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REGULAR ARTICLE

A REVISED LIST OF THE FRESHWATER MUSSELS (MOLLUSCA: BIVALVIA: UNIONIDA) OF THE UNITED STATES AND CANADA

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ABSTRACT

We present a revised list of freshwater mussels (order Unionida, families Margaritiferidae and Unionidae) of the United States and Canada, incorporating changes in nomenclature and systematic taxonomy since publication of the most recent checklist in 1998. We recognize a total of 298 species in 55 genera in the families Margaritiferidae (one genus, five species) and Unionidae (54 genera, 293 species). We propose one change in the Margaritiferidae: the placement of the formerly monotypic genus *Cumberlandia* in the synonymy of *Margaritifera*. In the Unionidae, we recognize three new genera, elevate four genera from synonymy, and place three previously recognized genera in synonymy. We recognize for the first time two species (one native and one nonindigenous) in the Asian genus *Sinanodonta* as occurring in North America. We recognize four new species and one subspecies and elevate 21 species from synonymy. We elevate 10 subspecies to species status and no longer recognize four subspecies. We change common names for five taxa, correct spelling for eight species, and correct the date of publication of original descriptions for four species.

KEY WORDS: Unionidae, Margaritiferidae, taxonomy, systematics, nomenclature, mussel scientific names, mussel common names

INTRODUCTION

During the past 50 yr, there has been considerable interest in freshwater mussels (order Unionida) in the United States and Canada. Much of this interest was brought about by passage of the U.S. Endangered Species Acts of 1966, 1969, and 1973 and the Canadian Species at Risk Act of 2002. These legislative actions and the environmental movement that accompanied them focused conservation attention on all animals and plants, as well as their habitats. This in turn led

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to assessment of species conservation status and the development of faunal lists for many states and provinces. The task of developing species lists was difficult for most invertebrates, including mussels, because so little attention had been given to the study of their biology, ecology, and systematics. In 1970, only six U.S. states had recent lists or books covering their mussel fauna. The first modern attempt to provide a comprehensive list of freshwater mussels of North America was published by Burch (1973, 1975).

The first comprehensive list of freshwater mussels of the United States and Canada was compiled in Turgeon et al. (1988) and revised a decade later (Turgeon et al. 1998). Williams et al. (1993) was another important resource during this period; although mainly an assessment of species conservation status, this paper also provided a comprehensive and widely used species list similar to those of Turgeon et al. (1988, 1998). These lists standardized and provided taxonomic stability to mussel common and scientific names to an extent that was previously unavailable. However, systematic taxonomy of mussels was poorly known at that time, and classifications at all taxonomic levels were based largely on concepts from the early 1900s.

Since publication of Turgeon et al. (1988, 1998) and Williams et al. (1993), many studies have refined our understanding of mussel systematic taxonomy. Several major publications have addressed systematic relationships within the class Bivalvia, including the order Unionida (Bieler et al. 2010; Carter et al. 2011; Bolotov et al. 2016; Araujo et al. 2017; Combosch et al. 2017). Major studies specific to the Unionida include Graf and Ó Foighil (2000), Hoeh et al. (2001, 2002, 2009), Roe and Hoeh (2003), Campbell et al. (2005), Walker et al. (2006), Graf and Cummings (2007, 2017), Cummings and Graf (2010), and Campbell and Lydeard (2012a, 2012b). In addition, many studies have examined systematic relationships at lower taxonomic levels (e.g., Serb et al. 2003; Jones et al. 2006; Lane et al. 2016). Together, this body of work depicts a view of mussel taxonomy that differs substantially from that of previous lists of the North American fauna.

We present a revised classification and list of the freshwater mussels of the United States and Canada (Tables 1 and 2). The primary purpose of this revision is to provide in a single resource a comprehensive list and taxonomic classification that reflects recent refinement of mussel systematics.

METHODS

We used as a starting point the list of Turgeon et al. (1998). We revised this list and its taxonomic classification based on a review of peer-reviewed mussel taxonomic and nomenclatural literature produced since 1998, unpublished research by the authors, and discussions with other experts on mussel systematics. We also corrected the spelling of specific epithets and publication dates of original descriptions based on the International Code of Zoological Nomenclature (http://www.iczn.org/iczn/index.jsp). Species mentioned in the text, but not included in Table 2, have author and date of publication following the name. Author and date of publication for all other species are given in Table 2.

Mussel common names follow Turgeon et al. (1998) with minor exceptions, but they are capitalized as is now the practice for many other animal groups (e.g., birds, reptiles, amphibians, fishes). Capitalization of common names helps avoid confusion by identifying standardized common names. For example, reference to a "fragile papershell" could apply to several thin-shelled species, but the capitalized "Fragile Papershell" is unambiguously recognized as the common name for *Leptodea fragilis*. We note and explain other instances where we changed common names from those of Turgeon et al. (1998) or where recognition of previously unrecognized species necessitated creation of a new common name.

We provide a rationale for and discussion of all taxonomic changes in the following accounts for each family and genus and in Table 2. There is a degree of uncertainty and subjectivity in our revised list that is unavoidable given our still imperfect understanding of mussel systematics. We attempted to reconcile divergent views regarding mussel systematics based on our assessment of the strength of evidence for these views. In cases where evidence did not allow reconciliation, we attempted to provide a plausible conclusion based on our professional judgment and experience; these conclusions were based on consensus among the authors to the extent possible.

