

REVIEW ARTICLE

A ‘big data’ approach to global freshwater mussel diversity (Bivalvia: Unionoida), with an updated checklist of genera and species

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ABSTRACT

The objective of this review is to update our previously published checklist of Recent freshwater mussel species and genera (Graf & Cummings, 2007, *J. Molluscan Stud.*: 291–314) to reflect the new data and research findings that have accumulated over the last decade. The MUSSEL Project Database was developed to synthesize the available taxonomic nomenclature, species ranges and published taxonomic hypotheses on genus–species combinations and synonymy. We have found 4,988 available species-group level nominal species representing 958 valid species in 192 genera worldwide, an increase of 118 species since 2007. The current patterns of species richness are discussed with regard to both taxonomy and geography, as is the general flux in the number of species recognized over time. A checklist is provided herein, with a bibliography to key faunistic and taxonomic references. The full dataset is maintained and updated on the MUSSEL Project Web Site (<http://mussel-project.net/>).

INTRODUCTION

It has been more than a decade since we published our checklist of the Recent species of the order Unionoida (= Unioniformes = Unionida) (Graf & Cummings, 2007b), and the new information that has since accumulated provides an opportunity to synthesize, update and revise our understanding of global freshwater mussel diversity. Freshwater mussels are of practical and aesthetic interest, both as molluscan canaries-in-the-coal-mines of globally threatened inland waterways (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010; Lopes-Lima *et al.*, 2018b; Reid *et al.*, 2019) and as fascinating, long-lived invertebrates with unusual parasitic life cycles adapted to life in flowing waters (Cummings & Graf, 2009; Haag, 2012; Graf, 2013). Ferreira-Rodríguez *et al.* (2019) listed determination of ‘species identity’ as a freshwater mussel conservation priority, and species inventories are a valuable first step towards conservation action. This is especially so for invertebrates, which are often overlooked in regional conservation assessments (Graf & Cummings, 2011; Collen *et al.*, 2014). We (as a community) need to agree which species of freshwater mussels occur where before we can prioritize which need protection and management.

Charles T. Simpson (1900, 1914) initiated the modern era of freshwater mussel systematics with comprehensive accounts of all of the then-known Recent species, and Fritz Haas (1969a) delivered the only other global, species-level appraisal during the 20th century. Each of those works provided a catalogue of valid species

and genera and the taxa synonymous with them. Valid taxa are those that are considered to be actual biological entities (i.e. clades and species), and they are a subset of the formal, type-bearing names introduced for taxonomic purposes (ICZN, 1999). We refer to the set of all available named species as nominal species. A valid species can circumscribe multiple synonymous nominal species (i.e. synonyms), and the nomenclatural principle of priority determines which of the available names should be applied. The validity of nominal species varies among authors, and any accounting of freshwater mussel diversity is enriched by considering both the biological taxa and the names that have been applied historically. During the nearly 40 years between Haas (1969a) and our first checklist (Graf & Cummings, 2007b), the imperilled conservation status of freshwater mussels attracted much needed attention (Bogan, 1993; Lydeard *et al.*, 2004; Strayer, 2006; Lopes-Lima *et al.*, 2018b), regional faunas were revised and there was an impetus for an updated global checklist of genera and species for the 21st century.

Since 2007, the pace of taxonomic and faunistic revision has increased worldwide, and the time is ripe for a reassessment of the patterns of global freshwater mussel richness and endemism, with an update of the underlying taxonomy. There have been recent, continent-scale regional assessments published for North America (Williams *et al.*, 2017), South America (Pereira *et al.*, 2014), Africa (Graf & Cummings, 2011), Europe (Lopes-Lima *et al.*, 2017b), East Asia (Zieritz *et al.*, 2018a) and Australasia (Walker, Jones & Klunzinger, 2014). Furthermore, grand phylogeny-based

suprageneric classifications have been proposed that have refined our concept of family-group level taxa (Whelan, Geneva & Graf, 2011; Bolotov *et al.*, 2017b; Lopes-Lima *et al.*, 2017a; Pfeiffer, Breinholt & Page, 2019b). However, there have also been numerous, valuable studies at local geographical and taxonomic scales that offer new insights into freshwater mussel diversity and biogeography. Our objectives herein are to (1) synthesize the current state of knowledge of freshwater mussel species richness and distributions into a consensus checklist of species and their geographical ranges and (2) provide an entrée into the copious literature that can serve as a resource for the freshwater mussel research community. The basis for achieving these objectives is the MUSSEL Project Database (MUSSELpdb).

THE MUSSEL PROJECT DATABASE

Since 2002, we have developed the MUSSELpdb as a tool to synthesize taxonomic, bibliographical, geographical and collections-based data about freshwater bivalves. The MUSSELpdb is implemented locally in FileMaker Pro Advanced v. 17 (<https://www.filemaker.com>) and served via the internet on the MUSSEL Project Web Site (<http://mussel-project.net/>). Python 3.6 (<https://www.python.org>) was used to automate queries and format the output for analysis, reporting and publication. We have applied the MUSSELpdb for previous diversity analyses (Graf, 2007, 2013; Graf & Cummings, 2007b, 2019), faunistic studies (Graf & Cummings, 2006, 2007a, 2009, 2011) and taxonomic catalogues (Graf, 2010, 2011). Moreover, the online version has been utilized by researchers around the world as a resource for taxonomic information and specimen data. In particular, multiple studies have utilized the taxonomic and specimen data on the MUSSEL Project Web Site as a primary or major data source (e.g. Linares & Vera, 2012; He & Zhuang, 2013; Do, Tuan & Bogan, 2018; Lopes-Lima *et al.*, 2018b; Zieritz *et al.*, 2018a).

The development of the MUSSELpdb was described previously (Graf & Cummings, 2007b), and our data model is illustrated and described on the MUSSEL Project Web Site. To produce the global checklist of Recent freshwater mussel species, we compiled a comprehensive catalogue of nominal species-, genus- and family-group level taxa from previous global syntheses (e.g. Simpson, 1900, 1914; Thiele, 1934; Modell, 1942, 1964; Haas, 1969a, b; Starobogatov, 1970; Vaught, 1989; Bieler, Carter & Coan, 2010). Nominal taxa were accounted for in regional faunistic studies and revisionary works (too numerous to list), as well as internet-based species inventories (e.g. <https://www.itis.gov>, <http://www.molluscabase.org>, <https://www.iucnredlist.org>), to determine currently accepted valid taxa and collate information about species' geographical ranges. Each nominal species was circumscribed within a valid species or treated as a *nomen dubium* based on published taxonomy. A *nomen dubium* is a described taxon with an uncertain or ambiguous connection to a biological species or clade. As described in Graf (2007), the MUSSELpdb also records the history of taxonomic opinions for each nominal taxon. A taxonomic opinion record serves as an associative entity between a nominal species and a published work that reports (1) whether the nomen was treated as valid, (2) the senior synonym in the author's circumscription of the species, (3) the combination of genus and species applied, and (4) verbatim data about the geographical and stratigraphic distributions of the species. There is also a field for notes, such as common names and conservation status. A similar data structure exists for genera and families.

The geographical range of each species was determined to the resolution of major physiographic regions and subregions that largely correspond to aggregations of freshwater ecoregions (<http://www.feow.org>) (Abell *et al.*, 2008). These are depicted in Figure 1A and described in Table 1 with references to key

area-specific sources to freshwater mussel taxonomy and distribution. The species distributions reported herein were derived largely from the published record, with some additional data from museum records, especially for South and Central America.

The checklist is arranged taxonomically by family-group level taxa, genera and species. In general, included taxa are listed alphabetically, although type taxa are listed first. For each species, the geographical distribution is summarized by listing the occupied subregions (Table 1). An indication of how each species relates to our previous checklist (Graf & Cummings, 2007b) (e.g. being lumped or split, assigned to a different genus or described as new to science) is also provided. Key references to taxonomy and diversity for genera are provided in the checklist to augment the geographically based sources listed in Table 1. It was not our intention to revise species and genera or offer new combinations. However, where logic and consistency dictated, we have done so. Suprageneric classification follows recent phylogenetic revisions (Whelan *et al.*, 2011; Bolotov *et al.*, 2017b; Lopes-Lima *et al.*, 2017a; Pfeiffer *et al.*, 2019b) (Table 2). The online version of the MUSSELpdb (<http://mussel-project.net>) provides a comprehensive account of the literature and specimen sources, as well as a searchable interface and complete synonymies for genera and species.

The comprehensive nature of the MUSSELpdb, though still a work in progress, provides the basis for our review, and it will continue to serve as a resource for the research community. The current checklist of Recent freshwater mussel genera and species based on the sources we have reviewed by the time of submission for publication is provided below, following our summary of the taxonomy and biogeographical patterns we have discovered. The checklist herein is a snapshot of one consensus of mussel taxonomy. We have endeavoured to provide a globally consistent synthesis of the names in use by the freshwater malacological community, including those for which the taxonomy has been neglected. For example, current species- and genus-level taxonomy in Central America is based mostly on Frierson (1927). Haas (1969a) followed Frierson (Johnson, 1999a), and Graf & Cummings (2007b) merely elevated subgenera to genera to better reflect ongoing taxonomic practice. Despite the dubiousness of projecting Frierson's (1927) barely annotated list of pre-biological species into a modern context, those taxa have been rarely considered in the intervening century (Goodrich & van der Schalie, 1937; Pfeiffer *et al.*, 2019a), and the system of Frierson remains the *best* estimate to date. However, this is an area of active research (Cummings *et al.*, 2018, 2019; Inoue *et al.*, 2020a). As taxonomy worldwide is revised, we will continue to revise the checklist and update supporting data on the MUSSEL Project Web Site. The website reports the complete synonymies and histories of species taxonomic opinions that are the basis for the taxonomy reported herein.

GLOBAL RICHNESS

Our current tally is 958 species of freshwater mussels in 192 genera (Table 3). This represents a substantial net increase in richness (118 spp., 14%) since Graf & Cummings (2007b), but the flux in diversity is more complicated than a simple increase in newly described species. We have identified 4,988 available nominal species of Recent freshwater mussels, 72 of which are regarded as *nomina dubia*, and our review of taxonomy is based on more than 65,500 taxonomic opinions from the published literature. The checklist as well as the global and regional tallies includes extinct Recent species as representative of the historical richness (Bogan, 1993). All of these data are available on the MUSSEL Project Web Site and will continue to be regularly updated. On average, there are more than five synonymous nominal species available per valid species. That is, the biological entities as we know them have typically been named multiple times. At the extremes, there are 446 valid species based on only a single nominal species each, while two species from Europe [*Anodonta cygnea* (Linnaeus, 1758) and *A. anatina* (Linnaeus, 1758)]

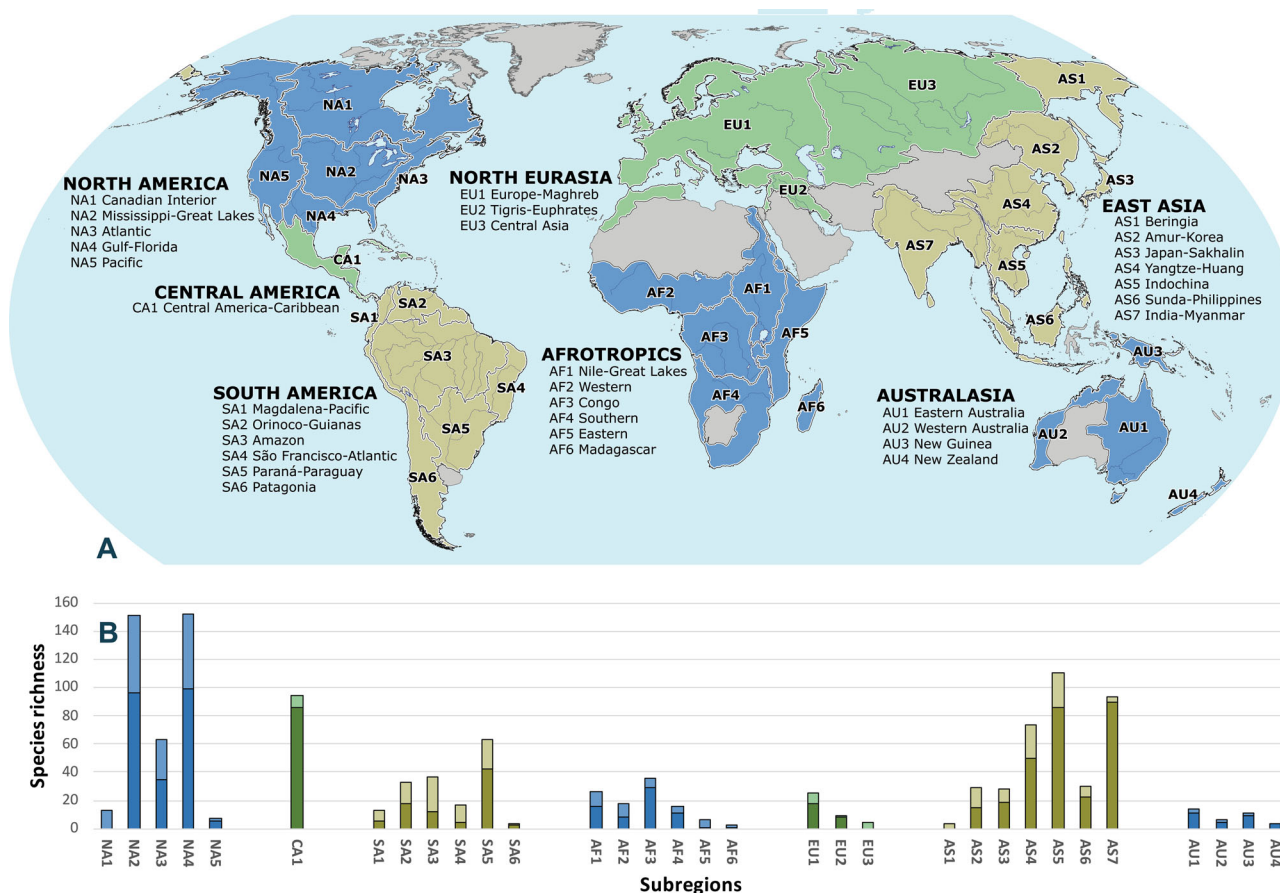


Figure 1. Freshwater mussel richness and endemism by subregion. **A.** Map of geographical regions and subregions. **B.** Total species richness (full extent of column) and endemic richness (darker portion) by subregion. Descriptions of subregions and key references are provided in Table 1.

account for 595 nominal species between them (12% of all available described species names).

History of freshwater mussel species assessment

The challenge of assessing the global diversity of freshwater mussels is accounting for all the nominal species and determining their alignment to actual valid species. Simpson (1914) recognized 1,323 valid species, Haas (1969a) listed 837 and Graf & Cummings (2007b) listed 840. Working contemporaneously but independently, Bogan (2008) reported 797 freshwater mussel species based on a review of several faunal accounts. We attribute the difference in near-simultaneous estimates to be the result of methodology. Whereas we (Graf & Cummings, 2007b) determined the global species list and then estimated the regional faunas from that synthesis, Bogan (2008) extrapolated from regional treatments to a global estimate. Since 2007, we have reported tallies of unionoid richness as high as 918 species (Graf, 2013; Graf & Cummings, 2019). Various internet initiatives have made available comprehensive species lists (e.g. <http://fada.biodiversity.be>, <http://www.bagniliggia.it/WMSD/WMSDhome.htm>, <https://itis.gov>, <http://mussel-project.uwsp.edu/fmuotwaolcb/>).

Our MUSSELpdb dataset allows us to reconstruct the history of freshwater mussel name usage since Linnaeus (1758) (Fig. 2). The method for constructing Figure 2 from the history of taxonomic opinions is explained in the figure caption. The flux in valid species over time (heavy green line) correlates well with the broad trends we might expect from the general history of taxonomy. There was a high number of species names in use through the 19th century while a typological species concept prevailed. That is, freshwater

mussel species, for most intents and purposes, corresponded to shell shapes, and the high within- and among-species variation exhibited by freshwater mussels (Ortmann, 1920; Zieritz & Aldridge, 2009) contributed to the description of thousands of nominal species. During the 20th century, the net trend in taxonomic effort was to consolidate ('lump') the described diversity. At mid-century, the Biological Species Concept (Mayr, 1963; Wheeler & Meier, 2000; de Queiroz, 2007) allowed for widespread, highly variable species with distinct-though-conspecific geographical 'subspecies'. Haas (1969a) was the nadir of recognized global species richness. In the 21st century, the number of recognized species has increased again as precladistic biological species were/are 'split' based on phylogenetic species concepts and algorithms for identifying species as genetic lineages (Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Yang & Rannala, 2010; Sukumaran & Knowles, 2017). As described below, the sampling effort has also recently increased. These broad trends fit the typical pattern for systematics and biogeographical research: a descriptive phase is followed by a narrative or explanatory phase that leads to an analytical phase (Ball, 1976).

The accumulation of nominal species and the flux in valid species over time depicted in Figure 2 also reflect the particular history of freshwater mussel taxonomy. Individual personalities had significant impacts on the endeavour to describe freshwater mussel diversity. For example, more than 50% of all available nominal species were introduced by only 11 men in Europe and North America: J.R. Bourguignat, T.A. Conrad, H. Drouët, L. Germain, M.P. Heude, W. Kobelt, I. Lea, A. Locard, E. von Martens, C.S. Rafinesque and C.T. Simpson. Isaac Lea (USA) alone named more than 860 freshwater mussels over nearly 50 years (1828–1874) (Scudder, 1885), and the spike in species names in the 1880–1890s

Table 1. Regions and subregions with key references.

Regions and subregions		Description	Freshwater ecoregions	Key references
NORTH AMERICA: Burch (1975b) ; Johnson (1980) ; Haag (2012) ; Williams et al. (1993, 2017)				
NA1	Canadian Interior	Arctic basins and those draining to Hudson Bay from the south and west; from the Mackenzie R. to the Nottaway R.	104–111	Clarke (1973, 1981a)
NA2	Mississippi–Great Lakes	Mississippi Basin including and above the Red River, as well as the Laurentian Great Lakes	116, 142–148, 149*, 150–152	Cummings & Mayer (1992) ; Parmalee & Bogan (1998) ; Watters et al. (2009)
NA3	Atlantic	Atlantic basins draining from Newfoundland south to the Satilla R. of Georgia; includes the St Lawrence below the Great Lakes	113–115, 117–119, 157–158	Johnson (1970) ; Strayer & Jirka (1997) ; Bogan (2002) ; Jones (2015)
NA4	Gulf–Florida	Gulf of Mexico basins from the R. Grande in Mexico, around peninsular Florida to the St Marys R.	132–141, 149*, 153–156, 161	Johnson (1972, 1999b) ; Howells, Neck & Murray (1996) ; Jones, Slack & Hartfield (2005) ; Williams et al. (2008, 2014) ; Williams, Butler & Wisniewski (2011)
NA5	Pacific	Pacific basins from the Aleutian Islands and the Yukon R. south to the Colorado R., Mexico	101–103, 120–131, 159–160	
CENTRAL AMERICA: Pilsbry (1910) ; Frierson (1927) ; Haas (1930) ; Goodrich & van der Schalie (1937)				
CA1	Central America–Caribbean	Basins in Mexico south of the Colorado R. and R. Grande, through Central America to R. Tuira in Panama; Caribbean islands of Cuba and Hispaniola	162–175, 201–211	
SOUTH AMERICA: Ortmann (1921) ; Morretes (1949) ; Simone (2006) ; Pereira et al. (2014)				
SA1	Magdalena–Pacific	R. Magdalena and Sinú in Colombia draining to the Caribbean, south along the Pacific basins to the R. Locumba, Peru	301–302, 336	Linares & Vera (2012)
SA2	Orinoco–Guianas	Caribbean basins from L. Maracaibo and R. Orinoco basins in Venezuela and Colombia east to the R. Oyapock, French Guiana; includes the islands of Trinidad and Tobago	303–311	Johnson (1981) ; Martinez, Cabrera & Lasso (2004) ; Lasso et al. (2009) ; Pointier (2015)
SA3	Amazon	Entire Amazon Basin and adjacent Atlantic basins east to the R. Parnaíba, Brazil	312–325	Ramírez, Paredes & Arenas (2003)
SA4	São Francisco–Atlantic	Atlantic coastal streams east of the R. Parnaíba to the R. São Francisco, and south to Rio de Janeiro, Brazil	326–329, 352	
SA5	Paraná–Paraguay	Entire R. de la Plata basin, including the Paraná, Paraguay and Uruguay R.; includes adjacent Atlantic coastal streams	330–335, 342–346	Rumi et al. (2008) ; Torres et al. (2018)
SA6	Patagonia	South and west of the Amazon and Paraná–Paraguay, from L. Titicaca, Peru through Chile to Tierra del Fuego, Argentina	337–341, 348–349	Parada & Peredo (2002, 2008)
AFROTROPICS: Mandahl-Barth (1988) ; Daget (1998) ; Graf & Cummings (2011)				
AF1	Nile–Great Lakes	Entire Nile R. basin, including L. Victoria, Albert and Edward; endorheic L. Turkana basin	521–524, 525*, 526, 530	Van Damme (1984) ; Graf & Cummings (2007a) ; Van Damme & Van Bocxlaer (2009)
AF2	Western	Atlantic streams from Cross and Wburi R. in the Gulf of Guinea, west to Senegal, including the Niger R.; endorheic L. Chad basin	505–520	
AF3	Congo	Entire Congo R. basin, including L. Tanganyika and the Malagarasi R.; Atlantic basins north to the Sanaga and Gabon R.	532–550	Graf & Cummings (2006)
AF4	Southern	Atlantic streams south of the Congo, including the Cuanza R., Angola; all basins south from the Cunene, Okavango and Zambezi R.; including L. Malawi	551–563, 569, 572–578	Appleton (1979) ; Graf & Cummings (2006)

GLOBAL FRESHWATER MUSSEL DIVERSITY

Table 1. Continued

Regions and subregions		Description	Freshwater ecoregions	Key references
AF5	Eastern	Coastal streams draining to the Indian Ocean and Red Sea north of the Zambezi R., Mozambique	525*, 527–529, 531, 564–568	
AF6	Madagascar	Madagascar	579–583	Fischer-Piette & Vukadinovic (1973); Graf & Cummings (2009)
NORTH EURASIA: Zhadin (1965); Starobogatov <i>et al.</i> (2004); Graf (2007); Vinarski & Kantor (2016)				
EU1	Europe–Maghreb	Volga R., other streams to the Caspian Sea, south to Turkey west of the Tigris–Euphrates, west to Iberia and the British and Irish Islands on the Atlantic; includes Atlantic and Mediterranean coastal streams in northern Africa, from the O. Sous, Morocco to the Gulf of Gabes, Tunisia	402–434, 452–453, 501–502	Falkner, Bank & von Proschwitz (2001); Falkner, Ripken & Falkner (2002); Araujo <i>et al.</i> (2009a); Lopes-Lima <i>et al.</i> (2017b)
EU2	Tigris–Euphrates	Tigris and Euphrates R. basins and adjacent streams draining to the Persian Gulf, south to the Mond R., Iran	436–438, 441–442, 444–446	Schütt (1983); Falkner (1994)
EU3	Central Asia	Aral Sea, L. Baikal and Arctic basins from the Ob R. through the Yenisei to the Lena R.	450, 601–608, 622, 624, 626–630	
EAST ASIA: Liu (1979); Starobogatov <i>et al.</i> (2004); Graf (2007); He & Zhuang (2013); Vinarski & Kantor (2016); Zieritz <i>et al.</i> (2018a); Lopes-Lima <i>et al.</i> (2020)				
AS1	Beringia	Arctic drainages from the Kolyma R. east; basins of the Bering Sea and Sea of Okhotsk, north of the Amur R.	609–614	
AS2	Amur–Korea	Amur R.; streams draining to the Sea of Japan and Yellow Sea, south to the Liao He R.	615–620, 637–640, 641*	Kil (1976); Kwon & Habe (1979)
AS3	Japan–Sakhalin	Streams draining Sakhalin Island and Kuril Islands, Russia and the islands of Japan, including L. Biwa	641*, 642–643	Kondo (2008)
AS4	Yangtze–Huang	Huang He and adjacent streams draining to Bo Hai, south through the Yangtze R., to coastal streams draining to the South China Sea, north of the Pearl R., China; Taiwan	633–636, 757–758, 764–767	Hu (2005); Prozorova <i>et al.</i> (2005); Xiong, Ouyang & Wu (2012); Liu <i>et al.</i> (2020)
AS5	Indochina	Pearl R., China south through the Mekong, Chao Phraya and Mae Klong R., the Malay Peninsula; Hainan Island	724–734, 735*, 759–763	Brandt (1974); Dang <i>et al.</i> (1980); Zieritz <i>et al.</i> (2016); Do <i>et al.</i> (2018)
AS6	Sunda–Philippines	Streams on the islands of Sumatra, Java, Borneo, east to Timor; north to Palawan and the Philippine Islands	735*, 736–746, 748, 752–753, 755–756	Van Benthem Jutting (1953); Marwoto (1987); Affandi <i>et al.</i> (2013); Zieritz <i>et al.</i> (2018b, 2020)
AS7	India–Myanmar	Salween and Tenasserim R. west through the Irrawaddy, Brahmaputra and Ganges to the Indus R., south to Sri Lanka	703, 705–706, 708–723	Subba Rao (1989); Nesemann <i>et al.</i> (2007); Ramakrishna & Dey (2007)
AUSTRALASIA: McMichael & Hiscock (1958); Smith (1992); Walker <i>et al.</i> (2001, 2014)				
AU1	Eastern Australia	Nicholson R., Northern Territory to the Murray–Darling, South Australia; interior Lake Eyre basin	805*, 806–810	
AU2	Western Australia	Basins draining to the Arafura Sea and Indian Ocean, from the Roper R., Northern Territory to southwestern Western Australia	801–803, 804*, 805*	
AU3	New Guinea	Basins on New Guinea, Bismarck and Solomon Islands	812–818	
AU4	New Zealand	North and South Islands	811	Marshall <i>et al.</i> (2014)

The freshwater ecoregions that comprise the subregions are identified by number (<http://www.feow.org>). An asterisk indicates an ecoregion divided among multiple subregions.

