River, 14
    mi S Chiredzi, Zimbabwe. — Ortmann (1912a, 1918a, 1918b), Heard and
    Vail (1976b).
Velesunio Iredale, 1934. — **V. ambigua* (Philippi, 1847) UMMZ 111839 Murray
    River, Australia. — rtmann (1912b), McMichael and Hiscock (1958), Bonetto
    and Ezcurra (1965a).

APPENDIX 2: CHARACTER DIAGNOSES

The key to the characters and their states as used for character analysis follows. Literature cited refers to relevant discussions of character evolution. See Methods and Materials for an explanation of the phylogenetic methodology. In all cases, *0* is hypothesized to be the plesiomorphic condition of the Paleoheterodonta.

Shell Characters

1. Hinge type: 0 = schizodont; 1 = taxodont (Thiele, 1934; but see discussions in Cox, 1969 and Morton, 1987).
2. Development of posterior (lateral) hinge teeth: 0 = well-developed; 1 = reduced or absent.
3. Morphology of posterior (lateral) hinge teeth: 0 = smooth; 1 = serrate (von Ihering, 1910; Ortmann, 1921).
4. Development of anterior (pseudocardinal) hinge teeth: 0 = rubust, generally with two teeth on the left, one on the right, 1 = delicate, generally with one on the left, two on the right; 2 = reduced or absent.
5. Angle between posterior and anterior hinge teeth: 0 = obtuse; 1 = acute.
6. Morphology of anterior (pseudocardinal) hinge teeth: 0 = tab-like; 1 = peg-like.
7. Shell shape: 0 = bilaterally symmetrical; 1 = asymmetrical due to cementation.
8. Adult adductor scars: 0 = dimyarian; 1 = monomyarian (Yonge, 1978).
9. External shell: 0 = sculptured; 1 = smooth (Stanley, 1970; Watters, 1994a).
10. Beak (umbo) sculpture: 0 = absent, concentric or double-looped; 1 = angular or zig-zag (including 'radial') (Bonetto, 1962a; Watters, 1994a).
11. Mantle muscle scars: 0 = present; 1 = absent (Smith, 1983).

Gross Soft-Anatomy Characters

12. Ctenidial morphology: 0 = filibranch; 1 = lamellibranch (Morton, 1987; Smith, 1998).
13. Association of ascending lamellae of outer demibranchs with the mantle: 0 = completely free (unfused) or free posteriorly, but separation of the infrabranchial from the suprabranchial chamber is achieved by a 'pallial ridge' or 'diaphragmatic septum'; 1 = fused to mantle along entire length or nearly so (Gould and Jones, 1974; Smith, 1980).
14. Association of ascending lamellae of inner demibranchs with the visceral mass: 0 = tending to be free of the visceral mass except at the anterior end; 1 = tending to be complete fused to the visceral mass.
15. Anterior attachment of the inner demibranchs to the visceral mass: 0 = distant from labial palps; 1 = in contact with or adjacent to the labial palps (Stasek, 1963).
16. Pallial fusion ventral to the incurrent aperture: 0 = absent; 1 = short.
17. Pallial fusion between the incurrent and excurrent apertures: 0 = absent; 1 = present.

18. Pallial fusion dorsal to excurrent aperture: 0 = absent; 1 = present but re-opening to form a supra-anal aperture; 2 = present but without a supra-anal aperture.
19. Pallial fusion between supra-anal and excurrent aperture: 0 = equal in length or longer than excurrent aperture; 1 = distinctly shorter than the excurrent aperture (Ortmann, 1912a).
20. Diaphragm formed by fusion of mantle with ctenidia: 0 = imperforate; 1 = perforate (McMichael and Hiscock, 1958).
21. Ctenidial filament morphology: 0 = homorhabdic (ctenidia smooth); 1 = heterorhabdic (ctenidia plicate) (Heard and Vail, 1976a).
22. Mantle ventral to the incurrent aperture: 0 = smooth or weakly elaborated; 1 = elaborated with conspicuous papillae or a ribbon-like flap (Ortmann, 1912a; Kraemer, 1970).

