

APPENDIX II
CORRECT FAMILY-GROUP NAMES OF THE UNIONOIDA, THOSE APPLIED
IN THIS DISSERTATION, AND A CONSENSUS CLASSIFICATION

There has been some confusion regarding the correct names of unionoid families, or, in some cases, there *should have been* some confusion but it has never been recognized. The likely reason has been the general lack of concern among freshwater malacologists to establish the correct familial nomenclature (as opposed to generic and trivial nomina) and disinterest in applying the recommendations of the ICZN. The lexicon of freshwater mussel families names presented here is not meant to be complete but rather a guide to the nomenclature applied in this dissertation. Thus, the numerous unionoid lineages that I do not consider in analyses are not listed; the majority of those ignored names presumably date from Modell (1942). The correct names of the Etheriidae, Iridinidae, and Mycetopodidae have been dealt with in detail by Kabat (1997).

All family-group names are listed in **Table II.1**. These names are largely non-problematical from a nomenclatural perspective, with two exceptions: Margaritiferidae and Diplodontidae. Margaritiferidae Haas, 1940 has been added to the official list of family-group names (Melville & Smith, 1987) based on ICZN O.495 (Hemming, 1957). This ruling ignores Henderson's (1935) earlier, correct application of that nomenclature. However, because (1) Margaritiferidae is one of only two freshwater mussel family-group nomina on the official list and (2) changing the authority will have no effect on unionoid nomenclature, the family-group name for *Margaritifera* will be maintained as Margaritiferidae Haas, 1940.

In the case of Diplodontidae von Ihering, 1901, the historically incorrect usage of that name is continued in this dissertation for the sake of consistency. Parodiz & Bonetto

(1963: 198-199) discussed the application of the family-group names Diplodontidae and Prisodontidae to the Hyriidae of South America:

“The family name Diplodontidae Ihering 1901... is not valid, being preoccupied by Diplodontidae Dall [1895], created for marine bivalves. Prisodontini Modell 1942 included the genus *Hyria* (= *Prisodon*) which cannot be separated as a subfamily by itself. The name Hyriidae Swainson 1840 has priority, but Diplodontini and Prisodontini can be used as tribal denominations.”

While Parodiz & Bonetto (1963) clearly recognized the problems with Diplodontidae and Prisodontidae, their designations did nothing to correct them. It seems clear from the quote above that they did not consider “tribal denominations” as family-groups names. They are, however, according to the ICZN (Art. 36). In the case of Prisodontini, that nomenclature is simply a junior synonym of Hyriini.

Dall (1895: 545) purposefully introduced Diplodontidae as a junior synonym of Ungulinidae H. & A. Adams, 1857, stating, “The name *Ungulinidae* has been used for very different assemblages of genera, and I prefer to use a name for the family about which there can be no uncertainty.” Despite the poor reasoning for introducing a new name, Diplodontidae Dall, 1895 is still available as a family-group name. Thus, either Dall’s or von Ihering’s use of that name will need to be suppressed. Such an act of nomenclatural providence is beyond the scope of this dissertation, and the incorrect use of Diplodontidae von Ihering, 1901 for the genus *Diplodon* will be retained.

Table II.2 is a consensus classification of the Unionoida based on the ‘correct’ family-group names in **Table II.1** and differing schools of malacological thought (e.g., Simpson, 1900, 1914; Ortmann, 1910a, 1911a, b, 1912b, 1921a; Frierson, 1927; Modell, 1942, 1949, 1964; Morrison, 1956, 1973; McMichael & Hiscock, 1958; Pain & Woodward, 1961; Parodiz and Bonetto, 1963; Haas, 1969a, b; Heard & Guckert, 1971; Davis & Fuller, 1981; Boss, 1982; Korniushev, 1998). Although there is widespread disagreement as to the ranks of the various family-group taxa, there are several points of agreement. Most malacologists since Parodiz & Bonetto (1963), have agreed that the

Unionoida should be divided into two superfamilies: Unionoidea and Etherioidea. The taxa with glochidium-type larvae — Margaritiferidae, Unionidae, and Hyriidae — comprise the Unionoidea, and in the Etherioidea resides those families with lasidium-type larvae: Iridinidae (= Mutelidae), Mycetopodidae, and Etheriidae. With the exception of the Unionidae (as listed in **Table II.2**), there seems to be general agreement with regard to the family-level taxa.