Subspecies is a taxonomic category applied to populations that are morphologically distinct and geographically separated but that exhibit intergradation in contact zones (Mayr et al. 1953; Gilbert 1961). We evaluated morphological and molecular evidence relating to the status of subspecies recognized by Turgeon et al. (1998) and subsequent workers (Jones and Neves 2010). In most cases, recent evidence did not support recognition of subspecies but supported either subsuming subspecies under the nominal species or elevating subspecies to species status; we discuss this evidence for each case. However, strong evidence with which to evaluate their status was lacking for several, mostly extinct, subspecies (see *Epioblasma*). The designation of subspecies versus species is arbitrary and inconsistent for many animal groups (Huang and Knowles 2016), and this has historically been the case for mussels (e.g., Ortmann 1918, 1920). For subspecies that lacked strong evidence for synonymization or elevation, we recognize all as species to provide more consistent null hypotheses regarding potential diversity in these groups.

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RESULTS

Freshwater bivalve higher classification continues to evolve as more data are generated and new techniques are developed. Fossil and modern bivalve higher classification has

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Table 1. Higher classification of the Unionoidea present in the United States and Canada.

CLASS Bivalvia Linnaeus, 1758
INFRACLASS Heteroconchia Hertwig, 1895
COHORT Uniomorphi Gray, 1854 [=Paleoheterodonta]
ORDER Unionida Gray, 1854
SUPERFAMILY Unionoidea Rafinesque, 1820
MARGARITIFERIDAE Henderson, 1929
Margaritifera Schumacher, 1816
UNIONIDAE Rafinesque, 1820
ANODONTINAE Rafinesque, 1820
Anodontini Rafinesque, 1820
Alasmidonta Say, 1818
Anodonta Lamarck, 1799
Anodontoides Simpson in Baker, 1898
Arcidens Simpson, 1900
Lasmigona Rafinesque, 1831
Pegias Simpson, 1900
Pyganodon Crosse and Fischer, 1894
Simpsonaias Frierson, 1914
Strophitus Rafinesque, 1820
Utterbackia Baker, 1927
Utterbackiana Frierson, 1927
Cristariini Lopes-Lima, Bogan, and Froufe, 2017
Sinanodonta Modell, 1945
GONIDEINAE Ortmann, 1916
Gonideini Ortmann, 1916
Gonidea Conrad, 1857
AMBLEMINAE Rafinesque, 1820
Amblemini Rafinesque, 1820
Amblema Rafinesque, 1820
Lampsilini Ihering, 1901
Actinonaias Crosse and Fischer, 1894
Cyprogenia Agassiz, 1852
Cyrtonaias Crosse and Fischer, 1894
Dromus Simpson, 1900
Ellipsaria Rafinesque, 1820
Epioblasma Rafinesque, 1831
Glebula Conrad, 1853
Hamiota Roe and Hartfield, 2005
Lampsilis Rafinesque, 1820
Lemiox Rafinesque, 1831
Leptodea Rafinesque, 1820
Ligumia Swainson, 1840
Medionidus Simpson, 1900
Obliquaria Rafinesque, 1820
Obovaria Rafinesque, 1819
Plectomerus Conrad, 1853
Potamilus Rafinesque, 1818
Ptychobranchus Simpson, 1900
Toxolasma Rafinesque, 1831
Truncilla Rafinesque, 1819
Venustaconcha Frierson, 1927
Villosa Frierson, 1927

Table 1, continued.

Pleurobemini Hannibal, 1912
Elliptio Rafinesque, 1819
Elliptoideus Frierson, 1927
Eurynia Rafinesque, 1820
Fusconaia Simpson, 1900
Hemistena Rafinesque, 1820
Parvaspina Perkins, Gangloff, and Johnson, 2017
Plethobasus Simpson, 1900
Pleurobema Rafinesque, 1819
Pleuronaia Frierson, 1927
Quadrulini Ihering, 1901
Cyclonaias Pilsbry in Ortmann and Walker, 1922
Megalonaias Utterback, 1915
Quadrula Rafinesque, 1820
Theliderma Swainson, 1840
Tritogonia Agassiz, 1852
Uniomerus Conrad, 1853
AMBLEMINAE (*incertae sedis*)
Disconaias Crosse and Fischer, 1894
Popenaias Frierson, 1927
Reginaia Campbell and Lydeard, 2012

recently been summarized by Carter et al. (2011), with standardized endings for higher taxa within Bivalvia. Recent evidence supports the order Unionida as a monophyletic clade (Combosch et al. 2017). There have been two recent assessments of the taxonomy for Margaritiferidae (Bolotov et al. 2016; Araujo et al. 2017). Higher level relationships within the Unionidae have recently been reviewed by Lopes-Lima et al. (2017). Based on these publications, we provide our assessment of higher classification of the Unionida and its position in the class Bivalvia (Table 1).