Table 2. Family-group level classification of the Unionoida.

Superfamily UNIONOIDEA Rafinesque, 1820
Family UNIONIDAE s.s.
Subfamily UNIONINAE s.s.
Tribe UNIONINI s.s.
Tribe LANCEOLARIINI Froufe, Lopes-Lima & Bogan in Lopes-Lima <i>et al.</i> , 2017
Tribe ANODONTINI Rafinesque, 1820
Subtribe ANODONTINA s.s.
Subtribe ALASMIDONTINA Rafinesque, 1820
Subtribe CRISTARIINA Lopes-Lima, Bogan & Froufe in Lopes-Lima <i>et al.</i> , 2017
Subfamily AMBLEMINAE Rafinesque, 1820
Tribe AMBLEMINI s.s.
Tribe LAMPSILINI Ihering, 1901
Tribe PLEUROBEMINI Hannibal, 1912
Tribe POPENAIIDINI Heard & Guckert, 1970
Tribe QUADRULINI Ihering, 1901
Subfamily GONIDEINAE Ortmann, 1916
Tribe GONIDEINI s.s.
Tribe CHAMBERLAINIINI Bogan, Froufe & Lopes-Lima in Lopes-Lima <i>et al.</i> , 2017
Tribe LAMPROTULINI Modell, 1942
Tribe PSEUDODONTINI Frierson, 1927
Subtribe PSEUDODONTINA s.s.
Subtribe PISLBRYOCONCHINA Bolotov, Vikhrev & Tumpeesuwan in Bolotov <i>et al.</i> , 2017
Subfamily RECTIDENTINAE Modell, 1942
Tribe RECTIDENTINI s.s.
Tribe CONTRADENTINI Modell, 1942
Subfamily MODELLNAINAE Brandt, 1974
Subfamily PARREYSIINAE Henderson, 1935
Tribe PARREYSIINI s.s.
Tribe COELATURINI Modell, 1942
Tribe INDOCHINELLINI Bolotov, Pfeiffer, Vikhrev & Konopleva in Bolotov <i>et al.</i> , 2018
Tribe LAMELLIDENTINI Modell, 1942
Tribe LEOPARREYSIINI Vikhrev, Bolotov & Kondakov in Bolotov <i>et al.</i> , 2017
Family MARGARITIFERIDAE Haas, 1940
Subfamily MARGARITIFERINAE s.s.
Subfamily GIBBOSULINAE Bogan, Bolotov, Froufe & Lopes-Lima in Lopes-Lima <i>et al.</i> , 2018
Superfamily HYRIOIDEA Swainson, 1840
Family HYRIIDAE s.s.
Subfamily HYRIIINAE s.s.
Tribe HYRIINI s.s.
Tribe CASTALIINI Morretes, 1949
Tribe HYRIDELLINI McMichael, 1956 (1934)
Tribe RHIPIDODONTINI Starobogatov, 1970
Subfamily VELESUNIONINAE Iredale, 1934
Superfamily ETHERIOIDEA Deshayes, 1830
Family ETHERIIDAE s.s.
Family IRIDINIDAE Swainson, 1840
Subfamily IRIDININAE s.s.
Subfamily ASPATHARIINAE Modell, 1942
Family MYCETOPODIDAE Gray, 1840
Subfamily MYCETOPODINAE s.s.
Subfamily ANODONTITINAE Modell, 1942
Subfamily LEILINAE Morretes, 1949
Subfamily MONOCONDYLAEINAE Modell, 1942

See text for references.

(Fig. 2) was to a large extent fostered by Bourguignat, Locard and others working in France (i.e. *Nouvelle École*) (Graf, 2010, 2011). In the late 20th century, beginning in the former Soviet Union and continuing into the modern Russian Federation, Ya.I. Starobogatov, V.V. Bogatov and others promoted a return to a typological species concept based on the ‘comparatory’ method. This led to a less extreme but still noticeable increase in the number of valid species names in use. For decades, biological and comparative taxonomies existed side-by-side in the literature (Korniushev, 1998; Graf, 2007; Vinarski & Kantor, 2016), but current phylogenetic work is bringing the two systems into better alignment (Bogatov *et al.*, 2018; Klishko *et al.*, 2018a). Since 2017, the pace of species description and revision has accelerated dramatically over previous rates owing to increased taxon sampling in diversity hotspots and vigorous application of molecular phylogenetic species concepts (Bolotov *et al.*, 2017b, 2019a, 2020b; Watters, 2018; Konopleva *et al.*, 2019b; Lopes-Lima *et al.*, 2020). More new species have been described since 2017 (54) than during the preceding 17 years (40) (Fig. 2B). The rules of zoological nomenclature are based on precedence and priority (ICZN, 1999) and, as such, historical trends and the idiosyncrasies of individual taxonomists are the necessary purview of modern taxonomists (whether they appreciate it or not).

Figure 2 also provides an alternative estimate of valid species name use by year. A 20-year cut-off (thin dotted line) removes a species from the annual tally of names if it had not been applied over the preceding 20 years. The taxonomic opinions we have captured in the MUSSELpdb represent only a sample of the available literature, but a general pattern in the data is evident. During the 1930–1960s (i.e. during and immediately after World War II), the majority of freshwater mussel species were not being mentioned in the publications that we surveyed (which are biased towards publications dealing with taxonomy) until Haas (1969a). A similar though smaller dip occurred following Haas (1969a) until the species were taken up again in our checklist (Graf & Cummings, 2007b).

Freshwater mussel richness vs other freshwater bivalves

With 958 Recent species in 192 genera, the Unionoida represents the most extensive radiation of bivalves into freshwaters. The other major freshwater bivalve radiations are considerably less species rich: the family Sphaeriidae (227 Recent species) and two genera of the family Cyrenidae, *Corbicula* Mühlfeld, 1811 (89 spp.) and *Cyanocyclus* Blainville, 1818 (6 spp.). Only eight other families have any species that inhabit inland freshwaters, though these lineages are predominantly marine (Bogan, 2008; Graf, 2013). It is instructive to compare the diversity of the Unionoida and Sphaeriidae (also known as fingernail, pill or pea clams) and hypothesize about the factors that created such a discrepancy in total richness between the two clades.

Both the Unionoida and the Sphaeriidae are worldwide in distribution, and both are of similar geological age. Each clade is represented in Cretaceous and older Mesozoic freshwater deposits, although molecular clocks support earlier stem-group origins (Haas, 1969b; Keen & Casey, 1969; Bieler *et al.*, 2014; Bolotov *et al.*, 2017a). Both have evolved parental care that involves brooding offspring in the interlamellar spaces of their ctenidia. However, the clades differ in their modes of reproduction, development and dispersal. Whereas sphaeriids are small (<2 cm), direct-developing, ovoviparous, self-fertile hermaphrodites capable of avian-assisted dispersal among isolated waterbodies, freshwater mussels are typically large, gonochoristic, indirect developers with a larval stage that is obligately parasitic on a host fish (or rarely amphibian) that is also the principal vector of dispersal (Cummings & Graf, 2009; Graf, 2013; Lee, 2019). As such, sphaeriids are adept colonizers, found in isolated and ephemeral waterbodies, and species often have large ranges. *Euglesa casertana* (Poli, 1791), for example,

GLOBAL FRESHWATER MUSSEL DIVERSITY

Table 3. Richness of species and genera arranged by taxonomy and region.

Taxonomy	Global	NA	CA	SA	AF	EU	AS	AU
Unionoida	958 (192)	302 (62)	94 (23)	115 (19)	81 (16)	34 (10)	320 (73)	30 (10)
Unionoidea	770 (157)	302 (62)	87 (21)	–	41 (10)	34 (10)	319 (72)	2 (1)
Unionidae	753 (153)	297 (60)	87 (21)	–	41 (10)	30 (8)	310 (70)	2 (1)
<i>incertae sedis</i>	3 (2)	–	–	–	1 (1)	–	–	2 (1)
Unioninae	166 (35)	51 (14)	5 (4)	–	3 (1)	23 (4)	93 (22)	–
Unionini	63 (13)	–	–	–	3 (1)	14 (1)	48 (13)	–
Anodontini	90 (21)	51 (14)	5 (4)	–	–	9 (3)	32 (8)	–
Anodontina	13 (2)	4 (1)	2 (1)	–	–	7 (2)	–	–
Alasmidontina	45 (11)	45 (11)	2 (2)	–	–	–	–	–
Cristariina	32 (8)	2 (2)	1 (1)	–	–	1 (1)	32 (8)	–
Lanceolariini	13 (1)	–	–	–	–	–	13 (1)	–
Ambleminae	325 (58)	245 (45)	82 (17)	–	–	–	3 (3)	–
Amblemini	7 (3)	7 (3)	–	–	–	–	2 (2)	–
Lampsilini	159 (31)	137 (26)	23 (7)	–	–	–	1 (1)	–
Pleurobemini	75 (9)	75 (9)	–	–	–	–	–	–
Popenaiadini	58 (9)	1 (1)	58 (9)	–	–	–	–	–
Quadrulini	26 (6)	25 (6)	1 (1)	–	–	–	–	–
Gonideinae	89 (25)	1 (1)	–	–	–	7 (4)	81 (20)	–
Gonideini	19 (9)	1 (1)	–	–	–	4 (3)	14 (5)	–
Chamberlainiini	5 (3)	–	–	–	–	–	5 (3)	–
Lamprotulini	25 (6)	–	–	–	–	3 (1)	22 (5)	–
Pseudodontini	40 (7)	–	–	–	–	–	40 (7)	–
Pseudodontina	13 (1)	–	–	–	–	–	13 (1)	–
Pilsbryoconchina	27 (6)	–	–	–	–	–	27 (6)	–
Modellnaiinae	1 (1)	–	–	–	–	–	1 (1)	–
Parreysiinae	116 (20)	–	–	–	37 (8)	–	79 (12)	–
Parreysiini	13 (1)	–	–	–	–	–	13 (1)	–
Coelaturini	37 (8)	–	–	–	37 (8)	–	–	–
Indochinellini	33 (7)	–	–	–	–	–	33 (7)	–
Lamellidentini	21 (3)	–	–	–	–	–	21 (3)	–
Leoparreysiini	12 (1)	–	–	–	–	–	12 (1)	–
Rectidentinae	53 (12)	–	–	–	–	–	53 (12)	–
Rectidentini	16 (6)	–	–	–	–	–	16 (6)	–
Contradentini	37 (6)	–	–	–	–	–	37 (6)	–
Margaritiferidae	17 (4)	5 (2)	–	–	–	4 (2)	9 (2)	–
Margaritiferinae	11 (3)	5 (2)	–	–	–	4 (2)	3 (1)	–
Gibbosulinae	6 (1)	–	–	–	–	–	6 (1)	–
Hyrioidea: Hyriidae	92 (15)	–	–	64 (6)	–	–	–	28 (9)
Hyriinae	76 (10)	–	–	64 (6)	–	–	–	12 (4)
<i>incertae sedis</i>	3 (1)	–	–	–	–	–	–	3 (1)
Hyriini	4 (2)	–	–	4 (2)	–	–	–	–
Castaliini	17 (3)	–	–	17 (3)	–	–	–	–
Hyridellini	9 (3)	–	–	–	–	–	–	9 (3)
Rhipidodontini	43 (1)	–	–	43 (1)	–	–	–	–
Velesunioninae	16 (5)	–	–	–	–	–	–	16 (5)
Etherioidea	96 (20)	–	7 (2)	51 (13)	40 (6)	–	1 (1)	–
Etheriidae	4 (4)	–	–	2 (2)	1 (1)	–	1 (1)	–
Iridinidae	39 (5)	–	–	–	39 (5)	–	–	–
Iridininae	17 (3)	–	–	–	17 (3)	–	–	–
Aspathariinae	22 (2)	–	–	–	22 (2)	–	–	–
Mycetopodidae	53 (11)	–	7 (2)	49 (11)	–	–	–	–
Mycetopodinae	5 (2)	–	1 (1)	5 (2)	–	–	–	–
Anodontitinae	28 (2)	–	6 (1)	24 (2)	–	–	–	–
Leilinae	2 (1)	–	–	2 (1)	–	–	–	–
Monocondylaeinae	18 (6)	–	–	18 (6)	–	–	–	–

Numbers in parentheses indicate the richness of genera. Region abbreviations: NA, North America; CA, Central America; SA, South America; AF, Afrotropics; EU, North Eurasia; AS, East Asia; AU, Australasia.

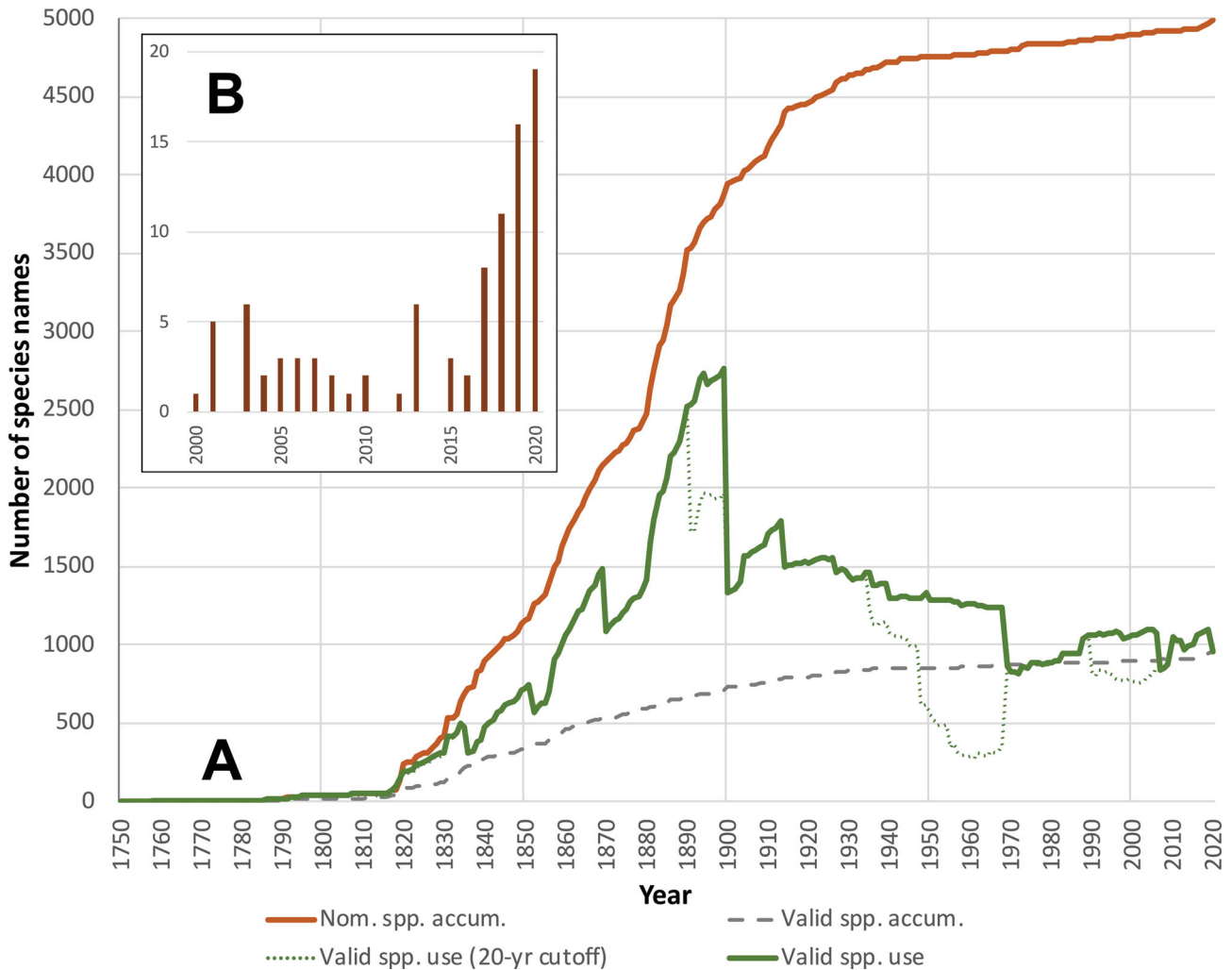


Figure 2. A. Accumulation of nominal and valid species. The red line traces the annual accumulation of available species-group names to the current tally of 4,988, and accumulation of the 958 valid species names over the same period is shown by the dash grey line. The green line depicts the history of name usage based on more than 65,500 species taxonomic opinions in the MUSSELpdb. For each year, an available nominal species was considered valid if it was regarded as such at that time or in the previous year and no one had treated the nomen as a junior synonym. For certain years with works that reported all valid freshwater mussel species known at the time (Lea, 1836, 1852, 1870; Simpson, 1900, 1914; Haas, 1969a; Graf & Cummings, 2007b), any nominal species not listed was implicitly synonymized. The dotted green line also shows the history of name usage, but any name that had not been treated as valid in the preceding 20 years was removed from the annual tally. **B.** Plot charting the number of available species published in each year since 2000, depicting the recent acceleration in species description.

is essentially cosmopolitan in distribution (Burch, 1975a). In contrast, freshwater mussels require aquatic connections for dispersal by their aquatic hosts. Unionoid species ranges are frequently endemic to permanent waters in single or adjacent basins, and disjunctions of taxa across terrestrial or marine barriers are strong evidence for past confluence (Graf & Cummings, 2011)—or human introduction, as with the case of *Sinanodonta woodiana* (Lea, 1834) (Sousa *et al.*, 2014).

Over the last 200 Myr, evolving terrestrial and marine barriers have created ample circumstances to disrupt gene flow and facilitate cladogenesis in allopatry (Futuyma, 2013). In addition, freshwater mussels have been co-evolving with their hosts (Barnhart, Haag & Roston, 2008; Hewitt, Wood & Ó Foighil, 2019) and perhaps even diversifying by host shifting (Graf, 1997). We hypothesize that these intrinsic and extrinsic factors of life history and biogeography have contributed to the high diversity of families, genera and species among freshwater mussels relative to the sphaeriids. Broad ranges and high vagility may have limited sphaeriid opportunities for isolation over evolutionary timescales.

FAMILY-LEVEL RICHNESS

There are six families of freshwater mussels worldwide. A detailed analysis of family-group level phylogenetic results to date is beyond the scope of this review. At this time, we seek only to provide justification for the classification utilized here (Table 2). The basis for the current consensus classification of Recent freshwater mussels originated with Bieler *et al.* (2010), as updated by several more recent studies. The most significant changes to the supra-generic classification since our previous review are: (1) recognition of the superfamily Hyrioidea (= Hyriidae) (Hoeh *et al.*, 2009; Graf *et al.*, 2015), (2) parsing of genera among subfamilies, tribes and subtribes in the Unionidae (Whelan *et al.*, 2011; Bolotov *et al.*, 2017b, 2018; Lopes-Lima *et al.*, 2017a; Pfeiffer *et al.*, 2019b) and (3) revision of the Margaritiferidae into multiple genera in two subfamilies (Smith, 2001; Lopes-Lima *et al.*, 2018a). The classification of the lasidium-bearing mussels of the Etherioidea (= Etheriidae + Mycetopodidae + Iridinidae) remains unchanged (but see below).

The richest family of freshwater mussels is the Unionidae with 753 species (153 genera), 79% of the species richness of the order (Table 3). Indeed, among freshwater mollusc families, its richness is exceeded only by the gastropod family Hydrobiidae (Strong *et al.*, 2008; Wilke & Delicado, 2019). The Unionidae is among the most species-rich bivalve families (freshwater or otherwise), and this is a consequence of not only evolutionary ‘success’ but also the dearth of available morphological synapomorphies to parcel the species richness into smaller, recognizable groups (Graf & Cummings, 2007b). Recent phylogenetic work has resolved the main branches of the Unionidae to six subfamilies. However, the diagnostic characters are largely molecular, and the monophyly and relationships among the subfamilies still depend on which character sets were analysed (Lopes-Lima *et al.*, 2017a; Frouffe *et al.*, 2019; Pfeiffer *et al.*, 2019b). Nevertheless, our understanding of the phylogenetic diversity of the Unionidae is much improved since 2007. The single richest unionid subfamily is the Ambleminae of North and Central America, with 325 species in 58 genera. Those tallies exceed the richness of the other five freshwater mussel families combined. At the other end of the spectrum, the East Asian (Indochina) Modellinae is represented by a single species that has yet to be included in any phylogenetic analysis. The Unionidae is also the most widespread freshwater mussel family, occurring in all regions except South America (Table 3).

