

## REVIEW ARTICLE

# REVIEW OF THE SYSTEMATICS AND GLOBAL DIVERSITY OF FRESHWATER MUSSEL SPECIES (BIVALVIA: UNIONOIDA)

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### ABSTRACT

Freshwater mussels (Bivalvia: Unionoida) are interesting because of their unique life cycles, global aggregate distribution and ancient origin. They are also of practical importance due to their worldwide, imperiled status. Of utmost utility for their continued study are a modern assessment of global and regional species diversity and a natural classification that reflects phylogenetic patterns. The freshwater malacological community has taken steps toward satisfying the latter of these requirements, but a consensus census of mussel species has not been published since Fritz Haas's revisions of the late 1960s. We set out to describe the species-level diversity of the Unionoida by reviewing the secondary literature and developing a comprehensive taxonomic database. Each valid species was assigned to one or more geographical regions (i.e. Nearctica, Neotropica, Afrotropica, Palearctica, Indotropica and Australasia) and one or more subregions, and each valid genus was assigned to the lowest possible level in a classification derived from our own, recent phylogenetic analyses. Based upon a consensus of numerous regional works, our global estimate of freshwater mussel diversity is 840 species. Regional diversity was determined as follows: Nearctica: 302 spp., Neotropica: 172, Afrotropica: 85, Palearctica: 45, Indotropica: 219 and Australasia: 33. The largest family is the Unionidae, with 674 species. However, the classification of that taxon is currently in flux, and many genera (corresponding to 225 spp.) were assigned to *incertae sedis* geographical assemblages. Diversity patterns are discussed, and it is suggested that reevaluation of these faunas with modern methods will likely increase recognized species diversity, especially on the southern continents. Our checklist and classification of freshwater mussel species is included as an appendix and mirrored on the MUSSEL Project Web Site (<http://www.mussel-project.net/>).

'The Naiades, or pearly fresh-water mussels, have a universal distribution throughout the ponds, lakes, and streams of the world, not only on the continents, but on most of the larger and some of the smaller islands. Some of the genera have probably extended back with but little change to the beginning of Mesozoic or possibly well into Paleozoic time; hence their study is an extremely interesting one, which may help us in obtaining a knowledge of the distribution of other life, and the mutations of land and sea in the time past.'

—Charles T. Simpson, 1896

### INTRODUCTION

The Recent species of the bivalve order Unionoida, colloquially known as freshwater mussels, pearly mussels or naiades, are conspicuous inhabitants of rivers and lakes on all continents except Antarctica. Freshwater mussels have generated significant interest over the last few decades due to their worldwide imperiled status, and a renaissance of sorts has improved the resolution of our understanding of supraspecific relationships and provincial diversity patterns beyond the latest global treatments of Modell (1942, 1949, 1964), Haas (1969a, b) and Starobogatov

(1970). However, a modern, synthetic perspective of global unionoid diversity is lacking, and its absence hinders the ability of ecologists, conservation biologists and freshwater malacologists, among other stakeholders, to apply patterns of freshwater mussel diversity and distribution to predictions derived from hypotheses of contemporary and historical biological processes. Our objective here is to review and summarize the global and regional diversity of the Unionoida. How many species of freshwater mussels are there and how are they distributed?

While freshwater mussels are indeed of practical interest, owing to their conservation status (Lydeard *et al.*, 2004; Strayer, 2006) and economic importance (Baker, 1993; Anthony & Downing, 2001), they are also extremely interesting from a biological perspective (Strayer *et al.*, 2004). Freshwater mussels have a unique life cycle incorporating both parental care (i.e. brooding) and larval parasitism upon freshwater fishes (and occasionally other vertebrates) (Graf, 1997; Wächtler, Mansur & Richter, 2001; and references therein). The Unionoida is also an ancient clade, the extant crown group having its origin by the Triassic (Haas, 1969b; Watters, 2001). The combined effects of these traits confer upon freshwater mussels characteristics useful for the study of such problems as speciation, zoogeography and life history evolution, to name a few. As has been discussed elsewhere (Simpson, 1896; Graf & Cummings, 2006b), the global patterns of unionoid phylogeny and diversity could be valuable tools for testing hypotheses of evolutionary processes at various scales of space and time.

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**Table 1.** Key references to the taxonomic and geographical diversity of the Unionoida.

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Nearctica:	Frierson (1927), Clench & Turner (1956), Johnson (1970, 1972, 1977, 1978, 1980, 1999), Clarke (1973, 1981, 1985), Burch (1975), Turgeon <i>et al.</i> (1998), Cummings & Mayer (1992), Williams <i>et al.</i> (1993), Ziuganov <i>et al.</i> (1994), Howells, Neck & Murray (1996), Parmalee & Bogan (1998), Brim-Box & Williams (2000), Smith (2001), Huff <i>et al.</i> (2004), Roe & Hartfield (2005)
Neotropica:	Ortmann (1921a), Frierson (1927), Haas (1929, 1930, 1931a–b), Baker (1930), Lange de Morretes (1949), Modell (1950), Bonetto (1962, 1964, 1965a–b, 1966, 1972), Figueiras (1965), Schade (1965), Pain & Woodward (1961), Parodiz (1968), Mansur (1970), Veitenheimer (1973), Johnson (1981), Quintana (1982), Mansur, Veitenheimer-Mendes & Marques de Almeida-Caon (1988), Mansur & Valer (1992), Parada & Peredo (2002), Ramírez, Paredes & Arenas (2003), Martínez, Cabrera & Lasso (2004), Mansur & Pereira (2006), Simone, 2006
Afrotropica:	Pilsbry & Bequaert (1927), Leloup (1950), Pain & Woodward (1961, 1964, 1968), Fischer-Piette & Vukadinovic (1973), Van Damme (1984), Mandahl-Barth (1988), Daget (1998), Ibrahim, Bishai & Khalil (1999), Scholz & Glaubrecht (2004), Graf & Cummings (2006a, in press)
Palearctica:	Zhadin (1938, 1965), Haas (1940), Habe (1977, 1991), Kondo (1982, 1997, 1998), Schütt (1983), Ziuganov <i>et al.</i> (1994), Falkner (1994), Korniusshin (1998), Bába (2000), Smith (2001), Falkner, Bank & von Proschwitz (2001), Falkner, Ripkin & Falkner (2002), Huff <i>et al.</i> (2004), Starobogatov <i>et al.</i> (2004), Kantor & Sysoev (2005), Graf (2007)
Indotropica:	Preston (1915), Prashad (1922), Pain & Woodward (1961), Moskvicheva & Starobogatov (1973), Brandt (1974), Liu (1979), Đang, Thái & Pham (1980), Subba Rao (1989), Neemann, Gopal & Ravindra (2003), Hu (2005), Prozorova <i>et al.</i> (2005)
Australasia:	Iredale (1934, 1943), McMichael & Hiscock (1958), Smith (1992), Walker <i>et al.</i> (2001), Ponder & Bayer (2004), Fenkwick & Marshall (2006)

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References are listed according to their geographical coverage, as most studies are typically faunistic. This is by no means a complete bibliography, only a gateway into the relevant literature on species taxonomy, diversity and distributions. Only two sets of synopses have covered the entire world to the species level: Simpson (1900, 1914) and Haas (1969a–b).

Because of their diversity, geographical breadth and chronological depth, the potential exists for freshwater mussels to become important model organisms for the study of evolutionary patterns. However, since the comprehensive syntheses of Simpson (1900, 1914) at the turn of the 20th century, only a few freshwater malacologists approached their science from a cosmopolitan perspective. Simpson consolidated the previous century's more than 4,000 named species to ca. 1,300 species and subspecies in fewer than 80 genera, and his synopsis provided both the benchmark for regional species accounts and a framework for family-level classification. In the 100 years since Simpson's *Magnum Opus*, numerous revisions have accumulated, but these have generally been provincial, faunistic studies (Table 1). At reasonably regular intervals, global syntheses appeared (e.g. Thiele, 1934; Modell, 1942, 1949, 1964; Haas, 1969a, b; Starobogatov, 1970; Vaught, 1989; Millard, 2001) but, among these, only Haas (1969a) worked below the genus level. Based upon Haas's work, there are over 830 species in about 180 genera, which are divided between two superfamilies with three families in each (Graf, 2000; Graf & Cummings, 2006b). However, subsequent revisions of the freshwater mussels of particular regions or of taxa often deviate significantly from Haas.

We have recently revised the family-group level classification of the Unionoida (Graf & Cummings, 2006b), and the time is ripe to take a new look at the species-level diversity of freshwater mussels on a global scale. We have undertaken a comprehensive review of the vast secondary taxonomic literature on the group

and assembled these disparate but often overlapping arrangements into a consistent framework that emphasizes current taxonomy and historical biogeographical patterns. Taken with a grain of salt, the resulting species checklist – reviewing the published geographic and taxonomic data from the last 200 or more years – can be used to examine patterns of freshwater mussel diversity across all continents. This research programme also provides the basis for the simplest method for estimating the number of known freshwater mussel species: counting.

## THE MUSSEL PROJECT DATABASE

The MUSSEL Project Database (MUSSELpdb) was created to store and manage freshwater mussel data from both the literature and specimen collections, and it has been invaluable to us for previous studies at smaller geographical scales (e.g. Graf & Cummings, 2006a, in press; Graf, 2007). The MUSSEL Project Web Site (<http://www.mussel-project.net/>) provides a description of our data model and example data sets. The MUSSELpdb was employed to analyse the vast data and to create a global checklist of freshwater mussel diversity, in order to estimate the taxonomic and geographical diversity of the Recent Unionoida.

We must emphasize that our checklist is a *review*, not a *revision* (despite the protestations of Davis, 2004; see Bouchet, 2006; Bank *et al.*, 2006 for rebuttals). Synonymies and geographical data have been gleaned from the literature, not from our own first-hand, collections-based research – except when we are reviewing articles based upon our own first-hand, collections-based research (i.e. Graf & Cummings, 2006a, b, in press). Although ours is not a significant deviation from previous approaches (e.g. Haas, 1969a), earlier synopses have not been particularly explicit about methods.

Our review of the modern literature began with Simpson (1900, 1914) and Haas (1969a, b), and then proceeded through the major works listed in Table 1 and numerous minor works. This effort is ongoing with regard to historical literature, but for our purpose here (i.e. determining taxa currently considered valid), those works not treated thus far are superseded by more modern revisions. In the MUSSELpdb, for each work, any reported synonymy was captured by associating a 'taxonomic opinion' with each nominal species following the method described by Graf (2007). For each nomen, there is a related set of taxonomic opinions indicating the author(s), date of publication, whether or not the nomen was considered valid, which nominal species was treated as the senior synonym (if invalid), and the combination of genus and species applied. Range data were also recorded.

Each nominal species was assigned to a valid species (or treated as a *nomen dubium*). Thus, in the MUSSELpdb, each valid species was related by synonymy to a comprehensive history of how the taxonomic components of that species were variously treated by different authorities. Through this system, areas of disagreement could be readily discovered and targeted for further study. An analogous arrangement of tables exists for genera. Circumscription of nominal species into valid species was done on the basis of genera. One or (usually) a few key revisionary works were selected as authoritative for each genus. In general, the criteria for selecting a reference as authoritative for a particular genus were that it was among the most recent treatments of all or most of the species of that genus. Our objective was not to compile a complete bibliography for each genus but rather a short list of key references to species-level classification and distributions that could serve as a gateway to the relevant literature.

Each valid species in our checklist was assigned to one or more geographic regions and to one or more subregions (Table 2 and Fig. 1). Taxa were arranged by family following Graf & Cummings (2006b, Table 3), although in the absence of a

**Table 2.** Geographic regions and subregions.

## (NA) NEARCTICA:

- (1) Interior Basin, including the Laurentian Great Lakes
- (2) Atlantic Slope
- (3) Gulf Coastal, from the Suwanee River west to the Rio Grande
- (4) Peninsular Florida
- (5) Pacific basins, including the Aleutian Islands

## (NT) NEOTROPICA:

- (1) Mesoamerica, including Cuba
- (2) Transandean, including the Magdalena and Maracaibo basins
- (3) Amazonas-Orinoco, including the Guyanas
- (4) Atlantic coastal streams, including the São Francisco
- (5) Paraná-Paraguay
- (6) Patagonia

## (AF) AFROTROPICA:

- (1) Nile Basin, including Lake Turkana
- (2) Atlantic basins in Western Africa
- (3) Congo, including Cameroon and Gabon
- (4) Southern Africa
- (5) Indian Ocean basins in eastern Africa
- (6) Madagascar, including the Mascarenes

## (PA) PALEARCTICA:

- (1) Europe, including the Maghreb
- (2) Middle East
- (3) Central Asia
- (4) Amur-Beringia, including northern China and Korea
- (5) Japan-Sakhalin Island, including the Kurils

## (IN) INDOTROPICA:

- (1) Yangtze-Huang, from the Pei south to the Qiantang and Taiwan
- (2) Indochina, including southern China and the Mekong west to the Salween
- (3) India-Burma, from the Indus to the Irrawaddy
- (4) Sunda Islands-Philippines

## (AU) AUSTRALASIA:

- (1) Eastern Australia, including Tasmania
- (2) Western-Northern Australia
- (3) New Guinea, including Misool and the Solomons
- (4) New Zealand

Geographic regions and subregions are depicted in Figure 1.

robust, global phylogeny for the Unionidae, lineages of Old World and Mesoamerican genera were arranged by geographic assemblage. These data were used to determine taxonomic and geographic tallies of species.

One of the strengths of our review is the electronic nature of the MUSSELpdb. The data that form the basis of our results and checklist are mirrored on the MUSSEL Project Web Site (<http://www.mussel-project.net/>), and that information can be periodically updated to reflect ongoing research. The online version provides a searchable interface, facilitating future revisions by interested taxonomists and ecologists without having to duplicate much of the effort we have already expended.

GLOBAL AND REGIONAL DIVERSITY  
OVERVIEW

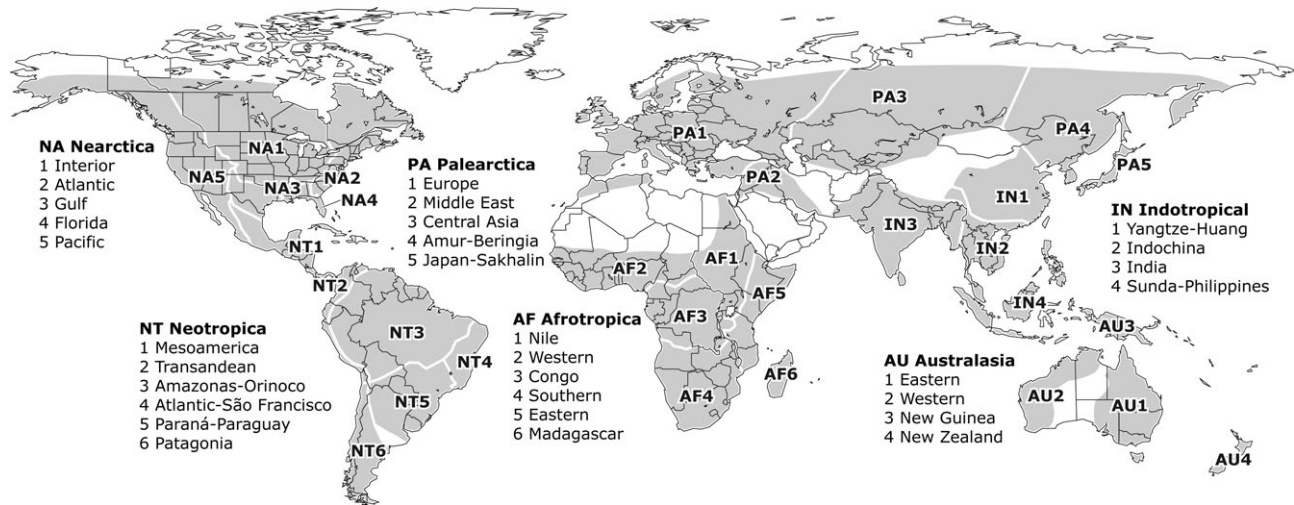
Based upon analysis of the secondary literature, we identified 4,839 species-group level nomina that had been treated as available in previous studies, and these were assigned to 840 valid species. An additional 116 specific nomina could not be assigned to any valid species (*nomina dubia*). Thus, the overwhelming majority of species-group nomina are not considered valid in recent treatments of freshwater mussel diversity. Many of these extra species-group nomina were introduced for European (and other) taxa by the French *Nouvelle École* in the late 19th century (Graf, 2007), but, on average, there is a roughly 6:1 synonyms-to-valid-species ratio worldwide.

Haas's (1969a) global revision of the Unionoida listed 837 valid species in 226 genera and subgenera. However, recent estimates have gone as high as 1,200 (Boss, 1972; Brusca & Brusca, 1990). We have recently reported estimates of freshwater mussel species diversity of 898 (Graf & Cummings, 2006b; Cummings & Bogan, 2006) and higher (Cummings & Graf, 2005). However, those counts included many Neotropical and Palearctic species that were subsequently synonymized (Simone, 2006; Graf, 2007). As expected, we found that species are not distributed randomly over the global range of the order Unionoida. Freshwater mussel diversity is parsed into its taxonomic and geographical components in Tables 4 and 5. The largest and most widespread of the six families is the Unionidae, with 674 species (Table 4). The other families all have fewer than 100 species each, and the Etheriidae has the fewest with only four. As shown in Table 5, most families have geographically restricted ranges, and only the Unionidae occur in all regions. The most speciose regions are Nearctica (302 spp.) and Indotropica (219). Australasia, as a region, has the fewest species (33), but Palearctica is the most sparse if land area is considered (45). The Checklist and Classification of Unionoid Genera and Species, which forms the basis for the tallies presented in Tables 4 and 5, follows as an appendix.