The two most recent classifications of the Unionoidea — Heard & Guckert (1971) and Davis & Fuller (1981; also Lydeard *et al.*, 1996) — differ with regard to whether or not the Unionidae should be regarded as a single family or as two. However, this difference seems only to be a question of taxon rank, and the system of Davis & Fuller (1981) with one family divided into two subfamilies is analogous to Heard & Guckert's (1971: Figure 1) two family system. Heard & Guckert (1971) included the genus *Unio* in the same family as *Anodonta*; thus, their two families were Unionidae and Amblemidae. Davis & Fuller (1981) and others (Ortmann, 1910a, 1912b) placed *Unio* in the same family as *Amblema*; thus, their two subfamilies were Anodontinae and “Ambleminae.” The classification presented in **Table II.2** follows Davis & Fuller's (1981) system except that “Ambleminae” is replaced with the correct nomenclature: Unioninae.

The Russian school of Unionoida taxonomy (*e.g.*, Starobogatov, 1970) can be reconciled with the Western consensus. The Russian system — reviewed by Shikov & Zatravkin, 1991 and Korniushev, 1998 — is mostly conchological and aimed at ‘splitting,’ emphasizing differences among taxa rather than their similarities. Their proliferation of genera and families, however, still follows the basic divisions of the Unionoida shown in **Table II.2**.

Totally separate and irreconcilable with this consensus classification is the system proposed by Hans Modell (1942, 1949, 1964). Admirably, Modell (translated by Stansbery & Soehnagen, 1964: 3) sought to objectively approach a “natural” system of the Unionoida, explaining,

“It is almost as if I had before me the material obtained on an expedition to an unexplored planet and I have used on it the experiences of a biological nature which I have obtained in better than 20 years of collecting.”

Reaching the misconceived conclusion that, “Simpson [1900, 1914], as Ortmann emphasized in 1912, paid too little attention to the shell and especially to the sculpture of the beaks...” (Stansbury & Soehnagen, 1964: 2), Modell used these latter two characters to divide the Unionoida into better than 30 subfamilies in four families. A glance at Modell’s phylogeny (1942, plate 5) suggests that he had no intention of discovering “natural” (*i.e.*, monophyletic) suprageneric categories.

The consensus arrangement shown in **Table II.2** serves to place the ‘classification’ of the Unionoida in a logically consistent framework. The ‘logical consistency of classification’ I am referring to is *not* in the sense of Wiley (1980) (*i.e.*, classification should accurately reflect phylogeny). Instead, I am referring to idea that all of the disparate systems of some portion of the Unionoida are reconciled to make an arrangement of the whole. The ‘logical consistency’ of the natural classification *sensu* Wiley (1980) is dealt with in **Chapter 7**.

Table II.1. Family-Group Names of the Unionoida. All names are listed alphabetically by their family-level rank (Principle of Coordination, ICZN Art. 36). For the lineages traditionally placed among the UNIONIDAE (**Table I.2**), only those specific lineages dealt with in this dissertation have been included. That is, among that group, only family-group names for genera here analyzed or discussed are listed. The family-group names under the ETHERIOIDEA (**Table I.2**), nomenclature follows Kabat (1997).

ACOSTAEIDAE Morrison, 1973.

ACOSTAEIDAE Morrison (1973: 45).

ALASMIDONTIDAE Swainson, 1840. — Spelling emended by Frierson (1927).

ALASMODONTINÆ Swainson (1840: 268, 381).

ALASMIDONTINAE Frierson (1927: 8-9, 18).