The Margaritiferidae is similarly widespread across North America, North Eurasia and East Asia, though with a considerably lower species richness: 17 in 4 genera (Table 3). Three of those genera (*Margaritifera*, *Cumberlandia* and *Pseudunio*) have traditionally been recognized in the family (Lopes-Lima *et al.*, 2018a), but *Gibbosula* was recently moved from the Unionidae (Huang *et al.*, 2018). That shift represents one of only two revisions of genera across families, the other being the move of *Moncetia* from the Iridinidae to Unionidae based on larval anatomy (Kondo, 1984; Ortiz-Sepulveda *et al.*, 2020).

The Recent Hyriidae is restricted to South America (64 spp., 6 genera) and Australasia (28 spp., 9 genera), and the families Mycetopodidae (53 spp., 11 genera) and Iridinidae (39 spp., 5 genera) are found in South America (and extending north into Central America) and the Afrotropics, respectively. The most species-poor freshwater mussel family is the Etheriidae, with only four monotypic genera. These have disjunct distributions in South America, Africa, Madagascar and India (Table 3). There is evidence that the species of the Etheriidae, known as freshwater oysters, are polyphyletic (Bogan & Hoeh, 2000; Hoeh *et al.*, 2009), but that hypothesis warrants further study (Graf & Cummings, 2010). A similar situation has been discovered for the Iridinidae, but the taxon sampling is limited (Walker *et al.*, 2006; Combsch *et al.*, 2017).

GEOGRAPHICAL DISTRIBUTION OF RICHNESS

Revisions of freshwater mussel species and genera have typically been based on geography rather than taxonomy. This pattern reflects how most systematists, ecologists and conservation biologists tend to organize their research: faunistic analysis by region (references cited in Table 1) rather than monography by taxon (references cited in the checklist). Each region has a distinct complement of genera and species, with only limited overlap among them. Of 958 freshwater mussel species, the only one that could not be precisely georeferenced to the scale of subregion was *Lamprotula plumbea* (Dillwyn, 1817). It is only known from the original figure (Chemnitz, 1795), and the type locality was given as “Südsee”, implying a marine locality (Haas, 1969a). However, since it is the type species of a valid genus, it has been regarded as a valid species of East Asia (Zieritz *et al.*, 2018a). We have provisionally placed *L. plumbea* in Indochina (AS5).

The regions and subregions that we have utilized herein to summarize biogeographical patterns of freshwater mussels (Fig. 1; Table 1) are modified from those of our previous assessment (Graf & Cummings, 2007b). Our goal in redefining the regions was to update the traditional boundaries to better summarize distributions according to areas of freshwater mussel endemism. Central America had been treated as a subregion of Neotropica, but we now recognize Central America as a separate region distinct from North and South America to reflect the endemic genera found there and to acknowledge the phylogenetic affinities of the assemblage with both North America (Ambleminae) and South America (Mycetopodidae). The far eastern subregions of the former Palearctica have been combined with Indotropica as East Asia. Europe, northern Africa, the Middle East and Central Asia remain grouped as North Eurasia. Australasia and the Afrotropics remain unchanged. Among subregions, we have (1) divided the former Interior subregion of North America (Nearctica) into the Canadian Interior and Mississippi–Great Lakes subregions, (2) combined Florida with the Gulf subregion and (3) treated the Salween River basin in East Asia as the eastern limit of the India–Myanmar subregion rather than the western extent of Indochina.

The freshwater mussel assemblage of each region has been reviewed and revised over the last decade, with additional species being described or resurrected from synonymy and other species being removed from the list by lumping them with other species or labelling them as *nomina dubia* (i.e. unrecognizable as species). Species have also been gained in regions because our current list includes introduced species (discussed below), whereas the previous checklist did not. The species richness by region and the nature of the changes since our previous checklist are depicted in Figure 3.

Richness by region

It has been ‘widely understood’ and heretofore uncontroversial that North America has the richest freshwater mussel fauna in the world (Graf & Cummings, 2007b: 296; Bogan, 2008; Graf, 2013, *ad nauseam*). Our realignment of major biogeographic regions and the recent vigorous pace of species- and genus-group level revisions (Fig. 2) have shifted East Asia into the premiere position. Whereas North America has 302 species (62 genera), East Asia has 320 species (73 genera) (Fig. 3; Table 3). North America and East Asia are the two regions that have experienced the most revisionary activity.

Since our previous assessment (Graf & Cummings, 2007b), there has been a net gain in East Asia of 78 species. Twenty-three species that were on our previous list have been subsequently demoted to junior synonyms, while 55 others have been resurrected from invalidity (55 – 23 = +32). In addition, 44 new species have been described and 2 that had been considered *nomina dubia* [*Indonaia rectangularis* (Tapparone Canefri, 1889) and *Cuneopsis kiangsiensis* Tchang & Li, 1965] are now treated as valid species (He & Zhuang, 2013; Zieritz *et al.*, 2018a; Bolotov *et al.*, 2019b) (32 + 44 + 2 = 78). Considering only the subregions of East Asia that correspond to the former Indotropical region (AS4–AS7, omitting AS1–AS3), the total species tally would be 281 (an increase of 62 species), and so some of the shift in patterns of species richness is due to our reconsideration of major regional boundaries.

The current tally of 302 species in North America is unchanged from our previous assessment of 302 (Graf & Cummings, 2007b), despite the addition of 13 subsequently described species, 1 species [*Reginaia apalachicola* (Williams & Fradkin, 1999)] that had not been treated as a Recent taxon (Williams *et al.*, 2014) and 25 more species split from existing taxa. Those 39 additions are exactly balanced by the 37 species that were lumped into synonymy (*Anodonta impura* Say, 1829 was removed from the regional tally) and 2 more that were removed from the list as *nomina dubia* [*Pleurobema altum* (Conrad, 1854) and *Sphenonaias taumilapana* (Conrad, 1855)]. In addition, *Sinanodonta woodiana*, an introduced species from East Asia, has been

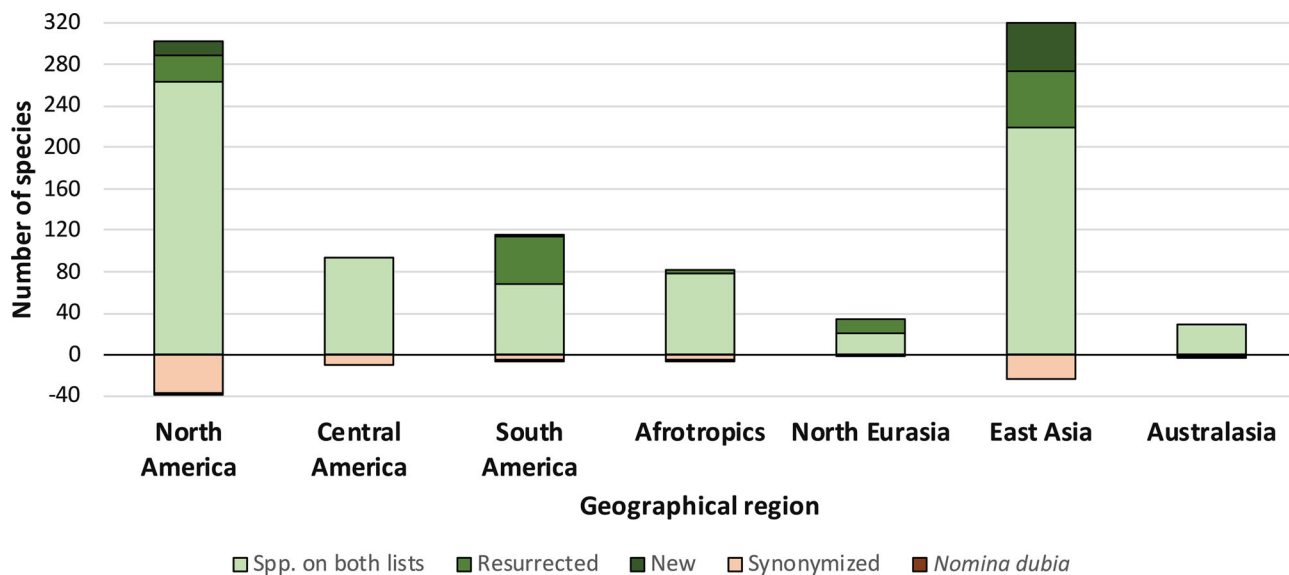


Figure 3. Species richness by region, illustrating the changes since Graf & Cummings (2007b). The extent of each column above the abscissa indicates the number of species, including gains through newly described species and those resurrected from prior synonymy. The negative extent depicts the removal of species from the previous checklist due to synonymy or categorization as *nomina dubia*.

reported from New Jersey, USA (Konečný *et al.*, 2018), and *Disconias fimbriata* (Frierson, 1907) was removed from the North American fauna as a Central American endemic. The taxonomic revisions—lumping, splitting and describing—in these two regions resulted from increased application of molecular phylogenetic methods to discover new lineages and greater taxon sampling (e.g. Kuehn, 2009; Bolotov *et al.*, 2017b, 2019a, 2020b; Vikhrev *et al.*, 2017; Smith *et al.*, 2018; Konopleva *et al.*, 2019b; Lopes-Lima *et al.*, 2019, 2020), as well as large-scale traditional revisions (Williams, Bogan & Garner, 2008; Watters, Hoggarth & Stansbery, 2009; Williams *et al.*, 2014; Watters, 2018).

South America has 115 species in 19 genera, well below half the richness of either North America or East Asia (Fig. 3; Table 3). However, the South American assemblage of freshwater mussels exhibits the second highest net gain in species, increasing from 74 to 115 (74 – 4 synonyms – 1 *nomen dubium* + 1 new + 45 resurrected from synonymy = 115). Unlike the two regions described above, the increase in species richness in South America by more than half ($41/74 = 55\%$) is not the result of a substantial increase in data over the last decade. Rather, the discrepancy is largely the result of disparity between two works: Simone (2006) and Pereira *et al.* (2014). We (Graf & Cummings, 2007b) had previously lamented the near lack of a synthesis of South American freshwater mussels since Haas (1969a). Simone's (2006) book on the freshwater molluscs of Brazil and adjacent areas was then the most recent re-evaluation of South American freshwater mollusc diversity, and we employed it as a primary resource for the continent. Simone's species were generally more lumped than those of Haas. Of the 340 nominal species cited in both works, Haas (1969a) circumscribed them into 92 species (117 including subspecies), whereas Simone (2006) recognized only 62. In contrast, Pereira *et al.* (2014) listed 106 as valid for the same set of nominal species, an increase of 44. Our preliminary work based on the MUSSELpdb agrees better (but not perfectly) with Pereira *et al.* (2014) (Cummings & Graf, unpubl.).

A similar relative increase in species richness was observed in North Eurasia, although the region is still among the poorest in richness with 34 species in 10 genera (Fig. 3; Table 3). This represents a net gain of 13 species from 21 (–1 lumped + 14 resurrected from synonymy) in Europe, the Middle East and Central Asia, a 62% increase. As with North America and East Asia, the revisions in this region were generally based on molecular phylogenetic re-

sults (Araujo *et al.*, 2009b, 2018; Khalloufi *et al.*, 2011; Froufe *et al.*, 2016b, 2017).

Central America, the Afrotropics and Australasia each show a net loss of species since our previous list (Graf & Cummings, 2007b) (Fig. 3; Table 3). While 3 species were added to the Central American and Caribbean assemblage either as introduced species (*Sinanodonta woodiana*) or because of revisions to their known ranges [*Anodonta impura* and *Utterbackia imbecillis* (Say, 1829)], 11 species were removed, decreasing the regional richness from 102 to 94 (23 genera). Ten former species were lumped into synonymy, and the range of *Anodontites trigona* (Spix in Wagner, 1827) was restricted to South America (Goodrich & van der Schalie, 1937; Watters, 1997; Johnson, 1998, 1999b). Ongoing research suggests that tally will be further reduced (Cummings *et al.*, 2018, 2019; Pfeiffer *et al.*, 2019a). Africa and Madagascar, with a total richness of 81 species in 16 genera, had 3 species resurrected from synonymy, but 4 more lost to synonymy, and 2 removed as *nomina dubia* (Van Damme & Van Bocxlaer, 2009; Graf & Cummings, 2011; Ortiz-Sepulveda *et al.*, 2020). The two *nomina dubia*, *Coelatura madagascariensis* (Sganzin, 1841) and *C. malgachensis* (Germain, 1911), as well as *C. cariei* (Germain, 1919) (= *C. aegyptiaca*) are regarded as extinct on the IUCN Red List (<https://www.iucnredlist.org>), but the statuses of those species (or the lack thereof) were discussed in detail by Graf & Cummings (2009). The Australasian freshwater mussel assemblage (30 species, 10 genera) is mostly unchanged except for the loss of 2 New Zealand species to synonymy and the relegation of *Velesunio ovata* to a *nomen dubium* (Marshall, Fenwick & Ritchie, 2014; Walker *et al.*, 2014). But for the few species in New Zealand (Marshall *et al.*, 2014) and Central Africa (Ortiz-Sepulveda *et al.*, 2020), the limited molecular phylogenetic work to date in these regions has not resulted in major taxonomic revisions at the species level (Hughes *et al.*, 2004; Graf *et al.*, 2014, 2015; Elderkin *et al.*, 2016; Pfeiffer *et al.*, 2019a).

Richness and endemism by subregion

Subregional (and regional) tallies of richness and endemism include species that are considered extinct as well as introduced freshwater mussels dispersed by human activities (Fig. 1B; Table 4). Other freshwater bivalve genera such as *Corbicula* Merg, 1811, *Dreissena* Van Beneden, 1835, *Limnoperna* Rochebrune, 1881, etc. are well known for their invasive species. Less attention has been paid to

Table 4. Species richness and subregional endemism by geography and family.

Region	Unionoidea	UN	MA	HY	ET	MY	IR
Global	958	753	17	92	4	53	39
North America	302	297	5	–	–	–	–
NA1	13 (0)	13 (0)	–	–	–	–	–
NA2	151 (96)	149 (95)	2 (1)	–	–	–	–
NA3	63 (35)	62 (35)	1 (0)	–	–	–	–
NA4	152 (99)	150 (97)	2 (2)	–	–	–	–
NA5	7 (5)	6 (5)	1 (0)	–	–	–	–
Central America	94	87	–	–	–	7	–
CA1	94 (86)	87 (82)	–	–	–	7 (4)	–
South America	115	–	–	64	2	49	–
SA1	13 (5)	–	–	1 (1)	1 (1)	11 (3)	–
SA2	33 (18)	–	–	15 (9)	–	18 (9)	–
SA3	37 (12)	–	–	14 (5)	1 (0)	22 (7)	–
SA4	17 (4)	–	–	8 (2)	–	9 (2)	–
SA5	63 (42)	–	–	39 (32)	1 (0)	23 (10)	–
SA6	3 (2)	–	–	2 (2)	–	1 (0)	–
Afrotropics	81	41	–	–	1	–	39
AF1	26 (16)	13 (11)	–	–	1 (0)	–	12 (5)
AF2	18 (8)	4 (2)	–	–	1 (0)	–	13 (6)
AF3	36 (29)	19 (19)	–	–	1 (0)	–	16 (10)
AF4	16 (11)	5 (4)	–	–	1 (0)	–	10 (7)
AF5	6 (1)	2 (1)	–	–	1 (0)	–	3 (0)
AF6	2 (1)	1 (1)	–	–	1 (0)	–	–
North Eurasia	34	30	4	–	–	–	–
EU1	25 (18)	22 (16)	3 (2)	–	–	–	–
EU2	9 (8)	8 (7)	1 (1)	–	–	–	–
EU3	4 (0)	4 (0)	–	–	–	–	–
East Asia	320	310	9	–	1	–	–
AS1	3 (0)	2 (0)	1 (0)	–	–	–	–
AS2	29 (15)	28 (14)	1 (1)	–	–	–	–
AS3	28 (19)	26 (18)	2 (1)	–	–	–	–
AS4	74 (50)	71 (47)	3 (3)	–	–	–	–
AS5	111 (86)	108 (93)	3 (3)	–	–	–	–
AS6	30 (22)	30 (22)	–	–	–	–	–
AS7	93 (90)	92 (89)	–	–	1 (1)	–	–
Australasia	30	2	–	28	–	–	–
AU1	14 (11)	–	–	14 (11)	–	–	–
AU2	6 (4)	–	–	6 (4)	–	–	–
AU3	11 (9)	2 (2)	–	9 (7)	–	–	–
AU4	3 (3)	–	–	3 (3)	–	–	–

Numbers within parentheses indicate the richness of endemic species in each subregion. Introduced species are listed in Table 5. Family abbreviations: UN, Unionoidea; MA, Margaritiferidae; HY, Hyriidae; ET, Etheriidae; MY, Mycetopodidae; IR, Iridinidae.

invasive freshwater mussel species than to the impacts of other invasive bivalves on native unionoid communities (Sousa *et al.*, 2014). Nevertheless, there are examples of introduced/invasive freshwater mussel populations (Table 5). We recognize three categories of introduced freshwater mussels: (1) the invasive species of *Sinanodonta*, (2) species introduced among regions and (3) species expanding their ranges to adjacent subregions. *Sinanodonta woodiana* is native to East Asia, from the Amur River and Korea south to Indochina (AS2, AS4–AS5). The species has been widely introduced through aquaculture to North and Central America (NA3, CA1), Europe (EU1), Central Asia (EU3), Japan (AS3), the Sunda and Philippine islands (AS6), and Myanmar (AS7) (Watters, 1997; Vikhrev *et al.*, 2017; Konečný *et al.*, 2018; Zieritz *et al.*, 2020). Recent scrutiny of the taxonomy of *S. woodiana* populations has resulted in the once highly variable, widespread, lumped taxon being split among at least nine species and multiple, as yet unnamed, lineages (Bolotov *et al.*, 2020a; Lopes-Lima *et al.*, 2020), and global

invasive populations may represent multiple invasive species. For example, *Sinanodonta lauta* (Martens, 1877), native to Japan and the adjacent continent (AS2–AS3), has also been found in Central Asia (EU3) and Borneo (AS6) (Bolotov *et al.*, 2020a; Zieritz *et al.*, 2020). Other species transported among regions include three species from North America introduced to the Yangtze–Huang subregion (AS4) by the freshwater pearl industry (He & Zhuang, 2013). Two European species of the genus *Unio* Philipsson in Retzius, 1788 are now found in the Amur Basin of Russia (AS2) (Bolotov *et al.*, 2020a) (Table 5).

Dispersal or transport of freshwater mussels among subregions of the same region has been harder to recognize. Eight Mississippi–Great Lakes (NA2) species in North America have been reported in the adjacent Atlantic Slope (NA3) (Table 5). The Erie Canal has been implicated in breaching the divide between the subregions for most of these (Strayer & Jirka, 1997; Sousa *et al.*, 2014). And, *Sinohyriopsis cumingii* from East Asia (AS4–AS5) has been reported

Table 5. Native and exotic ranges of introduced freshwater mussel species.

Species	North America				Central America	North Eurasia			East Asia				
	NA1	NA2	NA3	NA4	CA1	EU1	EU3	AS2	AS3	AS4	AS5	AS6	AS7
<i>Sinanodonta woodiana</i> (Lea, 1834)			I		I	I	I	N	I	N	N	I	I
<i>Sinanodonta lauta</i> (Martens, 1877)							I	N	N			I	
<i>Amblema plicata</i> (Say, 1817)	N	N		N						I			
<i>Potamilus alatus</i> (Say, 1817)	N	N	I							I			
<i>Reginaia ebenus</i> (Lea, 1831)		N		N						I			
<i>Unio pictorum</i> (Linnaeus, 1758)						N		I					
<i>Unio tumidus</i> Philipsson in Retzius, 1788						N		I					
<i>Cambarunio iris</i> (Lea, 1829)		N	I										
<i>Fusconaia flava</i> (Rafinesque)	N	N	I	N									
<i>Lampsilis cardium</i> Rafinesque, 1820	N	N	I										
<i>Lampsilis siliquoides</i> (Barnes, 1823)	N	N	I	N									
<i>Leptodea fragilis</i> (Rafinesque, 1820)		N	I	N									
<i>Ligumia recta</i> (Lamarck, 1819)	N	N	I	N									
<i>Pyganodon grandis</i> (Say, 1829)	N	N	I	N	N								
<i>Sinohyriopsis cumingii</i> (Lea, 1852)									I	N	N		

Species are arranged according to three categories: (1) *Sinanodonta* species, (2) species introduced among regions and (3) species introduced among subregions of the same region. *Potamilus alatus* represents both the second and third categories. Relevant references are cited in the text. Subregion abbreviations follow Table 1. Other abbreviations: N, native range; I, introduced.

Table 6. Widespread species occurring in four or more subregions, with other species that cross regional boundaries.

Species	Total	Regions					
		NA	CA	SA	AF	EU	AS
<i>Etheria elliptica</i> Lamarck, 1807	6				6		
<i>Anodontites trapesialis</i> (Lamarck, 1819)	6		1	5			
<i>Mycetopoda siliquosa</i> (Spix in Wagner, 1827)	6		1	5			
<i>Anodontites trigona</i> (Spix in Wagner, 1827)	5			5			
<i>Nodularia douglasiae</i> (Griffith & Pidgeon, 1833)	5						5
<i>Beringiana beringiana</i> (Middendorff, 1851)	4	1					3
<i>Chambardia wahlbergi</i> (Krauss, 1848)	4				4		
<i>Cristaria plicata</i> (Leach, 1814)	4						4
<i>Strophitus undulatus</i> (Say, 1817)	4	4					
<i>Pyganodon grandis</i> (Say, 1829)	4	3	1				
<i>Utterbackia imbecillis</i> (Say, 1829)	4	3	1				
<i>Anodontites tortilis</i> (Lea, 1852)	3		1	2			
<i>Cyrtonaias tampicoensis</i> (Lea, 1838)	2	1	1				
<i>Popenaias popeii</i> (Lea, 1857)	2	1	1				
<i>Margaritifera margaritifera</i> (Linnaeus, 1758)	2	1				1	

For each species, the total count of occupied ecoregions is provided, with the contribution by region. Region abbreviations follow Table 3.

from Lake Biwa in Japan (AS3) (Lopes-Lima *et al.*, 2020). More genetic sampling among widespread species will likely reveal additional examples.

The subregions utilized herein were designed to emphasize broad patterns of freshwater mussel endemism within each region. Almost all freshwater mussel species (918, >95%) have native (i.e. excluding introductions) geographical ranges limited to two or fewer subregions, and 808 species (84%) are endemic to single subregions. Conversely, only 11 species (1%) have native geographical ranges encompassing four or more subregions, and only 9 species are distributed across more than one region (Table 6). Many of these taxa may actually be composed of multiple separate evolutionary lineages, as evidenced by recent taxonomic splitting, traditionally recognized subspecies and/or cryptic genetic diversity (Graf & Cummings, 2011; Bolotov *et al.*, 2016; Elderkin *et al.*, 2016; Liu *et al.*, 2017).

Freshwater mussel species richness varies among the subregions from highs ≥ 150 species in Mississippi–Great Lakes (NA2) and Gulf–Florida (NA4) to as few as 2 in Madagascar (AF6) (Fig. 1B; Table 4). As shown in Figure 1A, arid and polar continental areas that lack mussels (i.e. species richness is 0) have not been assigned to any subregion. Among the 32 subregions, the median richness is 21.5 species, although the mean of 37.2 indicates a skewed tail in the distribution towards higher species richness.