Our global total, 840 species in 161 genera, is similar to that of Haas (1969a: 837 spp.), the last global tally. However, the current estimate is not merely 'Haas + species described since the late 1960s.' Regional diversity estimates based upon Haas's species illustrate this point. Assuming Haas's species would be assigned to the same regions as the corresponding valid species in the MUSSELpdb, for New World regions, his estimates would be 352 and 187 for Nearctica and Neotropica, respectively (539 total). That is 65 species (14%) more than our estimate of 474 (302 + 172; Table 5). For Old World regions, Haas's estimates would be as follows: Afrotropica, 73; Palearctica, 39; Indotropica, 172; Australasia, 29 (313 total). That is 69 species (18%) fewer than our estimate of 382 (85 + 45 + 219 + 33; Table 5). The discrepancy between the total of Haas's regional estimates (852) and his global count of 837 is accounted for by 16 species that each occur in two regions and one species that subsequent classifications have regarded as a *nomen dubium*. While Haas's contribution is tremendously important and remains intact for many species, it has been subsequently lumped or split for others and is now outdated. As a global accounting of freshwater mussel diversity, Haas's arrangement is no longer adequate.

## TAXONOMIC DIVERSITY

We have elsewhere (Graf & Cummings, 2006b) demonstrated the evidence supporting the higher classification of the Unionoida in a phylogenetic context, and that article provides a detailed review of data and methods applied to date to recover the higher-level pattern of cladogenesis of freshwater mussels. Figure 2 depicts a cladogram of the unionoid families based upon our analysis; nodes for which robust phylogenetic tests are wanting are left unresolved. Areas of disagreement based



**Figure 1.** Distribution of Freshwater Mussels Showing Geographic Regions and Subregions. Abbreviations and numbering of geographical subregions follows Table 2.

**Table 3.** Family-group level classification of the Unionoida.

Superfamily UNIONOIDEA Rafinesque, 1820
Family UNIONIDAE s.s.
Subfamily UNIONINAE s.s.
Tribe UNIONINI s.s.
Tribe ANODONTINI Rafinesque, 1820
Subfamily AMBLEMINEAE Rafinesque, 1820
the Amblemini Tribe group
Tribe AMBLEMINI s.s.
Tribe LAMPSILINI von Ihering, 1901
Tribe PLEUROBEMINI Hannibal, 1912
Tribe QUADRULINI von Ihering, 1901
Tribe GONIDEINI Ortmann, 1916
<i>incertae sedis</i> Mesoamerican amblemines
<i>incertae sedis</i> Western Palearctic unionids
<i>incertae sedis</i> Afrotropical unionids
<i>incertae sedis</i> Indotropical unionids
Family MARGARITIFERIDAE Haas, 1940
Superfamily ETHERIOIDEA Deshayes, 1830
Family HYRIIDAE Swainson, 1840
Subfamily HYRIINAE s.s.
the Hyriini Tribe group
Tribe HYRINI s.s.
Tribe CASTALIINI Parodiz & Bonetto, 1963
Tribe RHIPIDODONTINI Starobogatov (1970)
Tribe HYRIDELLINI McMichael, 1956 (1934)
Subfamily VELESUNIONINAE Iredale, 1934
the lasidium-bearing freshwater mussels
Family ETHERIIDAE s.s.
Family MYCETOPODIDAE Gray, 1840
Subfamily MYCETOPODINAE s.s.
Subfamily ANODONTITINAE Modell, 1942
Subfamily LEILINAE Lange de Morretes (1949)
Subfamily MONOCONDYLAEINAE Modell, 1942
Family IRIDINIDAE Swainson, 1840
Subfamily IRIDININAE s.s.
Subfamily ASPATHARIINAE Modell, 1942

Taxonomy follows Graf & Cummings (2006b), with various *incertae sedis* assemblages organized geographically. Taxa of the same rank are listed alphabetically following the type-taxon.

upon other studies and their relevance to assigning genera to family-group level taxa are discussed below.

The branching pattern hypothesized in Figure 2 is translated into a Linnaean classification in Table 3. The order Unionoida is monophyletic (sister to the marine genus *Neotrigonia*; Giribet & Wheeler, 2002; Graf & Cummings, 2006b) and divided into two superfamilies, Unionoidea and Etherioidea. The former is composed of the families Unionidae and Margaritiferidae, and the latter contains the Hyriidae, Etheriidae, Mycetopodidae and Iridinidae. The family Unionidae is by far the most diverse of the Unionoida, with 674 species (Table 4). Indeed, the Unionidae is among the most speciose of all bivalve families, the other contenders being the Lucinidae (ca. 500 spp.; Taylor & Glover, 2006) and Veneridae (ca. 800; Mikkelsen *et al.*, 2006). This is a rather dubious distinction belying the fact that phylogenetic work on the Unionidae to date has relied heavily upon molecular characters and incomplete sampling, and we are simply unaware of the morphological synapomorphies that could serve to subdivide it further.

The intergeneric relationships among members of the Nearctic unionid assemblage have been relatively well-studied using various molecular datasets (e.g. Davis & Fuller, 1981; Lydeard, Mulvey & Davis, 1996; Bogan & Hoeh, 2000; Graf & Ó Foighil, 2000a; Hoeh, Bogan & Heard, 2001; Graf, 2002; Hoeh *et al.*, 2002; Roe & Hoeh, 2003; Campbell *et al.*, 2005; Walker *et al.*, 2006), and the classification of those North American lineages generally conforms to the traditional, two-subfamily system: Unioninae and Ambleminae. The genera of Mesoamerica and the Old World, however, have not been studied in the same detail, and from the available phylogenies, a major revision of unionid subfamilies will be necessary to accommodate the global diversity in a natural classification. Haas (1969a, b), Heard & Guckert (1970), Heard (1974) and others erred by trying to shoehorn all unionid species into the arrangement conceived for the Nearctic fauna by Ortmann (1910, 1912, 1916). As discussed by Graf (2002), even Ortmann eventually questioned the accuracy of that classification. While the several molecular analyses cited above have refined our understanding of freshwater mussel evolution by falsifying the traditional arrangement, they do little to support a viable alternative system for the many taxa for which no molecular sequences are yet available.

No strictly Mesoamerican species have been included in published molecular phylogenetic studies to date, although certain genera can be assigned with confidence to tribes well diagnosed

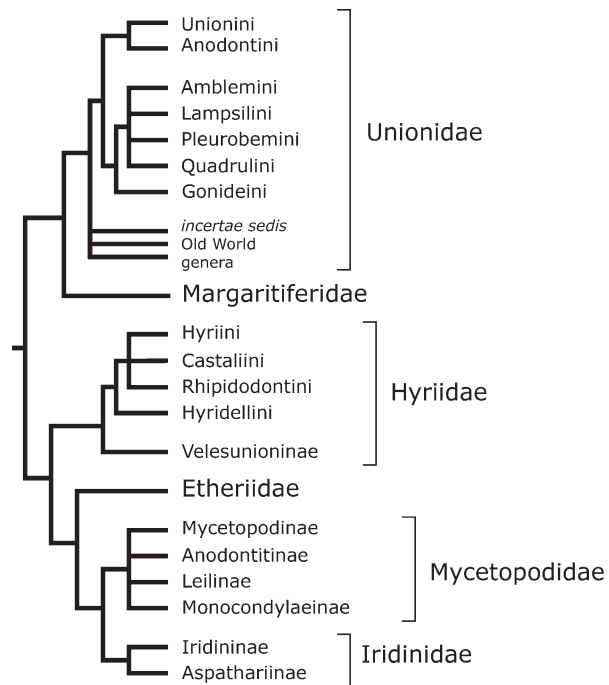
**Table 4.** Taxonomic diversity of the Unionoida.

Taxonomy	Geography						
	All	NA	NT	AF	PA	IN	AU
UNIONIDAE	674	297	94	41	38	217	2
Unioninae	107	44	2	3	26	42	–
Unionini	43	–	–	3	13	30	–
Anodontini	64	44	2	–	13	12	–
Ambleminae	342	253	92	–	–	–	–
Amblemini	3	3	–	–	–	–	–
Quadrulini	27	26	1	–	–	–	–
Pleurobemini	102	100	3	–	–	–	–
Lampsilini	148	122	28	–	–	–	–
Gonideini	1	1	–	–	–	–	–
<i>incertae sedis</i> ambl.	61	1	60	–	–	–	–
<i>incertae sedis</i> unionidae	225	–	–	38	12	175	2
MARGARITIFERIDAE	12	5	–	–	7	1	–
HYRIIDAE	71	–	40	–	–	–	31
Vesunioninae	17	–	–	–	–	–	17
Hyriinae	54	–	40	–	–	–	14
Hyridellini	14	–	–	–	–	–	14
Rhipidodontini	27	–	27	–	–	–	–
Castaliini	10	–	10	–	–	–	–
Hyriini	3	–	3	–	–	–	–
ETHERIIDAE	4	–	2	1	–	1	–
MYCETOPODIDAE	36	–	36	–	–	–	–
Anodontitinae	18	–	18	–	–	–	–
Mycetopodinae	4	–	4	–	–	–	–
Leilinae	2	–	2	–	–	–	–
Monocondylaeinae	12	–	12	–	–	–	–
IRIDINIDAE	43	–	–	43	–	–	–
Iridininae	17	–	–	17	–	–	–
Aspathariinae	26	–	–	26	–	–	–
TOTALS	840	302	172	85	45	219	33

Taxonomy follows Table 3. Geographic regions are abbreviated as in Table 2: NA, Nearctica; NT, Neotropica; AF, Afrotropica; PA, Palearctica; IN, Indotropica; AU, Australasia. Total diversity and regional subtotals may not match sums across rows, as certain species occur in the multiple areas.

by morphological characters, like the Anodontini (Unioninae) and Lampsilini (Ambleminae) (Graf & Cummings, 2006b). The 61 species of the remaining genera we leave as *incertae sedis* members of the Ambleminae, representing 18% of the species diversity of the subfamily. We assume, based upon geography and phylogenetic analyses performed to date, that the Ambleminae are a monophyletic lineage endemic to North and Central America, including Cuba in the Caribbean. The affinities of these taxa will be resolved as molecular analyses progress and the taxa of the Amblemini Tribe Group are better distinguished with morphological characters.

Several Old World taxa historically assigned to the Ambleminae (Brandt, 1974; Heard, 1974) have been included in molecular phylogenetic studies (reviewed by Graf & Cummings, 2006b). Analogous to the Ambleminae in Mesoamerica, certain Old World genera can be assigned to the Unioninae based upon diagnostic morphological characters and historical precedence. That is, the Unionini and Anodontini as recognized today correspond to traditional taxa. While too few genera and species have been analysed to place all the African and Eurasian lineages into a robust classification, phylogenetic studies have contradicted the hypothesis that they share any special affinity with the North American amblemines. Rather, those Old



**Figure 2.** Cladogram of Freshwater Mussel Family-Group Level Taxa. Based upon Graf & Cummings, 2006b.

World lineages seem to form a paraphyletic grade at the base of the Unionidae (Graf & Cummings, 2006b; but see Huang *et al.*, 2002; Roe & Hoeh, 2003; Walker *et al.*, 2006). Because the genera of those regions are typically restricted in distribution, it is convenient, in the absence of a robust classification, to group them geographically as *incertae sedis* assemblages within the Unionidae. The Afrotropical (38 spp.), Western Palearctic (5) and Indotropical (182) assemblages of *incertae sedis* species in combination represent a third (33%) of the diversity of the Unionidae, and that pattern demonstrates just how far the study of freshwater mussels systematics has yet to advance.

When discussing the historical over-simplification of unionid classification by the Western Malacological Establishment, it is appropriate to refer to the contributions of Modell (1942, 1949, 1964) and Starobogatov (1970). Both of these workers rebelled against what they apparently saw as the ‘lumping’ of Ortmann (1910, 1911, 1912, 1921a) and others by splitting the Unionidae (and indeed the whole Unionoida) into dozens of infrafamilial taxa (see Graf & Cummings, 2006b: their Appendix 3). In the interest of conservatism, we considered simply following these arrangements in our classification to handle the numerous *incertae sedis* genera. However, such a tack would have been both impractical and inconsistent. While Modell and Starobogatov both concurred that the families could be split into numerous subfamilies and tribes unrecognized by other authorities, that was the limit of their agreement. Their classifications are incompatible with each other and with the available phylogenetic evidence (Graf & Cummings, 2006b). An arrangement derived from a pragmatic chimera of the two systems or an arbitrary selection of one of them would have been misleading. However, as systematic studies proceed, many of the family-group level names introduced by Modell, Starobogatov and others will likely be resurrected, not because of any special insight, but simply because the nomina are available. For example, Leloup (1950) and Pain & Woodward (1968) introduced four subfamilies for four monotypic genera in the Lake Tanganyika region alone.

**Table 5.** Geographic diversity of the Unionoidea.

Geography	Taxonomy						
	All	UN	MA	HY	ET	MY	IR
NEARCTICA	302	297	5	–	–	–	–
1. Interior	131	129	2	–	–	–	–
2. Atlantic	56	55	1	–	–	–	–
3. Gulf	147	145	2	–	–	–	–
4. Florida	13	13	–	–	–	–	–
5. Pacific	9	8	1	–	–	–	–
NEOTROPICA	172	94	–	40	2	36	–
1. Mesoamerica	102	94	–	–	–	8	–
2. Transandean	12	–	–	1	1	10	–
3. Amazonas-Orinoco	42	–	–	17	1	24	–
4. Atlantic-São Francisco	18	–	–	10	–	8	–
5. Paraná-Paraguay	41	–	–	21	1	19	–
6. Patagonia	4	–	–	3	–	1	–
AFROTROPICA	85	41	–	–	1	–	43
1. Nile	26	13	–	–	1	–	12
2. Western	22	4	–	–	1	–	17
3. Congo	34	16	–	–	1	–	17
4. Southern	16	5	–	–	1	–	10
5. Eastern	4	2	–	–	1	–	1
6. Madagascar	5	4	–	–	1	–	–
PALEARCTICA	45	38	7	–	–	–	–
1. Europe	11	9	2	–	–	–	–
2. Middle East	11	10	1	–	–	–	–
3. Central Asia	3	3	–	–	–	–	–
4. Amur-Beringia	14	12	2	–	–	–	–
5. Japan-Sakhalin	17	14	3	–	–	–	–
INDOTROPICA	219	217	1	–	1	–	–
1. Yangtze-Huang	63	63	–	–	–	–	–
2. Indochina	91	90	1	–	–	–	–
3. India-Burma	54	53	–	–	1	–	–
4. Sunda-Philippines	30	30	–	–	–	–	–
AUSTRALASIA	33	2	–	31	–	–	–
1. Eastern Australia	14	–	–	14	–	–	–
2. Western Australia	6	–	–	6	–	–	–
3. New Guinea	12	2	–	10	–	–	–
4. New Zealand	5	–	–	5	–	–	–
TOTALS	840	674	12	71	4	36	43

Geographic areas are those listed in Table 2. Families are abbreviated as UN, Unionidae; MA, Margaritiferidae; HY, Hyriidae; ET, Etheriidae; MY, Mycetopodidae; IR, Iridinidae. The total diversity and regional subtotals may not match columnar sums, as certain species occur in the multiple geographical areas.

The sister-group to the Unionidae, the family Margaritiferidae, shares a similar Holarctic distribution, but diversity is significantly lower (12 spp.), and occurrences are patchier geographically. The classification of the family is contentious, having been recently treated from three different perspectives. Smith (2001) revised the species and genera of the global Margaritiferidae, Bogatov, Prozorova & Starobogatov (2003) treated the Russian species according to the ‘Comparatory’ method (Graf, 2007), and Huff *et al.* (2004) included several taxa in a molecular phylogenetic analysis. Smith’s (2001) revision departed from previous Western treatments (e.g. Haas, 1969a; Zúiganov *et al.*, 1994) most significantly in its system of genera, dividing the species of the family among *Margaritifera*, *Margaritanopsis* and *Pseudunio* based largely upon characters of

the hinge and ctenidia and hypothesized trends in morphological evolution. Bogatov *et al.* (2003) followed previous Russian applications of the ‘Comparatory’ method by recognizing *Dahurinaia* and *Kurilinaia* as distinct from *Margaritanopsis* sensu stricto and listing twice as many species. However, the analysis by Huff *et al.* (2004), while insufficient for a complete revision of the Margaritiferidae, suggested that simply calling all the species *Margaritifera* might be a reasonable solution.

Whereas the superfamily Unionoidea (=Unionidae + Margaritiferidae) is diverse (686 spp.) and widely distributed across the northern continents, the superfamily Etherioidea (=Hyriidae + Etheriidae + Mycetopodidae + Iridinidae) is relatively less speciose (154 spp.), and family-level etherioidean diversity is generally partitioned among the southern continents. Estimates of etherioidean diversity over the last few decades have been relatively more stable than those for unionoideans, but it is also true that the southern freshwater mussels have received considerably less attention. The largest etherioidean family, the Hyriidae (71 spp.), is currently known only from South America and Australasia (McMichael & Hiscock, 1958; Simone, 2006). The remaining three families of the Etherioidea are informally known as the ‘lasidium-bearing mussels,’ based upon their shared larval type (the Unionoidea and Hyriidae retain plesiomorphic glochidia; Graf & Cummings, 2006b). The Mycetopodidae (36 spp.; Haas, 1969a; Simone, 2006) and its sister group, Iridinidae (43 spp.; Mandahl-Barth, 1988; Daget, 1998), are known from Neotropica and Afrotropica, respectively. For these families of the Etherioidea, species concepts appear overly ‘lumped,’ and we hypothesize that etherioidean diversity has been under-estimated.