AMBLEMIDAE Rafinesque, 1820.

AMBLEMIDIA *Les Amblémides* Rafinesque (1820: 44, 1964: 46).

AMBLEMINAE Modell (1942: 180, 1949: 41, 1964: 90).

ANODONTIDAE Rafinesque, 1820.

ANODONTIDIA *Les Anodontides* Rafinesque (1820: 50, 1964: 48).

ANODONTINÆ Swainson (1840: 286, 381).

ANODONTINÆ Ortmann (1910a: 117, 1912b: 224).

ANODONTITIDAE Modell, 1942.

ANODONTITINAE Modell (1942: 175, 1949: 38, 1964: 81).

GLABARINAE Modell (1942: 175, 1949: 38, 1964: 81).

Table II.1 (continued). Family-Group Names of the Unionoida.

CAELATURIDAE Modell, 1942.

CAELATURINAE Modell (1942: 190, 1949: 46, 1964: 116).

CAFFERIIDAE Modell, 1942.

CAFFERIINAE Modell (1942: 188, 1949: 45).

CASTALIIDAE Morretes, 1949.

CASTALIINAE Morretes (1949: 21).

CASTALIINI Parodiz & Bonetto (1963: 201, 204).

CUCUMERUNIONIDAE Iredale, 1934. — Iredale's (1934) incorrect suffix emended by Modell (1942) in accordance with ICZN Article 29.

CUCUMERUNIONAE Iredale (1934: 58, 77, 1943a: 191).

CUCUMERUNIONINAE (Iredale, 1934) Modell (1942: 184, 1949: 42).

CUMBERLANDIIDAE Heard & Guckert, 1971. — The suffix applied by Heard & Guckert (1971) is not in accordance with ICZN Art. 29. It was corrected by Davis & Fuller (1981).

CUMBERLANDINAE Heard & Guckert (1971: 338).

CUMBERLANDIINAE Davis & Fuller (1981: 237, 250).

Table II.1 (continued). Family-Group Names of the Unionoida.

DIPLODONTIDAE von Ihering, 1901. — This name is a junior homonym of the DIPLODONTIDAE Dall, 1895 (= UNGULINIDAE H. & A. Adams, 1858). In the future, one of these nomina should be suppressed and renamed.

DIPLODONTIDAE von Ihering (1901: 52-53).

DIPLODONTINAE Morretes (1949: 17).

DIPLODONTINI Parodiz & Bonetto (1963: 199, 205).

ELLIPTIONIDAE Modell, 1942.

ELLIPTIONIDAE Modell (1942: 178, 180, 1949: 40, 1964: 88).

ETHERIIDAE Deshayes, 1830.

Ethéries Deshayes (1830: table, fam. 20).

ETHERIDÆ Swainson (1840: 258, 390).

FOSSULIDAE Bonetto, 1966.

FOSSULINI Bonetto (1966: 3, 5).

GONIDEIDAE Ortmann, 1916.

GONIDEINAE Ortmann (1916a: 53).

Table II.1 (continued). Family-Group Names of the Unionoida.

HYRIDELLIDAE McMichael, 1956 (1934). — The priority of HYRIDELLIDAE over PROPEHYRIDELLIDAE due to priority of the type genus is valid according to ICZN Article 40.2 because the replacement occurred before 1961.

PROPEHYRIDELLIDAE Iredale (1934: 58, 76-77, 1943a: 189-190, 1943b: 87).

HYRIDELLINAE McMichael (1956: 42, 1958: 427; McMichael & Hiscock, 1958: 435).

HYRIIDAE Swainson, 1840. — Swainson's (1840) incorrect suffix was emended by Ortmann (1910a) in accordance with ICZN Article 29. HYRIIDAE is retained over PRISODONTIDAE following ICZN Article 40.1.

HYRINÆ Swainson (1840: 268, 282). — Modell (1964: 103).

HYRIANÆ Swainson (1840: 379). — Agassiz (1845: 43).