Global patterns of richness within and among regions are more complex than simple latitudinal gradients (Rohde, 1992; Gaston, 2000). The 12 subregions ranked by richness in the bottom third (with ≤ 13 species) do include those of high latitudes: Canadian Interior (NA1), Central Asia (EU3), Beringia (AS1) and Patagonia (SA6). However, these least species-rich subregions also include temperate and tropical continental islands like Madagascar (AF6), New Zealand (AU4) and New Guinea (AU3), as well as temperate

arid subregions such as South Africa (AF5), East Australia (AU2) and the Middle East (EU2). Pacific North and South America (NA5 and SA1) are also included in this set. And, while the majority of the 11 subregions with the highest species richness (≥ 33 spp.) are predominantly tropical [Central America (CA1), Orinoco–Guianas (SA2), Amazon (SA3), Paraná–Paraguay (SA5), Congo (AF3), Indochina (AS5) and India–Myanmar (AS7)], the others are temperate, including those with the highest levels of species richness [Mississippi–Great Lakes (NA2), Atlantic Slope of North America (NA3), Gulf of Mexico and Florida (NA4) and Yangtze–Huang (AS4)] (Fig. 1B; Table 4).

We hypothesize that the major drivers of freshwater mussel diversity and richness are large river systems, as has been shown previously for fishes (Oberdorff, Guégan & Hugueny, 1995; Oberdorff *et al.*, 2011). Large, ancient river systems provide both habitat stability over geological time and dynamic opportunities for radiation in heterogeneous habitats (Bolotov *et al.*, 2017a). Mussel richness is positively correlated with fish richness and basin size (Watters, 1992; Graf & Cummings, 2011) and, with the exception of Central America (CA1), those of the richest subregions listed above are associated with some of the largest (by catchment area and/or discharge) river systems in the world. These include the Mississippi (NA2), Orinoco (SA2), Amazon (SA3), Paraná–Paraguay (La Plata) (SA5), Yangtze (AS4), Mekong (AS5) and Ganges–Brahmaputra (AS7) river systems. The Atlantic Slope (NA3) and Gulf of Mexico (NA4) subregions are adjacent to large rivers. Other large rivers may be too arid, like the Nile (AF1), or frozen, such as the Ob and Lena (EU3), to support a diverse freshwater mussel community. Freshwater mussel richness in such subregions may be directly limited by the primary productivity of the ecosystems and indirectly by the effects of energy availability on the host-fish community (Oberdorff *et al.*, 2011).

CONCLUSIONS

As regional freshwater mussel faunas receive renewed attention, we expect the number of recognized species and genera to continue to increase. In the decade since Graf & Cummings (2007b), the number of recognized species has increased from 840 to 958 and the number of genera has increased from 165 to 192. It is noteworthy that the tallies of species and genus richness increased by 43 and 10, respectively, just during the drafting of this article. These changes coincide with increased application of molecular phylogenetic techniques that provide powerful analytical tools for testing taxonomic hypotheses. The regions and taxa that have been analysed the most frequently have seen the most substantial revisions to species richness during that period. This is as expected. Molecular phylogenetic datasets are more extensive than they were a decade ago with regard to replicate sample sizes, diversity of taxa and number of nucleotides. Numerous studies (cited above), especially in North America, East Asia and Europe, have discovered (or rediscovered) species-level lineages and revised the taxonomy to assign names to new clades. However, this pattern is the result of not only new data but also changes in theory. Phylogenetic species (especially those where the criterion seems to be simply monophyly of mitochondrial DNA) are generally less inclusive (split) than widespread and variable (lumped) biological species (Sukumaran & Knowles, 2017). The result has been more species with narrower geographical ranges and higher endemism within basins, and this will likely impact conservation assessments (Agapow *et al.*, 2004; Franz, Peet & Weakley, 2008). A similar situation exists for supraspecific taxonomy: as new genus- and family-group level clades are recovered from analysis of molecular data, they are being named. This mentality of revising taxonomy post hoc based on molecular phylogenetic results alone is a change over the previous tendency of merely pointing out non-monophyly in anticipation of formal revisionary work (e.g. Campbell *et al.*, 2005; Graf *et al.*, 2015). We expect the splitting to continue, and this trend lends utility to the MUSSEL

Project Web Site (<http://mussel-project.net/>) to support those future revisions.

It is impractical, because of the large number of described species, to provide a complete synonymy for each species in the checklist published herein. Moreover, the majority of available species-group names have not been used as valid for more than a century (Fig. 2). However, synonymies are valuable for interpreting taxonomy, and our checklist is supported in that regard by the MUSSEL Project Web Site. For many freshwater mussel species, as aggregates of nominal species, using only a valid name may not be sufficient to unambiguously convey meaning. For example, *Elliptio icterina* of Williams *et al.* (2017) is not the same species as the one of the same name in Turgeon *et al.*'s (1998) study. As seen in our checklist, *E. icterina s.l.* has been split to include *E. icterina s.s.*, *E. occulta* and *E. pullata*. In addition, *E. icterina s.s.* has been combined with the former *E. cylindracea*, *E. errans*, *E. hepatica* and *E. raveneli*. This is not a strictly hypothetical issue. Pereira *et al.* (2014) listed no species in the genus *Iheringella* in South America, nor did they include the common and widespread *Anodontites trigona*. It is unclear from the context of their checklist whether those species were inadvertently omitted or simply relegated to junior synonyms somewhere else on their list. Thus, for many species, a reference to taxonomy, either by making synonyms explicit or providing a citation to a synonymy, can reduce unnecessary confusion.

It is evident (to us, anyway) that our previously published global checklist of freshwater mussel species and the availability of the data on the MUSSEL Project Web Site have had an impact on the way that the community of freshwater mussel researchers approach their work. We acknowledge, and it cannot be overemphasized, that our checklist will not be agreed upon by everyone (including the authors). Our objective has been to synthesize a current consensus from a diversity of sources, and while we have highlighted areas like Central America that have received a dearth of modern attention, other topics like the suprageneric classification of the Unionidae (Lopes-Lima *et al.*, 2017a; Pfeiffer *et al.*, 2019b) or the species diversity of East Asia (Bolotov *et al.*, 2017b, 2020a; Huang *et al.*, 2019; Lopes-Lima *et al.*, 2020) are opportunities for multiple interpretations. We hope that the checklist and summaries of genus and species richness provide a useful context to test specific hypotheses related to freshwater mussel systematics and biodiversity. When it comes to freshwater mussel biodiversity research, we aim to support *thinking globally while acting locally*.

CHECKLIST OF FRESHWATER MUSSEL GENERA AND SPECIES

For each genus, the list of occupied regions is provided as well as any additional taxonomic references to augment the faunistic works cited in Table 1. The type species is listed first with the remaining species listed alphabetically. For each species, the range is provided as a list of occupied subregions (Table 1).

A partial synonymy/chresonymy is provided that lists junior synonyms that are type species and references to species on our previous list (Graf & Cummings, 2007b), if different. The relationships among current and previous species can be more complicated than simply being lumped or split, and changes to species taxonomy can result from species- and/or genus-level revisions. We indicate the splitting of previous species with the notation 'in part'. For example, *Unio pictorum s.l.* is now recognized as at least four different species. An equal sign (=) is used to indicate that the combination of genus and species used in the previous checklist was different, and lumping of taxa is shown with a plus sign (+). These are intended to function analogously to mathematical operators. For example, *Venustaconcha trabalis* (Conrad, 1834) [= *Villosa trabalis s.l.* in part + *Villosa perpurpurea* (Lea, 1861)] should be read to mean that the species currently regarded as *Venustaconcha trabalis* was previously classified under *Villosa* and has been lumped with the species formerly recognized as *Villosa perpurpurea*. Moreover, the previous concept of

Villosa trabalis has been split. As can be seen in the checklist, *Venustaconcha troostensis* (Lea, 1834) is now treated as valid but had formerly been regarded as a junior synonym of *Villosa trabalis*. The absence of an equal sign in cases such as *Unio tigridis* Bourguignat, 1852 [+ *Unio terminalis* Bourguignat, 1852] indicates that the combination of genus and species used in the current list is unchanged, but that the current species has been lumped with (the entirety or part of) some previous species circumscription. Synonyms (indicated by ‘syn.’) are listed only when type species are junior synonyms of valid species.

The following additional abbreviations and symbols are used: *, type species; **, taxa added since Graf & Cummings (2007b); i = introduced to subregion; and Mp = subregion presence based on MUSSELPdb specimen records.

Order UNIONOIDA

Superfamily UNIONOIDEA

Family UNIONIDAE

incertae sedis Unionidae

***Germainia* Graf & Cummings, 2009:** Afrotropics.

1. **G. geayi* (Germain, 1911) [= *Coelatura geayi*]: AF6.

***Haasodonta* McMichael, 1956:** Australasia.

1. **H. fannyae* (R.I. Johnson, 1948): AU3.
2. *H. vanheurni* McMichael & Hiscock, 1958: AU3.

Subfamily UNIONINAE

Tribe UNIONINI

***Unio* Philipsson in Retzius, 1788:** North Eurasia, Afrotropics (introduced to East Asia); Khalloufi *et al.* (2011), Prie (2012), Prie & Puillandre (2014), Froufe *et al.* (2016a), Araujo *et al.* (2018), Marrone *et al.* (2019).

1. **U. pictorum* (Linnaeus, 1758) [= *U. pictorum s.l.* in part]: EU1, AS2 (i).
2. *U. abyssinicus* Martens, 1866: AF1.
3. *U. bruguierianus* Bourguignat, 1853 [= *U. crassus s.l.* in part]: EU1, EU2.
4. *U. caffer* Krauss, 1848 [= *Cafferia caffer*]: AF4.
5. *U. crassus* Philipsson in Retzius, 1788 [= *U. crassus s.l.* in part]: EU1.
6. *U. delphinus* Spengler, 1793 [= *U. pictorum s.l.* in part]: EU1.
7. *U. dembeae* Reeve, 1865 [= *U. mancus s.l.* in part]: AF1.
8. *U. durieui* Deshayes, 1847 [= *U. mancus s.l.* in part]: EU1.
9. *U. elongatulus* Pfeiffer, 1825 [= *U. mancus s.l.* in part]: EU1.
10. *U. foucauldianus* Pallary, 1936 [= *U. mancus s.l.* in part]: EU1.
11. *U. gibbus* Spengler, 1793 [= *U. pictorum s.l.* in part]: EU1.
12. *U. ionicus* Drouët, 1879 [= *U. crassus s.l.* in part]: EU1.
13. *U. mancus* Lamarck, 1819 [= *U. mancus s.l.* in part]: EU1.
14. *U. ravoisieri* Deshayes, 1848 [= *U. pictorum s.l.* in part]: EU1.
15. *U. tigridis* Bourguignat, 1852 [+ *U. terminalis* Bourguignat, 1852]: EU2.
16. *U. tumidiformis* Castro, 1885 [= *U. crassus s.l.* in part]: EU1.
17. *U. tumidus* Philipsson in Retzius, 1788: EU1, AS2 (i).

***Aculamprotula* Wu, Liang, Wang & Ouyang, 1999:** East Asia; Zhou *et al.* (2007), Pfeiffer & Graf (2013), Huang *et al.* (2019).

1. **A. fibrosa* (Heude, 1877) [= *Lamprotula fibrosa*]: AS4.
2. *A. coreana* (Martens, 1886) [= *Lamprotula coreana*]: AS2.
3. *A. grandidens* (Lea, 1862) [= *Lamprotula nodulosa s.l.* in part]: AS4.

4. *A. nodulosa* (Wood, 1815) [= *Lamprotula nodulosa s.l.* in part]: AS4, AS5.
5. *A. scripta* (Heude, 1875) [= *Lamprotula scripta*]: AS4.
6. *A. tientsinensis* (Crosse & Debeaux, 1863) [= *Lamprotula tientsinensis*]: AS4.
7. *A. tortuosa* (Lea, 1865) [= *Lamprotula tortuosa*]: AS4.
8. *A. zonata* (Heude, 1883) [= *Lamprotula zonata*]: AS4.

***Acuticosta* Simpson, 1900:** East Asia.

1. **A. chinensis* (Lea, 1868): AS4.
2. *A. retiaria* (Heude, 1883) [+ *A. ovata* (Simpson, 1900)]: AS4.
3. *A. sichuanica* Zeng & Liu, 1989: AS4.
4. *A. trisulcata* (Heude, 1883): AS4.

***Cuneopsis* Simpson, 1900:** East Asia.

1. **C. celtiformis* (Heude, 1874): AS4.
2. *C. capitatus* (Heude, 1874): AS4.
3. *C. demangei* Haas, 1929: AS5.
4. *C. heudei* (Heude, 1874): AS4.
5. *C. kiangsiensis* Tchang & Li, 1965**: AS4.
6. *C. pisciculus* (Heude, 1874): AS4.
7. *C. rufescens* (Heude, 1874): AS4.

***Diaurora* Cockerell, 1903:** East Asia.

1. **D. aurea* (Heude, 1883): AS4.

***Inversiuio* Habe, 1991:** East Asia; Kondo, Hyun & Seung-Ho (2007).

1. **I. reinianus* (Kobelt, 1879): AS3.
2. *I. jokohamensis* (Ihering, 1893): AS3.
3. *I. verrucosus* Kondo, Hyun & Seung-Ho, 2007**: AS2.
4. *I. yanagawensis* (Kondo, 1982): AS3.

***Lepidodesma* Simpson, 1896:** East Asia; Huang *et al.* (2019).

1. **L. languilati* (Heude, 1874): AS4.
2. *L. aligera* (Heude, 1877): AS4.

***Middendorffinaia* Moskvicheva & Starobogatov, 1973:** East Asia; Bolotov *et al.* (2020a).

1. **M. mongolica* (Middendorff, 1851) [= *Unio crassus s.l.* in part]: AS2.

***Nodularia* Conrad, 1853:** East Asia; Liu *et al.* (2017), Bolotov *et al.* (2018, 2020a), Klishko *et al.* (2018b, 2019).

1. **N. douglasiae* (Griffith & Pidgeon, 1833) [= *N. douglasiae s.l.* in part]: AS1, AS2, AS3, AS4, AS5.
2. *N. breviconcha* Lee, Kim, Bogan & Kondo in Lopes-Lima *et al.*, 2020**: AS2.
3. *N. diespiter* (Mabille, 1887) [= *Oxyaia diespiter*]: AS5.
4. *N. dorri* (Wattebled, 1886): AS5.
5. *N. gladiator* (Ancey, 1881) [= *Oxyaia gladiator*]: AS5.
6. *N. jourdyi* (Morlet, 1886) [= *Oxyaia jourdyi*]: AS5.
7. *N. micheloti* (Morlet, 1886) [= *Oxyaia micheloti*]: AS5.
8. *N. nipponensis* (Martens, 1877) [= *N. douglasiae s.l.* in part]: AS3.
9. *N. nuxpersicae* (Dunker, 1849) [= *N. douglasiae s.l.* in part]: AS5.
10. *N. persculpta* Haas, 1910 [= *Scabies crispata s.l.* in part]: AS4.

***Protunio* Haas, 1912:** East Asia; Bogan & Do (2018).

1. **P. messengeri* (Bavay & Dautzenberg, 1901): AS5.

***Pseudobaphia* Simpson, 1900:** East Asia; Bogan & Do (2018).

1. **P. biesiana* (Heude, 1877): AS4.
2. *P. banggiangensis* Bogan & Do, 2018**: AS5.
3. *P. huovatus* (He & Zhuang, 2013) [= *P. ovata* (Liu, Duan & Wang, 1994) non *Unio ovatus* Say, 1817]: AS4, AS5.

Rhombuniopsis Haas, 1920: East Asia; [Moskvicheva & Starobogatov \(1973\)](#).

1. **R. tauriformis* (Fulton, 1906): AS5.
2. *R. fulloni* [Moskvicheva & Starobogatov, 1973](#): AS5.
3. *R. superstes* (Neumayr, 1899): AS5.

Schistodesmus Simpson, 1900: East Asia; [Huang et al. \(2019\)](#).

1. **S. lampreyanus* (Baird & Adams, 1867): AS4.
2. *S. spinosus* ([Simpson, 1900](#)): AS4.

Tribe ANODONTINI
Subtribe ANODONTINA

Anodonta Lamarck, 1799: North Eurasia, North and Central America; [Chong et al. \(2008\)](#), [Mock et al. \(2013\)](#), [Froufe et al. \(2017\)](#).

1. **A. cygnea* ([Linnaeus, 1758](#)): EU1.
2. *A. anatina* ([Linnaeus, 1758](#)) [= *A. anatina* s.l. in part]: EU1, EU3.
3. *A. californiensis* [Lea, 1852](#) [+ *A. dejecta* [Lewis, 1875](#)]: NA5.
4. *A. cyrea* [Drouët, 1881](#): EU1, EU3.
5. *A. exulcerata* [Porro, 1838](#) [= *A. anatina* s.l. in part]: EU1.
6. *A. impura* [Say, 1829](#): CA1.
7. *A. kernerlyi* [Lea, 1860](#): NA5.
8. *A. lurulenta* ([Morelet, 1849](#)): CA1.
9. *A. nuttalliana* [Lea, 1838](#): NA5.
10. *A. oregonensis* [Lea, 1838](#): NA5.
11. *A. pseudodopsis* [Locard, 1883](#): EU2.
12. *A. vescoiana* [Bourguignat, 1856](#): EU2.

Pseudanodonta Bourguignat, 1876: North Eurasia.

1. **P. complanata* ([Rossmässler, 1835](#)): EU1.

Subtribe ALASMIDONTINA

Alasmidonta Say, 1818: North America; [Clarke \(1981b\)](#).

1. **A. undulata* ([Say, 1817](#)) [= *A. (Alasmidonta) undulata*]: NA3.
2. *A. arcua* ([Lea, 1838](#)) [= *A. (Alasmidonta) arcua*]: NA3.
3. *A. atropurpurea* ([Rafinesque, 1831](#)) [= *A. (Decurambis) atropurpurea*]: NA2.
4. *A. heterodon* ([Lea, 1829](#)) [= *A. (Pressodonta) heterodon*]: NA3.
5. *A. marginata* [Say, 1818](#) [= *A. (Decurambis) marginata*]: NA2, NA3.
6. *A. mccordi* [Athearn, 1964](#) [= *A. (Alasmidens) mccordi*]: NA4. Extinct.
7. *A. raveneliana* ([Lea, 1834](#)) [= *A. (Decurambis) raveneliana*]: NA2.
8. *A. robusta* [Clarke, 1981](#) [= *A. (Decurambis) robusta*]: NA3. Extinct.
9. *A. triangulata* ([Lea, 1858](#)) [= *A. (Alasmidonta) triangulata*]: NA4.
10. *A. varicosa* ([Lamarck, 1819](#)) [= *A. (Decurambis) varicosa*]: NA3.
11. *A. viridis* ([Rafinesque, 1820](#)) [= *A. (Pressodonta) viridis*]: NA2.
12. *A. wrightiana* ([Walker, 1901](#)) [= *A. (Alasmidonta) wrightiana*]: NA4. Extinct.

Anodontoides Simpson in F.C. Baker, 1898: North America; [Smith et al. \(2018\)](#).

1. **A. ferussacianus* ([Lea, 1834](#)) [= *A. ferussacianus* s.l. in part]: NA1, NA2, NA3.
2. *A. denigratus* ([Lea, 1852](#)) [= *A. ferussacianus* s.l. in part]: NA2.

Arcidens Simpson, 1900: North America; [Clarke \(1981b\)](#), [Inoue et al. \(2014\)](#).

1. **A. confragosus* ([Say, 1829](#)) [= *A. (Arcidens) confragosus*]: NA2, NA4.
2. *A. wheeleri* ([Ortmann & Walker, 1912](#)) [= *A. (Arkansia) wheeleri*]: NA2.

Lasmigona Rafinesque, 1831: North America; [Clarke \(1985\)](#).

1. **L. costata* ([Rafinesque, 1820](#)) [= *L. (Lasmigona) costata*]: NA1, NA2, NA3.
2. *L. alabamensis* [Clarke, 1985](#) [= *L. (Lasmigona) complanata* s.l. in part]: NA4.
3. *L. complanata* ([Barnes, 1823](#)) [= *L. (Lasmigona) complanata* s.l. in part]: NA1, NA2, NA4.
4. *L. compressa* ([Lea, 1829](#)) [= *L. (Platynaias) compressa*]: NA1, NA2, NA3.
5. *L. decorata* ([Lea, 1852](#)) [= *L. (Platynaias) decorata*]: NA3.
6. *L. etowaensis* ([Conrad, 1849](#)) [= *L. (Alasminota) holstonia* s.l. in part]: NA4.
7. *L. holstonia* ([Lea, 1838](#)) [= *L. (Alasminota) holstonia* s.l. in part]: NA2.
8. *L. subviridis* ([Conrad, 1835](#)) [= *L. (Platynaias) subviridis*]: NA2, NA3, NA4.

Pegias Simpson, 1900: North America; [Clarke \(1981b\)](#).

1. **P. fabula* ([Lea, 1838](#)): NA2.

Pseudodontoides Frierson, 1927: North America; [Smith et al. \(2018\)](#).

1. *P. connasaugaensis* ([Lea, 1858](#)) [= *Strophitus connasaugaensis*; syn. **Margaritana alabamensis* [Lea, 1861](#)]: NA4.
2. *P. subvexus* ([Conrad, 1834](#)) [= *Strophitus subvexus*]: NA4.

Pyganodon Crosse & Fischer, 1894: North and Central America; [Doucet-Beaupré et al. \(2012\)](#).

1. *P. grandis* ([Say, 1829](#)) [= *P. grandis* s.l. in part; syn. **Anodonta globosa* [Lea, 1841](#)]: NA1, NA2, NA3 (i), NA4, CA1.
2. *P. cataracta* ([Say, 1817](#)) [= *P. cataracta* s.l. in part]: NA3, NA4.
3. *P. fragilis* ([Lamarck, 1819](#)) [= *P. cataracta* s.l. in part]: NA3.
4. *P. gibbosa* ([Say, 1824](#)): NA3.
5. *P. lacustris* ([Lea, 1857](#)) [= *P. grandis* s.l. in part]: NA2, NA3.

Simpsonaias Frierson, 1914: North America; [Clarke \(1985\)](#).

1. **S. ambigua* ([Say, 1825](#)): NA2.

Strophitus Rafinesque, 1820: North America; [Smith et al. \(2018\)](#).

1. **S. undulatus* ([Say, 1817](#)): NA1, NA2, NA3, NA4.
2. *S. pascagoulaensis* [Smith, Johnson, Pfeiffer & Gangloff, 2018**](#): NA4.
3. *S. radiatus* ([Conrad, 1834](#)) [= *Anodontoides radiatus*]: NA4.
4. *S. williamsi* [Smith, Johnson, Pfeiffer & Gangloff, 2018**](#): NA4.

Utterbackia F.C. Baker, 1927: North and Central America.

1. **U. imbecillis* ([Say, 1829](#)): NA2, NA3, NA4, CA1.
2. *U. peggyae* ([R.I. Johnson, 1965](#)): NA4.
3. *U. peninsularis* [Bogan & Hoeh, 1995](#): NA4.

Utterbackiana Frierson, 1927: North America.

1. **U. suborbiculata* ([Say, 1831](#)) [= *Utterbackia suborbiculata*]: NA2, NA4.
2. *U. couperiana* ([Lea, 1840](#)) [= *Utterbackia couperiana*]: NA3, NA4.
3. *U. hartfieldorum* ([Williams, Bogan & Garner, 2009**](#)): NA4.
4. *U. heardi* ([Gordon & Hoeh, 1995](#)) [= *Utterbackia heardi*]: NA4.
5. *U. implicata* ([Say, 1829](#)) [= *Pyganodon implicata*]: NA3.