Traditionally, the family Etheriidae has been regarded as composed of four species of the cementing, freshwater oysters (Pain & Woodward, 1961; Graf, 2000). Three of those species – *Etheria elliptica*, *Acostaea rivoli* and *Pseudomulleria dalyi* – are proper cementers, and they exhibit varying degrees of ‘oysterization’ (Graf & Cummings, 2006b). The fourth, *Bartlettia stefanensis* of South America, is better described as a ‘wedger,’ and that characteristic has been used by some to argue that it would be better classified as a mycetopodid (Parodiz & Bonetto, 1963; but see Mansur & da Silva, 1990). The cementing habit, associated with asymmetrical shell morphology has arisen multiple times among freshwater bivalves, including the unionid genus *Modellinaia* Brandt, 1974 (Bogan & Hoeh, 2000). Further complicating our understanding of etheriid diversity are the molecular phylogenetic results reported by Bogan & Hoeh (2000) that even the core three genera may not form a clade. However, when we reanalysed the available data in the context of a larger data set including morphological characters, we found the core etheriid genera to support a monophyletic Etheriidae (*Bartlettia* was not included; Graf & Cummings, 2006b). We look forward to other molecular phylogenetic studies using a more varied combination of genes and including more individuals.

## GEOGRAPHICAL DIVERSITY

It is widely understood that Nearctica (more specifically, the southeastern United States) has the highest concentration of freshwater mussel diversity in the world. Our census reports 302 species from North America, including northern Mexico (Table 5). Only five of those are classified as margaritiferids, and the remaining species belong to the Unionidae. The bulk of this diversity is concentrated in the Interior Basin (131 spp.) and the Gulf Coastal (147 spp.) subregions, and various studies have already discussed more localized areas of endemism within those subregions (e.g. Johnson, 1980; Lydeard *et al.*, 1999; Brim-Box & Williams, 2000). While comprehensive lexicons of North American unionoid species diversity have been recently

compiled by Turgeon *et al.* (1988, 1998) and Williams *et al.* (1993), those lists (not unlike the present one) come without comprehensive synonymies, and thus it was difficult in many cases to find explanations for their deviations from the earlier, continent-wide revisions of Frierson (1927), Haas (1969a) and Burch (1975).

In the context of the interspecific relationships of the Nearctic freshwater mussel assemblage, it is appropriate to digress momentarily to discuss the effect of phylogenetic analyses of mitochondrial DNA on our understanding of the taxonomy of those taxa. Nucleic acid characters have been widely employed in recent years, and since the watershed work of Lydeard *et al.* (1996), numerous analyses have included multiple congeneric species. These studies have provided limited tests of species-level sister relationships and generic monophyly, and we divide them into two types: (1) those whose primary intention was testing interspecific relationships and (2) those whose primary intention (or actual accomplishment) was to test higher-level patterns of phylogeny. It is significant that, with the exception of the work of Roe, Hartfield & Lydeard (2001; Roe & Hartfield, 2005), type 1 phylogenetic work to date has not led to taxonomic revisions.

Studies of the second type, where species relationships were not as thoroughly examined, are analogous to scattered blasts at the branches of the unionid tree: they successfully falsify the traditional arrangement but they do not provide enough data to propose a reasonable alternative hypothesis of relationships. For example, the charge of 'prodigious polyphyly' has been leveled against the traditional taxon *Fusconaia* (Lydeard, Minton & Williams, 2000; Campbell *et al.*, 2005). Several '*Fusconaia*' species in those studies were recovered in various parts of the amblemine tree (depending upon the analysis), separate from *F. flava* (+*F. trigonia*, the type species). However, it is also true that no morphological characters were included in those analyses, and the mitochondrial markers utilized are notoriously homoplastic and inconsistent (reviewed for mussels by Graf & Cummings, 2006b). To be sure, studies like these provide interesting and important information. However, we do not consider phylogenetic hypotheses automatically equivalent to a revision, and so we have left the appropriate nomenclatural acts to future revisers.

The Mesoamerican assemblage of freshwater mussels is comprised mainly of species of the Unionidae (94 spp.), with only eight mycetopodids occurring as far north as Mexico from South America, their area of greatest diversity (Table 5). Historically, the unionids of Central America have been tacitly associated with Nearctic lineages (Ortmann, 1921b; Frierson, 1927), and Graf (2000) argued that the area was one of a few territories of overlap between the Unionoidea on the northern continents and the Etherioidea from the South. However, the Mesoamerican assemblage, with the exception of only a few species, is distinct from that of North America at the genus level and largely endemic to the American tropics. Accordingly, we have treated Mesoamerica as a subregion of Neotropica. Little current information is available on the unionid fauna of Central America, and we have relied largely upon Frierson (1927) and Haas (1969a) for our estimates of freshwater mussel diversity. Johnson (1981) described the mussel fauna of Cuba.

The South American freshwater mussel fauna is of Gondwanan origin (Graf, 2000), representing three families endemic to the fragments of the former super-continent. Overall, 74 species are currently recognized from South America (Haas, 1969a; Simone, 2006), less than half (43%) of the total, recognized Neotropical species diversity (172 spp.; Table 5). Two species belong to the widespread Etheriidae (but see above), but the two dominant families are the Mycetopodidae (32, +4 in Mesoamerica) and the Hyriidae (40), each presumably

representing a monophyletic South American radiation from a Gondwanan ancestor. The Mycetopodidae, composed of four endemic subfamilies (Tables 3 and 4), have recently been hypothesized to be sister to the Afrotropical Iridinidae (Graf & Cummings, 2006b; but see Graf, 2000; Bogan & Hoeh, 2000). The endemic hyriine tribes Hyriini, Rhipidodontini and Castaliini form a Neotropical clade sister to the Australasian Hyridellini (Graf & Ó Foighil, 2000b). The clade composed of those four tribes, subfamily Hyriinae, is diagnosed by radial beak sculpture, absent in the Australasian Velesunioninae (Graf & Cummings, 2006b).

Until recently, the only continent-wide revisions of the South American freshwater mussel assemblage were the global treatments of Simpson (1900, 1914) and Haas (1969a). There is a copious primary literature on the Neotropical malacofauna by such prolific authors as Bonetto and Mansur, as well as numerous species catalogues for more restricted areas (Table 1), but very little is available in the way of syntheses. Simone (2006), however, in his treatment of Brazil and adjacent areas provided an almost complete continental assessment that will be the likely starting place for further studies of the Neotropical assemblage, and for that reason, it was the primary source for South American genera and species in our checklist. Simone's revision is a significant departure from Haas (1969a), and we remain hopeful that it will be found to be an improvement.

The continent of Africa is inhabited by two, distinct freshwater mussel assemblages, the distributions of which are kept largely separate by the Sahara Desert (Van Damme, 1984; Graf & Cummings, in press). Certain Western Palearctic species and genera (Unionidae and Margaritiferidae) reach their southern limits in Northern Africa, from the Maghreb east to Egypt, and the sub-Saharan, Afrotropical fauna is largely endemic to tropical and southern Africa (Unionidae, Iridinidae and Etheriidae). It is only in the Nile Basin that the species of these two regions mingle. Those extralimital European taxa in northern Africa belong to the Palearctic assemblage, and our discussion of African freshwater mussel diversity will focus on the sub-Saharan and Nile faunas of Afrotropica.

Analogous to the situation in South America, the freshwater mussel assemblage of Afrotropica (85 spp.) is comprised of three families (Tables 3 and 4). There are two dominant families, the Unionidae (41 spp.) and Iridinidae (43), and a single, widespread species of the Etheriidae (*Etheria elliptica*). Extant iridinids are endemic to Africa (but see von Ihering, 1912; Morris & Williamson, 1988) and sister to the Neotropical Mycetopodidae (Graf & Cummings, 2006b). The unionid species form a heterogeneous assemblage, probably derived from at least two invasions of the Unionidae from the north (Graf, 2000). Three species are classified as members of the otherwise-Eurasian Unionini: *Unio abyssinicus* and *U. mancus* in the Blue Nile and *Cafferia caffra* in southern Africa (Graf & Ó Foighil, 2000a; Graf, 2002). The phylogenetic affinities of the remainder have either not been rigorously analysed or are confused. However, based upon what is known of their hard and soft anatomy and current phylogeny estimates, they can be confidently assigned to the Unionidae (Graf & Cummings, 2006b). We regard those 38, non-unionine species as *incertae sedis* Afrotropical Unionidae.

Africa is easily divided into a number of subregions based on the apparently high basin-endemism of freshwater mussel species (Fig. 1; see also the freshwater 'ecoregions' identified by Thieme *et al.*, 2005). Among these regions is the island subcontinent of Madagascar (with which we include the oceanic Mascarene Islands). The reported Malagasy diversity of five species in two families (Table 5) is meagre, and the current taxonomy is problematic regarding our current understanding of the biogeographical processes presumed to be involved. *Etheria elliptica* (Etheriidae), as currently conceived (Pilsbry & Bequaert,

1927; Pain & Woodward, 1961; Daget, 1998), is distributed widely on Africa and Madagascar. However, given the hypothesized difficulty of unionoid dispersal across oceanic barriers like the Mozambique Channel and the deep-time divergence associated with a Gondwanan vicariance scenario (ca. 160 Ma; Storey, 1995), it is hard for us to make sense of such a distribution for a single species. The four other recognized Malagasy species have been assigned to the catchall African genus *Coelatura*: *C. madagascarensis*, *C. malgachensis*, *C. geayi* and *C. cariei*; the last of these was described from Reunion (Haas, 1969a; Fischer-Peitte & Vukadinovic, 1973; Daget, 1998). In addition, we have seen specimens of various taxa reported from Mauritius, and indeed Haas (1969a) considered *Unio brevisialis* Lamarck, 1819, described from 'l'Isle de France,' to possibly be from that island. Classified as unionids, the presence of these species on these ancient, long-isolated fragments of Gondwana or oceanic islands is problematic. Unfortunately, extant specimens representing those species are rare, and the ones that are available are in poor condition. An alternative hypothesis – equally probable as a pre-Gondwanan origin of the Unionidae – could be that these taxa are actually hyriids, known to have been widely distributed on the southern supercontinent (Graf & Ó Foighil, 2000b) and difficult to distinguish from unionids based solely upon shell characters (Graf & Cummings, 2006b). For the specimens from Reunion and Mauritius it remains possible that these reports are simply the unfortunate result of miscommunication.

The entire African (and Malagasy) unionoid fauna has recently been revised (Mandahl-Barth, 1988; Daget, 1998), in addition to the earlier comprehensive treatments of Simpson (1900, 1914), Pilsbry & Bequaert (1927) and Haas (1969a, b) and the several more localized studies listed in Table 1. While the taxonomies used by Mandahl-Barth and Daget are broadly consistent with each other, they are a significant deviation from Haas (1969a), and indeed our experience has led us to the conclusion that Haas's system is a poor representation of the African diversity. Moreover, as portions of the Afrotropical freshwater mussel fauna have been considered on the basis of museum material or new collections, recent studies have found the accepted arrangement to be an under-estimate (e.g. Scholz & Glaubrecht, 2004; Graf & Cummings, 2006a, in press). We expect that as more of the species from Afrotropica come under scrutiny, the arrangements advocated by Mandahl-Barth (1988) and Daget (1998) will be further split to reflect the natural relationships among the various lineages of African unionoids.

The estimates of freshwater mussel diversity of Palearctica are arguably the most contentious due to the clash between disparate philosophies for diagnosing and classifying species and higher taxa: the Biological Species Concept vs. the eastern Russian 'Comparatory' Method (Korniushin, 1998; Graf, 2007). Further complicating any effort to thoroughly revise the Palearctic unionoid assemblage is the daunting number of available names, mostly described by 'splitters' of the French *Nouvelle École* (Dance, 1970). These challenges make it difficult to manage taxonomic information for Eurasian freshwater mussels.

The Palearctic Region, as applied here to freshwater mussel distributions, follows Graf (2007). It includes nearly all of Eurasia, excluding the Indotropical Region in the southeast: from Europe, northern Africa and the Middle East, east across Siberia to Japan and Kamchatka (Table 2 and Fig. 1). We consider five species of the Western Palearctic freshwater mussel assemblage to be *incertae sedis* unionids. These belong to the monotypic genera *Potomida*, *Microcondylaea* and *Pseudodontopsis*, and to *Leguminaria* (2 spp.), known from southern Europe and the Middle East (Falkner, 1994; Falkner, Bank & von Proschwitz, 2001; Falkner, Ripkin & Falkner, 2002). Recent works have assigned these taxa to various Nearctic lineages

(Nagel, Badino & Celebrano, 1998; Nagel & Badino, 2001) but, as discussed by Graf (2002), the characters upon which those arrangements were based are generally plesiomorphic among the Unionoidea.

At the family level, the Palearctic unionoid assemblage is composed of representatives from two families, Unionidae and Margaritiferidae. However, depending upon which School of Malacology one chooses to follow, estimates of Palearctic freshwater mussel species diversity can range over a factor of three. Based upon the works of the 'lumpers,' including Zhadin (1938, 1965), Haas (1940, 1969a), Habe (1977, 1991), Bába (2000) and Falkner *et al.* (2001, 2002), the consensus estimate is 45 spp., with numerous recognized subspecies. Adding all the 'species' recognized by the 'Comparatory' malacologists, such as Zatravkin (1983, 1987), Bogatov *et al.* (2003), Bogatov, Starobogatov & Prozorova (2005), Starobogatov *et al.* (2004) and Kantor & Sysoev (2005), increases the Palearctic regional tally to 156 species (Graf, 2007). Taxonomic revision of the unionoid species in the region will require an exhaustive, synthetic approach featuring not only reexamination of morphological characters and incorporation of molecular phylogenetic analyses, but also a thorough reevaluation of the last 200+ years of alpha taxonomy.

Indotropica in southeastern Asia extends from Central China southward and east from the Indus Basin of Pakistan and India, through Indochina and the larger islands of the Philippines and Indonesia (excluding New Guinea; Table 2). The region is the second-most diverse, with 219 freshwater mussel species in three families (Table 5). Only one of those species, *Pseudomulleria dalyi* in India, represents the Etherioidea and (presumably) the Gondwanan freshwater mussel assemblage (Graf & Cummings, 2006b; but see Bogan & Hoeh, 2000). The remaining Indotropical species represent the Unionoidea and the northern continents. All but one of these (*Margaritifera laosensis*) are classified as Unionidae (217 spp.), but 182 (84%) belong to *incertae sedis* unionid genera. The Indotropical *incertae sedis* unionids have been traditionally treated among the Nearctic amblemines. Although phylogenetic studies have only touched upon the Asian freshwater mussel assemblage, they have been sufficient to demonstrate that the traditional classification does not reflect natural relationships (Graf, 2002; Huang *et al.*, 2002; Walker *et al.*, 2006).

Our current tally of freshwater mussel species for the Indotropical Region has been compiled from a variety of sources, most of rather parochial focus and often with competing views of unionoid diversity (Table 1). While the freshwater mussel faunas of India and Burma (Subba Rao, 1989), Thailand (Brandt, 1974), Vietnam (Đang *et al.*, 1980) and China (Liu, 1979; Prozorova *et al.*, 2005) have been recently dealt with in detail, for other areas of southeastern Asia, we have had to rely upon Haas (1969a). As with other tropical areas of the world, we expect that as Indotropical unionoids are reexamined using modern methods, the species (and higher level) diversity will be found to be even greater than currently understood.

The freshwater mussels of the Australasian region were completely revised in 1958 by McMichael & Hiscock. Though somewhat dated, especially with regard to phylogenetic and biogeographic conclusions, their taxonomic arrangement has remained largely intact (Haas, 1969a; Smith, 1992; Walker *et al.*, 2001). We currently estimate 33 unionoid species in the Australasian region (Table 5). While species diversity is low relative to other continental areas of similar size (and latitude), at least three family-group level lineages occur in the Australasian region (Table 5; Graf & Ó Foighil, 2000b; Graf & Cummings, 2006b). The Unionidae are represented by a single genus, *Haasodonta*, in New Guinea. Assuming that this classification (based solely upon shell characters) is accurate, it may represent an invasion of the Australasian



region by the Unionidae from the Sunda Islands of Indonesia. However, the actual phylogenetic affinities of *Haasodonta* are unknown, and we treat it as part of the Indotropical assemblage of *incertae sedis* genera. Hyriids are represented by at least two clades that have persisted since before the breakup of Gondwana (ca. 150 Ma; Storey, 1995; Jokat *et al.*, 2003). However, ongoing research in Australia and New Zealand continues to reveal novel diversity at the genus, species and cyto-plasmid levels (Baker *et al.*, 2004; Hughes *et al.*, 2004; Ponder & Bayer, 2004; Fenwick & Marshall, 2006; Marshall & Fenwick, 2006).

## CONCLUSIONS AND COMMENTS

We hope our discussion and checklist of global freshwater mussel diversity will have the same effect that Simpson's (1900, 1914) did a century earlier: interest and discussion in the Unionoida will increase (von Ihering, 1901; Sterki, 1903; Frierson, 1910; Ortmann, 1910; etc.), and new data and analyses will test and refine the patterns we have described. Our effort to compile and analyse diverse literature sources provided an interesting perspective on the history of freshwater malacological research. Besides the challenges associated with the near absence of a global perspective in most species-level revisionary studies and the ridiculous number of available species names, freshwater mussel systematics (indeed, systematics in general) has historically been based upon authoritarian essays. Since most practising systematists, regardless of their philosophical background, regard species to be the lone objective level of taxonomy (i.e. species are real; Wheeler & Meier, 2000), it is paradoxical that species delineation should have proceeded in such a casual manner. Since the New Synthesis (Mayr, 1963; and earlier, e.g. Darwin, 1859), the systematic community has continually reevaluated 'species concepts', and various schemes provide criteria for recognizing natural, terminal lineages (Eldredge & Cracraft, 1980). However, while the taxonomic community has collectively conceded that species *should* be natural entities, by not reevaluating the traditional arrangements, we have tacitly laundered an out-moded system into legitimacy by assuming that they *are* natural until demonstrated otherwise.