HYRIOIDÆ Agassiz (1846: 192).

HYRIINÆ Ortmann (1910a: 115, 1911a: 108, 120, 130, 1912b: 225, 1912c: 103, 1921a: 457). — Modell (1942: 186, 1949: 43).

PRISODONTINAE Modell (1942: 174, 1949: 38, 1964: 80).

PRISODONTIDAE Morretes (1949: 17, 23).

PRISODONTINI Parodiz & Bonetto (1963: 201, 204).

IRIDINIDAE Swainson, 1840

IRIDININÆ Swainson (1840: 261, 286, 380).

Table II.1 (continued). Family-Group Names of the Unionoida.

LAMPSILIDAE von Ihering, 1901.

LAMPSILINÆ von Ihering (1901: 53).

LAMPSILINÆ Ortmann (1910a: 118, 1912b: 224).

LEILIDAE Morretes, 1949.

LEILINAE Morretes (1949: 28).

LORTIELLIDAE Iredale, 1934.

LORTIELLINAE Iredale (1934: 58, 77, 1943a: 190).

MARGARITIFERIDAE Haas, 1940. — The ICZN (O.495 Hemming, 1957) ruled that MARGARITIFERIDAE Haas, 1940 was the official family name following suppression of MARGARITANIDAE Ortmann, 1910a (Melville & Smith, 1987).

MARGARITANINÆ Ortmann (1910a: 114, 1912b: 223).

MARGARITIFERINAE Henderson (1935: 68).

MARGARITIFERIDAE Haas (1940: 119).

MARGARITIFERINAE Modell (1942: 184, 1949: 42, 1964: 97).

MEGALONAIADINAE Heard & Guckert, 1971.

MEGALONAIADINAE Heard & Guckert (1971: 338).

MONOCONDYLAEIDAE Modell, 1942.

MONOCONDYLAEINAE Modell (1942: 175, 1949: 38, 1964: 81).

Table II.1 (continued). Family-Group Names of the Unionoida.

MUTELIDAE Gray, 1847.

MUTELADAE Gray (1847:197).

MYCETOPODIDAE Gray, 1840.

MYCETOPODIDAE Gray (1840: 142, 155).

PARREYSIIDAE Henderson, 1935.

PARREYSIINAE Henderson (1935: 69). — Modell (1964: 107).

PARREYSIINAE Modell (1942: 186, 1949: 43).

PLEUROBEMIDAE Hannibal, 1912.

PLEUROBEMINÆ Hannibal (1912: 119). — Modell (1949: 40).

PLEUROBEMINAE Modell (1942: 179, 1964: 88).

PSEUDODONTIDAE Frierson, 1927.

PSEUDODONTINAE Frierson (1927: 67).

PSEUDOMULLERIIDAE Starobogatov, 1970.

PSEUDOMULLERIIDAE Starobogatov (1970: 75, 288).

PSEUDOMULLERIDAE Morrison (1973: 46).

Table II.1 (continued). Family-Group Names of the Unionoida.

QUADRULIDAE von Ihering, 1901.

QUADRULINÆ von Ihering (1901: 53). — Hannibal (1912: 119). — Modell (1949: 44, 1964: 106).

QUADRULINAE Haas (1929: 333). — Modell (1942: 187).

RECTIDENTIDAE Modell, 1942. — The genus *Uniandra* has been placed in CONTRADENTINAE and ANODONTINAE by Modell (1942, 1949, 1964). CONTRADENTINAE, the type genus of which is *Uniandra*, was considered a synonym of the RECTIDENTINAE by Brandt (1974).

RECTIDENTINAE Modell (1942: 189, 1949: 45, 1964: 113). — Brandt (1974: 287).

CONTRADENTINAE Modell (1942: 189, 1949: 45).

STROPHITIDAE Starobogatov, 1970.

STROPHITINAE Starobogatov (1970: 69, 287). — Bogan (1985: 141-142).