Subtribe CRISTARIINA

Cristaria Schumacher, 1817: East Asia; [Bogatov & Prozorova \(2017\)](#).

1. *C. plicata* (Leach, 1814) [= *C. plicata* s.l. in part; syn. **Cristaria tuberculata* Schumacher, 1817]: AS2, AS3, AS4, AS5.
2. *C. beirensis* Liu & Zhang, 1982 [= *C. plicata* s.l. in part]: AS2.
3. *C. clessini* (Kobelt, 1879) [= *C. plicata* s.l. in part]: AS3.
4. *C. radiata* Simpson, 1900: AS4.
5. *C. truncata* Dang, Thai & Pham, 1980: AS5.

Amuranodonta Moskvicheva, 1973: East Asia; Bolotov *et al.* (2020a).

1. **A. kijaensis* Moskvicheva, 1973 [= *Anemina arcaeformis* s.l. in part]: AS2.

Anemina Haas, 1969: East Asia; Bogatov & Prozorova (2017).

1. **A. arcaeformis* (Heude, 1877) [= *A. arcaeformis* s.l. in part]: AS2, AS3, AS4.
2. *A. euscaphys* (Heude, 1879): AS2, AS4.
3. *A. fluminea* (Heude, 1877): AS4.
4. *A. globosula* (Heude, 1878): AS4.

Beringiana Starobogatov in Zatravkin, 1983: East Asia and North America; Bolotov *et al.* (2020a).

1. **B. beringiana* (Middendorff, 1851) [= *Anodonta beringiana*]: NA5, AS1, AS2 AS3.
2. *B. fukuharai* San, Hattori & Kondo in Lopes-Lima *et al.*, 2020**: AS3.
3. *B. gosannensis* San, Hattori & Kondo in Lopes-Lima *et al.*, 2020**: AS3.
4. *B. japonica* (Clessin, 1874) [= *Sinanodonta woodiana* s.l. in part]: AS3.

Buldowskia Moskvicheva, 1973: East Asia; Bolotov *et al.* (2020a).

1. **B. suifunica* (Lindholm, 1925) [= *Anemina arcaeformis* s.l. in part]: AS2.
2. *B. flavotincta* (Martens, 1905) [= *Anemina arcaeformis* s.l. in part]: AS2.
3. *B. iwakawai* (Suzuki, 1939) [= *Anemina arcaeformis* s.l. in part]: AS2, AS3.
4. *B. kamiyai* San, Hattori & Kondo in Lopes-Lima *et al.*, 2020**: AS3.
5. *B. shadini* (Moskvicheva, 1973) [= *Anemina arcaeformis* s.l. in part]: AS2.

Pletholophus Simpson, 1900: East Asia.

1. *P. tenuis* (Griffith & Pidgeon, 1833) [= **Cristaria discoidea* (Lea, 1834)]: AS4, AS5.
2. *P. reinianus* (Martens, 1875) [= *Cristaria discoidea* s.l. in part]: AS3.

Simpsonella Cockerell, 1903: East Asia.

1. **S. purpurea* (Valenciennes, 1827): AS6.
2. *S. gracilis* (Lea, 1850): AS6.

Sinanodonta Modell, 1945: East Asia (introduced to North and Central America, and North Eurasia); Sano *et al.* (2017), Bolotov *et al.* (2020a).

1. **S. woodiana* (Lea, 1834) [= *S. woodiana* s.l. in part]: NA3 (i), CA1 (i), EU1 (i), EU3 (i), AS2, AS3 (i), AS4, AS5, AS6 (i), AS7 (i).
2. *S. angula* (Tchang, Li & Liu, 1965) [= *Anemina angula*]: AS4.
3. *S. calipygos* (Kobelt, 1879) [= *S. woodiana* s.l. in part]: AS3.
4. *S. elliptica* (Heude, 1878) [= *S. woodiana* s.l. in part]: AS4, AS5.
5. *S. jourdyi* (Morlet, 1886) [= *S. woodiana* s.l. in part]: AS5.

6. *S. lauta* (Martens, 1877) [= *S. woodiana* s.l. in part]: EU3 (i), AS2, AS3, AS6 (i).
7. *S. lucida* (Heude, 1877) [= *S. woodiana* s.l. in part]: AS4, AS5.
8. *S. schrenkii* (Lea, 1870) [= *S. woodiana* s.l. in part]: AS2.
9. *S. tumens* (Haas, 1910) [= *S. woodiana* s.l. in part + *S. oguruae* (Kuroda & Habe, 1987)]: AS3.

Tribe LANCEOLARIINI

Lanceolaria Conrad, 1853: East Asia.

1. *L. grayii* (Griffith & Pidgeon, 1833) [= **L. grayana* (Lea, 1834) s.l. in part]: AS2, AS4, AS5.
2. *L. acrorhyncha* (Martens, 1894): AS2.
3. *L. bilirata* (Martens, 1902) [= *L. oxyrhyncha* s.l. in part]: AS5.
4. *L. bogani* Thach, 2016**: AS5.
5. *L. cylindrica* (Simpson, 1900): AS2.
6. *L. eucylindrica* Lin, 1962: AS4.
7. *L. fruhstorferi* (Dautzenberg, 1900) [= *L. grayana* s.l. in part]: AS5.
8. *L. gladiola* (Heude, 1877): AS4, AS5.
9. *L. kihirai* Kondo & Hattori, 2019**: AS3.
10. *L. laevis* (Martens, 1902) [= *L. grayana* s.l. in part]: AS5.
11. *L. lanceolata* (Lea, 1856) [+ *Arconaia mutica* (Heude, 1877) + *Arconaia huaiensis* Huang & Li, 2003]: AS4.
12. *L. oxyrhyncha* (Martens, 1861) [= *L. oxyrhyncha* s.l. in part]: AS3.
13. *L. triformis* (Heude, 1877): AS4.

Subfamily AMBLEMINEAE

Tribe AMBLEMINI

Amblema Rafinesque, 1820: North America (introduced to East Asia); Mulvey *et al.* (1997).

1. *A. plicata* (Say, 1817) [syn. **Amblema costata* Rafinesque, 1820]: NA1, NA2, NA4, AS4 (i).
2. *A. elliotii* (Lea, 1857): NA4.
3. *A. neislerii* (Lea, 1858): NA4.

Plectomerus Conrad, 1853: North America.

1. *P. dombeyanus* (Valenciennes in Humboldt & Bonpland, 1827) [syn. **Unio trapezoides* Lea, 1831]: NA2, NA4.

Reginaia Campbell & Lydeard, 2012: North America (introduced to East Asia); Campbell & Lydeard (2012a).

1. **R. ebenus* (Lea, 1831) [= *Fusconia ebena*]: NA2, NA4, AS4 (i).
2. *R. apalachicola* (Williams & Fradkin, 1999)**: NA4.
3. *R. rotulata* (B.H. Wright, 1899) [= *Obovaria rotulata*]: NA4.

Tribe LAMPASILINI

Lampsilis Rafinesque, 1820: North America; Inoue *et al.* (2020b).

1. **L. ovata* (Say, 1817): NA2.
2. *L. abrupta* (Say, 1831): NA2.
3. *L. bergmanni* Inoue & Randklev in Inoue *et al.*, 2020**: NA4.
4. *L. binominata* Simpson, 1900: NA4. Extinct.
5. *L. bracteata* (Gould, 1855): NA4.
6. *L. brittsi* Simpson, 1900 [= *L. reeviana* s.l. in part]: NA2.
7. *L. cardium* Rafinesque, 1820: NA1, NA2, NA3 (i).
8. *L. cariosa* (Say, 1817): NA3.
9. *L. dolabraeformis* (Lea, 1838): NA3.
10. *L. fasciola* Rafinesque, 1820: NA2.
11. *L. floridensis* (Lea, 1852) [= *L. teres* s.l. in part]: NA4.

12. *L. higginsii* (Lea, 1857): NA2.
13. *L. hydiana* (Lea, 1838): NA2, NA4.
14. *L. ornata* (Conrad, 1835): NA4.
15. *L. powellii* (Lea, 1852): NA2.
16. *L. radiata* (Gmelin, 1791) [+ *L. fullerkeri* R.I. Johnson, 1984]: NA3.
17. *L. rafinesqueana* Frierson, 1927: NA2.
18. *L. reeveiana* (Lea, 1852) [= *L. reeviana s.l.* in part]: NA2.
19. *L. satura* (Lea, 1852): NA2, NA4.
20. *L. sietmani* Keogh & Simons, 2019**: NA2, NA4.
21. *L. siliquoides* (Barnes, 1823): NA1, NA2, NA3 (i), NA4.
22. *L. splendida* (Lea, 1838): NA3.
23. *L. straminea* (Conrad, 1834): NA4.
24. *L. streckeri* Frierson, 1927: NA2.
25. *L. teres* (Rafinesque, 1820) [= *L. teres s.l.* in part]: NA2, NA4.
26. *L. virescens* (Lea, 1858): NA2.

Actinonaias Crosse & Fischer, 1894: Central America.

1. **A. sapotalensis* (Lea, 1841): CA1.
2. *A. computata* (Crosse & Fischer, 1893): CA1.
3. *A. coyensis* (Pilsbry, 1910): CA1.
4. *A. medellina* (Lea, 1838): CA1.
5. *A. moctezumensis* (Pilsbry, 1910): CA1.
6. *A. signata* (Pilsbry, 1910): CA1.
7. *A. undivaga* (Pilsbry, 1910): CA1.

Arotonaias Martens, 1900: Central America.

1. **A. cyrenoides* (Philippi, 1847): CA1.
2. *A. gabbianus* (Lea, 1868) [+ *Arotonaias nicaraguensis* (Lea, 1868)]: CA1.
3. *A. imbricata* (Mörch, 1861): CA1.

Cambarunio Watters, 2018: North America; Watters (2018).

1. **C. iris* (Lea, 1829) [= *Villosa iris s.l.* in part]: NA2, NA3 (i).
2. *C. dactylus* (Lea, 1840) [= *Villosa iris s.l.* in part]: NA2.
3. *C. hesperus* Watters, 2018**: NA2.
4. *C. jonesii* (Lea, 1859) [= *Villosa nebulosa s.l.* in part]: NA2, NA4.
5. *C. nebulosus* (Conrad, 1834) [= *Villosa nebulosa s.l.* in part]: NA2, NA4.
6. *C. simus* (Lea, 1838) [= *Villosa iris s.l.* in part]: NA2.
7. *C. taeniatus* (Conrad, 1834) [= *Villosa taeniata*]: NA2.

Cyprogenia Agassiz, 1852: North America; Serb & Barnhart (2008), Grobler *et al.* (2011), Chong, Harris & Roe (2016).

1. *C. stegaria* (Rafinesque, 1820) [syn. **Unio irroratus* Lea, 1828]: NA2.
2. *C. aberti* (Conrad, 1850): NA2.

Cyrtonaias Crosse & Fischer, 1894: North and Central America; R.I. Johnson (1998), Pfeiffer *et al.* (2019a).

1. *C. tampicoensis* (Lea, 1838) [+ *C. saladoensis* (Lea, 1860); syn. **Unio berlandierii* Lea, 1857]: NA4, CA1.
2. *C. explicata* (Morelet, 1849) [+ *C. livida* (Simpson, 1900)]: CA1.
3. *C. sapperi* (Ihering, 1901): CA1.
4. *C. umbrosa* (Lea, 1856) [+ *Potamilus rovirosai* (Pilsbry, 1900)]: CA1.

Delphinonaias Crosse & Fischer, 1894: Central America.

1. *D. largillierti* (Philippi, 1847) [= *Potamilus largillierti* + **D. delphinulus* (Morelet, 1849) + *D. paludosa* (Morelet, 1849) + *D. planivalvis* (Morelet, 1851)]: CA1.
2. *D. scutulata* (Morelet, 1849): CA1.

Disconaias Crosse & Fischer, 1894: North and Central America; R.I. Johnson (1998).

1. **D. disca* (Lea, 1838) [+ *D. panacoensis* (von dem Busch in Philippi, 1843)]: CA1.
2. *D. conchos* Taylor, 1997: NA4.
3. *D. fimbriata* (Frierson, 1907): CA1.
4. *D. novoleonis* (Pilsbry, 1910): CA1.
5. *D. purpurata* (Say, 1831): CA1.

Dromus Simpson, 1900: North America; Serb & Barnhart (2008), Grobler *et al.* (2011), Chong *et al.* (2016).

1. **D. dromas* (Lea, 1834): NA2.

Ellipsaria Rafinesque, 1820: North America.

1. *E. lineolata* (Rafinesque, 1820) [syn. **Obliquaria ellipsaria* Rafinesque, 1820]: NA2, NA4.

Epioblasma Rafinesque, 1831: North America; R.I. Johnson (1978).

1. *E. rangiana* (Lea, 1838) [= *E. torulosa s.l.* in part; syn. **Epioblasma biloba* Rafinesque, 1831]: NA2.
2. *E. ahlstedti* Jones & Neves, 2010**: NA2.
3. *E. arcaeformis* (Lea, 1831): NA2. Extinct.
4. *E. aureola* Jones & Neves, 2010**: NA2.
5. *E. biemarginata* (Lea, 1857): NA2. Extinct.
6. *E. brevidens* (Lea, 1831): NA2.
7. *E. capsaeformis* (Lea, 1834): NA2.
8. *E. cincinnatiensis* (Lea, 1840) [= *E. torulosa s.l.* in part]: NA2.
9. *E. curtisii* (Frierson & Utterback in Utterback, 1916) [= *E. florentina s.l.* in part]: NA2.
10. *E. flexuosa* (Rafinesque, 1820): NA2. Extinct.
11. *E. florentina* (Lea, 1857) [= *E. florentina s.l.* in part]: NA2. Extinct.
12. *E. gubernaculum* (Reeve, 1865) [= *E. torulosa s.l.* in part]: NA2. Extinct.
13. *E. haysiana* (Lea, 1834): NA2. Extinct.
14. *E. lenior* (Lea, 1842): NA2. Extinct.
15. *E. lewisii* (Walker, 1910): NA2. Extinct.
16. *E. metastrata* (Conrad, 1838): NA4.
17. *E. obliquata* (Rafinesque, 1820) [= *E. obliquata s.l.* in part]: NA2.
18. *E. othcaloogensis* (Lea, 1857): NA4.
19. *E. penit a* (Conrad, 1834): NA4.
20. *E. perobliqua* (Conrad, 1836) [= *E. obliquata s.l.* in part]: NA2.
21. *E. personata* (Say, 1829): NA2. Extinct.
22. *E. propinqua* (Lea, 1857): NA2. Extinct.
23. *E. sampsonii* (Lea, 1862): NA2. Extinct.
24. *E. stewardsonii* (Lea, 1852): NA2. Extinct.
25. *E. torulosa* (Rafinesque, 1820) [= *E. torulosa s.l.* in part]: NA2. Extinct.
26. *E. triquetra* (Rafinesque, 1820): NA2.
27. *E. turgidula* (Lea, 1858): NA2. Extinct.
28. *E. walkeri* (Wilson & Clark, 1914) [= *E. florentina s.l.* in part]: NA2.

Friersonia Ortmann, 1912: Central America.

1. **F. indella* (Pilsbry & Frierson, 1908): CA1.

Glebulula Conrad, 1853: North America.

1. **G. rotundata* (Lamarck, 1819): NA2, NA4.

Hamiota Roe & Hartfield, 2005: North America; Roe, Hartfield & Lydeard (2001), Roe & Hartfield (2005).

1. **H. subangulata* (Lea, 1840): NA4.
2. *H. altilis* (Conrad, 1834): NA4.
3. *H. australis* (Simpson, 1900): NA4.
4. *H. perovalis* (Conrad, 1834): NA4.

Leaunio Watters, 2018: North America; Watters (2018).

1. **L. lienosus* (Conrad, 1834) [= *Villosa lienosa*]: NA2, NA4.
2. *L. ortmanni* (Walker, 1925) [= *Villosa ortmanni*]: NA2.
3. *L. pataecus* Watters, 2018**: NA2.
4. *L. umbrans* (Lea, 1857) [= *Villosa vanuxemensis s.l.* in part]: NA2, NA4.
5. *L. vanuxemensis* (Lea, 1838) [= *Villosa vanuxemensis s.l.* in part]: NA2.

Lemiox Rafinesque, 1831: North America.

1. **L. rimosus* (Rafinesque, 1831): NA2.

Leptodea Rafinesque, 1820: North America; Smith *et al.* (2019).

1. **L. fragilis* (Rafinesque, 1820) [+ *Medionidus meglameriae* van der Schalie, 1939]: NA2, NA3 (i), NA4.
2. *L. leptodon* (Rafinesque, 1820): NA2.
3. *L. ochracea* (Say, 1817): NA3.

Ligumia Swainson, 1840: North America.

1. **L. recta* (Lamarck, 1819): NA1, NA2, NA3 (i), NA4.

Medionidus Simpson, 1900: North America; R.I. Johnson (1977).

1. **M. conradicus* (Lea, 1834): NA2.
2. *M. acutissimus* (Lea, 1831): NA4.
3. *M. parvulus* (Lea, 1860): NA4.
4. *M. penicillatus* (Lea, 1857): NA4.
5. *M. simpsonianus* Walker, 1905: NA4.
6. *M. walkeri* (B.H. Wright, 1897): NA4.

Obliquaria Rafinesque, 1820: North America.

1. **O. reflexa* Rafinesque, 1820: NA2, NA4.

Obovaria Rafinesque, 1819: North America; Inoue *et al.* (2013), Watters (2018).

1. **O. retusa* (Lamarck, 1819): NA2.
2. *O. arkansasensis* (Lea, 1862) [+ *O. jacksoniana* (Frierson, 1912)]: NA2, NA4.
3. *O. choctawensis* (Athearn, 1964) [= *Villosa choctawensis*]: NA4.
4. *O. haddletoni* (Athearn, 1964) [= *Lampsilis haddletoni*]: NA4.
5. *O. olivaria* (Rafinesque, 1820): NA2.
6. *O. subrotunda* (Rafinesque, 1820): NA2.
7. *O. unicolor* (Lea, 1845): NA4.

Ortmanniana Frierson, 1927: North America.

1. *O. ligamentina* (Lamarck, 1819) [= *Actinonaias ligamentina*; syn. **Unio carinatus* Barnes, 1823]: NA2.
2. *O. pectorosa* (Conrad, 1834) [= *Actinonaias pectorosa*]: NA2.

Pachynaias Crosse & Fischer, 1894: Central America.

1. **P. spheniopsis* (Morelet, 1849): CA1.
2. *P. rugososulcata* (Lea, 1866) [= *P. rugosulcata (sic)*]: CA1.

Paetulunio Watters, 2018: North America; Watters (2018).

1. **P. fabalis* (Lea, 1831) [= *Villosa fabalis*]: NA2.

Potamilus Rafinesque, 1818: North America (introduced to East Asia); Roe & Lydeard (1998), Smith *et al.* (2019).

1. **P. alatus* (Say, 1817): NA1, NA2, NA3 (i), AS4 (i).
2. *P. amphichaenus* (Frierson, 1898): NA4.
3. *P. capax* (Green, 1832): NA2.
4. *P. inflatus* (Lea, 1831): NA4.
5. *P. metnecktayi* R.I. Johnson, 1998: NA4.
6. *P. ohioensis* (Rafinesque, 1820): NA2, NA4.
7. *P. purpuratus* (Lamarck, 1819): NA2, NA4.
8. *P. streckersoni* Smith, Johnson, Inoue, Doyle & Randklev, 2019**: NA4.

Ptychobranthus Simpson, 1900: North America; Roe (2013).

1. *P. fasciolaris* (Rafinesque, 1820) [syn. **Unio phaseolus* Hildreth, 1828]: NA2.
2. *P. foremanianus* (Lea, 1842) [= *P. greenii s.l.* in part]: NA4.
3. *P. greenii* (Conrad, 1834) [= *P. greenii s.l.* in part]: NA4.
4. *P. jonesi* (van der Schalie, 1934): NA4.
5. *P. occidentalis* (Conrad, 1836): NA2.
6. *P. subtentus* (Say, 1825): NA2.

Sagittunio Watters, 2018: North America; Watters (2018).

1. **S. nasutus* (Say, 1817) [= *Ligumia nasuta*]: NA2, NA3.
2. *S. aldermani* Watters, 2018**: NA3.
3. *S. subrostratus* (Say, 1831) [= *Ligumia subrostrata*]: NA2, NA4.
4. *S. vauhanianus* (Lea, 1838) [= *Villosa vauhaniana*]: NA3.

Toxolasma Rafinesque, 1831: North America.

1. **T. lividum* Rafinesque, 1831: NA2.
2. *T. corvunculus* (Lea, 1868): NA4.
3. *T. cylindrellus* (Lea, 1868): NA2.
4. *T. parvum* (Barnes, 1823): NA2, NA4.
5. *T. paulum* (Lea, 1840): NA4.
6. *T. pullus* (Conrad, 1838): NA3.
7. *T. texasiense* (Lea, 1857) [+ *T. mearnsi* (Simpson, 1900)]: NA2, NA4.

Truncilla Rafinesque, 1819: North America; Burlakova, Campbell & Karatayev (2019).

1. **T. truncata* Rafinesque, 1820: NA2, NA4.
2. *T. cognata* (Lea, 1860): NA4.
3. *T. donaciformis* (Lea, 1828): NA2, NA4.
4. *T. macrodon* (Lea, 1859): NA4.

Venustaconcha Frierson, 1927: North America; Watters (2018).

1. *V. ellipsiformis* (Conrad, 1836) [syn. **Unio venustus* Lea, 1838]: NA2.
2. *V. constricta* (Conrad, 1838) [= *Villosa constricta*]: NA3.
3. *V. pleasii* (Marsh, 1891): NA2.
4. *V. trabalis* (Conrad, 1834) [= *Villosa trabalis s.l.* in part + *Villosa perpurpurea* (Lea, 1861)]: NA2.
5. *V. troostensis* (Lea, 1834) [= *Villosa trabalis s.l.* in part]: NA2.

Villosa Frierson, 1927: North America; Watters (2018).

1. **V. villosa* (B.H. Wright, 1898): NA4.
2. *V. amygdalum* (Lea, 1843): NA4.
3. *V. delumbis* (Conrad, 1834): NA3.
4. *V. vibex* (Conrad, 1834): NA2, NA3, NA4.

Tribe PLEUROBEMINI

Pleurobema Rafinesque, 1819: North America; [Burlakova et al. \(2012\)](#), [Campbell & Lydeard \(2012a\)](#), [Inoue et al. \(2018\)](#).