Supraspecific taxa have recently come under scrutiny (reviewed by Roe & Hoeh, 2003; Campbell *et al.*, 2005; Graf & Cummings, 2006b; Walker *et al.*, 2006), and that work, though just beginning, has moved our understanding of the historical pattern of freshwater mussel diversity into a modern framework. But what of species? For the vast majority of unionoid species, the data are as yet unavailable to test whether or not they conform to biological species, evolutionary species, phylogenetic species or other modern concepts. Rather, our collections mostly of shells require the application of a morphological basis for recognition: if species are reproductively isolated lineages (biological species) with their own evolutionary trajectories (evolutionary species) and derived diagnostic or autapomorphic characters inherited from a shared ancestor (phylogenetic species), then members of that species should look similar to each other. Thus, freshwater mussels that look different from each other belong to different species, of course taking into account morphological variation (often extreme; Ortmann, 1920). A strictly morphological basis for circumscribing specimens into the various species concepts is not ideal, but it is better than nothing. Specimens can be arranged into (figurative) piles with similar morphology, and including type specimens provides the basis for turning piles into named taxa. Unfortunately, freshwater mussel systematics has too often proceeded without explicit reference to specimens or types. Synonymies have been treated as something to look up rather than assemble from collections research, and little attention has been paid to the assumptions and methods behind the circumscription of freshwater mussel specimens – representing

various populations and/or morphological variants – into species.

Our checklist follows in the tradition of reviewing rather than revising. Given the caveats that we have laid out, it might seem that our tally of global freshwater mussel diversity is so flawed that it cannot be trusted. However, while certainly not perfect and unlikely to be agreed upon in its entirety by all interested parties (including the authors!), it is an explicit summary of what is known about the global, species-level diversity of the Unionoida. Rather than throwing the baby out with the bathwater, we can provisionally accept this summary and checklist of freshwater mussel diversity as the most complete synthesis available. We are optimistic that highlighting the numerous areas of inconsistency in the classification of freshwater mussels will prove to be a useful resource and catalyse future revisions of the Unionoida.

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## APPENDIX

*Checklist and classification of unionoid genera and species*

The following checklist forms the basis for our global and regional tallies of freshwater mussel diversity. The classification follows Graf & Cummings (2006b) except for numerous *incertae sedis* unionid genera, which are assigned to geographical assemblages to facilitate data retrieval and discussion (Table 3). Taxa at the same hierarchical level are arranged alphabetically except for the type taxon, which is always listed first. Junior synonyms (at all levels) are listed only to indicate type taxa. Key references for establishing species diversity and ranges are provided for each genus. Species-level taxa missing from other modern checklists are marked with a question mark (?). Each species is assigned to one or more geographical subregions (Table 2). Regions are abbreviated as follows: AF, Afrotropica; AU,

Australasia; IN, Indotropica; NA, Nearctica; NT, Neotropica; PA, Palearctica.

## Order UNIONOIDA

### Superfamily UNIONOIDEA Rafinesque, 1820

#### Family UNIONOIDEA s.s.

#### Subfamily UNIONINAE s.s.

#### Tribe UNIONINI s.s.

*Unio* Philipsson in Retzius, 1788: Haas (1940, 1969a), Falkner (1994), Falkner *et al.* (2001, 2002).

*U. pictorum* (Linnaeus, 1758): PA(Europe).

*U. abyssinicus* von Martens, 1866: AF(Nile).

*U. crassus* Philipsson in Retzius, 1788: PA(Europe, Middle East, Amur-Beringia).

*U. mancus* Lamarck, 1819: PA(Europe, Middle East), AF(Nile).

*U. terminalis* Bourguignat, 1852: PA(Middle East).

*U. tigridis* Bourguignat, 1852: PA(Middle East).

*U. tumidus* Philipsson in Retzius, 1788: PA(Europe).

*Acuticosta* Simpson, 1900: Liu (1979), Hu (2005), Prozorova *et al.* (2005).

*A. chinensis* (Lea, 1868): IN(Yangtze-Huang).

*A. ovata* (Simpson, 1900): IN(Yangtze-Huang).

*A. retiararia* (Heude, 1883): IN(Yangtze-Huang).

*A. sichuanica* Zeng & Liu, 1989: IN(Yangtze-Huang).

*A. trisulcata* (Heude, 1883): IN(Yangtze-Huang).

*Arconaia* Conrad, 1865: Liu (1979), Hu (2005), Prozorova *et al.* (2005).

*A. lanceolata* (Lea, 1856): IN(Yangtze-Huang).

*A. huaiensis* Huang & Li, 2003: IN(Yangtze-Huang).

*A. mutica* (Heude, 1877): IN(Yangtze-Huang).

*Cafferia* Simpson, 1900: Mandahl-Barth (1988), Daget (1998).

*C. caffra* (Krauss, 1848): AF(South).

*Cuneopsis* Simpson, 1900: Liu (1979), Đang *et al.* (1980), Hu (2005), Prozorova *et al.* (2005).

*C. celtiformis* (Heude, 1874): IN(Yangtze-Huang).

*C. capitatus* (Heude, 1874): IN(Yangtze-Huang).

*C. demangei* Haas, 1929: IN(Indochina).

*C. heudei* (Heude, 1874): IN(Yangtze-Huang, Indochina).

*C. pisciculus* (Heude, 1874): IN(Yangtze-Huang).

*C. rufescens* (Heude, 1874): IN(Yangtze-Huang).

*Inversiunio* Habe, 1991: Habe (1991), Kondo (1998).

*I. reinianus* (Kobelt, 1879): PA(Japan-Sakhalin).

*I. jokohamensis* (von Ihering, 1893): PA(Japan-Sakhalin).

*I. yanagawensis* (Kondo, 1982): PA(Japan-Sakhalin).

*Lanceolaria* Conrad, 1853: Haas (1969a), Liu (1979), Habe (1991), Prozorova *et al.* (2005).

*L. grayana* (Lea, 1834): IN(Indochina).

*L. acrorrhyncha* (von Martens, 1894): PA(Amur-Beringia).

*L. cylindrica* (Simpson, 1900): PA(Amur-Beringia).

*L. eucylindrica* Lin, 1962: IN(Yangtze-Huang).

*L. gladiola* (Heude, 1877): IN(Yangtze-Huang, Indochina).

*L. oxyrhyncha* (von Martens, 1861): IN(Indochina), PA(Japan-Sakhalin).

*L. triformis* (Heude, 1877): IN(Yangtze-Huang).

*Lepidodesma* Simpson, 1896: Liu (1979), Hu (2005), Prozorova *et al.* (2005).

*L. languilati* (Heude, 1874): IN(Yangtze-Huang).

*L. aligera* (Heude, 1877): IN(Yangtze-Huang).

*Nodularia* Conrad, 1853: Haas (1969a), Habe (1991), Liu (1979), Đang *et al.* (1980), Kondo (1997).

*N. douglasiae* (Griffith & Pidgeon, 1834): PA(Amur-Beringia, Japan-Sakhalin), IN(Yangtze-Huang).

*N. denserugata* Haas, 1910: IN(Indochina).

*N. dorri* (Wattebled, 1886): IN(Indochina).

*N. schoedei* (Haas, 1930): IN(Indochina).

*Rhombuniopsis* Haas, 1920: Haas (1969a), Moskvicheva & Starobogatov (1973).

*R. tauriformis* (Fulton, 1906): IN(Indochina).

*R. fultoni* Moskvicheva & Starobogatov, 1973: IN(Indochina).

*R. superstes* (Neumayr, 1899): IN(Indochina).

*Schistodesmus* Simpson, 1900: Liu (1979), Hu (2005), Prozorova *et al.* (2005).

*S. lampreyanus* (Baird & Adams, 1867): IN(Yangtze-Huang).

*S. spinosus* Simpson, 1900: IN(Yangtze-Huang).

## Tribe ANODONTINI Rafinesque, 1820

(Old World and Pacific Nearctic anodontines)

*Anodonta* Lamarck, 1799: Haas (1940, 1969a), Burch (1975), Turgeon *et al.* (1998), Williams *et al.* (1993), Falkner (1994), Daget (1998), Falkner *et al.* (2001, 2002).

*A. cygnea* (Linnaeus, 1758): PA(Europe).

*A. anatina* (Linnaeus, 1758): PA(Europe, Central).

*A. beringiana* Middendorff, 1851: PA(Amur-Beringia), NA(Pacific).

*A. californiensis* Lea, 1852: NA(Pacific).

*A. cyrea* Drouët, 1881: PA(Central).

*A. dejecta* Lewis, 1875: NA(Pacific).

*A. impura* Say, 1829: NA(Pacific).

*A. kennerlyi* Lea, 1860: NA(Pacific).

*A. lurulenta* Morelet, 1849: NT(Mesoamerica).

*A. nuttalliana* Lea, 1838: NA(Pacific).

*A. oregonensis* Lea, 1838: NA(Pacific).

*A. pseudodopsis* Locard, 1883: PA(Middle East).

*A. vescoiana* Bourguignat, 1856: PA(Middle East).

*Anemina* Haas, 1969: Haas (1969a), Liu (1979), Habe (1991), Hu (2005), Prozorova *et al.*, (2005).

*A. arcaeformis* (Heude, 1877): IN(Yangtze-Huang), PA(Amur-Beringia, Japan-Sakhalin).

*A. angula* Tchang, Li & Liu, 1965: IN(Yangtze-Huang).

*A. euscaphys* (Heude, 1879): IN(Yangtze-Huang), PA(Amur-Beringia).

*A. fluminea* (Heude, 1877): IN(Yangtze-Huang).

*A. globosula* (Heude, 1878): IN(Yangtze-Huang).

*Cristaria* Schumacher, 1817: Brandt (1974), Liu (1979), Đang *et al.* (1980), Habe (1991), Prozorova *et al.* (2005).

*C. plicata* (Leach, 1815): IN(Yangtze-Huang, Indochina), PA(Amur-Beringia, Japan-Sakhalin).

+ *Cristaria tuberculata* Schumacher, 1817

*C. discoidea* (Lea, 1834): IN(Yangtze-Huang, Indochina), PA(Japan-Sakhalin).

?*C. radiata* Simpson, 1900: IN(Yangtze-Huang).

*C. truncata* Đang, Thái & Pham, 1980: IN(Indochina).

*Pseudanodonta* Bourguignat, 1876: Falkner *et al.* (2001, 2002).

*P. complanata* (Rossmässler, 1835): PA(Europe).

*Simpsonella* Cockerell, 1903: Haas (1969a).

*S. purpurea* (Valenciennes in Humboldt & Bonpland, 1821): IN(Sunda-Philippines).

*S. gracilis* (Lea, 1850): IN(Sunda-Philippines).

*Sinanodonta* Modell, 1945: Haas (1969a), Liu (1979), Đang *et al.* (1980), Habe (1991), Prozorova *et al.* (2005).

- S. woodiana* (Lea, 1834): IN(Yangtze-Huang, Indochina), PA(Central, Amur-Beringia, Japan-Sakhalin) [widely introduced].  
*S. ogurae* (Kuroda & Habe, 1987) [nov. comb.]: PA(Japan-Sakhalin).

(eastern Nearctic anodontines)

- Alasmidonta* Say, 1818: Clarke (1981), Brim-Box & Williams (2000).  
*A. (Alasmidonta) undulata* (Say, 1817): NA(Atlantic).  
*A. (Alasmidonta) arcula* (Lea, 1838): NA(Atlantic).  
*A. (Alasmidonta) triangulata* (Lea, 1858): NA(Gulf).  
*A. (Alasmidonta) wrightiana* (B. Walker, 1901): NA(Gulf).  
*A. (Alasmidens) mccordi* Athearn, 1964: NA(Gulf).  
*A. (Decurambis) marginata* Say, 1818: NA(Interior, Atlantic).  
 + *Decurambis scriptum* Rafinesque, 1831  
*A. (Decurambis) atropurpurea* (Rafinesque, 1831): NA(Interior).  
*A. (Decurambis) raveneliana* (Lea, 1834): NA(Interior).  
*A. (Decurambis) robusta* Clarke, 1981: NA(Atlantic).  
*A. (Decurambis) varicosa* (Lamarck, 1819): NA(Atlantic).  
*A. (Pressodonta) viridis* (Rafinesque, 1820): NA(Interior).  
 + *Unio calceolus* Lea, 1828  
*A. (Pressodonta) heterodon* (Lea, 1829): NA(Atlantic).  
*Anodontoides* Simpson in F.C. Baker, 1898: Burch (1975), Parmalee & Bogan (1998).  
*A. ferussacianus* (Lea, 1834): NA(Interior).  
*A. radiatus* (Conrad, 1834): NA(Gulf).  
*Arcidens* Simpson, 1900: Burch (1975), Clarke (1981).  
*A. (Arcidens) confragosus* (Say, 1829): NA(Interior, Gulf).  
*A. (Arkansia) wheeleri* (Ortmann & B. Walker, 1912): NA(Interior).  
*Lasmigona* Rafinesque, 1831: Clarke (1985).  
*L. (Lasmigona) costata* (Rafinesque, 1820): NA(Interior).  
*L. (Lasmigona) complanata* (Barnes, 1823): NA(Interior, Gulf).  
*L. (Alasminota) holstonia* (Lea, 1838): NA(Interior, Gulf).  
*L. (Platynaias) compressa* (Lea, 1829): NA(Interior).  
*L. (Platynaias) decorata* (Lea, 1852): NA(Atlantic).  
*L. (Platynaias) subviridis* (Conrad, 1835): NA(Interior, Atlantic).  
*Pegias* Simpson, 1900: Clarke (1981), Parmalee & Bogan (1998).  
*P. fabula* (Lea, 1838): NA(Interior).  
*Pyganodon* Crosse & Fischer, 1894: Johnson (1970), Parmalee & Bogan (1998).  
*P. grandis* (Say, 1829): NA(Interior, Gulf), NT(Mesoamerica).  
 + *Anodonta globosa* Lea 1841  
*P. cataracta* (Say, 1817): NA(Atlantic, Gulf).  
*P. gibbosa* (Say, 1824): NA(Atlantic).  
*P. implicata* (Say, 1829): NA(Atlantic).  
*Simpsonaias* Frierson, 1914: Haas (1969a), Clarke (1985), Parmalee & Bogan (1998).  
*S. ambigua* (Say, 1825): NA(Interior).  
*Strophitus* Rafinesque, 1820: Burch (1975), Parmalee & Bogan (1998).  
*S. undulatus* (Say, 1817): NA(Interior, Atlantic).  
*S. comasaugaensis* (Lea, 1858): NA(Gulf).  
*S. subvexus* (Conrad, 1834): NA(Gulf).  
*Utterbackia* F.C. Baker, 1927: Burch (1975), Parmalee & Bogan (1998), Brim-Box & Williams (2000).  
*U. imbecillis* (Say, 1829): NA(Interior, Gulf).  
*U. couperiana* (Lea, 1840): NA(Atlantic, Florida).  
*U. heardi* (Gordon & Hoeh, 1995) [nov. comb.]: NA(Gulf).  
*U. peggyae* (Johnson, 1965): NA(Gulf).

- U. peninsularis* Bogan & Hoeh, 1995: NA(Florida).  
*U. suborbiculata* (Say, 1831): NA(Interior, Gulf).

**Subfamily AMBLEMINEAE Rafinesque, 1820**  
**the AMBLEMINI Tribe group**  
**Tribe AMBLEMINI s.s.**

- Amblema* Rafinesque, 1820: Parmalee & Bogan (1998), Brim-Box & Williams (2000).  
*A. plicata* (Say, 1817): NA(Interior, Gulf).  
 + *Amblema costata* Rafinesque, 1820  
*A. elliottii* (Lea, 1856): NA(Gulf).  
*A. neislerii* (Lea, 1858): NA(Gulf).

**Tribe LAMPSILINI von Ihering, 1901**

- Lampsilis* Rafinesque, 1820: Haas (1969a), Burch (1975), Johnson (1980), Parmalee & Bogan (1998).  
*L. ovata* (Say, 1817): NA(Interior).  
*L. abrupta* (Say, 1831): NA(Interior).  
*L. binominata* Simpson, 1900: NA(Gulf).  
*L. bracteata* (Gould, 1855): NA(Gulf).  
*L. cardium* Rafinesque, 1820: NA(Interior).  
*L. cariosa* (Say, 1817): NA(Atlantic).  
*L. dolabraeformis* (Lea, 1838): NA(Atlantic).  
*L. fasciola* Rafinesque, 1820: NA(Interior).  
*L. fullerkeri* R.I. Johnson, 1984: NA(Atlantic).  
*L. haddletomi* Athearn, 1964: NA(Gulf).  
*L. higginsii* (Lea, 1857): NA(Interior).  
*L. hydiana* (Lea, 1838): NA(Interior, Gulf).  
*L. ornata* (Conrad, 1835): NA(Gulf).  
*L. powellii* (Lea, 1852): NA(Interior).  
*L. radiata* (Gmelin, 1791): NA(Atlantic).  
*L. rafinesqueana* Frierson, 1927: NA(Interior).  
*L. reeviana* (Lea, 1852): NA(Interior).  
*L. satura* (Lea, 1852): NA(Interior, Gulf).  
*L. siliquioidea* (Barnes, 1823): NA(Interior).  
*L. splendida* (Lea, 1838): NA(Atlantic).  
*L. straminea* (Conrad, 1834): NA(Gulf).  
*L. streckeri* Frierson, 1927: NA(Interior).  
*L. teres* (Rafinesque, 1820): NA(Interior, Gulf).  
*L. virescens* (Lea, 1858): NA(Interior).  
*Actinonaias* Crosse & Fischer, 1894: Frierson (1927), Haas (1969a), Parmalee & Bogan (1998).  
*A. sapotalensis* (Lea, 1841): NT(Mesoamerica).  
*A. computata* (Crosse & Fischer, 1893): NT(Mesoamerica).  
*A. coyensis* (Pilsbry, 1910): NT(Mesoamerica).  
*A. ligamentina* (Lamarck, 1819): NA(Interior).  
*A. medellina* (Lea, 1838): NT(Mesoamerica).  
*A. moctezumensis* (Pilsbry, 1910): NT(Mesoamerica).  
*A. pectorosa* (Conrad, 1834): NA(Interior).  
*A. signata* (Pilsbry, 1910): NT(Mesoamerica).  
*A. undivaga* (Pilsbry, 1910): NT(Mesoamerica).  
*Arotonaias* von Martens, 1900: Frierson (1927).  
*A. cyrenoides* (Philippi, 1847): NT(Mesoamerica).  
*A. imbricata* (Mörch, 1861): NT(Mesoamerica).  
*A. nicaraguensis* (Lea, 1868): NT(Mesoamerica).  
*Cyprogenia* Agassiz, 1852: Johnson (1980), Parmalee & Bogan (1998).  
*C. stegaria* (Rafinesque, 1820): NA(Interior).  
 + *Unio irroratus* Lea, 1828  
*C. aberti* (Conrad, 1850): NA(Interior).  
*Cyrtonaias* Crosse & Fischer, 1894: Haas (1969a).  
*C. tampicoensis* (Lea, 1838): NA(Gulf), NT(Mesoamerica).