STROPHITINI Gordon (1981: 58, 1985: 8).

UNIONIDAE Rafinesque, 1820. — Originally, the ICZN (O.495 Hemming, 1957) had ruled the UNIONIDAE Fleming, 1828 was the official family name. This was subsequently corrected by Melville & Smith (1987).

UNIODIA *Les Uniodés* Rafinesque (1820: 24, 1964: 35).

UNIONIDAE Fleming (1828: 408, 415).

UNIONIDÆ Swainson (1840: 257, 264, 377).

Table II.1 (continued). Family-Group Names of the Unionoida.

VELESUNIONIDAE Iredale, 1934. — Iredale's (1934) incorrect suffix emended by Modell (1942) in accordance with ICZN Article 29.

VELESUNIONAE Iredale (1934: 58, 76, 1943a: 189).

VELESUNIONINAE (Iredale, 1934) Modell (1942: 178, 1949: 39, 1964: 87).

Table II.2. An Annotated Consensus Classification of the Unionoida. See text for discussion.

Order UNIONOIDA

Superf. UNIONOIDEA Rafinesque, 1820.

Fam. UNIONIDAE *s.s.*

Subf. UNIONINAE *s.s.*

Tr. UNIONINI *s.s.* (= CAFFERIINI Modell, 1942)

Tr. AMBLEMINI Rafinesque, 1820

(= MEGALONAIADINAE Heard & Guckert, 1971)

(= QUADRULINI von Ihering, 1901).

Tr. CAELATURINI Modell, 1942.

Tr. GONIDEINI Ortmann, 1916a.

(=PSEUDODONTINI Frierson, 1927).

Tr. LAMPSILINI von Ihering, 1901.

Tr. PARREYSIINI Henderson, 1935.

Tr. PLEUROBEMINI Hannibal, 1912

(= ELLIPTIONINI Modell, 1942).

Tr. PSEUDODONTINI Frierson, 1927.

Tr. RECTIDENTINI Modell, 1942.

Subf. ANODONTINAE Rafinesque, 1820.

Tr. ANODONTINI *s.s.*

Tr. ALASMIDONTINI Swainson, 1840.

Tr. STROPHITINI Starobogatov, 1970.

Table II.2 (continued). An Annotated Consensus Classification of the Unionoida.

Fam. MARGARITIFERIDAE Haas, 1940.
Subf. MARGARITIFERINAE <i>s.s.</i>
Subf. CUMBERLANDIINAE Heard & Guckert, 1971.
Fam. HYRIIDAE Swainson, 1840.
Subf. HYRIINAE <i>s.s.</i>
Tr. HYRIINI <i>s.s.</i>
Tr. CASTALIINI Morretes, 1949.
Tr. DIPLODONTINI von Ihering, 1901.
Subf. HYRIDELLINAE McMichael, 1956 (1934).
Tr. HYRIDELLINI <i>s.s.</i>
Tr. CUCUMERUNIONINI Iredale, 1934.
Tr. LORTIELLINI Iredale, 1934.
Tr. VELESUNIONINI Iredale, 1934.
Superf. ETHERIOIDEA Deshayes, 1830.
Fam. ETHERIIDAE <i>s.s.</i>
Subf. ETHERIINAE <i>s.s.</i>
Subf. ACOSTAEINAE Morrison, 1973.
(= PSEUDOMULLERIINAE Starobogatov, 1970).
Fam. MYCETOPODIDAE Gray, 1840.
Subf. MYCETOPODINAE <i>s.s.</i>
Subf. ANODONTITINAE Modell, 1942.
Subf. LEILINAE Morretes, 1949.
Subf. MONOCONDYLAEINAE Modell, 1942.

Table II.2 (continued). An Annotated Consensus Classification of the Unionoida.

Tr. MONOCONDYLAEINI *s.s.*

Tr. FOSSULINI Bonetto, 1966.

Fam. IRIDINIDAE Swainson, 1840.

(= MUTELINAE Gray, 1847).