There is general agreement on the three subfamily divisions within the Unionidae in North America and seven subfamilies worldwide, but there remains some uncertainty regarding classification at lower levels. We adopted a subfamily-, tribe-, and generic-level classification for the United States and Canada based on recent phylogenetic research (Table 1). We recognize the Anodontinae as a subfamily with two tribes in the United States and Canada. We recognize the subfamily Gonideinae, containing the genus *Gonidea*. We recognize the subfamily Ambleminae as consisting of four tribes: Amblemini, Lampsilini, Pleurobemini, and Quadrulini. The placement of many genera within tribes in the Ambleminae is well supported and consistent among studies, but the placement of others is less certain and varies among studies (e.g., *Plectomerus*, Campbell et al. 2005). The Mexican and Central American genera *Disconaias* and *Popenaias* and North American *Reginaia* lack sufficient phylogenetic information to be confidently assigned to a classification, and we placed them in Ambleminae incertae sedis (Table 1).

Our revised list includes many taxonomic changes at the

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Table 2. List of Margaritiferidae and Unionidae of the United States and Canada. Currently recognized taxa are bolded. Taxa preceded by an asterisk and not bolded appeared in Turgeon et al. (1998) but are no longer recognized or reassigned to other genera.

Scientific Name	Common Name	Changes in Scientific and Common Names
MARGARITIFERIDAE Henderson, 1929		
**Cumberlandia* Ortmann, 1912		Synonym of *Margaritifera*
**Cumberlandia monodonta* (Say, 1829)	Spectaclecase	Reassigned to *Margaritifera*
***Margaritifera* Schumacher, 1816**		
***Margaritifera falcata* (Gould, 1850)**	Western Pearlshell	
***Margaritifera hembeli* (Conrad, 1838)**	Louisiana Pearlshell	
***Margaritifera margaritifera* (Linnaeus, 1758)**	Eastern Pearlshell	
***Margaritifera marrianae* Johnson, 1983**	Alabama Pearlshell	
***Margaritifera monodonta* (Say, 1829)**	Spectaclecase	Reassigned from *Cumberlandia*
UNIONIDAE Rafinesque, 1820		
***Actinonaias* Crosse and Fischer, 1894**		
***Actinonaias ligamentina* (Lamarck, 1819)**	Mucket	
***Actinonaias pectorosa* (Conrad, 1834)**	Pheasantshell	
***Alasmidonta* Say, 1818**		
***Alasmidonta arcula* (Lea, 1838)**	Altamaha Arcmussel	
***Alasmidonta atropurpurea* (Rafinesque, 1831)**	Cumberland Elktoe	
***Alasmidonta heterodon* (Lea, 1829)**	Dwarf Wedgemussel	Publication date corrected
***Alasmidonta marginata* Say, 1818**	Elktoe	
***Alasmidonta mccordi* Athearn, 1964**	Coosa Elktoe	
***Alasmidonta raveneliana* (Lea, 1834)**	Appalachian Elktoe	
***Alasmidonta robusta* Clarke, 1981**	Carolina Elktoe	
***Alasmidonta triangulata* (Lea, 1858)**	Southern Elktoe	
***Alasmidonta undulata* (Say, 1817)**	Triangle Floater	
***Alasmidonta varicosa* (Lamarck, 1819)**	Brook Floater	
***Alasmidonta viridis* (Rafinesque, 1820)**	Slippershell Mussel	
***Alasmidonta wrightiana* (Walker, 1901)**	Ochlockonee Arcmussel	
***Amblema* Rafinesque, 1820**		
***Amblema elliottii* (Lea, 1856)**	Coosa Fiveridge	
***Amblema neislerii* (Lea, 1858)**	Fat Threeridge	
***Amblema plicata* (Say, 1817)**	Threeridge	
***Anodonta* Lamarck, 1799**		
**Anodonta beringiana* Middendorff, 1851	Yukon Floater	Reassigned to *Sinanodonta*
***Anodonta californiensis* Lea, 1852**	California Floater	
**Anodonta couperiana* Lea, 1840	Barrel Floater	Reassigned to *Utterbackiana*
***Anodonta dejecta* Lewis, 1875	Woebegone Floater	Synonym of *Anodonta californiensis*
**Anodonta heardi* Gordon and Hoeh, 1995	Apalachicola Floater	Reassigned to *Utterbackiana*
**Anodonta implicata* Say, 1829	Alewife Floater	Reassigned to *Utterbackiana*
***Anodonta kennerlyi* Lea, 1860**	Western Floater	
***Anodonta nuttalliana* Lea, 1838**	Winged Floater	
***Anodonta oregonensis* Lea, 1838**	Oregon Floater	
**Anodonta suborbiculata* Say, 1831	Flat Floater	Reassigned to *Utterbackiana*
***Anodontoides* Simpson in Baker, 1898**		
***Anodontoides denigrata* (Lea, 1852)**	Cumberland Papershell	Elevated from synonymy
***Anodontoides ferussacianus* (Lea, 1834)**	Cylindrical Papershell	
***Anodontoides radiatus* (Conrad, 1834)**	Rayed Creekshell	
***Arcidens* Simpson, 1900**		
***Arcidens confragosus* (Say, 1829)**	Rock Pocketbook	
***Arcidens wheeleri* (Ortmann and Walker, 1912)**	Ouachita Rock Pocketbook	Reassigned from *Arkansia*
**Arkansia* Ortmann and Walker, 1912		Synonym of *Arcidens*
**Arkansia wheeleri* Ortmann and Walker, 1912	Ouachita Rock Pocketbook	Reassigned to *Arcidens*