1. *P. clava* (Lamarck, 1819) [+ *P. bournianum* (Lea, 1840); syn. **Pleurobema mytiloides* Rafinesque, 1820]: NA2.
2. *P. athearni* Gangloff, Williams & Feminella, 2006: NA4.
3. *P. beadleianum* (Lea, 1861): NA4.
4. *P. cordatum* (Rafinesque, 1820): NA2.
5. *P. curtum* (Lea, 1859): NA4.
6. *P. decimum* (Lea, 1831) [+ *P. chattanoogaense* (Lea, 1858)]: NA4.
7. *P. fibuloides* (Lea, 1859): NA4.
8. *P. georgianum* (Lea, 1841) [+ *P. nucleopsis* (Conrad, 1849) + *P. troschelianum* (Lea, 1852)]: NA4.
9. *P. hanleyianum* (Lea, 1852): NA4.
10. *P. hartmanianum* (Lea, 1860): NA4.
11. *P. marshalli* Frierson, 1927: NA4.
12. *P. oviforme* (Conrad, 1834): NA2.
13. *P. perovatum* (Conrad, 1834) [+ *P. johannis* (Lea, 1859) + *P. flavidulum* (Lea, 1861)]: NA4. Extinct.
14. *P. plenum* (Lea, 1840): NA2.
15. *P. pyriforme* (Lea, 1857): NA4.
16. *P. riddellii* (Lea, 1862): NA4.
17. *P. rubellum* (Conrad, 1834) [= *P. rubellum* s.l. in part + *P. avellanum* Simpson, 1900 + *P. furvum* (Conrad, 1834) + *P. hagleri* (Frierson, 1900)]: NA4.
18. *P. rubrum* (Rafinesque, 1820): NA2.
19. *P. sintoxia* (Rafinesque, 1820): NA2.
20. *P. stabile* (Lea, 1861) [= *P. rubellum* s.l. in part + *P. murrayense* (Lea, 1868)]: NA4.
21. *P. strodeanum* (B.H. Wright, 1898): NA4.
22. *P. taitianum* (Lea, 1834): NA4.
23. *P. verum* (Lea, 1861): NA4.

Elliptio Rafinesque, 1819: North America; [Perkins, Johnson & Gangloff \(2017\)](#), [Inoue et al. \(2018\)](#).

1. *E. crassidens* (Lamarck, 1819) [syn. **Unio nigra* Rafinesque, 1820]: NA2, NA4.
2. *E. ahenea* (Lea, 1843) [+ *E. waltoni* (B.H. Wright, 1888)]: NA4.
3. *E. angustata* (Lea, 1831): NA3.
4. *E. arca* (Conrad, 1834): NA4.
5. *E. arctata* (Conrad, 1834): NA3, NA4.
6. *E. chipolaensis* (Walker, 1905): NA4.
7. *E. cistellaeformis* (Lea, 1863): NA3.
8. *E. complanata* (Lightfoot, 1786) [= *E. complanata* s.l. in part]: NA2, NA3.
9. *E. congaraea* (Lea, 1831) [+ *E. waccamawensis* (Lea, 1863)]: NA3.
10. *E. dariensis* (Lea, 1842): NA3, NA4.
11. *E. downiei* (Lea, 1858): NA3.
12. *E. fisheriana* (Lea, 1838): NA3.
13. *E. folliculata* (Lea, 1838): NA3.
14. *E. fraterna* (Lea, 1852): NA3, NA4.
15. *E. fumata* (Lea, 1857) [= *E. complanata* s.l. in part]: NA4.
16. *E. hopetonensis* (Lea, 1838): NA3.
17. *E. icterina* (Conrad, 1834) [= *E. icterina* s.l. in part + *E. cylindracea* Frierson, 1927 + *E. errans* (Lea, 1856) + *E. hepatica* (Lea, 1859) + *E. raveneli* (Conrad, 1834)]: NA3.
18. *E. jayensis* (Lea, 1838) [+ *E. buckleyi* (Lea, 1841)]: NA4.
19. *E. lanceolata* (Lea, 1828): NA3, NA4.
20. *E. marsupiobesa* Fuller, 1972: NA3.
21. *E. mcmichaeli* Clench & Turner, 1956: NA4.
22. *E. monroensis* (Lea, 1843): NA4.

23. *E. nigella* (Lea, 1852): NA4.
24. *E. occulta* (Lea, 1843) [= *E. icterina* s.l. in part]: NA4.
25. *E. producta* (Conrad, 1836): NA3.
26. *E. pullata* (Lea, 1857) [= *E. icterina* s.l. in part]: NA4.
27. *E. purpurella* (Lea, 1857): NA4.
28. *E. roanokensis* (Lea, 1838) [+ *E. judithae* Clarke, 1986]: NA3.
29. *E. shepardiana* (Lea, 1834): NA3.
30. *E. spinosa* (Lea, 1836): NA3.

Elliptoideus Frierson, 1927: North America.

1. **E. sloatianus* (Lea, 1840): NA4.

Eurynia Rafinesque, 1820: North America.

1. **E. dilatata* (Rafinesque, 1820) [= *Elliptio dilatata*]: NA2.

Fusconaia Simpson, 1900: North America; [Burlakova et al. \(2012\)](#), [Campbell & Lydeard \(2012a, 2012b\)](#), [Inoue et al. \(2018\)](#), [Pieri et al. \(2018\)](#).

1. *F. flava* (Rafinesque, 1820) [+ *F. hebetata* (Conrad, 1854); syn. **Unio trigonus* Lea, 1831]: NA1, NA2, NA3 (i), NA4.
2. *F. burkei* (Walker in Ortmann & Walker, 1922) [= *Quincuncina burkei*]: NA4.
3. *F. cerina* (Conrad, 1838) [+ *F. rubidula* (Frierson, 1905)]: NA4.
4. *F. chumii* (Lea, 1862) [= *F. askewi* (Marsh, 1896) + *F. lananensis* (Frierson, 1901)]: NA4.
5. *F. cor* (Conrad, 1834): NA2.
6. *F. cuneolus* (Lea, 1840): NA2.
7. *F. escambia* Clench & Turner, 1956: NA4.
8. *F. masoni* (Conrad, 1834) [+ *Lexingtonia subplana* (Conrad, 1837) + *Lexingtonia utricula* (Lea, 1845)]: NA3.
9. *F. mitchelli* (Simpson in Dall, 1896) [= *Quincuncina mitchelli*]: NA4.
10. *F. ozarkensis* (Call, 1887): NA2.
11. *F. subrotunda* (Lea, 1831): NA2.

Hemistena Rafinesque, 1820: North America.

1. **H. lata* (Rafinesque, 1820): NA2.

Parvaspina Perkins, Johnson & Gangloff, 2017: North America; [Johnson & Clarke \(1983\)](#), [Perkins et al. \(2017\)](#).

1. **P. collina* (Conrad, 1837) [= *Pleurobema collina*]: NA3.
2. *P. steinstansana* (Johnson & Clarke, 1983) [= *Elliptio steinstansana*]: NA3.

Plethobasus Simpson, 1900: North America; [Campbell & Lydeard \(2012a\)](#).

1. *P. cyphus* (Rafinesque, 1820) [syn. **Unio aesopus* Green, 1827]: NA2.
2. *P. cicatricosus* (Say, 1829): NA2.
3. *P. cooperianus* (Lea, 1834): NA2.

Pleuronaia Frierson, 1927: North America; [Campbell & Lydeard \(2012a\)](#), [Perkins et al. \(2017\)](#), [Inoue et al. \(2018\)](#).

1. **P. barnesiana* (Lea, 1838) [= *Fusconaia barnesiana*]: NA2.
2. *P. dolabelloides* (Lea, 1840) [= *Lexingtonia dolabelloides*]: NA2.
3. *P. gibber* (Lea, 1838) [= *Pleurobema gibberum*]: NA2.

Tribe POPENAIADINI

Popenaias Frierson, 1927: North and Central America.

1. **P. popeii* (Lea, 1857): NA4, CA1.
2. *P. metallica* (Say, 1831): CA1.
3. *P. tehuantepecensis* (Crosse & Fischer, 1893): CA1.

Barynaias Crosse & Fischer, 1894: Central America.

1. **B. pigerrima* (Crosse & Fischer, 1893): CA1.
2. *B. caldwelii* (Lea, 1858): CA1.
3. *B. opacata* (Crosse & Fischer, 1893): CA1.
4. *B. plexus* (Conrad, 1838): CA1.
5. *B. sallei* (Crosse & Fischer, 1893): CA1.

Martensnaias Frierson, 1927: Central America.

1. **M. rubicunda* (Martens, 1900): CA1.

Micronaias Simpson, 1900: Central America.

1. **M. arata* (Lea, 1843): CA1.
2. *M. fallaciosa* (Simpson, 1914): CA1.
3. *M. granadensis* (Lea, 1868): CA1.

Nephritica Frierson, 1927: Central America.

1. **N. poeyana* (Lea, 1857): CA1.
2. *N. haricotti* (Frierson, 1927): CA1.

Nephronaias Crosse & Fischer, 1894: Central America.

1. **N. plicatula* (Küster, 1856): CA1.
2. *N. aeruginosa* (Morelet, 1849): CA1.
3. *N. aztecorum* (Philippi, 1847): CA1.
4. *N. calamitarum* (Morelet, 1849): CA1.
5. *N. championi* (Martens, 1900): CA1.
6. *N. copanensis* (Martens, 1900): CA1.
7. *N. dysonii* (Lea, 1859): CA1.
8. *N. goascoranensis* (Lea, 1858): CA1.
9. *N. gundlachi* (Dunker, 1858): CA1.
10. *N. hermanni* (Haas, 1929): CA1.
11. *N. hjalmarsoni* (Dunker, 1858): CA1.
12. *N. lempensis* Marshall, 1926: CA1.
13. *N. macnielii* (Lea, 1869): CA1.
14. *N. mellea* (Lea, 1859): CA1.
15. *N. oregonensis* (Lea, 1852): CA1.
16. *N. ravistella* (Morelet, 1849): CA1.
17. *N. rowellii* (Lea, 1859): CA1.
18. *N. rugulosa* (Küster, 1856): CA1.
19. *N. sajensis* (Frierson, 1927): CA1.
20. *N. scamnata* (Morelet, 1849): CA1.
21. *N. sphenorhyncha* (Crosse & Fischer, 1893): CA1.
22. *N. tabascoensis* (Küster, 1856): CA1.
23. *N. tempisquensis* Pilsbry, 1920: CA1.
24. *N. yzabalensis* (Crosse & Fischer, 1892): CA1.

Psoronaias Crosse & Fischer, 1894: Central America; Pfeiffer *et al.* (2019a).

1. *P. semigranosa* (von dem Busch in Philippi, 1843) [+ *P. crocodilorum* (Morelet, 1849) + *P. morini* (Morelet, 1851) + *Psorula rudis* (Simpson, 1900); syn. **Unio psoricus* Morelet, 1851]: CA1.
2. *P. distincta* (Crosse & Fischer, 1893): CA1.
3. *P. guatemalensis* (Simpson, 1900) [= *Psorula guatemalensis*]: CA1.
4. *P. herrenae* (Marshall, 1923): CA1.
5. *P. kuxensis* Frierson, 1917: CA1.
6. *P. martensi* Frierson, 1927: CA1.
7. *P. ostreata* (Morelet, 1849): CA1.
8. *P. percompressa* (Martens, 1887) [= *Psorula percompressa*]: CA1.
9. *P. profunda* (Simpson, 1914) [= *Psorula profunda*]: CA1.
10. *P. quadrata* (Simpson, 1914) [= *Psorula quadrata*]: CA1.
11. *P. salinarum* (Haas, 1929) [= *Psorula salinarum*]: CA1.
12. *P. usumasintae* (Crosse & Fischer, 1892) [= *Psorula usumasintae*]: CA1.

Reticulatus Frierson, 1927: Central America.

1. **R. reticulatus* (Simpson, 1900): CA1.
2. *R. elvae* (Walker, 1924): CA1.

Sphenonaias Crosse & Fischer, 1894: Central America.

1. **S. liebmanni* (Philippi, 1847): CA1.
2. *S. callosa* (Lea, 1841): CA1-Mp.
3. *S. colorata* (Küster, 1856): CA1.
4. *S. flucki* (Bartsch, 1906): CA1.
5. *S. mexicana* (Philippi, 1847): CA1.
6. *S. microdon* (Martens, 1887): CA1.

Tribe QUADRULINI**Quadrula Rafinesque, 1820:** North America; Lopes-Lima *et al.* (2019).

1. **Q. quadrula* (Rafinesque, 1820) [= *Q. quadrula s.l.* in part + *Q. apiculata* (Say, 1829) + *Q. rumphiana* (Lea, 1852)]: NA1, NA2, NA4.
2. *Q. couchiana* (Lea, 1860) [= *Amphinaias couchiana*]: NA4.
3. *Q. fragosa* (Conrad, 1836): NA2.

Cyclonaias Pilsbry in Ortmann & Walker, 1922: North America; Johnson *et al.* (2018), Lopes-Lima *et al.* (2019).

1. **C. tuberculata* (Rafinesque, 1820): NA2.
2. *C. infucata* (Conrad, 1834) [= *Quincuncina infucata s.l.* in part]: NA4.
3. *C. kieneriana* (Lea, 1852) [= *Amphinaias pustulosa s.l.* in part + *A. asperata* (Lea, 1861)]: NA4.
4. *C. kleimiana* (Lea, 1852) [= *Quincuncina infucata s.l.* in part]: NA4.
5. *C. necki* Burlakova, Karatayev, Lopes-Lima & Bogan in Burlakova *et al.*, 2018**: NA4.
6. *C. nodulata* (Rafinesque, 1820) [= *Amphinaias nodulata*]: NA2, NA4.
7. *C. petrina* (Gould, 1855) [= *Amphinaias petrina*]: NA4.
8. *C. pustulosa* (Lea, 1831) [= *Amphinaias pustulosa s.l.* in part + *A. archeri* (Frierson, 1905) + *A. aurea* (Lea, 1859) + *A. houstonensis* (Lea, 1859) + *A. refulgens* (Lea, 1868)]: NA2, NA4.
9. *C. succissa* (Lea, 1852) [= *Fusconaia succissa*]: NA4.

Megalonaias Utterback, 1915: North and Central America; Pfeiffer *et al.* (2018b).

1. *M. nervosa* (Rafinesque, 1820) [+ *M. boykiniana* (Lea, 1840); syn. **Unio heros* Say, 1829]: NA2, NA4.
2. *M. nickliniana* (Lea, 1834): CA1.

Theliderma Swainson, 1840: North America; Serb, Buhay & Lydeard (2003), Lopes-Lima *et al.* (2019).

1. **T. metanevra* (Rafinesque, 1820) [+ *T. tuberosa* (Lea, 1840)]: NA2, NA4.
2. *T. cylindrica* (Say, 1817): NA2.
3. *T. intermedia* (Conrad, 1836): NA2.
4. *T. johnsoni* Bogan & Lopes-Lima in Lopes-Lima & Bogan, 2019**: NA4.
5. *T. sparsa* (Lea, 1841): NA2.
6. *T. stapes* (Lea, 1831): NA4.

Tritogonia Agassiz, 1852: North America; Lopes-Lima *et al.* (2019).

1. **T. verrucosa* (Rafinesque, 1820): NA2, NA4.
2. *T. nobilis* (Conrad, 1854) [= *Quadrula quadrula s.l.* in part]: NA2, NA4.

Unio **Conrad, 1853**: North America; [Campbell & Lydeard \(2012a\)](#), [Lopes-Lima et al. \(2019\)](#).

1. **U. declivis* (Say, 1831): NA2, NA4.
2. *U. carolinianus* (Bosc, 1801) [= *U. caroliniana s.l.* in part]: NA3, NA4.
3. *U. columbensis* (Lea, 1857) [= *U. caroliniana s.l.* in part]: NA4.
4. *U. tetralasmus* (Say, 1831): NA2, NA4.

Subfamily GONIDEINAE

Tribe GONIDEINI

Gonidea **Conrad, 1857**: North America.

1. *G. angulata* (Lea, 1838) [syn. **Anodonta randalli* Trask, 1855]: NA5.

Koreosolenia **Lee, Kim, Lopes-Lima & Bogan in Lopes-Lima et al., 2020**: East Asia.

1. **K. sityensis* Lee, Kim, Lopes-Lima & Bogan, 2020**: AS2.

Leguminaia **Conrad, 1865**: North Eurasia.

1. *L. wheatleyi* (Lea, 1862) [syn. **Monocondyloea mardinensis* Lea, 1865]: EU2.
2. *L. saulcyi* (Bourguignat, 1852): EU2.

Microcondylaea **Vest, 1866**: North Eurasia.

1. **M. bonellii* (Férussac, 1827) [previously as by Rossmässler, 1835]: EU1.

Obovalis **Simpson, 1900**: East Asia.

1. *O. omiensis* (Heimburg, 1884) [= *Pseudodon (Obovalis) omiensis*; syn. **Pseudodon loomisii* Simpson, 1900]: AS3.

Parvasolenia **Huang & Wu in Huang et al., 2019**: East Asia; [Huang et al. \(2019\)](#).

1. **P. rivularis* (Heude, 1877) [= *Solenia iridinea s.l.* in part]: AS4.
2. *P. neotriangularis* (He & Zhuang, 2013)**: AS4.
3. *P. triangularis* (Heude, 1885) [= *Solenia triangularis*]: AS2, AS4.

Pseudodontopsis **Kobelt, 1913**: North Eurasia.

1. **P. euphratica* (Bourguignat, 1852): EU2.

Ptychorhynchus **Simpson, 1900**: East Asia.

1. **P. pfisteri* (Heude, 1874): AS4, AS5.
2. *P. denserugatum* (Haas, 1910) [= *Nodularia denserugata*]: AS5.
3. *P. murinum* (Heude, 1883): AS4.
4. *P. schoedei* (Haas, 1930) [= *Nodularia schoedei*]: AS5.
5. *P. schomburgianum* (Heude, 1885): AS4, AS5.

Solenia **Conrad, 1869**: East Asia.

1. **S. emarginata* (Lea, 1860): AS5.
2. *S. carinata* (Heude, 1877) [= *S. iridinea s.l.* in part]: AS4.
3. *S. iridinea* (Heude, 1874) [= *S. iridinea s.l.* in part]: AS4, AS5.
4. *S. khwaeniensis* Panha & Deekin in Deekin et al., 2004: AS5.

Tribe CHAMBERLAINIINI

Chamberlainia **Simpson, 1900**: East Asia.

1. **C. hainesiana* (Lea, 1856) [+ *C. paviei* (Morelet, 1891)]: AS5.

Caudiculatus **Simpson, 1900**: East Asia.

1. **C. caudiculatus* (Martens, 1867): AS6.

Sinohyriopsis **Starobogatov, 1970**: East Asia; [Lopes-Lima et al. \(2017a\)](#).

1. **S. cumingii* (Lea, 1852) [= *Hyriopsis cumingii s.l.* in part]: AS3 (i), AS4, AS5.

2. *S. goliath* (Rolle, 1904) [= *Hyriopsis cumingii s.l.* in part]: AS5.
3. *S. schlegelii* (Martens, 1861) [= *Hyriopsis schlegelii*]: AS3.

Tribe LAMPROTULINI

Lamprotula **Simpson, 1900**: East Asia; [Zhou et al. \(2007\)](#), [Pfeiffer & Graf \(2013\)](#).

1. **L. plumbea* (Dillwyn, 1817): AS5?
2. *L. bazini* (Heude, 1877): AS4, AS5.
3. *L. blaisei* (Dautzenberg & Fischer, 1905): AS5.
4. *L. caveata* (Heude, 1877): AS4, AS5.
5. *L. chiai* Chow, 1958**: AS4.
6. *L. cornuumlunae* (Heude, 1883) [= *L. cornuumlunae s.l.* in part]: AS4.
7. *L. divergens* (Benson in Cantor, 1842): AS4.
8. *L. elongata* Liu, Zhang & Wang, 1980: AS4.
9. *L. kouangensis* (Simpson, 1900): AS4.
10. *L. laeii* (Gray in Griffith & Pidgeon, 1833) [+ *L. gottschei* (von Martens, 1894)]: AS2, AS4, AS5.
11. *L. liniae* He & Zhuang, 2013**: AS4.
12. *L. microsticta* (Heude, 1877): AS4.
13. *L. paschalis* (Heude, 1883) [= *L. cornuumlunae s.l.* in part]: AS4.
14. *L. salaputium* (Martens, 1902): AS5.
15. *L. seonjinensis* (Kondo, Hyun & Seung-Ho, 2007)**: AS2.
16. *L. triclava* (Heude, 1877): AS4.

Discomya **Simpson, 1900**: East Asia.

1. **D. radulosa* (Drouet & Chaper, 1892): AS6.

Inversidens **Haas, 1911**: East Asia.

1. **I. brandtii* (Kobelt, 1879): AS3.
2. *I. pantoensis* (Neumayr, 1899): AS2, AS4.

Potomida **Swainson, 1840**: North Eurasia; [Froufe et al. \(2016b\)](#).

1. *P. littoralis* (Cuvier, 1798) [= *P. littoralis s.l.* in part; syn. **Mysca corrugata* Swainson, 1840]: EU1.
2. *P. acarnanica* (Kobelt, 1879) [= *P. littoralis s.l.* in part]: EU1.
3. *P. semirugata* (Lamarck, 1819) [= *P. littoralis s.l.* in part]: EU2.

Pronodularia **Starobogatov, 1970**: East Asia; [Kondo et al. \(2007\)](#).

1. **P. japonensis* (Lea, 1859) [= *Inversidens japonensis*]: AS3.

Schepmania **Haas, 1910**: East Asia.

1. **S. nieuwenhuisi* (Schepman, 1898): AS6.
2. *S. parcesculpta* (Martens, 1903): AS6.

Tribe PSEUDODONTINI

Subtribe PSEUDODONTINA

Pseudodon **Gould, 1844**: East Asia; [Bolotov et al. \(2017b, 2020b\)](#).

1. **P. inoscularis* (Gould, 1844) [= *P. (Pseudodon) inoscularis* in part]: AS5, AS7.
2. *P. aureus* Heude, 1885 [= *P. (Chrysopseudodon) aureus*]: AS4.
3. *P. avae* (Theobald, 1873) [= *P. (Indopseudodon) avae*]: AS7.
4. *P. bogani* Bolotov, Kondakov & Konopleva in Bolotov et al., 2017**: AS7.
5. *P. crebristriatus* (Anthony, 1865) [= *P. (Pseudodon) crebristriata*]: AS7.
6. *P. kayimensis* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020**: AS7.
7. *P. manueli* Konopleva, Kondakov & Vikrev in Bolotov et al., 2017**: AS7.

8. *P. nankingensis* (Heude, 1874) [= *P. (Nasus) nankingensis*]: AS4.
9. *P. peguensis* (Anthony, 1865) [= *P. (Pseudodon) peguensis*]: AS7.
10. *P. pinchonianus* (Heude, 1883) [+ *P. (Pseudodon) solidus* Haas, 1911]: AS4.
11. *P. resupinatus* Martens, 1902 [= *P. (Cosmopseudodon) resupinatus*]: AS5.
12. *P. salweenianus* (Gould, 1844) [= *P. (Indopseudodon) salweeniana*]: AS7.
13. *P. secundus* Heude, 1877 [= *P. (Nasus) secundus*]: AS4.

Subtribe PILSBRYOCONCHINA

Pilsbryoconcha Simpson, 1900: East Asia; Bolotov *et al.* (2020b).

1. **P. exilis* (Lea, 1838): AS5 AS6.
2. *P. carinifera* (Conrad, 1837): AS5 AS6.
3. *P. compressa* (Martens, 1860): AS5.
4. *P. expressa* (Martens, 1900): AS6.
5. *P. lemeslei* (Morelet, 1875): AS5.

Bineurus Simpson, 1900: East Asia; Bolotov *et al.* (2017b, 2020b).