- + *Unio berlandierii* Lea, 1857  
*C. explicata* (Morelet, 1849): NT(Mesoamerica).  
*C. livida* (Simpson, 1900): NT(Mesoamerica).  
*C. saladoensis* (Lea, 1860): NA(Gulf).  
*C. sapperi* (von Ihering, 1901): NT(Mesoamerica).  
*C. umbrosa* (Lea, 1856): NT(Mesoamerica).
- Delphinonaias* Crosse & Fischer, 1894: Haas (1969a).  
*D. delphinulus* (Morelet, 1849): NT(Mesoamerica).  
*D. paludosa* (Morelet, 1849): NT(Mesoamerica).  
*D. planivalvis* (Morelet, 1851): NT(Mesoamerica).  
*D. scutulata* (Morelet, 1849): NT(Mesoamerica).
- Disconaias* Crosse & Fischer, 1894: Haas (1969a).  
*D. disca* (Lea, 1838): NT(Mesoamerica).  
*D. conchos* Taylor, 1997: NA(Gulf).  
*D. fimbriata* (Frierson, 1907): NA(Gulf), NT(Mesoamerica).  
*D. novoleonis* (Pilsbry, 1910): NT(Mesoamerica).  
*D. panacoensis* (von dem Busch in Philippi, 1843):  
 NT(Mesoamerica).  
*D. purpurata* (Say, 1831): NT(Mesoamerica).
- Dromus* Simpson, 1900: Parmalee & Bogan (1998).  
*D. dromas* (Lea, 1834): NA(Interior).
- Ellipsaria* Rafinesque, 1820: Parmalee & Bogan (1998).  
*E. lineolata* (Rafinesque, 1820): NA(Interior, Gulf).  
 + *Obliquaria* (*Ellipsaria*) *ellipsaria* Rafinesque, 1820
- Epioblasma* Rafinesque, 1831: Johnson (1978), Parmalee & Bogan (1998).  
*E. flexuosa* (Rafinesque, 1820): NA(Interior).  
 + *Epioblasma biloba* Rafinesque, 1831  
*E. arcaeformis* (Lea, 1831): NA(Interior).  
*E. biemarginata* (Lea, 1857): NA(Interior).  
*E. brevidens* (Lea, 1831): NA(Interior).  
*E. capsaeformis* (Lea, 1834): NA(Interior).  
*E. florentina* (Lea, 1857): NA(Interior).  
*E. haysiana* (Lea, 1834): NA(Interior).  
*E. lenior* (Lea, 1840): NA(Interior).  
*E. lewisii* (B. Walker, 1910): NA(Interior).  
*E. metastrata* (Conrad, 1838): NA(Gulf).  
*E. obliquata* (Rafinesque, 1820): NA(Interior).  
*E. othcaloogensis* (Lea, 1857): NA(Gulf).  
*E. penita* (Conrad, 1834): NA(Gulf).  
*E. personata* (Say, 1829): NA(Interior).  
*E. propinqua* (Lea, 1857): NA(Interior).  
*E. sampsonii* (Lea, 1862): NA(Interior).  
*E. stewardsonii* (Lea, 1852): NA(Interior).  
*E. torulosa* (Rafinesque, 1820): NA(Interior).  
*E. triquetra* (Rafinesque, 1820): NA(Interior).  
*E. turgidula* (Lea, 1858): NA(Interior).
- Frierionia* Ortmann, 1912: Haas (1969a).  
*F. iridella* (Pilsbry & Frierson, 1907): NT(Mesoamerica).
- Glebulia* Conrad, 1853: Burch (1975).  
*G. rotundata* (Lamarck, 1819): NA(Gulf).
- Hamiota* Roe & Hartfield, 2005: Roe & Hartfield (2005).  
*H. subangulata* (Lea, 1840): NA(Gulf).  
*H. altilis* (Conrad, 1834): NA(Gulf).  
*H. australis* (Simpson, 1900): NA(Gulf).  
*H. perovalis* (Conrad, 1834): NA(Gulf).
- Lemiox* Rafinesque, 1831: Parmalee & Bogan (1998).  
*L. rimosus* (Rafinesque, 1831): NA(Interior).
- Leptodea* Rafinesque, 1820: Johnson (1970), Parmalee & Bogan (1998).  
*L. fragilis* (Rafinesque, 1820): NA(Interior, Gulf).
- L. leptodon* (Rafinesque, 1820): NA(Interior).  
*L. ochracea* (Say, 1817): NA(Atlantic).
- Ligumia* Swainson, 1840: Burch (1975), Parmalee & Bogan (1998).  
*L. recta* (Lamarck, 1819): NA(Interior, Gulf).  
*L. nasuta* (Say, 1817): NA(Interior, Atlantic).  
*L. subrostrata* (Say, 1831): NA(Interior).
- Medionidus* Simpson, 1900: Johnson (1977), Parmalee & Bogan (1998).  
*M. conradicus* (Lea, 1834): NA(Interior).  
*M. acutissimus* (Lea, 1831): NA(Gulf).  
*M. mcglameriae* van der Schalie, 1939: NA(Gulf).  
*M. parvulus* (Lea, 1860): NA(Gulf).  
*M. penicillatus* (Lea, 1857): NA(Gulf).  
*M. simpsonianus* B. Walker, 1905: NA(Gulf).  
*M. walkerii* (S.H. Wright, 1897): NA(Gulf).
- Obliquaria* Rafinesque, 1820: Parmalee & Bogan (1998).  
*O. reflexa* Rafinesque, 1820: NA(Interior, Gulf).
- Obovaria* Rafinesque, 1819: Burch (1975), Parmalee & Bogan (1998).  
*O. retusa* (Lamarck, 1819): NA(Interior).  
 + *Obovaria torsa* Rafinesque, 1820  
*O. jacksoniana* (Frierson, 1912): NA(Interior, Gulf).  
*O. olivaria* (Rafinesque, 1820): NA(Interior).  
*O. rotulata* (B.H. Wright, 1899): NA(Gulf).  
*O. subrotunda* (Rafinesque, 1820): NA(Interior).  
*O. unicolor* (Lea, 1845): NA(Gulf).
- Potamilus* Rafinesque, 1818: Simpson (1914), Haas (1969a), Burch (1975), Johnson (1980), Parmalee & Bogan (1998).  
*P. alatus* (Say, 1817): NA(Interior, Gulf).  
*P. amphichaenus* (Frierson, 1898): NA(Gulf).  
*P. capax* (Green, 1832): NA(Interior).  
*P. inflatus* (Lea, 1831): NA(Gulf).  
 ?*P. largillierti* (Philippi, 1847): NT(Mesoamerica).  
*P. metnecktayi* R.I. Johnson, 1998: NA(Gulf).  
*P. ohioensis* (Rafinesque, 1820): NA(Interior, Gulf).  
*P. purpuratus* (Lamarck, 1819): NA(Interior, Gulf).  
*P. rovirosai* (Pilsbry, 1900): NT(Mesoamerica).
- Ptychobranthus* Simpson, 1900: Burch (1975), Johnson (1980), Parmalee & Bogan (1998).  
*P. fasciolaris* (Rafinesque, 1820): NA(Interior).  
 + *Unio phaseolus* Hildreth, 1828  
*P. greenii* (Conrad, 1834): NA(Gulf).  
*P. jonesi* (van der Schalie, 1934): NA(Gulf).  
*P. occidentalis* (Conrad, 1836): NA(Interior).  
*P. subtentum* (Say, 1825): NA(Interior).
- Toxolasma* Rafinesque, 1831: Haas (1969a), Burch (1975), Parmalee & Bogan (1998).  
*T. lividus* Rafinesque, 1831: NA(Interior).  
*T. corvunculus* (Lea, 1868): NA(Gulf).  
*T. cylindrellus* (Lea, 1868): NA(Interior).  
*T. mearnsi* (Simpson, 1900): NA(Gulf).  
*T. parvus* (Barnes, 1823): NA(Interior, Gulf).  
*T. paulus* (Lea, 1840): NA(Gulf).  
*T. pullus* (Conrad, 1838): NA(Atlantic).  
*T. texasiensis* (Lea, 1857): NA(Interior, Gulf).
- Truncilla* Rafinesque, 1819: Haas (1969a), Parmalee & Bogan (1998).  
*T. truncata* Rafinesque, 1820: NA(Interior).  
*T. cognata* (Lea, 1860): NT(Mesoamerica).  
*T. donaciformis* (Lea, 1828): NA(Interior, Gulf).  
*T. macrodon* (Lea, 1859): NA(Gulf).



*Venustaconcha* Frierson, 1927: Frierson (1927), Haas (1969a).

- V. ellipsiformis* (Conrad, 1836): NA(Interior).
- + *Unio venustus* Lea, 1838
- V. pleasii* (Marsh, 1891): NA(Interior).

*Villosa* Frierson, 1927: Johnson (1970, 1972, 1980), Burch (1975), Turgeon *et al.* (1998), Parmalee & Bogan (1998).

- V. villosa* (B.H. Wright, 1898): NA(Florida, Gulf).
- V. amygdala* (Lea, 1843): NA(Florida).
- V. arkansasensis* (Lea, 1862): NA(Interior).
- V. choctawensis* Athearn, 1964: NA(Gulf).
- V. constricta* (Conrad, 1838): NA(Atlantic).
- V. delumbis* (Conrad, 1834): NA(Atlantic).
- V. fabalis* (Lea, 1831): NA(Interior).
- V. iris* (Lea, 1829): NA(Interior).
- V. lienosa* (Conrad, 1834): NA(Interior, Gulf).
- V. nebulosa* (Conrad, 1834): NA(Gulf).
- V. ortmanni* (B. Walker, 1925): NA(Interior).
- V. perpurpurea* (Lea, 1861): NA(Interior).
- V. taeniata* (Conrad, 1834): NA(Interior).
- V. trabalis* (Conrad, 1834): NA(Interior).
- V. vanuxemensis* (Lea, 1838): NA(Interior, Gulf).
- V. vaughaniana* (Lea, 1838): NA(Atlantic).
- V. vibex* (Conrad, 1834): NA(Atlantic, Florida, Gulf).

### Tribe PLEUROBEMINI Hannibal, 1912

*Pleurobema* Rafinesque, 1819: Haas (1969a), Burch (1975), Turgeon *et al.* (1998), Williams *et al.* (1993), Parmalee & Bogan (1998).

- P. clava* (Lamarck, 1819): NA(Interior).
- + *Pleurobema mytiloides* Rafinesque, 1820
- P. altum* (Conrad, 1854): NA(Gulf).
- P. athearni* Gangloff, Williams & Feminella, 2006: NA(Gulf).
- P. avellanum* Simpson, 1900: NA(Gulf).
- P. beadleianum* (Lea, 1861): NA(Gulf).
- P. bourmianum* (Lea, 1840): NA(Interior).
- P. chattanoogaense* (Lea, 1858): NA(Gulf).
- P. collina* (Conrad, 1837): NA(Atlantic).
- P. cordatum* (Rafinesque, 1820): NA(Interior).
- P. curtum* (Lea, 1859): NA(Gulf).
- P. decisum* (Lea, 1831): NA(Gulf).
- P. fibuloides* (Lea, 1859): NA(Gulf).
- P. flavidulum* (Lea, 1861): NA(Gulf).
- P. furvum* (Conrad, 1834): NA(Gulf).
- P. georgianum* (Lea, 1841): NA(Gulf).
- P. gibberum* (Lea, 1838): NA(Interior).
- P. hagleri* (Frierson, 1900): NA(Gulf).
- P. hanleyianum* (Lea, 1852): NA(Gulf).
- P. hartmanianum* (Lea, 1860): NA(Gulf).
- P. johannis* (Lea, 1859): NA(Gulf).
- P. marshalli* Frierson, 1927: NA(Gulf).
- P. murrayense* (Lea, 1868): NA(Gulf).
- P. nucleopsis* (Conrad, 1849): NA(Gulf).
- P. oviforme* (Conrad, 1834): NA(Interior).
- P. perovatum* (Conrad, 1834): NA(Gulf).
- P. plenum* (Lea, 1840): NA(Interior).
- P. pyriforme* (Lea, 1857): NA(Gulf).
- P. riddellii* (Lea, 1862): NA(Gulf).
- P. rubellum* (Conrad, 1834): NA(Gulf).
- P. rubrum* (Rafinesque, 1820): NA(Interior).
- P. sintoxia* (Rafinesque, 1820): NA(Interior).
- P. strodeanum* (B.H. Wright, 1898): NA(Gulf).
- P. taitianum* (Lea, 1834): NA(Gulf).
- P. troschelium* (Lea, 1852): NA(Gulf).
- P. verum* (Lea, 1861): NA(Gulf).

*Cyclonaias* Pilsbry in Ortmann & B. Walker, 1922: Parmalee & Bogan (1998).

- C. tuberculata* (Rafinesque, 1820): NA(Interior).

*Elliptio* Rafinesque, 1819: Johnson (1970, 1972), Turgeon *et al.* (1998), Williams *et al.* (1993).

- E. crassidens* (Lamarck, 1819): NA(Interior, Gulf).
- + *Unio (Elliptio) nigra* Rafinesque, 1820
- E. ahenea* (Lea, 1841): NA(Florida).
- E. angustata* (Lea, 1831): NA(Atlantic).
- E. arca* (Conrad, 1834): NA(Gulf).
- E. arctata* (Conrad, 1834): NA(Atlantic, Gulf).
- E. buckleyi* (Lea, 1841): NA(Florida).
- E. chipolaensis* (B. Walker, 1905): NA(Gulf).
- E. cistellaeformis* (Lea, 1863): NA(Atlantic).
- E. complanata* (Lightfoot, 1786): NA(Interior, Atlantic, Gulf).
- E. congaraea* (Lea, 1831): NA(Atlantic).
- E. cylindracea* Frierson, 1927: NA(Atlantic).
- E. dariensis* (Lea, 1842): NA(Atlantic, Florida).
- E. dilatata* (Rafinesque, 1820): NA(Interior).
- E. downiei* (Lea, 1858): NA(Atlantic).
- E. errans* (Lea, 1856): NA(Atlantic).
- E. fisheriana* (Lea, 1838): NA(Atlantic).
- E. folliculata* (Lea, 1838): NA(Atlantic).
- E. fraterna* (Lea, 1852): NA(Atlantic, Gulf).
- E. hepatica* (Lea, 1859): NA(Atlantic).
- E. hopetonensis* (Lea, 1838): NA(Atlantic).
- E. ictervina* (Conrad, 1834): NA(Atlantic, Florida, Gulf).
- E. jayensis* (Lea, 1838): NA(Florida, Gulf).
- E. judithae* Clarke, 1986: NA(Atlantic).
- E. lanceolata* (Lea, 1828): NA(Atlantic, Gulf).
- E. marsupiobesa* Fuller, 1972: NA(Atlantic).
- E. mcmichaeli* Clench & Turner, 1956: NA(Gulf).
- E. monroensis* (Lea, 1843): NA(Florida).
- E. nigella* (Lea, 1852): NA(Gulf).
- E. producta* (Conrad, 1836): NA(Atlantic).
- E. purpurella* (Lea, 1857): NA(Gulf).
- E. raveneli* (Conrad, 1834): NA(Atlantic).
- E. roanokensis* (Lea, 1838): NA(Atlantic).
- E. shepardiana* (Lea, 1834): NA(Atlantic).
- E. spinosa* (Lea, 1836): NA(Atlantic).
- E. steinstansana* R.I. Johnson & Clarke, 1983: NA(Atlantic).
- E. waccamawensis* (Lea, 1863): NA(Atlantic).
- E. waltoni* (B.H. Wright, 1888): NA(Florida).

*Elliptioideus* Frierson, 1927: Burch (1975), Brim-Box & Williams (2000).

- E. sloatianus* (Lea, 1840): NA(Gulf).

*Fusconaia* Simpson, 1900: Burch (1975), Parmalee & Bogan (1998).

- F. flava* (Rafinesque, 1820): NA(Interior, Gulf).
- + *Unio trigonus* Lea, 1831
- F. askevi* (Marsh, 1896): NA(Gulf).
- F. barnesiana* (Lea, 1838): NA(Interior).
- F. cerina* (Conrad, 1838): NA(Gulf).
- F. cor* (Conrad, 1834): NA(Interior).
- F. cuneolus* (Lea, 1840): NA(Interior).
- F. ebena* (Lea, 1831): NA(Interior, Gulf).
- F. escambia* Clench & Turner, 1956: NA(Gulf).
- ?*F. hebetata* (Conrad, 1854): NA(Gulf).
- F. lananensis* (Frierson, 1901): NA(Gulf).
- F. masoni* (Conrad, 1834): NA(Atlantic).
- F. ozarkensis* (Call, 1887): NA(Interior).
- ?*F. rubidula* (Frierson, 1905): NA(Gulf).
- F. subrotunda* (Lea, 1831): NA(Interior).
- F. succissa* (Lea, 1852): NA(Gulf).