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Cyclonaias* Pilsbry in Ortmann and Walker, 1922**		
***Cyclonaias archeri* (Frierson, 1905)**	Tallapoosa Orb	Elevated from synonymy
***Cyclonaias asperata* (Lea, 1861)**	Alabama Orb	Reassigned from *Quadrula*
***Cyclonaias aurea* (Lea, 1859)**	Golden Orb	Reassigned from *Quadrula*
***Cyclonaias houstonensis* (Lea, 1859)**	Smooth Pimpleback	Reassigned from *Quadrula*
***Cyclonaias infucata* (Conrad, 1834)**	Sculptured Pigtoe	Reassigned from *Quincuncina*
***Cyclonaias kieneriana* (Lea, 1852)**	Coosa Orb	Elevated from synonymy
***Cyclonaias kleiniana* (Lea, 1852)**	Florida Mapleleaf	Elevated from synonymy
***Cyclonaias mortoni* (Conrad, 1835)**	Western Pimpleback	Species elevated from subspecies; reassigned from *Quadrula*
***Cyclonaias nodulata* (Rafinesque, 1820)**	Wartyback	Reassigned from *Quadrula*
***Cyclonaias petrina* (Gould, 1855)**	Texas Pimpleback	Reassigned from *Quadrula*
***Cyclonaias pustulosa* (Lea, 1831)**	Pimpleback	Reassigned from *Quadrula*
***Cyclonaias refulgens* (Lea, 1868)**	Purple Pimpleback	Reassigned from *Quadrula*
***Cyclonaias succissa* (Lea, 1852)**	Purple Pigtoe	Reassigned from *Fusconaia*
***Cyclonaias tuberculata* (Rafinesque, 1820)**	Purple Wartyback	
***Cyprogenia* Agassiz, 1852**		
***Cyprogenia aberti* (Conrad, 1850)**	Western Fanshell	
***Cyprogenia stegaria* (Rafinesque, 1820)**	Fanshell	
***Cyrtonaias* Crosse and Fischer, 1894**		
***Cyrtonaias tampicoensis* (Lea, 1838)**	Tampico Pearlymussel	
***Disconaias* Crosse and Fischer, 1894**		
***Disconaias fimbriata* (Frierson, 1907)**	Fringed Mucket	Elevated from synonymy
**Disconaias salinasensis* (Simpson, 1908)	Salina Mucket	Synonym of *Disconaias fimbriata*
***Dromus* Simpson, 1900**		
***Dromus dromas* (Lea, 1834)**	Dromedary Pearlymussel	
***Ellipsaria* Rafinesque, 1820**		
***Ellipsaria lineolata* (Rafinesque, 1820)**	Butterfly	
***Elliptio* Rafinesque, 1819**		
***Elliptio ahenea* (Lea, 1843)**	Southern Lance	
***Elliptio angustata* (Lea, 1831)**	Carolina Lance	
***Elliptio arca* (Conrad, 1834)**	Alabama Spike	
***Elliptio arctata* (Conrad, 1834)**	Delicate Spike	
**Elliptio buckleyi* (Lea, 1843)	Florida Shiny Spike	Synonym of *Elliptio jayensis*
***Elliptio chipolaensis* (Walker, 1905)**	Chipola Slabshell	
***Elliptio cistellaeformis* (Lea, 1863)**	Box Spike	
***Elliptio complanata* (Lightfoot, 1786)**	Eastern Elliptio	
***Elliptio congaraea* (Lea, 1831)**	Carolina Slabshell	
***Elliptio crassidens* (Lamarck, 1819)**	Elephantear	
***Elliptio dariensis* (Lea, 1842)**	Georgia Elephantear	
**Elliptio dilatata* (Rafinesque, 1820)	Spike	Reassigned to *Eurynia*
***Elliptio downiei* (Lea, 1858)**	Satilla Elephantear	
**Elliptio errans* (Lea, 1856)	Oval Elliptio	Synonym of *Elliptio icterina*; publication date corrected
***Elliptio fisheriana* (Lea, 1838)**	Northern Lance	
***Elliptio folliculata* (Lea, 1838)**	Pod Lance	
***Elliptio fraterna* (Lea, 1852)**	Brother Spike	
***Elliptio fumata* (Lea, 1857)**	Gulf Slabshell	Elevated from synonymy
**Elliptio hepatica* (Lea, 1859)	Brown Elliptio	Synonym of *Elliptio icterina*
***Elliptio hopetonensis* (Lea, 1838)**	Altamaha Slabshell	
***Elliptio icterina* (Conrad, 1834)**	Variable Spike	