Brooding and Life History Characters

23. Habitat: 0 = marine; 1 = freshwater.
24. Parental care: 0 = none, fertilization is external; 1 = female broods embryos and larvae in ctenidial marsupium (Coker et al., 1921; Kat, 1984).
25. Demibranchs occupied by marsupium: 0 = all four; 1 = inner pair only; 2 = outer pair only (Heard and Guckert, 1971).
26. Outer marsupial demibranch: 0 = entire demibranch marsupial or nearly so; 1 = a restricted portion of the demibranch marsupial (Ortmann, 1912a).
27. Inner marsupial demibranch: 0 = entire demibranch marsupial or nearly so; 1 = a restricted portion of the demibranch marsupial (Ortmann, 1921).
28. Interlamellar connections of non-marsupial demibranchs, including those of males: 0 = none or scattered; 1 = complete septa; 2 = perforated septa.
29. Interlamellar connection of marsupial demibranchs: 0 = absent or scattered; 1 = perforated septa; 2 = complete septa.
30. Marsupial water tubes: 0 = undivided; 1= divided by lateral septa ('tripartite') (Ortmann, 1910a, 1910d, 1911c).
31. Interlamellar septa of marsupium: 0 = without a swelling protruding into the water tubes; 1= bearing a 'marked swelling' (Ortmann, 1911a).
32. Edge of marsupium: 0 = remains sharp when gravid; 1 = expands greatly when gravid (Ortmann, 1911c).
33. Ventral extent of marsupium: 0 = ventral margin of marsupium does not extend past the non-marsupial portion; 1 = ventral margin of marsupium extends past the non-marsupial portion (Lefevre and Curtis, 1910).
34. Larval discharged: 0 = larvae discharged out the excurrent aperture with the respiratory current; 1 = larvae discharge through the ventral margin of the demibranch and out the incurrent aperture (Ortmann, 1910c; 1911c; Kraemer, 1970).

Larval Characters

35. Larval type: 0 = free-living; 1 = parasitic; 2 = secondarily non-parasitic (Lefevre and Curtis, 1912; Parodiz and Bonetto, 1963; Kondo, 1990).
36. Parasitic larval type: 0 = glochidium; 1 = lasidium (Parodiz and Bonetto, 1963).

37. Glochidium morphology: 0 = unhooked; 1 = hooked (Ortmann, 1912a, 1921; Parodiz and Bonetto, 1963; Jones *et al.,* 1986).
38. Lasidium morphology: 0 = attaches by tubular appendages (haustorium-type); 1 = attaches by forming a cyst (lasidium-type) (Fryer, 1961; Parodiz and Bonetto, 1963).

APPENDIX 3: CHARACTER TRANSFORMATIONS AND STATISTICS

The following is an accounting of the character transformations suggested by this phylogenetic analysis. The character numbers are the same as in Appendix 2. An s refers to the number of transformations (*i.e.*, steps) each character undergoes; CI and RC are the Consistency and Rescaled Consistency Indices, respectively. A dagger ('†') indicates that the RC is taken to be unity when the Retension Index is undefined (Farris, 1989). Nomenclature follows the taxonomy listed in Table 3, and character transformations are mapped in Fig. 2.

Shell Characters

1. Synapomorphy of *Iridina* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
2. There are three independent reductions in *Margaritifera*, *Pyganodon*, and (Iridinidae, Etheriidae) ($s = 3$, $CI = 0.333$, $RC = 0.222$).
3. Arises as independent synapomorphies of both *Neotrigonia* and *Castalina* ($s = 2$, $CI = 0.500$, $RC = 0$).
4. Independent synapomorphies of *Parreysia* and (*Diplodon*, (*Hyridella*, *Velesunio*)), with two independent transformations to *2* in *Pyganodon* and (Iridinidae, Etheriidae) ($s = 4$, $CI = 0.500$, $RC = 0.375$).
5. Arises as independent synapomorphies of both *Elliptio* and *Castalina* ($s = 2$, $CI = 0.500$, $RC = 0$).
6. Arises as independent synapomorphies of *Margaritifera*, *Elliptio*, and *Castalina* ($s = 3$, $CI = 0.333$, $RC = 0$).
7. Synapomorphy of (*Etheria*, *Acostaea*) ($s = 1$, $CI = 1.0$, $RC = 1.0$).
8. Autapomorphy of *Acostaea* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
9. Synapomorphy of the Unionoida with an reversal to *0* in *Grandidieria* ($s = 2$, $CI = 0.500$, $RC = 0$).
10. Synapomorphy of (*Parreysia*, (*Grandidieria*, Etherioidea)), with independent reversions to *0* in *Velesunio* and (Iridinidae, Etheriidae) ($s = 3$, $CI = 0.333$, $RC = 0.167$).
11. Synapomorphy of ("Unionidae," Etherioidea) ($s = 1$, $CI = 1.0$, $RC = 1.0$).