1. **B. mouhotii* (Lea, 1863) [= *Pseudodon (Bineurus) mouhotii s.l.* in part]: AS5.
2. *B. exilis* (Morelet, 1866) [= *Pseudodon (Bineurus) mouhotii s.l.* in part]: AS5.

Monodontina Conrad, 1853: East Asia; Bolotov *et al.* (2017b, 2020b).

1. **M. vondembuschiana* (Lea, 1840) [= *Pseudodon (Monodontina) vondembuschianus* + *Pseudodon (Bineurus) hageni* (Strubell, 1897)]: AS5, AS6.
2. *M. aeneola* (Drouet & Chaper, 1892) [= *Pseudodon (Cosmopseudodon) aeneolus*]: AS6.
3. *M. cambodjensis* (Petit, 1865) [= *Pseudodon (Monodontina) cambodjensis*]: AS5.
4. *M. laosica* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS5.
5. *M. lenyanensis* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS7.
6. *M. mekongi* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS5.
7. *M. walpolei* (Hanley, 1871) [+ *Pseudodon (Diplopseudodon) crassus* (Drouët & Chaper, 1892)]: AS6.

Nyeinchanconcha Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020: East Asia.

1. **N. nyeinchani* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS5.

Sundadontina Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020: East Asia.

1. **S. cumingii* (Lea, 1851) [= *Pseudodon (Pseudodon) cumingii s.l.* in part + *Pseudodon (Monodontina) chaperi* (Morgan, 1885)]: AS5.

2. *S. brandti* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS5.
3. *S. harmandi* (Crosse & Fischer, 1876) [= *Pseudodon (Pseudodon) inoscularis s.l.* in part]: AS5.
4. *S. mabilli* (Rochebrune, 1882) [= *Pseudodon (Bineurus) mouhotii s.l.* in part]: AS5.
5. *S. moreleti* (Crosse & Fischer, 1876) [= *Pseudodon (Monodontina) tumidus s.l.* in part]: AS5.
6. *S. ponderosa* (Preston, 1909) [= *Pseudodon (Monodontina) ellipticus s.l.* in part]: AS5.
7. *S. sulcata* (Rochebrune, 1882) [= *Pseudodon (Pseudodon) cumingii s.l.* in part]: AS5.
8. *S. tanintharyiensis* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS7.
9. *S. taskaevi* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS5.
10. *S. tumida* (Morelet, 1866) [= *Pseudodon (Monodontina) tumidus s.l.* in part]: AS5.

Thaiconcha Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020: East Asia.

1. **T. callifera* (Martens, 1860) [= *Pseudodon (Bineurus) thomsoni* Morelet (*sic*), 1884 + *Pseudodon (Monodontina) ellipticus s.l.* in part + *Pseudodon (Pseudodon) inoscularis s.l.* in part]: AS5.
2. *T. ovalis* (Morlet, 1889) [= *Pseudodon (Monodontina) ellipticus s.l.* in part]: AS5.

Subfamily MODELINAIIINAE

Modellinaia Brandt, 1974: East Asia.

1. **M. siamensis* Brandt, 1974: AS5.

Subfamily PARREYSIINAE

Tribe PARREYSIINI

Parreysia Conrad, 1853: East Asia.

1. *P. corrugata* (Müller, 1774) [= *P. (Parreysia) corrugata*; syn. **Unio multidentatus* Philippi, 1847]: AS7.
2. *P. annandalei* Preston, 1912 [= *P. (Parreysia) annandalei*]: AS7.
3. *P. corbis* (Hanley, 1856) [= *P. (Parreysia) corbis*]: AS7.
4. *P. cylindrica* Annandale & Prashad, 1919 [= *P. (Parreysia) cylindrica*]: AS7.
5. *P. favidens* (Benson, 1862) [= *P. (Parreysia) favidens s.l.* in part]: AS7.
6. *P. govhattensis* (Theobald, 1873) [= *P. (Parreysia) govhattensis*]: AS7.
7. *P. rajahensis* (Lea, 1841) [= *P. (Parreysia) rajahensis*]: AS7.
8. *P. rakhinensis* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020*: AS7.
9. *P. rugosa* (Gmelin, 1791) [= *P. (Parreysia) rugosa*]: AS7.
10. *P. sikkimensis* (Lea, 1859) [= *P. (Parreysia) sikkimensis*]: AS7.
11. *P. smaragdites* (Benson, 1862) [= *P. (Parreysia) smaragdites*]: AS7.
12. *P. triembola* (Benson, 1862) [= *P. (Parreysia) triembola*]: AS7.
13. *P. viridula* (Benson, 1862) [= *P. (Parreysia) favidens s.l.* in part]: AS7.

Tribe COELATURINI

Coelatura Conrad, 1853: Afrotropics; Scholz & Glaubrecht (2004), Graf *et al.* (2014), Ortiz-Sepulveda *et al.* (2020).

1. **C. aegyptiaca* (Cailliaud, 1827) [+ *C. cariei* (Germain, 1919)]: AF1, AF2.
2. *C. alluaudi* (Dautzenberg, 1908): AF1.
3. *C. bakeri* (H. Adams, 1866): AF1.
4. *C. briarti* (Dautzenberg, 1901): AF3.
5. *C. choziensis* (Preston, 1910): AF3.
6. *C. cridlandi* Mandahl-Barth, 1954: AF1.
7. *C. disciformis* (Rochebrune, 1886) [= *C. rotula* Pilsbry & Bequaert, 1927]: AF3.
8. *C. essoensis* (Chaper, 1885): AF2.
9. *C. gabonensis* (Küster, 1862) [= *C. gabonensis s.l.* in part]: AF3.
10. *C. hauttecoeri* (Bourguignat, 1883): AF1.
11. *C. horei* (E.A. Smith, 1880): AF3.
12. *C. hypsiprymna* (Martens, 1897): AF4.
13. *C. kipopoensis* Mandahl-Barth, 1968: AF3.
14. *C. kunenensis* (Mousson, 1887): AF4.
15. *C. leopoldvillensis* (Putzeys, 1898): AF3.
16. *C. lobensis* (Frierson, 1913): AF3.
17. *C. luapulaensis* (Preston, 1913): AF3.
18. *C. mesafricana* Pilsbry & Bequaert, 1927 [= *C. gabonensis s.l.* in part]: AF3.
19. *C. mossambicensis* (Martens, 1860): AF4, AF5.
20. *C. ratidota* (Charmes, 1885): AF5.
21. *C. rothschildi* (Neuvill & Anthony, 1906): AF1. Extinct.
22. *C. stagnorum* (Dautzenberg, 1890): AF3.
23. *C. stanleyvillensis* Pilsbry & Bequaert, 1927 [= *C. gabonensis s.l.* in part]: AF3.
24. *C. stuhlmanni* (Martens, 1897): AF1.

Brazzaea Bourguignat, 1886: Afrotropics; Pain & Woodward (1968).

1. **B. anceyi* Bourguignat, 1886: AF3.

Grandidieria Bourguignat, 1885: Afrotropics; Ortiz-Sepulveda *et al.* (2020).

1. **G. burtoni* (Woodward, 1859): AF3.

Moncetia Bourguignat, 1886: Afrotropics; Ortiz-Sepulveda *et al.* (2020).

1. **M. anceyi* Bourguignat, 1886: AF3.

Nitia Pallary, 1924: Afrotropics; Ortiz-Sepulveda *et al.* (2020).

1. **N. teretiuscula* (Philippi, 1847): AF1, AF2.
2. *N. acuminata* (H. Adams, 1866): AF1.
3. *N. chefnexi* (Neuvill & Anthony, 1906): AF1.
4. *N. monceti* (Bourguignat, 1883): AF1.
5. *N. mutelaeformis* (Germain, 1906): AF2.

Nyassunio Haas, 1936: Afrotropics; Scholz & Glaubrecht (2004), Ortiz-Sepulveda *et al.* (2020).

1. **N. nyassaensis* (Lea, 1864): AF4.
2. *N. ujjiensis* (Crosse, 1881): AF3.

Prisodontopsis Tomlin, 1928: Afrotropics; Pain & Woodward (1968), F.R. Woodward (1991), Graf *et al.* (2014), Ortiz-Sepulveda *et al.* (2020).

1. *P. aviculaeformis* F.R. Woodward, 1991 [syn. **Unio johnstoni* E.A. Smith, 1893]: AF3.
2. *P. mweruensis* (E.A. Smith, 1908) [= *Mweruella mweruensis*]: AF3.

Pseudospatha Simpson, 1900: Afrotropics; Pain & Woodward (1968), Ortiz-Sepulveda *et al.* (2020).

1. **P. tanganyicensis* (E.A. Smith, 1880): AF3.

Tribe INDOCHINELLINI

Indochinella Bolotov, Pfeiffer, Vikhrev & Konopleva in Bolotov *et al.*, 2018: East Asia. Bolotov *et al.* (2018), Pfeiffer *et al.* (2018a).

1. **I. pugio* (Benson, 1862) [= *Oxynaia pugio*]: AS7.

Harmandia Rochebrune, 1882: East Asia; Pfeiffer *et al.* (2018a).

1. **H. somborensis* Rochebrune, 1882: AS5.

Indonaiia Prashad, 1918: East Asia; Bolotov *et al.* (2018), Konopleva *et al.* (2019b).

1. **I. caerulea* (Lea, 1831) [= *Parreysia (Radiatula) caerulea*]: AS7.
2. *I. andersontana* (Nevill, 1877) [= *Parreysia (Radiatula) andersontana*]: AS7.
3. *I. involuta* (Hanley, 1856) [= *Parreysia (Radiatula) involuta*]: AS7.
4. *I. khadakvaslaensis* Ray, 1966 [= *Parreysia (Radiatula) khadakvaslaensis*]: AS7.
5. *I. lima* (Simpson, 1900) [= *Parreysia (Radiatula) lima*]: AS7.
6. *I. nuttalliana* (Lea, 1856) [= *Parreysia (Radiatula) nuttalliana*]: AS7.
7. *I. occata* (Lea, 1860) [= *Parreysia (Radiatula) occata*]: AS7.
8. *I. olivaria* (Lea, 1831) [= *Parreysia (Radiatula) olivaria*]: AS7.
9. *I. pachysoma* (Benson, 1862) [= *Parreysia (Radiatula) pachysoma*]: AS7.
10. *I. rectangularis* (Tapparone Canefri, 1889)**: AS7.
11. *I. shurtleffiana* (Lea, 1856) [= *Parreysia (Radiatula) shurtleffiana*]: AS7.
12. *I. subclathrata* (Martens, 1899) [= *Trapezoideus exolescens s.l.* in part]: AS7.
13. *I. substriata* (Lea, 1856) [+ *Parreysia pecten* (Preston, 1912)]: AS5.
14. *I. theobaldi* (Preston, 1912) [= *Parreysia (Radiatula) theobaldi*]: AS7.

Radiatula Simpson, 1900: East Asia; Bolotov *et al.* (2017b), Jeratthitukul, Sucharit & Prasankok (2019b).

1. **R. crispisulcata* (Benson, 1862) [= *Parreysia (Radiatula) crispisulcata*]: AS7.
2. *R. bonneaudii* (Eydoux, 1838) [= *Parreysia (Radiatula) bonneaudii*]: AS7.
3. *R. chauthurii* (Preston, 1912) [= *Parreysia (Radiatula) chauthurii*]: AS7.
4. *R. chindwinensis* Bolotov, Konopleva, Vikrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Konkodakov, 2019**: AS7.
5. *R. mouhoti* Vikhrev, Bolotov & Konopleva in Bolotov *et al.*, 2017**: AS7.
6. *R. myitkyinae* (Prashad, 1930) [= *Parreysia (Parreysia) burmana s.l.* in part]: AS7.

7. *R. myithanensis* Bolotov, Konopleva, Vikrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019**: AS7.

Scabiellus Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020: East Asia.

1. **S. songkramensis* (Kongim & Panha in Kongim *et al.*, 2015)**: AS5.

Scabies Haas, 1911: East Asia; Pfeiffer *et al.* (2018a), Jeraththitikul *et al.* (2019b), Bolotov *et al.* (2020b).

- *S. scobinatus* (Lea, 1856) [= *S. crispata* s.l. in part]: AS5.
- S. anceps* (Deshayes in Deshayes & Jullien, 1876) [= *Contradens graciosus* s.l. in part]: AS5.
- S. crispata* (Gould, 1843) [= *S. crispata* s.l. in part + *S. chinensis* Liu, Duan & Lai, 1991 + *S. longata* Liu, Duan & Lai, 1991]: AS5, AS7.
- S. humilis* (Lea, 1856) [= *Parreysia (Radiatula) humilis*]: AS5.
- S. mandarinus* (Morelet, 1864) [= *S. crispata* s.l. in part]: AS5.
- S. nucleus* (Lea, 1856): AS5.
- S. phaseus* (Lea, 1856): AS5.
- S. pilata* (Lea, 1866) [= *Parreysia (Radiatula) pilata*]: AS5.

Unionetta Haas, 1955: East Asia; Pfeiffer *et al.* (2018a).

1. **U. fabagina* (Deshayes in Deshayes & Jullien, 1876) [+ *U. broti* (DeShayes & Jullien, 1874)]: AS5.

Tribe LAMELLIDENTINI

Lamellidens Simpson, 1900: East Asia.

- *L. marginalis* (Lamarck, 1819) [= *L. marginalis* s.l. in part]: AS7.
- L. brandti* Bolotov, Konopleva & Vikhrev in Bolotov *et al.*, 2017**: AS7.
- L. consobrinus* (Lea, 1860): AS7.
- L. corrianus* (Lea, 1834) [= *L. corrianus* s.l. in part]: AS7.
- L. ferrugineus* (Annandale, 1918) [= *Physumio ferrugineus*]: AS7.
- L. generosus* (Gould, 1847) [= *L. generosus* s.l. in part + *Physumio micropteroides* Annandale, 1918]: AS7.
- L. jenkinsianus* (Benson, 1862): AS7.
- L. lamellatus* (Lea, 1838): AS7.
- L. mainwaringi* Preston, 1912 [= *L. corrianus* s.l. in part]: AS7.
- L. narainporensis* Preston, 1912: AS7.
- L. phenchooganjensis* Preston, 1912: AS7.
- L. rhadinaeus* Annandale & Prashad, 1921 [= *L. marginalis* s.l. in part]: AS7.
- L. savadiensis* (Nevill, 1877) [= *L. indawgyiensis* Prashad, 1930]: AS7.
- L. theca* (Benson, 1862) [= *Trapezoideus theca*]: AS7.
- L. unioides* Nesemann & Sharma in Nesemann *et al.*, 2007**: AS7.

Arcidopsis Simpson, 1900: East Asia; Konopleva *et al.* (2019b).

1. **A. footei* (Theobald, 1876) [+ *Trapezoideus prashadi* Haas, 1922]: AS7.

Trapezidens Bolotov, Vikhrev & Konopleva in Bolotov *et al.*, 2017: East Asia; Bolotov *et al.* (2017b), Konopleva *et al.* (2020).

1. **T. exolecens* (Gould, 1843) [= *Trapezoideus exolecens* s.l. in part]: AS7.

- T. angustior* (Hanley & Theobald, 1876) [= *Lamellidens generosus* s.l. in part]: AS7.
- T. dolichorhynchus* (Tapparone Canefri, 1889) [= *Lamellidens corrianus* s.l. in part]: AS7.
- T. scutum* (Sowerby, 1868) [= *Lamellidens scutum*]: AS7.
- T. yeti* Konopleva, Bolotov, Kondakov, Kononov, Gofarov, Tomilova, Lunn, Chan, Win & Vikhrev, 2020**: AS7.

Tribe LEOPARREYSIINI

Leoparreysia Vikhrev, Bolotov & Aksenova in Bolotov *et al.*, 2017: East Asia; Bolotov *et al.* (2017b).

- *L. canefrii* Vikhrev, Bolotov & Kondakov in Bolotov *et al.*, 2017**: AS7.
- L. bhomoensis* (Theobald, 1873) [+ *Parreysia (Parreysia) mandalayensis* (Theobald, 1874)]: AS7.
- L. burmana* (Blanford, 1869) [= *Parreysia (Parreysia) burmana* s.l. in part]: AS7.
- L. choprae* (Prashad, 1930) [= *Parreysia (Parreysia) choprae*]: AS7.
- L. feae* (Tapparone Canefri, 1889) [= *Parreysia (Parreysia) feae*]: AS7.
- L. feddeni* (Theobald, 1873) [= *Parreysia (Parreysia) feddeni*]: AS7.
- L. hougdarauica* (Tapparone Canefri, 1889) [= *Parreysia (Parreysia) hougdarauica* (sic)]: AS7.
- L. olivacea* (Prashad, 1930) [= *Parreysia (Parreysia) olivacea*]: AS7.
- L. perconvexa* (Preston, 1912) [= *Parreysia (Parreysia) perconvexa*]: AS7.
- L. tavoyensis* (Gould, 1843) [= *Parreysia (Parreysia) tavoyensis*]: AS7.
- L. vulcanus* (Hanley, 1876) [= *Parreysia (Parreysia) burmana* s.l. in part]: AS7.
- L. whitteni* Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019**: AS7.

Subfamily RECTIDENTINAE

Tribe RECTIDENTINI

Rectidens Simpson, 1900: East Asia.

- R. lingulatus* (Drouet & Chaper, 1892) [syn. **Unio prolongatus* Drouët, 1894]: AS6.
- R. sumatrensis* (Dunker, 1852): AS5, AS6.

Ctenodesma Simpson, 1900: East Asia.

- *C. borneensis* (Issel, 1874): AS6.
- C. scheibeneri* Haas, 1927: AS6.

Elongaria Haas, 1911: East Asia.

- *E. orientalis* (Lea, 1840): AS6.
- E. trompi* (Drouet & Chaper, 1892): AS6.

Ensidents Frierson, 1911: East Asia; Muanta *et al.* (2019), Konopleva *et al.* (2019a), Bolotov *et al.* (2020b).

- *E. ingallsianus* (Lea, 1852) [= *E. ingallsianus* s.l. in part]: AS5.
- E. pazü* (Lea, 1862) [= *E. ingallsianus* s.l. in part]: AS5.
- E. sagittarius* (Lea, 1856): AS5.

Hyriopsis Conrad, 1853: East Asia; Konopleva *et al.* (2019a), Bolotov *et al.* (2020b).

- H. bialata* Simpson, 1900 [= *H. bialata* s.l. in part; syn. **Unio delphinus* Gruner, 1841 non Spengler, 1793]: AS5.
- H. delaportei* (Crosse & Fischer, 1876): AS5.

3. *H. desowitzi* Brandt, 1974: AS5.
4. *H. gracilis* Haas, 1910 [= *H. bialata s.l.* in part]: AS5.
5. *H. myersiana* (Lea, 1856): AS5.
6. *H. velthuizeni* (Schepman, 1896): AS6.

Prohyriopsis Haas, 1914: East Asia.

1. **P. stolata* (Martens, 1900): AS6.

Tribe CONTRADENTINI**Contradens Haas, 1911:** East Asia; [Konopleva et al. \(2019a, b\)](#), [Jeratthitukul et al. \(2019a\)](#).

1. **C. contradens* (Lea, 1838) [= *C. contradens s.l.* in part]: AS5, AS6.
2. *C. comptus* (Deshayes in Deshayes & Jullien, 1876) [= *Trapezoideus exolegens s.l.* in part + *Harmandia munensis* Brandt, 1974]: AS5.
3. *C. crossi* (Deshayes in Deshayes & Jullien, 1876) [= *C. contradens s.l.* in part]: AS5.
4. *C. eximius* (Lea, 1856) [= *Physunio eximius*]: AS5.
5. *C. fultoni* Haas, 1930 [= *C. semmelinki s.l.* in part]: AS5.
6. *C. fulvaster* (Drouet & Chaper, 1892): AS6.
7. *C. gratusus* (Philippi, 1843) [= *C. gratusus s.l.* in part]: AS5.
8. *C. inaequalis* (Rochebrune, 1882): AS5.
9. *C. misellus* (Morelet, 1865) [= *Trapezoideus exolegens s.l.* in part]: AS5.
10. *C. novoselovi* Konopleva, Bolotov, Spitsyn, Kondakov, Gofarov & Vikhrev, 2019**: AS5.
11. *C. pallegoixi* (Sowerby, 1867) [= *Trapezoideus exolegens s.l.* in part]: AS5.
12. *C. peninsularis* (Simpson, 1900) [= *Trapezoideus peninsularius (sic)*]: AS6.
13. *C. rolfbrandti* Jeratthitukul & Panha in Jeratthitukul et al., 2019**: AS5.
14. *C. semmelinki* (Martens, 1891) [= *C. semmelinki s.l.* in part]: AS6.
15. *C. subcircularis* (Brandt, 1974): AS5.

Balwantia Prashad, 1919: East Asia; [Bolotov et al. \(2020b\)](#).

1. **B. soleniformis* (Benson, 1836) [= *Solenaia soleniformis*]: AS7.
2. *B. baniensis* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020**: AS7.
3. *B. elongatula* (Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019)**: AS7.

Physunio Simpson, 1900: East Asia; [Konopleva et al. \(2019b\)](#).

1. *P. superbus* (Lea, 1843) [syn. **Unio gravidus* Lea, 1856]: AS5, AS6.
2. *P. cambodiensis* (Lea, 1856): AS5.
3. *P. friersoni* Simpson, 1914: AS7.
4. *P. inornatus* (Lea, 1856): AS5.
5. *P. micropterus* (Morelet, 1866) [+ *P. semialatus* (DeShayes & Jullien, 1874)]: AS5.
6. *P. modelli* Brandt, 1974: AS5.

Pressidens Haas, 1910: East Asia.

1. **P. moellendorffi* Haas, 1910: AS6.
2. *P. exanthematicus* (Küster, 1861): AS6.
3. *P. insularis* (Drouet, 1894): AS6.

Trapezoideus Simpson, 1900: East Asia; [Bolotov et al. \(2017b, 2020b\)](#).

1. **T. foliaceus* (Gould, 1843) [= *T. exolegens s.l.* in part]: AS5.
2. *T. lenya* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020**: AS7.

Yaukthwa Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019: East Asia; [Konopleva et al. \(2019a, b\)](#), [Bolotov et al. \(2020b\)](#).

1. **Y. nesemanni* (Konopleva, Vikhrev & Bolotov in Bolotov et al., 2017)**: AS7.
2. *Y. avansensis* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020**: AS7.
3. *Y. dalliana* (Frierson, 1913) [= *Trapezoideus exolegens s.l.* in part]: AS7.
4. *Y. inlenensis* Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019**: AS7.
5. *Y. paiensis* Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019**: AS7.
6. *Y. panhai* (Konopleva, Bolotov & Kondakov in Bolotov et al., 2017)**: AS7.
7. *Y. peguensis* (Anthony, 1865) [= *Trapezoideus exolegens s.l.* in part]: AS7.
8. *Y. zayleymanensis* (Preston, 1912) [= *Trapezoideus exolegens s.l.* in part]: AS7.

Family MARGARITIFERIDAE
Subfamily MARGARITIFERINAE**Margaritifera Schumacher, 1816:** East Asia, North America and North Eurasia; [Ziuganov et al. \(1994\)](#), [D.G. Smith \(2001\)](#), [Araujo et al. \(2016\)](#), [Lopes-Lima et al. \(2018a\)](#).