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Elliptio jayensis* (Lea, 1838)**	Florida Spike	Common name changed from Flat Spike
**Elliptio judithae* Clarke, 1986	Plicate Spike	Synonym of *Elliptio roanokensis*
***Elliptio lanceolata* (Lea, 1828)**	Yellow Lance	
**Elliptio lugubris* (Lea, 1834)	Sad Elliptio	Synonym of *Elliptio icterina*
***Elliptio marsupiobesa* Fuller, 1972**	Cape Fear Spike	
***Elliptio mcmichaeli* Clench and Turner, 1956**	Fluted Elephantear	
***Elliptio monroensis* (Lea, 1843)**	St. Johns Elephantear	
***Elliptio nigella* (Lea, 1852)**	Winged Spike	
***Elliptio occulta* (Lea, 1843)**	Hidden Spike	Elevated from synonymy
***Elliptio producta* (Conrad, 1836)**	Atlantic Spike	
***Elliptio pullata* (Lea, 1856)**	Gulf Spike	Elevated from synonymy
***Elliptio purpurella* (Lea, 1857)**	Inflated Spike	Elevated from synonymy
**Elliptio raveneli* (Conrad, 1834)	Carolina Spike	Synonym of *Elliptio icterina*
***Elliptio roanokensis* (Lea, 1838)**	Roanoke Slabshell	
***Elliptio shepardiana* (Lea, 1834)**	Altamaha Lance	
***Elliptio spinosa* (Lea, 1836)**	Altamaha Spinymussel	
**Elliptio steinstansana* Johnson and Clarke, 1983	Tar River Spinymussel	Reassigned to *Parvaspina*
**Elliptio waccamawensis* (Lea, 1863)	Waccamaw Spike	Synonym of *Elliptio congaraea*
**Elliptio waltoni* (Wright, 1888)	Florida Lance	Synonym of *Elliptio ahenea*
***Elliptoideus* Frierson, 1927**		
***Elliptoideus sloatianus* (Lea, 1840)**	Purple Bankclimber	
***Epioblasma* Rafinesque, 1831**		
***Epioblasma ahlstedti* Jones and Neves, 2010**	Duck River Dartersnapper	Described as new species
***Epioblasma arcaeformis* (Lea, 1831)**	Sugarspoon	
***Epioblasma aureola* Jones and Neves, 2010**	Golden Riffleshell	Species elevated from subspecies
***Epioblasma biemarginata* (Lea, 1857)**	Angled Riffleshell	
***Epioblasma brevidens* (Lea, 1831)**	Cumberlandian Combshell	
***Epioblasma capsaeformis* (Lea, 1834)**	Oyster Mussel	
***Epioblasma cincinnatiensis* (Lea, 1840)**	Ohio Riffleshell	Elevated from synonymy
***Epioblasma curtisii* (Frierson and Utterback, 1916)**	Curtis Pearlymussel	Species elevated from subspecies
***Epioblasma flexuosa* (Rafinesque, 1820)**	Leafshell	
***Epioblasma florentina* (Lea, 1857)**	Yellow Blossom	
**Epioblasma florentina aureola* Jones and Neves, 2010	Golden Riffleshell	Described as new subspecies; elevated to species
**Epioblasma florentina curtisii* (Frierson and Utterback, 1916)	Curtis Pearlymussel	Subspecies elevated to species
**Epioblasma florentina florentina* (Lea, 1857)	Yellow Blossom	Nominotypical subspecies not required
**Epioblasma florentina walkeri* (Wilson and Clark, 1914)	Tan Riffleshell	Subspecies elevated to species
***Epioblasma gubernaculum* (Reeve, 1865)**	Green Blossom	Species elevated from subspecies
***Epioblasma haysiana* (Lea, 1834)**	Acornshell	
***Epioblasma lenior* (Lea, 1842)**	Narrow Catspaw	
***Epioblasma lewisii* (Walker, 1910)**	Forkshell	
***Epioblasma metastriata* (Conrad, 1838)**	Upland Combshell	
***Epioblasma obliquata* (Rafinesque, 1820)**	Catspaw	
**Epioblasma obliquata obliquata* (Rafinesque, 1820)	Catspaw	Nominotypical subspecies not required
**Epioblasma obliquata perobliqua* (Conrad, 1836)	White Catspaw	Subspecies elevated to species
***Epioblasma othcaloogensis* (Lea, 1857)**	Southern Acornshell	
***Epioblasma penita* (Conrad, 1834)**	Southern Combshell	
***Epioblasma perobliqua* (Conrad, 1836)**	White Catspaw	Species elevated from subspecies
***Epioblasma personata* (Say, 1829)**	Round Combshell	
***Epioblasma propinqua* (Lea, 1857)**	Tennessee Riffleshell	
***Epioblasma rangiana* (Lea, 1838)**	Northern Riffleshell	Species elevated from subspecies