Gross Soft-Anatomy Characters

12. Synapomorphy of the Unionoida. ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
13. Synapomorphy of ("Unionidae," Etherioidea) ($s = 1$, $CI = 1.0$, $RC = 1.0$).
14. Arises independently as synapomorphies of (*Parreysia*, (*Grandidieria*, Etherioidea)) and *Lampsilis* ($s = 2$, $CI = 0.500$, $RC = 0.375$).
15. Synapomorphy of the Etherioidea ($s = 1$, $CI = 1.0$, $RC = 1.0$).
16. Arises independently as synapomorphies of the Iridinidae and *Castalina* ($s = 2$, $CI = 0.500$, $RC = 0.250$).
17. Synapomorphy of the Etherioidea ($s = 1$, $CI = 1.0$, $RC = 1.0$).
18. Synapomorphy of ("Unionidae," Etherioidea). Transformation to *2* in the Etherioidea and reversion to *0* in the Etheriidae ($s = 3$, $CI = 0.667$, $RC = 0.600$).
19. Synapomorphy of *Elliptio* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).

20. Synapomorphy of (*Hyridella, Velesunio*) ($s = 1$, $CI = 1.0$, $RC = 1.0$).
21. Synapomorphy of (*Etheria, Acostaea*) ($s = 1$, $CI = 1.0$, $RC = 1.0$).
22. Synapomorphy of *Lampsilis* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).

Brooding and Life History Characters

23. Synapomorphy of the Unionoida ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
24. Synapomorphy of the Unionoida ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
25. Synapomorphy of (*Grandidieria*, Etherioidea), and *2* is a synapomorphy of (*Unio*, (*Elliptio* (*Lampsilis, Pyganodon*))) ($s = 2$, $CI = 1.0$, $RC = 1.0$).
26. Synapomorphy of *Lampsilis* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
27. Synapomorphy of Hyriidae ($s = 1$, $CI = 1.0$, $RC = 1.0$).
28. Synapomorphy of ("Unionidae," Etherioidea). Reversion to *0* in the Hyriidae, but with *2* a synapomorphy of (*Hyridella, Velesunio*) ($s = 3$, $CI = 0.667$, $RC = 0.500$).
29. Synapomorphy of ("Unionidae," Etherioidea), with independent transformations to *2* in (*Elliptio*, (*Lampsilis, Pyganodon*)) and (Iridinidae, Etheriidae) ($s = 3$, $CI = 0.667$, $RC = 0.533$).
30. Synapomorphy of *Pyganodon* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
31. Synapomorphy of (Iridinidae, Etheriidae) ($s = 1$, $CI = 1.0$, $RC = 1.0$).
32. Synapomorphy of (*Pyganodon, Lampsilis*) ($s = 1$, $CI = 1.0$, $RC = 1.0$).
33. Synapomorphy of *Lampsilis* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).
34. Synapomorphy of *Lampsilis* ($s = 1$, $CI = 1.0$, $RC = 1.0$†).

Larval Characters

35. Synapomorphy of the Unionoida, with a transformation to *2* in *Grandidieria* ($s = 2$, $CI = 1.0$, $RC = 1.0$†).
36. Synapomorphy of (Iridinidae, Etheriidae) ($s = 1$, $CI = 1.0$, $RC = 1.0$).
37. Arises as independent synapomorphies of in *Pyganodon*, *Unio*, and the Hyriidae ($s = 3$, $CI = 0.333$, $RC = 0.111$).
38. Synapomorphy of the Etheriidae ($s = 1$, $CI = 1.0$, $RC = 1.0$†).