*Hemistena* Rafinesque, 1820: Parmalee & Bogan (1998).

- H. lata* (Rafinesque, 1820): NA(Interior).

*Lexingtonia* Ortmann, 1914: Burch (1975), Parmalee & Bogan (1998).

- L. subplana* (Conrad, 1837): NA(Atlantic).  
*L. dolabelloides* (Lea, 1840): NA(Interior).  
 ?*L. utricula* (Lea, 1845): NA(Atlantic).

*Plethobasus* Simpson, 1900: Parmalee & Bogan (1998).

- P. cyphus* (Rafinesque, 1820): NA(Interior).  
 + *Unio aesopus* Green, 1827  
*P. cicatricosus* (Say, 1829): NA(Interior).  
*P. cooperianus* (Lea, 1834): NA(Interior).

*Popenaias* Frierson, 1927: Frierson (1927), Haas (1969a).

- P. popeii* (Lea, 1857): NA(Gulf), NT(Mesoamerica).  
*P. metallica* (Say, 1831): NT(Mesoamerica).  
*P. tehuantepecensis* (Crosse & Fischer, 1893):  
 NT(Mesoamerica).

*Uniomereus* Conrad, 1853: Parmalee & Bogan (1998), Turgeon *et al.* (1998), Brim-Box & Williams (2000).

- U. declivis* (Say, 1831): NA(Gulf).  
 + *Unio excultus* Conrad, 1838  
*U. caroliniana* (Bosc, 1801): NA(Atlantic, Florida, Gulf).  
*U. tetralasmus* (Say, 1831): NA(Interior, Gulf).

### Tribe QUADRULINI von Ihering, 1901

*Quadrula* Rafinesque, 1820: Burch (1975), Parmalee & Bogan (1998). Recent phylogenetic work by Serb, Buhay & Lydeard (2003) has shown that *Quadrula* (in the broad sense) included several distinct lineages that we here treat as separate genera: *Quadrula s.s.*, *Amphinaias*, *Theliderma* and *Tritogonia*.

- Q. quadrula* (Rafinesque, 1820): NA(Interior, Gulf).  
*Q. apiculata* (Say, 1829): NA(Gulf). [introduced to Tennessee River]  
*Q. fragosa* (Conrad, 1836): NA(Interior).  
*Q. rumphiana* (Lea, 1852): NA(Gulf).

*Amphinaias* Crosse & Fischer, 1894: Burch (1975), Howells *et al.* (1996), Parmalee & Bogan (1998).

- A. couchiana* (Lea, 1860): NA(Gulf).  
*A. archeri* (Frierson, 1905): NA(Gulf).  
*A. asperata* (Lea, 1861): NA(Gulf).  
*A. aurea* (Lea, 1859): NA(Gulf).  
*A. houstonensis* (Lea, 1859): NA(Gulf).  
*A. nodulata* (Rafinesque, 1820): NA(Interior).  
*A. petrina* (Gould, 1855): NA(Gulf).  
*A. pustulosa* (Lea, 1831): NA(Interior, Gulf).  
*A. refulgens* (Lea, 1868): NA(Gulf).

*Megaloniaias* Utterback, 1915: Clench & Turner (1956), Haas (1969a), Parmalee & Bogan (1998).

- M. nervosa* (Rafinesque, 1820): NA(Interior, Gulf).  
 + *Unio heros* Say, 1829  
*M. boykiniana* (Lea, 1840): NA(Gulf).  
*M. nickliniana* (Lea, 1834): NT(Mesoamerica).

*Plectomerus* Conrad, 1853: Burch (1975), Parmalee & Bogan (1998).

*P. dombeyanus* (Valenciennes in Humboldt & Bonpland, 1827): NA(Interior, Gulf).

*Quincuncina* Ortmann & B. Walker, 1922: Howells *et al.* (1996), Brim-Box & Williams (2000).

- Q. burkei* B. Walker in Ortmann & B. Walker, 1922:  
 NA(Gulf).  
*Q. infucata* (Conrad, 1834): NA(Gulf).  
*Q. mitchelli* (Simpson in Dall, 1896): NA(Gulf).

*Theliderma* Swainson, 1840: Burch (1975), Johnson (1980), Parmalee & Bogan (1998).

*T. metaneura* (Rafinesque, 1820): NA(Interior, Gulf).

*T. cylindrica* (Say, 1817): NA(Interior).

*T. intermedia* (Conrad, 1836): NA(Interior).

*T. sparsa* (Lea, 1841): NA(Interior).

*T. stapes* (Lea, 1831): NA(Gulf).

*T. tuberosa* (Lea, 1840): NA(Interior).

*Tritogonia* Agassiz, 1852: Parmalee & Bogan (1998).

*T. verrucosa* (Rafinesque, 1820): NA(Interior, Gulf).

### Tribe GONIDEINI Ortmann, 1916

*Gonidea* Conrad, 1857: Haas (1969a), Burch (1975).

*G. angulata* (Lea, 1838): NA(Pacific).

+ *Anodonta randallii* Trask, 1855

### *incertae sedis* AMBLEMINEAE

The amblemine fauna of Mesoamerica will probably end up distributed among the Nearctic tribes following rigorous phylogenetic analyses. Certain taxa from that area with anatomical data sufficient to do so have been placed in the LAMP SILINI and ANODONTINI.

*Barynaias* Crosse & Fischer, 1894: Frierson (1927), Haas (1969a).

- B. pigerrima* (Crosse & Fischer, 1893): NT(Mesoamerica).  
*B. caldwelii* (Lea, 1858): NT(Mesoamerica).  
*B. opacata* (Crosse & Fischer, 1893): NT(Mesoamerica).  
*B. plexus* (Conrad, 1838): NT(Mesoamerica).  
*B. sallei* (Crosse & Fischer, 1893): NT(Mesoamerica).

*Martensnaias* Frierson, 1927: Frierson (1927), Haas (1969a).

*M. rubicunda* (von Martens, 1900): NT(Mesoamerica).

*Micronaias* Simpson, 1900: Frierson (1927), Haas (1969a).

- M. arata* (Lea, 1845): NT(Mesoamerica).  
*M. fallaciosa* (Simpson, 1914): NT(Mesoamerica).  
*M. granadensis* (Lea, 1868): NT(Mesoamerica).

*Nephritica* Frierson, 1927: Frierson (1927), Haas (1969a).

- N. poeyana* (Lea, 1857): NT(Mesoamerica).  
*N. haricotti* (Frierson, 1927): NT(Mesoamerica).

*Nephronaias* Crosse & Fischer, 1894: Simpson (1914), Frierson (1927), Haas (1969a).

- N. plicatula* (Charpentier in Küster, 1856):  
 NT(Mesoamerica).  
*N. aeruginosa* (Morelet, 1849): NT(Mesoamerica).  
*N. aztecorum* (Philippi, 1847): NT(Mesoamerica).  
*N. calamitarum* (Morelet, 1849): NT(Mesoamerica).  
*N. championi* (von Martens, 1900): NT(Mesoamerica).  
*N. copanensis* (von Martens, 1900): NT(Mesoamerica).  
*N. dysonii* (Lea, 1859): NT(Mesoamerica).  
*N. goascoranensis* (Lea, 1858): NT(Mesoamerica).  
*N. gundlachi* (Dunker, 1858): NT(Mesoamerica).  
*N. hermanni* (Haas, 1929): NT(Mesoamerica).  
*N. hjalmarsoni* (Dunker, 1858): NT(Mesoamerica).  
*N. lempensis* Marshall, 1926: NT(Mesoamerica).  
*N. macnielii* (Lea, 1869): NT(Mesoamerica).  
*N. mellea* (Lea, 1859): NT(Mesoamerica).  
*N. oregonensis* (Lea, 1852): NT(Mesoamerica).  
*N. ravistella* (Morelet, 1849): NT(Mesoamerica).  
*N. rowellii* (Lea, 1859): NT(Mesoamerica).  
*N. rugulosa* (Charpentier in Küster, 1856):  
 NT(Mesoamerica).  
*N. sajensis* (Frierson, 1927): NT(Mesoamerica).  
*N. scamnata* (Morelet, 1849): NT(Mesoamerica).  
*N. sphenorhyncha* (Crosse & Fischer, 1893):  
 NT(Mesoamerica).

- N. tabascoensis* (Charpentier in Küster, 1856): NT (Mesoamerica).  
*N. tempisqueensis* Pilsbry, 1920: NT(Mesoamerica).  
*N. yzabalensis* (Crosse & Fischer, 1892): NT(Mesoamerica).
- Pachynaias* Crosse & Fischer, 1894: Frierson (1927), Haas (1969a).  
*P. speniopsis* (Morelet, 1849): NT(Mesoamerica).  
*P. rugosulcata* (Lea, 1866): NT(Mesoamerica).
- Psoronaias* Crosse & Fischer, 1894: Frierson (1927), Haas (1969a).  
*P. semigranosa* (von dem Busch in Philippi, 1845): NT(Mesoamerica).  
 + *Unio psoricus* Morelet, 1851  
*P. crocodilorum* (Morelet, 1849): NT(Mesoamerica).  
*P. distincta* (Crosse & Fischer, 1893): NT(Mesoamerica).  
*P. herrerae* (Marshall, 1923): NT(Mesoamerica).  
*P. kuxensis* Frierson, 1917: NT(Mesoamerica).  
*P. martensi* Frierson, 1927: NT(Mesoamerica).  
*P. morini* (Morelet, 1851): NT(Mesoamerica).  
*P. ostreata* (Morelet, 1849): NT(Mesoamerica).
- Psorula* Haas, 1930: Frierson (1927), Haas (1969a).  
*P. rudis* (Simpson, 1900): NT(Mesoamerica).  
*P. guatemalensis* (Simpson, 1900): NT(Mesoamerica).  
*P. percompressa* (von Martens, 1887): NT(Mesoamerica).  
*P. profunda* (Simpson, 1914): NT(Mesoamerica).  
*P. quadrata* (Simpson, 1914): NT(Mesoamerica).  
*P. salinarum* (Haas, 1929): NT(Mesoamerica).  
*P. usumasintae* (Crosse & Fischer, 1892): NT(Mesoamerica).
- Reticulatus* Frierson, 1927: Frierson (1927), Haas (1969a).  
*R. reticulatus* (Simpson, 1900): NT(Mesoamerica).  
*R. elvae* (B. Walker, 1924): NT(Mesoamerica).
- Sphenonaias* Crosse & Fischer, 1894: Frierson (1927), Haas (1969a).  
*S. liebmanni* (Philippi, 1847): NT(Mesoamerica).  
*S. callosa* (Lea, 1841): NT(Mesoamerica).  
*S. colorata* (Charpentier in Küster, 1856): NT(Mesoamerica).  
*S. flucki* (Bartsch, 1906): NT(Mesoamerica).  
*S. mexicana* (Philippi, 1847): NT(Mesoamerica).  
*S. microdon* (von Martens, 1887): NT(Mesoamerica).  
*S. taumilapana* (Conrad, 1855): NA(Gulf).
- incertae sedis* UNIONIDAE**
- Traditionally, numerous Old World genera were included among the Ambleminae (Heard & Guckert, 1970; Heard, 1974). However, recent phylogenetic analyses have raised doubts about the monophyly of that subfamily (Graf & Cummings, 2006b and references therein). Unfortunately, only enough study has been undertaken to demonstrate the flawed nature of the traditional arrangement, and the data to-date are insufficient to make a robust hypothesis about the phylogenetic placement of Old World ‘amblemine’ genera. For convenience, we group those taxa geographically.
- (*Afrotropical*)
- Brazzaea* Bourguignat, 1885: Pain & Woodward (1968), Daget (1998).  
*B. anceyi* Bourguignat, 1885: AF(Congo).
- Coelatura* Conrad, 1853: Daget (1998), Scholz & Glaubrecht (2004), Graf & Cummings (2006a).  
*C. aegyptiaca* (Cailliaud, 1827): AF(Nile, West).
- C. alluaudi* (Dautzenberg, 1908): AF(Nile).  
*C. bakeri* (H. Adams, 1866): AF(Nile).  
*C. briarti* (Dautzenberg, 1901): AF(Congo).  
*C. cariei* (Germain, 1919): AF(Madagascar).  
*C. choziensis* (Preston, 1910): AF(Congo).  
*C. cridlandi* Mandahl-Barth, 1954: AF(Nile).  
*C. essoensis* (Chaper, 1885): AF(West).  
*C. gabonensis* (Küster, 1862): AF(Congo).  
*C. geayi* (Germain, 1911): AF(Madagascar).  
*C. hauttecoeurii* (Bourguignat, 1883): AF(Nile).  
*C. horei* (E.A. Smith, 1880): AF(Congo).  
*C. hypsiprymna* (von Martens, 1897): AF(South).  
*C. kipopoensis* Mandahl-Barth, 1968: AF(Congo).  
*C. kunenensis* (Mousson, 1887): AF(South).  
*C. leopoldvillensis* (Putzeys, 1898): AF(Congo).  
*C. lobensis* (Frierson, 1913): AF(Congo).  
*C. luapulaensis* (Preston, 1913): AF(Congo).  
*C. madagascariensis* (Sganzin, 1841): AF(Madagascar).  
*C. malgachensis* (Germain, 1911): AF(Madagascar).  
*C. mossambicensis* (von Martens, 1860): AF(East, South).  
*C. ratidota* (Charmes, 1885): AF(East).  
*C. rothschildi* (Neuville & Anthony, 1906): AF(Nile).  
*C. rotula* Pilsbry & Bequaert, 1927: AF(Congo).  
*C. stagnorum* (Dautzenberg, 1890): AF(Congo).  
*C. stuhlmanni* (von Martens, 1897): AF(Nile).
- Grandidieria* Bourguignat, 1885: Daget (1998), Scholz & Glaubrecht (2004).  
*G. burtoni* (Woodward, 1859): AF(Congo).
- Mweruella* Haas, 1936: Pain & Woodward (1968), Daget (1998).  
*M. mweruensis* (E.A. Smith, 1908): AF(Congo).
- Nitia* Pallary, 1924: Daget (1998), Scholz & Glaubrecht (2004), Graf & Cummings (in press).  
*N. teretiuscula* (Philippi, 1847): AF(Nile, West).  
*N. acuminata* (H. Adams, 1866): AF(Nile).  
*N. chefnuexi* (Neuville & Anthony, 1906): AF(Nile).  
*N. monceti* (Bourguignat, 1883): AF(Nile).  
*N. mutelaeformis* (Germain, 1906): AF(West).
- Nyassunio* Haas, 1936: Daget (1998), Scholz & Glaubrecht (2004).  
*N. nyassaensis* (Lea, 1864): AF(South).  
*N. ujjiensis* (Crosse, 1881): AF(Congo).
- Prisodontopsis* Tomlin, 1928: Pain & Woodward (1968), Daget (1998).  
*P. aviculaeformis* Woodward, 1991: AF(Congo).  
 + *Unio (Metaptera) johnstoni* E.A. Smith, 1893
- Pseudospatha* Simpson, 1900: Pain & Woodward (1968), Daget (1998).  
*P. tanganyicensis* (E.A. Smith, 1880): AF(Congo).
- (*Western Palearctic*)
- Leguminaia* Conrad, 1865: Schütt (1983), Falkner (1994).  
*L. wheatleyi* (Lea, 1862): PA(Middle East).  
 + *Monocondylaea mardinensis* Lea, 1865  
*L. saulcyi* (Bourguignat, 1852): PA(Middle East).
- Microcondylaea* von Vest, 1866: Haas (1940, 1969a), Falkner *et al.* (2001).  
*M. bonellii* (Rossmässler, 1835): PA(Europe).
- Potomida* Swainson, 1840: Haas (1940, 1969a), Falkner (1994), Falkner *et al.* (2001, 2002).  
*P. littoralis* (Cuvier, 1798): PA(Europe, Middle East).  
 + *Mysca (Potomida) corrugata* Swainson, 1840