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Epioblasma sampsonii* (Lea, 1861)**	Wabash Riffleshell	
***Epioblasma stewardsonii* (Lea, 1852)**	Cumberland Leafshell	
***Epioblasma torulosa* (Rafinesque, 1820)**	Tubercled Blossom	
**Epioblasma torulosa gubernaculum* (Reeve, 1865)	Green Blossom	Subspecies elevated to species
**Epioblasma torulosa rangiana* (Lea, 1838)	Northern Riffleshell	Subspecies elevated to species
**Epioblasma torulosa torulosa* (Rafinesque, 1820)	Tubercled Blossom	Nominotypical subspecies not required
***Epioblasma triquetra* (Rafinesque, 1820)**	Snuffbox	
***Epioblasma turgidula* (Lea, 1858)**	Turgid Blossom	
***Epioblasma walkeri* (Wilson and Clark, 1914)**	Tan Riffleshell	Species elevated from subspecies
***Eurynia* Rafinesque, 1820**		Elevated from synonymy
***Eurynia dilatata* Rafinesque, 1820**	Spike	Reassigned from *Elliptio*
***Fusconaia* Simpson, 1900**		
**Fusconaia askewi* (Marsh, 1896)	Texas Pigtoe	Synonym of *Fusconaia chunii*
**Fusconaia barnesiana* (Lea, 1838)	Tennessee Pigtoe	Reassigned to *Pleuronaia*
***Fusconaia burkei* (Walker, 1922)**	Tapered Pigtoe	Reassigned from *Quincuncina*
***Fusconaia cerina* (Conrad, 1838)**	Gulf Pigtoe	Common name changed from Southern Pigtoe
***Fusconaia chunii* (Lea, 1861)**	Texas Pigtoe	Elevated from synonymy
***Fusconaia cor* (Conrad, 1834)**	Shiny Pigtoe	
***Fusconaia cuneolus* (Lea, 1840)**	Finerayed Pigtoe	
**Fusconaia ebena* (Lea, 1831)	Ebonyshell	Reassigned to *Reginaia*
***Fusconaia escambia* Clench and Turner, 1956**	Narrow Pigtoe	
***Fusconaia flava* (Rafinesque, 1820)**	Wabash Pigtoe	
**Fusconaia lananensis* (Frierson, 1901)	Triangle Pigtoe	Synonym of *Fusconaia chunii*
***Fusconaia masoni* (Conrad, 1834)**	Atlantic Pigtoe	
***Fusconaia mitchelli* (Simpson, 1895)**	False Spike	Reassigned from *Quincuncina*
***Fusconaia ozarkensis* (Call, 1887)**	Ozark Pigtoe	
***Fusconaia subrotunda* (Lea, 1831)**	Longsolid	
**Fusconaia succissa* (Lea, 1852)	Purple Pigtoe	Reassigned to *Cyclonaias*
***Glebula* Conrad, 1853**		
***Glebula rotundata* (Lamarck, 1819)**	Round Pearlshell	
***Gonidea* Conrad, 1857**		
***Gonidea angulata* (Lea, 1838)**	Western Ridged Mussel	
***Hamiota* Roe and Hartfield, 2005**		Described as new genus
***Hamiota altilis* (Conrad, 1834)**	Finelined Pocketbook	Reassigned from *Lampsilis*
***Hamiota australis* (Simpson, 1900)**	Southern Sandshell	Reassigned from *Lampsilis*
***Hamiota perovalis* (Conrad, 1834)**	Orangenacre Mucket	Reassigned from *Lampsilis*
***Hamiota subangulata* (Lea, 1840)**	Shinyrayed Pocketbook	Reassigned from *Lampsilis*
***Hemistena* Rafinesque, 1820**		
***Hemistena lata* (Rafinesque, 1820)**	Cracking Pearlymussel	
***Lampsilis* Rafinesque, 1820**		
***Lampsilis abrupta* (Say, 1831)**	Pink Mucket	
**Lampsilis altilis* (Conrad, 1834)	Finelined Pocketbook	Reassigned to *Hamiota*
**Lampsilis australis* Simpson, 1900	Southern Sandshell	Reassigned to *Hamiota*
***Lampsilis binominata* Simpson, 1900**	Lined Pocketbook	
***Lampsilis bracteata* (Gould, 1855)**	Texas Fatmucket	
***Lampsilis brittsi* Simpson, 1900**	Northern Brokenray	Species elevated from subspecies
***Lampsilis cardium* Rafinesque, 1820**	Plain Pocketbook	
***Lampsilis cariosa* (Say,1817)**	Yellow Lampmussel	
***Lampsilis dolabraeformis* (Lea, 1838)**	Altamaha Pocketbook	
***Lampsilis fasciola* Rafinesque, 1820**	Wavyrayed Lampmussel	