1. **M. margaritifera* (Linnaeus, 1758): NA3, EU1.
2. *M. dahurica* (Middendorff, 1850): AS2.
3. *M. falcata* (Gould, 1850): NA2, NA5.
4. *M. hembeli* (Conrad, 1838): NA4.
5. *M. laevis* (Haas, 1910): AS3.
6. *M. marrianae* R.I. Johnson, 1983: NA4.
7. *M. middendorffi* (Rosén, 1926) [+ *M. togakushiensis* Kondo & Kobayashi, 2005]: AS1, AS3.

Cumberlandia Ortmann, 1912: North America; [D.G. Smith \(2001\)](#), [Araujo et al. \(2016\)](#), [Lopes-Lima et al. \(2018a\)](#).

1. **C. monodonta* (Say, 1829) [= *Margaritifera monodonta*]: NA2.

Pseudunio Haas, 1910: North Eurasia; [D.G. Smith \(2001\)](#), [Araujo et al. \(2016\)](#), [Lopes-Lima et al. \(2018a\)](#).

1. *P. auricularius* (Spengler, 1793) [= *Margaritifera auricularia s.l.* in part; syn. **Unio sinuata* Lamarck, 1819]: EU1.
2. *P. homsensis* (Lea, 1865) [= *Margaritifera homsensis*]: EU2.
3. *P. marocanus* (Pallary, 1918) [= *Margaritifera auricularia s.l.* in part]: EU1.

Subfamily GIBBOSULINAE**Gibbosula Simpson, 1900:** East Asia; [Huang et al. \(2018\)](#), [Lopes-Lima et al. \(2018a\)](#).

1. **G. crassa* (Wood, 1815) [= *Lamprotula crassa* + *Lamprotula mansuyi* (Dautzenberg & Fischer, 1908)]: AS5.
2. *G. confragosa* Frierson, 1928 [= *Lamprotula confragosa*]: AS4.

3. *G. laosensis* (Lea, 1863) [= *Margaritifera laosensis*]: AS5.
4. *G. nanmingensis* Qian, Fang & He, 2015***: AS5.
5. *G. polysticta* (Heude, 1877) [+ *Lamprotula similaris* (Simpson, 1900)]: AS4.
6. *G. rochechouartii* (Heude, 1875) [= *Lamprotula rochechouartii*]: AS4.

Superfamily HYRIOIDEA
Family HYRIIDAE
Subfamily HYRIINAE
***incertae sedis* Hyriinae**

- Echyridella* McMichael & Hiscock, 1958:** Australasia; Fenwick & Marshall (2006), Marshall *et al.* (2014).
1. **E. menziesii* (Gray, 1843) [+ *E. lucasi* (Suter, 1905)]: AU4.
 2. *E. aucklandica* (Gray, 1843) [+ *Cucumerunio websteri* (Simpson, 1902)]: AU4.
 3. *E. onekaka* Fenwick & Marshall, 2006: AU4.

Tribe HYRIINI

- Triplodon* Spix in Wagner, 1827:** South America; Mansur & Pimpão (2008).
1. *T. corrugatus* (Lamarck, 1819) [= *Prisodon* (*Triplodon*) *corrugatus*; syn. **Unio rugosus* Spix in Wagner, 1827]: SA2, SA3.
 2. *T. chodo* Mansur & Pimpão, 2008***: SA3.

***Prisodon* Schumacher, 1817:** South America.

1. **P. obliquus* Schumacher, 1817 [= *P. (Prisodon) obliquus*]: SA2, SA3.
2. *P. syrmatophorus* (Gmelin, 1791) [= *P. (Paxyodon) syrmatophorus*]: SA2, SA3.

Tribe CASTALIINI

***Castalia* Lamarck, 1819:** South America; Bonetto (1965).

1. **C. ambigua* Lamarck, 1819 [= *C. ambigua s.l.* in part]: SA2, SA3, SA5.
2. *C. cordata* Swainson, 1840 [= *C. multisulcata s.l.* in part]: SA2.
3. *C. crosseana* Hidalgo, 1865 [= *C. ambigua s.l.* in part]: SA3.
4. *C. ecarinata* Mousson, 1869 [= *C. multisulcata s.l.* in part]: SA1.
5. *C. inflata* d'Orbigny, 1835: SA5.
6. *C. martensi* (Ihering, 1891): SA5.
7. *C. multisulcata* Hupé, 1857 [= *C. multisulcata s.l.* in part]: SA5 (Mp).
8. *C. nehringi* (Ihering, 1891): SA5.
9. *C. orbignyvi* (Deville & Hupé, 1850) [= *Castaliella sulcata s.l.* in part]: SA3.
10. *C. orinocensis* Morrison, 1943: SA2.
11. *C. psammoica* (d'Orbigny, 1835): SA5.
12. *C. stevensi* (H.B. Baker, 1930) [= *C. multisulcata s.l.* in part]: SA2.
13. *C. undosa* Martens, 1885: SA5.

***Callonaia* Simpson, 1900:** South America.

1. **C. duprei* (Récluz, 1842): SA3.

***Castaliella* Simpson, 1900:** South America; Bonetto (1965).

1. **C. sulcata* (Krauss, 1848) [= *C. sulcata s.l.* in part]: SA2.
2. *C. quadrata* (Sowerby, 1869) [= *C. sulcata s.l.* in part]: SA2.
3. *C. schombergiana* (Sowerby, 1869) [= *C. sulcata s.l.* in part]: SA2.

Tribe HYRIDELLINI

***Hyridella* Swainson, 1840:** Australasia.

1. **H. australis* (Lamarck, 1819) [= *H. (Hyridella) australis*]: AU1.
2. *H. depressa* (Lamarck, 1819) [= *H. (Hyridella) depressa*]: AU1.
3. *H. drapeta* (Iredale, 1934) [= *H. (Hyridella) drapeta*]: AU1.
4. *H. glenelgensis* (Dennant, 1898) [= *H. (Protohyridella) glenelgensis*]: AU1.
5. *H. guppyi* (E.A. Smith, 1885) [= *H. (Nesonaia) guppyi*]: AU3.
6. *H. misoolensis* (Schepman, 1897) [= *H. (Hyridella) misoolensis*]: AU3.
7. *H. narracanensis* (Cotton & Gabriel, 1932) [= *H. (Hyridella) narracanensis*]: AU1.

***Cucumerunio* Iredale, 1934:** Australasia.

1. **C. novaehollandiae* (Gray, 1834): AU1.

***Virgus* Simpson, 1900:** Australasia.

1. **V. beccarianus* (Tapparone Canefri, 1883): AU3.

Tribe RHIPIDODONTINI

***Diplodon* Spix in Wagner, 1827:** South America; Parodiz (1968).

1. **D. ellipticus* Spix in Wagner, 1827 [+ *D. besckeanus* (Dunker, 1849)]: SA4, SA5.
2. *D. aethiops* (Lea, 1860) [= *Rhipidodonta charruana s.l.* in part]: SA5.
3. *D. berthae* Ortmann, 1921 [= *Rhipidodonta charruana s.l.* in part]: SA5.
4. *D. burroughianus* (Lea, 1834) [= *Rhipidodonta burroughiana s.l.* in part]: SA5.
5. *D. caipira* (Ihering, 1893) [= *D. expansus s.l.* in part]: SA5.
6. *D. charruanus* (d'Orbigny, 1835) [= *Rhipidodonta charruana s.l.* in part]: SA5.
7. *D. chilensis* (Gray, 1828) [+ *D. patagonicus* (d'Orbigny, 1835)]: SA6.
8. *D. delodontus* (Lamarck, 1819): SA5.
9. *D. fontainianus* (d'Orbigny, 1835): SA4, SA5.
10. *D. funebris* (Lea, 1860) [= *Rhipidodonta funebris*]: SA5.
11. *D. garbei* (Ihering, 1910) [= *Rhipidodonta suavidica s.l.* in part]: SA4.
12. *D. granosus* (Bruguière, 1792): SA2.
13. *D. gratus* (Lea, 1860) [= *Rhipidodonta grata*]: SA5.
14. *D. greeffeanus* (Ihering, 1893) [= *D. expansus s.l.* in part]: SA5.
15. *D. guaporensis* Bonetto & Tassara, 1987: SA3.
16. *D. guaranianus* (d'Orbigny, 1835) [= *Rhipidodonta hylaea s.l.* in part]: SA3, SA5.
17. *D. hildae* Ortmann, 1921 [= *Rhipidodonta charruana s.l.* in part]: SA5.
18. *D. hylaeus* (d'Orbigny, 1835) [= *Rhipidodonta hylaea s.l.* in part]: SA3 SA5.
19. *D. iheringi* Simpson, 1914 [= *Rhipidodonta burroughiana s.l.* in part]: SA5.
20. *D. imitator* Ortmann, 1921 [= *Rhipidodonta charruana s.l.* in part]: SA5.
21. *D. koseritzi* (Clessin, 1888) [= *Rhipidodonta charruana s.l.* in part]: SA5.
22. *D. losadae* Haas, 1966: SA2.
23. *D. martensi* (Ihering, 1893) [= *Rhipidodonta charruana s.l.* in part]: SA5.

24. *D. multistriatus* (Lea, 1831) [= *D. multistriatus* s.l. in part + *D. expansus* (Küster, 1856) in part]: SA4, SA5.
25. *D. obsolescens* F. Baker, 1913 [= *Rhipidodonta suavidica* s.l. in part]: SA2, SA3.
26. *D. parallelopipedon* (Lea, 1834): SA5.
27. *D. paranensis* (Lea, 1834) [= *Rhipidodonta variabilis* s.l. in part]: SA5.
28. *D. parodizi* Bonetto, 1962: SA5.
29. *D. paulista* (Ihering, 1893) [= *D. expansus* s.l. in part]: SA5.
30. *D. peraeformis* (Lea, 1860) [= *Rhipidodonta charruana* s.l. in part]: SA5.
31. *D. pfeifferi* (Dunker, 1849) [= *D. multistriatus* s.l. in part]: SA4.
32. *D. piceus* (Lea, 1860) [= *D. rhuacoicus* s.l. in part]: SA5.
33. *D. rhombeus* Spix in Wagner, 1827 [= *Rhipidodonta rhombea* s.l. in part]: SA3, SA4.
34. *D. rhuacoicus* (d'Orbigny, 1835) [= *D. rhuacoicus* s.l. in part]: SA5.
35. *D. rotundus* Spix in Wagner, 1827 [= *Rhipidodonta rhombea* s.l. in part]: SA4, SA5.
36. *D. solidulus* (Philippi, 1869): SA6.
37. *D. solisianus* (d'Orbigny, 1835) [= *Rhipidodonta variabilis* s.l. in part]: SA5.
38. *D. suavidicus* (Lea, 1856) [= *Rhipidodonta suavidica* s.l. in part + *D. flucki* Morrison, 1943]: SA2, SA3, SA4.
39. *D. uruguayensis* (Lea, 1860) [= *D. wymanii* s.l. in part]: SA5.
40. *D. variabilis* (Maton, 1811) [= *Rhipidodonta variabilis* s.l. in part]: SA5.
41. *D. vicarius* Ortmann, 1921 [= *Rhipidodonta charruana* s.l. in part]: SA5.
42. *D. voltzi* Vernhout, 1914: SA2.
43. *D. wymanii* (Lea, 1860) [= *D. wymanii* s.l. in part]: SA5.

Subfamily VELESUNIONINAE

Velesunio Iredale, 1934: Australasia.

1. *V. ambiguus* (Philippi, 1847) [syn. **Unio balonnensis* Conrad, 1850]: AU1.
2. *V. angasi* (Sowerby, 1867): AU1, AU2.
3. *V. moretonicus* (Reeve, 1865): AU1.
4. *V. sentaniensis* (Haas, 1924): AU3.
5. *V. wilsonii* (Lea, 1859): AU1, AU2, AU3.

Alathyria Iredale, 1934: Australasia.

1. **A. jacksoni* Iredale, 1934: AU1.
2. *A. condola* Iredale, 1943: AU1.
3. *A. pertexta* Iredale, 1934: AU1, AU3.
4. *A. profuga* (Gould, 1850): AU1.

Lortiella Modell, 1942: Australasia; Ponder & Bayer (2004).

1. **L. rugata* (Sowerby, 1868): AU2.
2. *L. froggatti* Iredale, 1934: AU2.
3. *L. opertanea* Ponder & Bayer, 2004: AU2.

Microdontia Tapparone Canefri, 1883: Australasia.

1. **M. anodontaeformis* (Tapparone Canefri, 1883): AU3.

Westralunio Iredale, 1934: Australasia.

1. **W. carteri* Iredale, 1934: AU2.
2. *W. albertisi* Clench, 1957: AU3.
3. *W. flyensis* (Tapparone Canefri, 1883): AU3.

Superfamily ETHERIOIDEA

Family ETHERIIDAE

Etheria Lamarck, 1807: Afrotropics; Elderkin *et al.* (2016).

1. *E. elliptica* Lamarck, 1807 [syn. **Etheria semilunata* Lamarck, 1807]: AF1, AF2, AF3, AF4, AF5, AF6.

Acostaea d'Orbigny, 1851: South America; Pain & Woodward (1961b).

1. *A. rivoli* (Deshayes, 1827) [+ **Acostaea guaduasana* d'Orbigny, 1851]: SA1.

Bartlettia H. Adams, 1866: South America; Pain & Woodward (1961b).

1. **B. stefanensis* (Moricand, 1856): SA3, SA5.

Pseudomulleria R. Anthony, 1907: East Asia; Pain & Woodward (1961b).

1. **P. dalyi* (E.A. Smith, 1898): AS7.

Family IRIDINIDAE

Subfamily IRIDININAE

Mutela Scopoli, 1777: Afrotropics.

1. **M. dubia* (Gmelin, 1791): AF1, AF2, AF3.
2. *M. alata* (Lea, 1864): AF4.
3. *M. alluaudi* Germain, 1909: AF1.
4. *M. bourguignati* Bourguignat, 1886: AF1.
5. *M. franci* Daget, 1964: AF2.
6. *M. hargeri* E.A. Smith, 1908: AF3.
7. *M. joubini* (Germain, 1904): AF2, AF3.
8. *M. langi* Pilsbry & Bequaert, 1927: AF3.
9. *M. legumen* (Rochebrune, 1886): AF3.
10. *M. mabilli* (Rochebrune, 1886): AF3.
11. *M. rostrata* (Rang, 1835): AF1, AF2, AF3.
12. *M. soleniformis* Bourguignat, 1886: AF3.
13. *M. wistarmorrisi* Graf & Cummings, 2006: AF4.
14. *M. zambiensis* Mandahl-Barth, 1988: AF4.

Chelidonopsis Ancey, 1887: Afrotropics.

1. **C. hirundo* (Martens, 1881): AF3.

Pleiodon Conrad, 1834: Afrotropics; Pain & Woodward (1961a).

1. *P. ovatus* (Swainson, 1823) [syn. **Pleiodon macmurtriei* Conrad, 1834]: AF2.
2. *P. speki* (Woodward, 1859): AF3.

Subfamily ASPATHARIINAE

Aspatharia Bourguignat, 1885: Afrotropics.

1. *A. rugifera* (Dunker, 1858) [syn. **Margaritana vignouana* Bernardi, 1859]: AF3, AF4.
2. *A. chaiziana* (Rang, 1835) [+ *A. tawaii* (Rang, 1835)]: AF1, AF2.
3. *A. dahomeyensis* (Lea, 1859): AF2.
4. *A. divaricata* (Martens, 1897): AF1.
5. *A. droueti* (Chaper, 1885): AF2.
6. *A. ganciniensis* (Rochebrune, 1886) [= *A. semicorrugata* (Preston, 1909)]: AF3.
7. *A. marnoi* (Jickeli, 1874): AF1, AF5.
8. *A. pangallensis* (Rochebrune, 1882) [+ *A. mabillei* (Jousseume, 1886)]: AF2.
9. *A. pfeifferiana* (Bernardi, 1860): AF3.

10. *A. rochebrunei* (Jousseume, 1886) [+ *A. tristis* (Jousseume, 1886)]: AF2.
 11. *A. subreniformis* (Sowerby, 1867): AF4.

Chambardia Bourguignat in Servain, 1890: Afrotropics.

- **C. letourneuxi* Bourguignat in Servain, 1890: AF1. Extinct.
- C. bourguignati* (Bourguignat, 1886): AF1, AF5.
- C. flava* (Pilsbry & Bequaert, 1927) [= *C. dautzenbergi* (Haas, 1936)]: AF3.
- C. moutai* (Darteville, 1939): AF4.
- C. nyassaensis* (Lea, 1864): AF3, AF4.
- C. petersi* (Martens, 1860): AF4.
- C. rubens* (Lamarck, 1819): AF1, AF2.
- C. trapezia* (Martens, 1897): AF1.
- C. wahlbergi* (Krauss, 1848): AF1, AF2, AF4, AF5.
- C. welwitschii* (Morelet, 1868): AF4.
- C. wissmanni* (Martens, 1883): AF2, AF3.

Family MYCETOPODIDAE
Subfamily MYCETOPODINAE

Mycetopoda d'Orbigny, 1835: South and Central America.

- **M. soleniformis* d'Orbigny, 1835: SA2, SA3, SA5.
- M. legumen* (Martens, 1888): SA5.
- M. pittieri* Marshall, 1927 [= *M. siliquosa* s.l. in part]: SA2.
- M. siliquosa* (Spix in Wagner, 1827) [= *M. siliquosa* s.l. in part]: CA1, SA1, SA2, SA3, SA4, SA5.

Mycetopodella Marshall, 1927: South America.

- **M. falcata* (Higgins, 1868): SA2 (Mp), SA3.

Subfamily ANODONTITINAE**Anodontites Bruguière, 1792:** South and Central America.

- **A. crispata* Bruguière, 1792 [= *A. crispatus* s.l. in part]: SA1, SA2, SA3.
- A. aroana* H.B. Baker, 1930 [= *A. trapesialis* s.l. in part]: SA2.
- A. carinata* (Dunker, 1858) [= *A. crispatus* s.l. in part]: SA1, SA2.
- A. colombiensis* Marshall, 1922 [= *A. tenebricosus* s.l. in part]: SA1.
- A. cylindracea* (Lea, 1838): CA1.
- A. depexa* (Martens, 1900): CA1.
- A. elongata* (Swainson, 1823) [= *A. elongatus* s.l. in part]: SA1, SA3, SA5.
- A. ferrarisii* (d'Orbigny, 1835): SA5.
- A. guanarensis* Marshall, 1927 [= *A. trigonus* s.l. in part]: SA2.
- A. iheringi* (Clessin, 1882) [= *A. patagonicus* s.l. in part]: SA5.
- A. infossa* H.B. Baker, 1930 [= *A. patagonicus* s.l. in part]: SA2.
- A. leotaudi* (Guppy, 1866): SA2.
- A. lucida* (d'Orbigny, 1835) [= *A. obtusus* s.l. in part]: SA5.
- A. montezuma* (Lea, 1841) [= *A. inaequivulva* (Lea, 1868)]: CA1.
- A. moricandii* (Lea, 1860): SA4.
- A. obtusa* (Spix in Wagner, 1827) [= *A. obtusus* s.l. in part]: SA3, SA4, SA5.
- A. patagonica* (Lamarck, 1819) [= *A. patagonicus* s.l. in part]: SA5.
- A. pittieri* Marshall, 1922: SA2.
- A. schomburgiana* (Sowerby, 1870) [= *A. crispatus* s.l. in part]: SA2.
- A. solenidea* (Sowerby, 1867) [= *A. tenebricosus* s.l. in part]: SA4 (Mp), SA5.
- A. tehuantepecensis* (Crosse & Fischer, 1893): CA1.

- A. tenebricosus* (Lea, 1834) [= *A. tenebricosus* s.l. in part]: SA3, SA5.
- A. tortilis* (Lea, 1852): CA1, SA1, SA2.
- A. trapesialis* (Lamarck, 1819) [= *A. trapesialis* s.l. in part]: CA1, SA1, SA2, SA3, SA4, SA5.
- A. trapezea* (Spix in Wagner, 1827): SA3, SA4, SA5.
- A. trigona* (Spix in Wagner, 1827) [= *A. trigonus* s.l. in part]: SA1, SA2, SA3, SA5, SA6.

Lamproscapha Swainson, 1840: South America.

- **L. ensiformis* (Spix in Wagner, 1827) [= *L. ensiformis* s.l. in part]: SA2, SA3, SA5.
- L. falsa* (Simpson, 1900) [= *L. ensiformis* s.l. in part]: SA2.

Subfamily LEILINAE**Leila Gray, 1840:** South America; [Veitenheimer \(1973\)](#).

- **L. esula* (d'Orbigny, 1835): SA3.
- L. blainvilliana* (Lea, 1834): SA3, SA5.

Subfamily MONOCONDYLAEINAE**Monocondylaea d'Orbigny, 1835:** South America.

- **M. paraguayana* (d'Orbigny, 1835) [= *M. paraguayana* s.l. in part]: SA5.
- M. corrientensis* (d'Orbigny, 1835) [= *M. corrientensis* s.l. in part]: SA3, SA4, SA5.
- M. costulata* (Moricand, 1858) [= *M. paraguayana* s.l. in part]: SA3.
- M. franciscana* (Moricand, 1837) [= *M. corrientensis* s.l. in part]: SA4.
- M. guarayana* (d'Orbigny, 1835) [= *M. paraguayana* s.l. in part]: SA3.
- M. jaspidea* (Hupé, 1857) [= *M. paraguayana* s.l. in part]: SA3.
- M. minuana* (d'Orbigny, 1835) [= *M. minuana* s.l. in part]: SA5.
- M. parchappii* (d'Orbigny, 1835) [= *M. minuana* s.l. in part]: SA5.

Diplodontites Marshall, 1922: South America; [Olsson & Wurtz \(1951\)](#).

- **D. cookei* Marshall, 1922: SA1, SA3.
- D. olssoni* Pilsbry, 1933: SA1.
- D. pilsbryana* Olsson & Wurtz, 1951: SA1.

Fossula Lea, 1870: South America.

- **F. fossiculifera* (d'Orbigny, 1835): SA3, SA4, SA5.

Haasica Strand, 1932: South America.

- **H. balzani* (Ihering, 1893): SA5.

Iheringella Pilsbry, 1893: South America.

- **I. isocardioides* (Lea, 1856): SA5.
- I. semisulcata* (H. Adams, 1870): SA3.

Tamsiella Haas, 1931: South America; [Bonetto \(1972\)](#).

- **T. tamsiana* (Dunker, 1858): SA2.
- T. amazonica* Bonetto, 1972: SA3.
- T. schroeteriana* (Lea, 1852) [= *Anodontites elongatus* s.l. in part]: SA3.

Nomina dubia

These are species that were included by [Graf & Cummings \(2007b\)](#) but are now regarded as doubtful species of uncertain affinities.

1. *Unio altus* Conrad, 1854 [= *Pleurobema altum*]: type locality unknown.
2. *Unio fluctiger* Lea, 1859 [= *Diplodon fluctiger*]: type locality unknown.
3. *Unio madagascariensis* Sganzin, 1841 [= *Coelatura madagascariensis*]: described from the Mahoupa River, near Tamatave, Madagascar.
4. *Unio* (—?) *malgachensis* Germain, 1911 [= *Coelatura malgachensis*]: described from Madagascar.
5. *Microdonia ovata* Haas, 1910 [= *Velesunio ovata*]: described from New Guinea, perhaps the Fly River.
6. *Unio taumilapanus* Conrad, 1855 [= *Sphenonaias taumilapanus*]: described from the San Juan River, Tamaulipas, Mexico.

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