- Pseudodontopsis* Kobelt, 1913: Schütt (1983), Falkner (1994).  
*P. euphratica* (Bourguignat, 1852): PA(Middle East).  
 (Indotropical & Eastern Palearctic)
- Arcidopsis* Simpson, 1900: Subba Rao (1989).  
*A. footei* (Theobald, 1876): IN(India-Burma).
- Caudiculatus* Simpson, 1900: Haas (1969a).  
*C. caudiculatus* (von Martens, 1866): IN(Sunda-Philippines).
- Chamberlainia* Simpson, 1900: Haas (1969a), Brandt (1974).  
*C. hainesiana* (Lea, 1856): IN(Indochina).  
*C. paviei* (Morelet, 1891): IN(Indochina).
- Conradens* Haas, 1913: Haas (1969a), Brandt (1974).  
*C. contradens* (Lea, 1838): IN(Indochina, Sunda-Philippines).  
*C. fulvaster* (Drouët & Chaper, 1892): IN(Sunda-Philippines).  
*C. gratiosus* (Philippi, 1845): IN(Indochina).  
*C. inaequalis* (Rochebrune, 1882): IN(Indochina).  
*C. semmelinki* (von Martens, 1891): IN(Indochina, Sunda-Philippines).  
*C. subcircularis* (Brandt, 1974): IN(Indochina).
- Ctenodesma* Simpson, 1900: Haas (1969a).  
*C. borneensis* (Issel, 1874): IN(Sunda-Philippines).  
*C. scheibeneri* Haas, 1927: IN(Sunda-Philippines).
- Diaurora* Cockerell, 1903: Haas (1969a), Prozorova *et al.* (2005).  
*D. aurea* (Heude, 1883): IN(Yangtze-Huang).
- Discomya* Simpson, 1900: Haas (1969a).  
*D. radulosa* (Drouët & Chaper, 1892): IN(Sunda-Philippines).
- Elongaria* Haas, 1913: Haas (1969a).  
*E. orientalis* (Lea, 1840): IN(Sunda-Philippines).  
*E. trompi* (Drouët & Chaper, 1892): IN(Sunda-Philippines).
- Ensidens* Frierson, 1911: Haas (1969a), Brandt (1974).  
*E. ingallsianus* (Lea, 1852): IN(Indochina).  
*E. sagittarius* (Lea, 1856): IN(Indochina).
- Haasodonta* McMichael, 1956: McMichael & Hiscock (1958).  
*H. fannyae* (R.I. Johnson, 1948): AU(New Guinea).  
*H. vanheurni* McMichael & Hiscock, 1958: AU(New Guinea).
- Harmandia* Rochebrune, 1882: Brandt (1974).  
*H. somboriensis* Rochebrune, 1882: IN(Indochina).  
*H. munensis* Brandt, 1974: IN(Indochina).
- Hyriopsis* Conrad, 1853: Haas (1969a), Brandt (1974), Đang *et al.* (1980), Habe (1991).  
*H. bialata* Simpson, 1900: IN(Indochina).  
 + *Unio delphinus* Gruner, 1841 *non* Spengler, 1793  
*H. cumingii* (Lea, 1852): IN(Yangtze-Huang, Indochina).  
*H. delaportei* (Crosse & Fischer, 1876): IN(Indochina).  
*H. desowitzi* Brandt, 1974: IN(Indochina).  
*H. myersiana* (Lea, 1856): IN(Indochina).  
 ?*H. pinchomiana* (Heude, 1883): IN(Indochina).  
*H. schlegelii* (von Martens, 1861): PA(Japan-Sakhalin).  
*H. velthuiszeni* (Schepman, 1895): IN(Sunda-Philippines).
- Inversidens* Haas, 1911: Haas (1969a), Kondo (1982), Habe (1991).  
*I. brandtii* (Kobelt, 1879): PA(Japan-Sakhalin).  
*I. japonensis* (Lea, 1859): PA(Japan-Sakhalin).  
*I. pantoensis* (Neumayr, 1899): IN(Yangtze-Huang), PA(Amur-Beringia).
- Lamellidens* Simpson, 1900: Subba Rao (1989), Neseemann *et al.* (2003).  
*L. marginalis* (Lamarck, 1819): IN(India-Burma).
- L. consobrinus* (Lea, 1860): IN(India-Burma).  
*L. corrianus* (Lea, 1834): IN(India-Burma).  
*L. generosus* (Gould, 1847): IN(India-Burma).  
*L. indawgyiensis* Prashad, 1930: IN(India-Burma).  
*L. jenkinsianus* (Benson, 1862): IN(India-Burma).  
*L. lamellatus* (Lea, 1838): IN(India-Burma).  
*L. narainporensis* Preston, 1912: IN(India-Burma).  
*L. phenchooganjensis* Preston, 1912: IN(India-Burma).  
*L. scutum* (Sowerby, 1868): IN(Indochina).
- Lamprotula* Simpson, 1900: Haas (1969a), Liu (1979), Đang *et al.* (1980), Prozorova *et al.* (2005).  
*L. plumbea* (Chemnitz, 1795): IN(?).  
*L. bazini* (Heude, 1877): IN(Yangtze-Huang).  
*L. blaisei* (Fischer & Dautzenberg, 1905): IN(Indochina).  
*L. caveata* (Heude, 1877): IN(Yangtze-Huang).  
*L. confragosa* (Frierson, 1928): IN(Yangtze-Huang).  
*L. coreana* (von Martens, 1886): PA(Amur-Beringia).  
*L. cornuulmae* (Heude, 1883): IN(Yangtze-Huang).  
*L. crassa* (Wood, 1815): IN(Indochina).  
*L. divergens* (Benson, 1855): IN(Yangtze-Huang).  
*L. elongata* Liu, Zhang & Wang, 1980: IN(Yangtze-Huang).  
*L. fibrosa* (Heude, 1877): IN(Yangtze-Huang).  
*L. gottschei* (von Martens, 1894): IN(Yangtze-Huang), PA(Amur-Beringia).  
*L. kouangensis* (Simpson, 1900): IN(Yangtze-Huang).  
*L. leai* (Gray in Griffith & Pidgeon, 1834): IN(Yangtze-Huang, Indochina).  
*L. mansuyi* (Dautzenberg & Fischer, 1908): IN(Indochina).  
*L. microsticta* (Heude, 1877): IN(Yangtze-Huang).  
*L. nodulosa* (Wood, 1815): IN(Indochina).  
*L. polysticta* (Heude, 1877): IN(Yangtze-Huang).  
*L. rochechouartii* (Heude, 1875): IN(Yangtze-Huang).  
*L. salaputium* (von Martens, 1902): IN(Indochina).  
*L. scripta* (Heude, 1875): IN(Yangtze-Huang).  
*L. similaris* (Simpson, 1900): IN(Yangtze-Huang).  
*L. tiensinensis* (Crosse & Debeaux, 1863): IN(Yangtze-Huang).  
*L. tortuosa* (Lea, 1865): IN(Yangtze-Huang).  
*L. triclava* (Heude, 1877): IN(Yangtze-Huang).  
*L. zonata* (Heude, 1883): IN(Yangtze-Huang).
- Modellnaia* Brandt, 1974: Brandt (1974).  
*M. siamensis* Brandt, 1974: IN(Indochina).
- Oxynia* Haas, 1913: Haas (1969a), Đang *et al.* (1980), Subba Rao (1989).  
*O. jourdyi* (Morelet, 1886): IN(Indochina).  
*O. diespiter* (Mabille, 1887): IN(Indochina).  
*O. gladiator* (Ancey, 1881): IN(Indochina).  
*O. micheloti* (Morelet, 1886): IN(Indochina).  
*O. pugio* (Benson, 1862): IN(Indochina, India-Burma).
- Parreysia* Conrad, 1853: Brandt (1974), Subba Rao (1989), Neseemann *et al.* (2003).  
*P. (Parreysia) corrugata* (Müller, 1774): IN(India-Burma).  
 + *Unio multidentatus* Philippi, 1847  
*P. (Parreysia) amandalei* Preston, 1912: IN(India-Burma).  
*P. (Parreysia) bhomoensis* (Theobald, 1874): IN(Indochina, India-Burma).  
*P. (Parreysia) burmana* (Blanford, 1869): IN(Indochina, India-Burma).  
*P. (Parreysia) choprae* Prashad, 1930: IN(India-Burma).  
*P. (Parreysia) corbis* (Hanley, 1856): IN(India-Burma).  
*P. (Parreysia) cylindrica* Annandale & Prashad, 1919: IN(India-Burma).  
*P. (Parreysia) favidens* (Benson, 1862): IN(India-Burma).  
*P. (Parreysia) feae* (Tapparone Canefri, 1889): IN(Indochina).

- P. (Parreysia) feddeni* (Theobald, 1874): IN(India-Burma).  
*P. (Parreysia) gowhattensis* (Theobald, 1874): IN(India-Burma).  
*P. (Parreysia) hougdararica* (Tapparone Canefri, 1889): IN(Indochina).  
*P. (Parreysia) mandalayensis* (Theobald, 1874): IN(India-Burma).  
*P. (Parreysia) olivacea* Prashad, 1930: IN(India-Burma).  
*P. (Parreysia) perconvexa* Preston, 1912: IN(India-Burma).  
*P. (Parreysia) rajahensis* (Lea, 1841): IN(India-Burma).  
*?P. (Parreysia) rugosa* (Gmelin, 1791): IN(India-Burma).  
*P. (Parreysia) sikkimensis* (Lea, 1859): IN(India-Burma).  
*P. (Parreysia) smaragdites* (Benson, 1862): IN(India-Burma).  
*P. (Parreysia) tavoyensis* (Gould, 1843): IN(Indochina, India-Burma).  
*P. (Parreysia) triembola* (Benson, 1855): IN(India-Burma).  
*P. (Radiatula) crispisulcata* (Benson, 1862): IN(India-Burma).  
*P. (Radiatula) andersoniana* (Nevill, 1877): IN(India-Burma).  
*P. (Radiatula) bonneaudi* (Eydox, 1838): IN(India-Burma).  
*P. (Radiatula) caerulea* (Lea, 1831): IN(India-Burma).  
*P. (Radiatula) chauthurii* (Preston, 1912): IN(India-Burma).  
*P. (Radiatula ?) humilis* (Lea, 1856): IN(Indochina).  
*P. (Radiatula) involuta* (Benson in Hanley, 1856): IN(India-Burma).  
*P. (Radiatula) khadakvaslaensis* (Ray, 1966): IN(India-Burma).  
*P. (Radiatula) lima* (Simpson, 1900): IN(India-Burma).  
*P. (Radiatula) nuttalliana* (Lea, 1856): IN(India-Burma).  
*P. (Radiatula) occata* (Lea, 1860): IN(India-Burma).  
*P. (Radiatula) olivaria* (Lea, 1831): IN(India-Burma).  
*P. (Radiatula) pachysoma* (Benson, 1862): IN(India-Burma).  
*P. (Radiatula) pilata* (Lea, 1866): IN(Indochina).  
*P. (Radiatula) shurtleffiana* (Lea, 1856): IN(India-Burma).  
*P. (Radiatula) substriata* (Lea, 1856): IN(Indochina).  
*P. (Radiatula) theobaldi* (Preston, 1912): IN(India-Burma).  
*?P. pecten* (Preston, 1912): IN(Indochina).
- Physunio* Simpson, 1900: Haas (1969a), Brandt (1974), Subba Rao (1989).  
*P. superbus* (Lea, 1841): IN(Indochina, Sunda-Philippines).  
 + *Unio gravidus* Lea, 1856  
*P. cambodiensis* (Lea, 1856): IN(Indochina).  
*P. eximius* (Lea, 1856): IN(Indochina).  
*P. ferrugineus* Annandale, 1918: IN(Indochina).  
*P. friersoni* Simpson, 1914: IN(India-Burma).  
*P. inornatus* (Lea, 1856): IN(Indochina).  
*P. micropteroides* Annandale, 1918: IN(Indochina).  
*P. micropterus* (Morelet, 1866): IN(Indochina).  
*P. modelli* Brandt, 1974: IN(Indochina).  
*P. semialatus* (DeShayes & Jullien, 1874): IN(Indochina).
- Pilsbryconcha* Simpson, 1900: Haas (1969a), Brandt (1974).  
*P. exilis* (Lea, 1838): IN(Indochina, Sunda-Philippines).  
*P. carinifera* (Conrad, 1837): IN(Indochina, Sunda-Philippines).  
*P. compressa* (von Martens, 1860): IN(Indochina).  
*P. expressa* (von Martens, 1900): IN(Sunda-Philippines).  
*P. lemeslei* (Morelet, 1875): IN(Indochina).
- Pressidens* Haas, 1910: Haas (1969a).  
*P. moellendorffi* Haas, 1910: IN(Sunda-Philippines).  
*P. exanthematicus* (Küster, 1861): IN(Sunda-Philippines).  
*P. insularis* (Drouët, 1894): IN(Sunda-Philippines).
- Prohyriopsis* Haas, 1914: Haas (1969a).  
*P. stolata* (von Martens, 1900): IN(Sunda-Philippines).
- Protunio* Haas, 1913: Haas (1969a), Đang *et al.* (1980).  
*P. messengeri* (Bavay & Dautzenberg, 1901): IN(Indochina).
- Pseudobaphia* Simpson, 1900: Haas (1969a), Prozorova *et al.* (2005).  
*P. biesiana* (Heude, 1877): IN(Yangtze-Huang).  
*P. ovata* (Liu, Duan & Wang in Liu *et al.* 1994) *non* Say, 1817: IN(Yangtze-Huang).
- Pseudodon* Gould, 1844: Haas (1969a), Brandt (1974), Subba Rao (1989), Prozorova *et al.* (2005).  
*P. (Pseudodon) inoscularis* (Gould, 1844): IN(Indochina).  
*P. (Pseudodon) crebristriata* (Anthony, 1865): IN(India-Burma).  
*P. (Pseudodon) cumingii* (Lea, 1850): IN(Indochina).  
*P. (Pseudodon) peguensis* (Anthony, 1865): IN(India-Burma).  
*P. (Pseudodon) solidus* Haas, 1911: IN(Yangtze-Huang).  
*P. (Pseudodon) walpolei* (Hanley, 1871): IN(Sunda-Philippines).  
*P. (Bineurus) mouhotii* (Lea, 1863): IN(Indochina).  
*P. (Bineurus) hageni* (Strubell, 1897): IN(Sunda-Philippines).  
*P. (Bineurus) thomsoni* Morelet, 1884: IN(Indochina).  
*P. (Chrysosepsodon) aureus* Heude, 1885: IN(Yangtze-Huang).  
*P. (Cosmopseudodon) resupinatus* von Martens, 1902: IN(Indochina).  
*P. (Cosmopseudodon) aeneolus* Drouët & Chaper, 1892: IN(Sunda-Philippines).  
*P. (Diplopseudodon) crassus* Drouët & Chaper, 1892: IN(Sunda-Philippines).  
*P. (Indopseudodon) salweeniana* (Gould, 1844): IN(Indochina).  
*P. (Indopseudodon) avae* (Theobald, 1873): IN(India-Burma).  
*P. (Monodontina) vondembuschianus* (Lea, 1840): IN(Indochina, Sunda-Philippines).  
*P. (Monodontina) cambodjensis* (Petit, 1865): IN(Indochina).  
*P. (Monodontina) chaperi* (Morgan, 1885): IN(Indochina).  
*P. (Monodontina) ellipticus* Conrad, 1865: IN(Indochina).  
*P. (Monodontina) tumidus* (Morelet, 1866): IN(Indochina).  
*P. (Nasus) nankingensis* (Heude, 1874): IN(Yangtze-Huang).  
*P. (Nasus) secundus* Heude, 1877: IN(Yangtze-Huang).  
*P. (Obovalis) omiensis* (von Heimburg, 1884): PA(Japan-Sakhalin).  
 + *Pseudodon loomisi* Simpson, 1900
- Ptychorhynchus* Simpson, 1900: Haas (1969a), Prozorova *et al.* (2005).  
*P. pfisteri* (Heude, 1874): IN(Yangtze-Huang).  
*P. murinum* (Heude, 1883): IN(Yangtze-Huang).  
*P. schomburgianum* (Heude, 1885): IN(Indochina).
- Rectidens* Simpson, 1900: Haas (1969a).  
*R. lingulatus* (Drouët & Chaper, 1892): IN(Sunda-Philippines).  
 + *Unio prolongatus* Drouët, 1894  
*R. sumatrensis* (Dunker, 1852): IN(Sunda-Philippines).
- Scabies* Haas, 1911: Brandt (1974), Subba Rao (1989), Hu (2005).  
*S. crispata* (Gould, 1843): IN(Yangtze-Huang, Indochina, India-Burma).  
 + *Unio scobinatus* Lea, 1856  
*S. chinensis* Liu, Duan & Lai, 1991: IN(Indochina).  
*S. longata* Liu, Duan & Lai, 1991: IN(Indochina).  
*S. nucleus* (Lea, 1856): IN(Indochina).  
*S. phaselus* (Lea, 1856): IN(Indochina).
- Schepmania* Haas, 1912: Haas (1969a).  
*S. nieuwenhuisi* (Schepman, 1898): IN(Sunda-Philippines).  
*S. parcesculpta* (von Martens, 1903): IN(Sunda-Philippines).
- Solenia* Conrad, 1869: Haas (1969a), Liu (1979), Subba Rao (1989), Prozorova *et al.* (2005).  
*S. emarginata* (Lea, 1860): IN(Indochina).

- S. iridinea* (Heude, 1874): IN(Yangtze-Huang).  
*S. khwaeniensis* Panha & Dezin in Dezin *et al.*, 2004:  
 IN(Indochina).  
*S. soleniformis* (Benson, 1836): IN(India-Burma).  
*S. triangularis* (Heude, 1885): IN(Yangtze-Huang).

*Trapezoides* Simpson, 1900: Simpson (1914), Preston (1915),  
 Brandt (1974), Subba Rao (1989).

- T. exolescens* (Gould, 1843): IN(Indochina, India-Burma).  
 + *Unio foliaceus* Gould, 1843  
*T. peninsularis* Simpson, 1900: IN(Sunda-Philippines).  
 ?*T. prashadi* Haas, 1922: IN(India-Burma).  
 ?*T. theca* (Benson, 1862): IN(India-Burma).

*Unionetta* Haas, 1955: Haas (1969a), Brandt (1974).

- U. fabagina* (DeShayes & Jullien, 1874): IN(Indochina).  
*U. broti* (DeShayes & Jullien, 1874): IN(Indochina).

### Family MARGARITIFERIDAE Haas, 1940

*Margaritifera* Schumacher, 1816: Ziuganov *et al.* (1994), D.G.  
 Smith (2001), Huff *et al.* (2004).

- M. margaritifera* (Linnaeus, 1758): NA(Atlantic),  
 PA(Europe).  
*M. auricularia* (Spengler, 1793): PA(Europe).  
*M. dahurica* (Middendorff, 1850): PA(Amur-Beringia, Japan-  
 Sakhalin).  
*M. falcata* (Gould, 1850): NA(Pacific, Interior).  
*M. hembeli* (Conrad, 1838): NA(Gulf).  
*M. homsensis* (Lea, 1864): PA(Middle East).  
*M. laevis* (Haas, 1910): PA(Japan-Sakhalin).  
*M. laosensis* (Lea, 1863): IN(Indochina).  
*M. marrianae* R.I. Johnson, 1983: NA(Gulf).  
*M. middendorffi* (Rosén, 1926): PA(Amur-Beringia).  
*M. monodonta* (Say, 1829): NA(Interior).  
*M. togakushiensis* Kondo & Kobayashi, 2005: PA(Japan-  
 Sakhalin).