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Lampsilis floridensis* (Lea, 1852)**	Florida Sandshell	Elevated from synonymy
**Lampsilis fullerkati* Johnson, 1984	Waccamaw Fatmucket	Synonym of *Lampsilis radiata*
**Lampsilis haddletoni* Athearn, 1964	Haddleton Lampmussel	Reassigned to *Obovaria*
***Lampsilis higginsii* (Lea, 1857)**	Higgins Eye	
***Lampsilis hydiana* (Lea, 1838)**	Louisiana Fatmucket	
***Lampsilis ornata* (Conrad, 1835)**	Southern Pocketbook	
***Lampsilis ovata* (Say, 1817)**	Pocketbook	
**Lampsilis perovalis* (Conrad, 1834)	Orangenacre Mucket	Reassigned to *Hamiota*
***Lampsilis powellii* (Lea, 1852)**	Arkansas Fatmucket	
***Lampsilis radiata* (Gmelin, 1791)**	Eastern Lampmussel	
**Lampsilis radiata conspicua* (Lea, 1872)	Carolina Fatmucket	Subspecies no longer recognized
**Lampsilis radiata radiata* (Gmelin, 1791)	Eastern Lampmussel	Nominotypical subspecies not required
***Lampsilis rafinesqueana* Frierson, 1927**	Neosho Mucket	
***Lampsilis reeveiana* (Lea, 1852)**	Arkansas Brokenray	
**Lampsilis reeveiana brevicula* (Call, 1887)	Ozark Brokenray	Subspecies no longer recognized
**Lampsilis reeveiana brittsi* Simpson, 1900	Northern Brokenray	Subspecies elevated to species
**Lampsilis reeveiana reeviana* (Lea, 1852)	Arkansas Brokenray	Nominotypical subspecies not required
***Lampsilis satura* (Lea, 1852)**	Sandbank Pocketbook	
***Lampsilis siliquoidea* (Barnes, 1823)**	Fatmucket	
***Lampsilis splendida* (Lea, 1838)**	Rayed Pink Fatmucket	
***Lampsilis straminea* (Conrad, 1834)**	Rough Fatmucket	
**Lampsilis straminea claibornensis* (Lea, 1838)	Southern Fatmucket	Subspecies no longer recognized
**Lampsilis straminea straminea* (Conrad, 1834)	Rough Fatmucket	Nominotypical subspecies not required
***Lampsilis streckeri* Frierson, 1927**	Speckled Pocketbook	
**Lampsilis subangulata* (Lea, 1840)	Shinyrayed Pocketbook	Reassigned to *Hamiota*
***Lampsilis teres* (Rafinesque, 1820)**	Yellow Sandshell	
***Lampsilis virescens* (Lea, 1858)**	Alabama Lampmussel	
***Lasmigona* Rafinesque, 1831**		
***Lasmigona alabamensis* Clarke, 1985**	Alabama Heelsplitter	Species elevated from subspecies
***Lasmigona complanata* (Barnes, 1823)**	White Heelsplitter	
**Lasmigona complanata alabamensis* Clarke, 1985	Alabama Heelsplitter	Subspecies elevated to species
**Lasmigona complanata complanata* (Barnes, 1823)	White Heelsplitter	Nominotypical subspecies not required
***Lasmigona compressa* (Lea, 1829)**	Creek Heelsplitter	
***Lasmigona costata* (Rafinesque, 1820)**	Flutedshell	
***Lasmigona decorata* (Lea, 1852)**	Carolina Heelsplitter	
***Lasmigona etowaensis* (Conrad, 1849)**	Etowah Heelsplitter	Elevated from synonymy
***Lasmigona holstonia* (Lea, 1838)**	Tennessee Heelsplitter	
***Lasmigona subviridis* (Conrad, 1835)**	Green Floater	
***Lemiox* Rafinesque, 1831**		
***Lemiox rimosus* (Rafinesque, 1831)**	Birdwing Pearlymussel	
***Leptodea* Rafinesque, 1820**		
***Leptodea fragilis* (Rafinesque, 1820)**	Fragile Papershell	
***Leptodea leptodon* (Rafinesque, 1820)**	Scaleshell	
***Leptodea ochracea* (Say, 1817)**	Tidewater Mucket	
**Lexingtonia* Ortmann, 1914		Synonym of *Fusconaia*
**Lexingtonia dolabelloides* (Lea, 1840)	Slabside Pearlymussel	Reassigned to *Pleuronaia*
**Lexingtonia subplana* (Conrad, 1837)	Virginia Pigtoe	Synonym of *Fusconaia masoni*
***Ligumia* Swainson, 1840**		
***Ligumia nasuta* (Say, 1817)**	Eastern Pondmussel	
***Ligumia recta* (Lamarck, 1819)**	Black Sandshell	
***Ligumia subrostrata* (Say, 1831)**	Pondmussel	