### Superfamily ETHERIOIDEA Deshayes, 1830

#### Family HYRIIDAE Swainson, 1840

##### Subfamily HYRIINAE s.s.

##### the Hyrini Tribe group

##### Tribe HYRIINI s.s.

- Prisodon* Schumacher, 1817: Haas (1969a), Simone (2006).  
 + *Hyrja* Lamarck, 1819  
*P. (Prisodon) obliquus* Schumacher, 1817: NT(Amazonas-  
 Orinoco).  
*P. (Paxyodon) symatophorus* (Meuschen in Gronovius, 1781):  
 NT(Amazonas-Orinoco).  
 + *Paxyodon ponderosus* Schumacher, 1817  
*P. (Triplodon) corrugatus* (Lamarck, 1819): NT(Amazonas-  
 Orinoco).  
 + *Unio rugosus* Spix & Wagner, 1827

### Tribe CASTALIINI Parodiz & Bonetto, 1963

- Castalia* Lamarck, 1819: Modell (1950), Bonetto (1965b), Haas  
 (1969a), Simone (2006).  
*C. ambigua* Lamarck, 1819: NT(Amazonas-Orinoco,  
 Atlantic-São Francisco).  
*C. inflata* d'Orbigny, 1835: NT(Paraná).  
*C. martensi* (von Ihering, 1891): NT(Paraná).  
*C. multisulcata* Hupé, 1857: NT(Transandean, Amazonas-  
 Orinoco).  
*C. nehringi* (von Ihering, 1891): NT(Paraná).  
*C. orinocensis* Morrison, 1943: NT(Amazonas-Orinoco).

- C. psammoica* (d'Orbigny, 1835): NT(Paraná).  
*C. undosa* von Martens, 1895: NT(Paraná).

*Callonia* Simpson, 1900: Haas (1969a), Simone (2006).

- C. duprei* (Récluz, 1842): NT(Amazonas-Orinoco).

*Castaliella* Simpson, 1900: Martinez *et al.* (2004), Simone (2006).

- C. sulcata* (Krauss, 1849): NT(Amazonas-Orinoco).

### Tribe RHIPIDODONTINI Starobogatov, 1970

*Rhipidodonta* Mörch, 1853: Modell (1950), Parodoiz (1968),  
 Haas (1969a), Simone (2006).

- R. variabilis* (Maton, 1811): NT(Paraná).  
 + *Unio paranensis* Lea, 1834  
*R. burroughiana* (Lea, 1834): NT(Paraná).  
*R. charruana* (d'Orbigny, 1835): NT(Atlantic-São Francisco,  
 Paraná).  
*R. funebris* (Lea, 1860): NT(Paraná).  
*R. grata* (Lea, 1860): NT(Paraná).  
*R. hylaea* (d'Orbigny, 1835): NT(Amazonas-Orinoco,  
 Paraná).  
*R. rhombea* (Spix & Wagner, 1827): NT(Amazonas-Orinoco,  
 Atlantic-São Francisco).  
*R. suavidica* (Lea, 1856): NT(Amazonas-Orinoco, Atlantic-  
 São Francisco).

*Diplodon* Spix & Wagner, 1827: Modell (1950), Parodoiz (1968),  
 Haas (1969a), Simone (2006).

- D. ellipticus* (Spix & Wagner, 1927): NT(Atlantic-São  
 Francisco, Paraná).  
*D. besckeanus* (Dunker, 1848): NT(Atlantic-São Francisco).  
*D. chilensis* (Gray, 1828): NT(Patagonia).  
*D. delodontus* (Lamarck, 1819): NT(Paraná).  
*D. expansus* (Küster, 1856): NT(Paraná).  
*D. flucki* Morrison, 1943: NT(Amazonas-Orinoco).  
*D. fluctiger* (Lea, 1859): NT(Amazonas-Orinoco).  
*D. fontainianus* (d'Orbigny, 1835): NT(Atlantic-São  
 Francisco, Paraná).  
*D. granosus* (Bruguère, 1792): NT(Amazonas-Orinoco,  
 Atlantic-São Francisco, Paraná).  
*D. guaporensis* Bonetto & Tassara, 1987: NT(Amazonas-  
 Orinoco).  
*D. losadae* Haas, 1966: NT(Amazonas-Orinoco).  
*D. multistriatus* (Lea, 1831): NT(Atlantic-São Francisco,  
 Paraná).  
*D. parallelopipedon* (Lea, 1834): NT(Paraná).  
*D. parodizi* Bonetto, 1962: NT(Paraná).  
*D. patagonicus* (d'Orbigny, 1835): NT(Patagonia).  
*D. rhuacoicus* (d'Orbigny, 1835): NT(Atlantic-São Francisco,  
 Paraná).  
*D. solidulus* (Philippi, 1869): NT(Patagonia).  
*D. voltzi* Vernhout, 1914: NT(Amazonas-Orinoco).  
*D. wymanii* (Lea, 1860): NT(Paraná).

### Tribe HYRIDELLINI McMichael, 1956 (1934)

*Hyridella* Swainson, 1840: McMichael & Hiscock (1958), B.J.  
 Smith (1992).

- H. (Hyridella) australis* (Lamarck, 1819): AU(East).  
*H. (Hyridella) aucklandica* (Gray, 1843): AU(New Zealand).  
*H. (Hyridella) depressa* (Lamarck, 1819): AU(East).  
*H. (Hyridella) drapeta* (Iredale, 1934): AU(East).  
*H. (Hyridella) misoolensis* (Schepman, 1897): AU(New  
 Guinea).  
*H. (Hyridella) narracanensis* (Cotton & Gabriel, 1932):  
 AU(East).  
*H. (Nesonaia) guppyi* (E.A. Smith, 1885): AU(New Guinea).  
*H. (Protohyride)*

LLA) GLENELGENSIS (DENNANT, 1898):  
AU(EAST).

*Cucumerunio* Iredale, 1934: McMichael & Hiscock (1958), B.J. Smith (1992).

*C. novaehollandiae* (Gray, 1834): AU(East).

*C. websteri* (Simpson, 1902): AU(New Zealand).

*Echydridella* McMichael & Hiscock, 1958: McMichael & Hiscock (1958), Fenwick & Marshall (2006).

*E. menziesii* (Gray, 1843): AU(New Zealand).

*E. lucasi* (Suter, 1905): AU(New Zealand).

*E. onekaka* Fenwick & Marshall, 2006: AU(New Zealand).

*Virgus* Simpson, 1900: McMichael & Hiscock (1958), Haas (1969a).

*V. beccarianus* (Tapparone Canefri, 1883): AU(New Guinea).

**Subfamily VELESUNIONINAE Iredale, 1934**

*Velesunio* Iredale, 1934: McMichael & Hiscock (1958), B.J. Smith (1992).

*V. ambiguus* (Philippi, 1847): AU(East).

+ *Unio balonnensis* Conrad, 1850

*V. angasi* (Sowerby, 1867): AU(East, West).

*V. moretonicus* (Reeve, 1865): AU(East).

?*V. ovata* (Haas, 1910): AU(New Guinea).

*V. sentaniensis* (Haas, 1924): AU(New Guinea).

*V. wilsonii* (Lea, 1859): AU(East, West, New Guinea).

*Alathyria* Iredale, 1934: McMichael & Hiscock (1958), B.J. Smith (1992).

*A. jacksoni* Iredale, 1934: AU(East).

*A. condola* Iredale, 1934: AU(East).

*A. profuga* (Gould, 1851): AU(East).

*A. pertexta* Iredale, 1934: AU(East, New Guinea).

*Lortiella* Iredale, 1934: McMichael & Hiscock (1958), B.J. Smith (1992), Ponder & Bayer (2004).

*L. rugata* (Sowerby, 1868): AU(West).

*L. froggattii* Iredale, 1934: AU(West).

*L. opertanea* Ponder & Bayer, 2004: AU(West).

*Microdontia* Tapparone Canefri, 1883: McMichael & Hiscock (1958).

*M. anodontaeformis* (Tapparone Canefri, 1883): AU(New Guinea).

*Westralunio* Iredale, 1934: McMichael & Hiscock (1958), B.J. Smith (1992).

*W. carteri* Iredale, 1934: AU(West).

*W. albertsi* Clench, 1957: AU(New Guinea).

*W. flyensis* (Tapparone Canefri, 1883): AU(New Guinea).

**the lasidium-bearing freshwater mussels**  
**Family ETHERIIDAE s.s.**

*Etheria* Lamarck, 1807: Pilsbry & Bequaert (1927), Pain & Woodward (1961).

*E. elliptica* Lamarck, 1807: AF(Nile, West, Congo, East, South, Madagascar).

+ *Etheria semilumata* Lamarck, 1807

*Acostaea* d'Orbigny, 1851: Pain & Woodward (1961), Haas (1969a).

*A. rivolii* (Deshayes, 1827): NT(Transandean).

+ *Acostaea guaduasana* d'Orbigny, 1851

*Bartlettia* H. Adams, 1866: Pain & Woodward (1961), Haas (1969a), Simone (2006).

*B. stefanensis* (Moricand, 1856): NT(Amazonas-Orinoco, Paraná).

*Pseudomulleria* Anthony, 1907: Pain & Woodward (1961), Subba Rao (1989).

*P. dalyi* (E.A. Smith, 1898): IN(India-Burma).

**Family MYCETOPODIDAE Gray, 1840**

**Subfamily MYCETOPODINAE s.s.**

*Mycetopoda* d'Orbigny, 1835: Lange de Morretes (1949), Bonetto (1962), Haas (1969a), Simone (2006).

*M. soleniformis* d'Orbigny, 1835: NT(Amazonas-Orinoco, Paraná).

*M. legumen* (von Martens, 1888): NT(Paraná).

*M. siliquosa* (Spix & Wagner, 1827): NT(Mesoamerica, Transandean, Amazonas-Orinoco, Atlantic-São Francisco, Paraná).

*Mycetopodella* Marshall, 1927: Haas (1969a), Ramírez *et al.* (2003), Simone (2006).

*M. falcata* (Higgins, 1868): NT(Amazonas-Orinoco).

**Subfamily ANODONTITINAE Modell, 1942**

*Anodontites* Bruguière, 1792: Frierson (1927), Haas (1969a), Johnson (1981), Martínez *et al.* (2004), Simone (2006).

*A. crispatus* Bruguière, 1792: NT(Transandean, Amazonas-Orinoco).

*A. cylindraceus* (Lea, 1838): NT(Mesoamerica).

*A. depexus* (von Martens, 1900): NT(Mesoamerica).

*A. elongatus* (Swainson, 1823): NT(Transandean, Amazonas-Orinoco, Paraná).

*A. ferrarisii* (d'Orbigny, 1835): NT(Paraná).

*A. inaequivalva* (Lea, 1868): NT(Mesoamerica).

*A. leotaudi* (Guppy, 1864): NT(Amazonas-Orinoco).

*A. moricandii* (Lea, 1860): NT(Atlantic-São Francisco).

*A. obtusus* (Spix & Wagner, 1827): NT(Amazonas-Orinoco, Atlantic-São Francisco, Paraná).

*A. patagonicus* (Lamarck, 1819): NT(Amazonas-Orinoco, Paraná).

*A. pittieri* Marshall, 1922: NT(Amazonas-Orinoco).

*A. tehuantepecensis* (Crosse & Fischer, 1894): NT(Mesoamerica).

*A. tenebricosus* (Lea, 1834): NT(Transandean, Amazonas-Orinoco, Atlantic-São Francisco, Paraná).

*A. tortilis* (Lea, 1852): NT(Mesoamerica, Transandean, Amazonas-Orinoco).

*A. trapesimalis* (Lamarck, 1819): NT(Mesoamerica, Transandean, Amazonas-Orinoco, Atlantic-São Francisco, Paraná).

*A. trapezeus* (Spix & Wagner, 1827): NT(Amazonas-Orinoco, Atlantic-São Francisco, Paraná).

*A. trigonus* (Spix & Wagner, 1827): NT(Mesoamerica, Transandean, Amazonas-Orinoco, Paraná, Patagonia).

*Lamproscapha* Swainson, 1840: Lange de Morretes (1949), Quintana (1982), Martínez *et al.* (2004), Simone (2006).

*L. ensiformis* (Spix & Wagner, 1827): NT(Amazonas-Orinoco, Paraná).

**Subfamily LEILINAE Lange de Morretes, 1949**

*Leila* Gray, 1840: Veitenheimer (1973).

*L. esula* (d'Orbigny, 1835): NT(Amazonas-Orinoco).

*L. blainvilliana* (Lea, 1834): NT(Amazonas-Orinoco, Paraná).

**Subfamily MONOCONDYLAEINAE Modell,  
1942**

- Monocondylaea* d'Orbigny, 1835: Bonetto (1966), Haas (1969a), Simone (2006).  
*M. paraguayana* (d'Orbigny, 1835): NT(Amazonas-Orinoco, Paraná).  
*M. corrientensis* (d'Orbigny, 1835): NT(Amazonas-Orinoco, Atlantic-São Francisco, Paraná).  
*M. minuana* (d'Orbigny, 1835): NT(Paraná).  
*Diplodontites* Marshall, 1922: Simone (2006).  
*D. cookei* Marshall, 1922: NT(Transandean, Amazonas-Orinoco).  
*D. olssoni* Pilsbry, 1933: NT(Transandean).  
*D. pilsbryana* Olsson & Wurtz, 1951: NT(Transandean).  
*Fossula* Lea, 1870: Bonetto (1966), Simone (2006).  
*F. fossiculifera* (d'Orbigny, 1835): NT(Amazonas-Orinoco, Atlantic-São Francisco, Paraná).  
*Haasica* Strand, 1932: Bonetto (1966), Simone (2006).  
*H. balzani* (von Ihering, 1893): NT(Paraná).  
*Iheringella* Pilsbry, 1893: Bonetto (1966), Simone (2006).  
*I. isocardioides* (Lea, 1856): NT(Paraná).  
*I. semisulcata* (H. Adams, 1870): NT(Amazonas-Orinoco).  
*Tamsiella* Haas, 1931: Bonetto (1972), Simone (2006).  
*T. tamsiana* (Dunker, 1858): NT(Amazonas-Orinoco).  
*T. amazonica* Bonetto, 1972: NT(Amazonas-Orinoco).

**Family IRIDINIDAE Swainson, 1840**

**Subfamily IRIDININAE s.s.**

- Mutela* Scopoli, 1777: Daget (1998), Graf & Cummings (2006a).  
 + *Iridina* Lamarck, 1819  
*M. dubia* (Gmelin, 1791): AF(Nile, West, Congo).  
*M. alata* (Lea, 1864): AF(South).  
*M. alluaudi* Germain, 1909: AF(Nile).  
*M. bourguignati* Bourguignat, 1885: AF(Nile).  
*M. franci* Daget, 1964: AF(West).  
*M. hargeri* E.A. Smith, 1908: AF(Congo).  
*M. joubini* (Germain, 1904): AF(West, Congo).  
*M. langi* Pilsbry & Bequaert, 1927: AF(Congo).  
*M. legumen* (Rochebrune, 1886): AF(Congo).  
*M. mabilli* (Rochebrune, 1886): AF(Congo).  
*M. rostrata* (Rang, 1835): AF(Nile, West, Congo).  
*M. soleniformis* Bourguignat, 1885: AF(Congo).

- M. wistarmorrisi* Graf & Cummings 2006: AF(South).  
*M. zambesensis* Mandahl-Barth, 1988: AF(South).

- Chelidonopsis* Ancey, 1887: Daget (1998).  
*C. hirundo* (von Martens, 1881): AF(Congo).  
*Pleiodon* Conrad, 1834: Pain & Woodward (1964), Daget (1998).  
*P. ovata* (Swainson, 1823): AF(West).  
 + *Pleiodon macmurtriei* Conrad, 1834  
*P. spekii* (Woodward, 1859): AF(Congo).

**Subfamily ASPATHARIINAE Modell, 1942**

- Aspatharia* Bourguignat, 1885: Daget (1998), Graf & Cummings (2006a, in press).  
*A. rugifera* (Dunker, 1858): AF(Congo, South).  
 + *Margaritana vignouana* Bernardi, 1859  
*A. chaziana* (Rang, 1835): AF(Nile, West).  
*A. dahomeyensis* (Lea, 1859): AF(West).  
*A. divaricata* (von Martens, 1897): AF(Nile).  
*A. droueti* (Chaper, 1885): AF(West).  
*A. mabillei* (Jousseume, 1886): AF(West).  
*A. marnoi* (Jickeli, 1874): AF(Nile).  
*A. pangallensis* (Rochebrune, 1882): AF(West).  
*A. pfeifferiana* (Bernardi, 1860): AF(West, Congo).  
*A. rochebrunei* (Jousseume, 1886): AF(West).  
*A. semicorrugata* (Preston, 1909): AF(Congo).  
*A. subreniformis* (Sowerby, 1867): AF(South).  
*A. tawaii* (Rang, 1835): AF(West).  
*A. tristis* (Jousseume, 1886): AF(West).  
*Chambardia* Bourguignat in Servain, 1890: Daget (1998), Graf & Cummings (2006a, in press).  
*C. letourneuxi* Servain, 1890: AF(Nile).  
*C. bourguignati* (Bourguignati, 1885): AF(Nile).  
*C. dautzenbergi* (Haas, 1936): AF(Congo).  
*C. moutai* (Darteville, 1939): AF(South).  
*C. nyassaensis* (Lea, 1864): AF(Congo, South).  
*C. petersi* (von Martens, 1860): AF(South).  
*C. rubens* (Lamarck, 1819): AF(Nile, West).  
*C. trapezia* (von Martens, 1897): AF(Nile).  
*C. wahlbergi* (Krauss, 1848): AF(Nile, West, East, South).  
*C. weltwitschii* (Morelet, 1868): AF(South).  
*C. wissmanni* (von Martens, 1883): AF(West, Congo).  
*Moncetia* Bourguignat, 1885: Daget (1998).  
*M. anceyi* Bourguignat, 1885: AF(Congo).