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Medionidus* Simpson, 1900**		
***Medionidus acutissimus* (Lea, 1831)**	Alabama Moccasinshell	
***Medionidus conradicus* (Lea, 1834)**	Cumberland Moccasinshell	
**Medionidus mcglameriae* van der Schalie, 1939	Tombigbee Moccasinshell	Synonym of *Leptodea fragilis*
***Medionidus parvulus* (Lea, 1860)**	Coosa Moccasinshell	
***Medionidus penicillatus* (Lea, 1857)**	Gulf Moccasinshell	
***Medionidus simpsonianus* Walker, 1905**	Ochlockonee Moccasinshell	
***Medionidus walkeri* (Wright, 1897)**	Suwannee Moccasinshell	
***Megalonaias* Utterback, 1915**		
***Megalonaias nervosa* (Rafinesque, 1820)**	Washboard	
***Obliquaria* Rafinesque, 1820**		
***Obliquaria reflexa* Rafinesque, 1820**	Threehorn Wartyback	
***Obovaria* Rafinesque, 1819**		
***Obovaria arkansasensis* (Lea, 1862)**	Southern Hickorynut	Reassigned from *Villosa*
***Obovaria choctawensis* (Athearn, 1964)**	Choctaw Bean	Reassigned from *Villosa*
***Obovaria haddletoni* (Athearn, 1964)**	Haddleton Lampmussel	Reassigned from *Lampsilis*
**Obovaria jacksoniana* (Frierson, 1912)	Southern Hickorynut	Synonym of *Obovaria arkansasensis*
***Obovaria olivaria* (Rafinesque, 1820)**	Hickorynut	
***Obovaria retusa* (Lamarck, 1819)**	Ring Pink	
**Obovaria rotulata* (Wright, 1899)	Round Ebonyshell	Reassigned to *Reginaia*
***Obovaria subrotunda* (Rafinesque, 1820)**	Round Hickorynut	
***Obovaria unicolor* (Lea, 1845)**	Alabama Hickorynut	
***Parvaspina* Perkins, Gangloff, and Johnson, 2017**		Described as new genus
***Parvaspina collina* (Conrad, 1836)**	James Spinymussel	Reassigned from *Pleurobema*; publication date corrected
***Parvaspina steinstansana* (Johnson and Clarke, 1983)**	Tar River Spinymussel	Reassigned from *Elliptio*
***Pegias* Simpson, 1900**		
***Pegias fabula* (Lea, 1838)**	Littlewing Pearlymussel	
***Plectomerus* Conrad, 1853**		
***Plectomerus dombeyanus* (Valenciennes, 1827)**	Bankclimber	
***Plethobasus* Simpson, 1900**		
***Plethobasus cicatricosus* (Say, 1829)**	White Wartyback	
***Plethobasus cooperianus* (Lea, 1834)**	Orangefoot Pimpleback	
***Plethobasus cyphyus* (Rafinesque, 1820)**	Sheepnose	
***Pleurobema* Rafinesque, 1819**		
**Pleurobema altum* (Conrad, 1854)	Highnut	Considered a *nomen dubium*
***Pleurobema athearni* Gangloff, Williams, and Feminella, 2006**	Canoe Creek Clubshell	Described as new species
**Pleurobema avellanum* Simpson, 1900	Hazel Pigtoe	Synonym of *Pleurobema rubellum*
***Pleurobema beadleianum* (Lea, 1861)**	Mississippi Pigtoe	
**Pleurobema bournianum* (Lea, 1840)	Scioto Pigtoe	Synonym of *Pleurobema clava*
**Pleurobema chattanoogaense* (Lea, 1858)	Painted Clubshell	Synonym of *Pleurobema decisum*
***Pleurobema clava* (Lamarck, 1819)**	Clubshell	
**Pleurobema collina* (Conrad, 1836)	James Spinymussel	Reassigned to *Parvaspina*
***Pleurobema cordatum* (Rafinesque, 1820)**	Ohio Pigtoe	
***Pleurobema curtum* (Lea, 1859)**	Black Clubshell	
***Pleurobema decisum* (Lea, 1831)**	Southern Clubshell	
***Pleurobema fibuloides* (Lea, 1859)**	Kusha Pigtoe	Elevated from synonymy
**Pleurobema flavidulum* (Lea, 1861)	Yellow Pigtoe	Synonym of *Pleurobema perovatum*
**Pleurobema furvum* (Conrad, 1834)	Dark Pigtoe	Synonym of *Pleurobema rubellum*
***Pleurobema georgianum* (Lea, 1841)**	Southern Pigtoe	

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
**Pleurobema gibberum* (Lea, 1838)	Cumberland Pigtoe	Reassigned to *Pleuronaia*
**Pleurobema hagleri* (Frierson, 1900)	Brown Pigtoe	Synonym of *Pleurobema rubellum*
***Pleurobema hanleyianum* (Lea, 1852)**	Georgia Pigtoe	
***Pleurobema hartmanianum* (Lea, 1860)**	Cherokee Pigtoe	Elevated from synonymy
**Pleurobema johannis* (Lea, 1859)	Alabama Pigtoe	Synonym of *Pleurobema perovatum*
***Pleurobema marshalli* Frierson, 1927**	Flat Pigtoe	
**Pleurobema murrayense* (Lea, 1868)	Coosa Pigtoe	Synonym of *Pleurobema stabile*
**Pleurobema nucleopsis* (Conrad, 1849)	Longnut	Synonym of *Pleurobema georgianum*
***Pleurobema oviforme* (Conrad, 1834)**	Tennessee Clubshell	
***Pleurobema perovatum* (Conrad, 1834)**	Ovate Clubshell	
***Pleurobema plenum* (Lea, 1840)**	Rough Pigtoe	
***Pleurobema pyriforme* (Lea, 1857)**	Oval Pigtoe	
***Pleurobema riddellii* (Lea, 1861)**	Louisiana Pigtoe	
***Pleurobema rubellum* (Conrad, 1834)**	Warrior Pigtoe	
***Pleurobema rubrum* (Rafinesque, 1820)**	Pyramid Pigtoe	
***Pleurobema sintoxia* (Rafinesque, 1820)**	Round Pigtoe	
***Pleurobema stabile* (Lea, 1861)**	Coosa Pigtoe	Elevated from synonymy
***Pleurobema strodeanum* (Wright, 1898)**	Fuzzy Pigtoe	
***Pleurobema taitianum* (Lea, 1834)**	Heavy Pigtoe	
**Pleurobema troschelianum* (Lea, 1852)	Alabama Clubshell	Synonym of *Pleurobema georgianum*
***Pleurobema verum* (Lea, 1861)**	True Pigtoe	
***Pleuronaia* Frierson, 1927**		Elevated from synonymy
***Pleuronaia barnesiana* (Lea, 1838)**	Tennessee Pigtoe	Reassigned from *Fusconaia*
***Pleuronaia dolabelloides* (Lea, 1840)**	Slabside Pearlymussel	Reassigned from *Lexingtonia*
***Pleuronaia gibber* (Lea, 1838)**	Cumberland Pigtoe	Reassigned from *Pleurobema*; spelling correction of species name
***Popenais* Frierson, 1927**		
***Popenais popeii* (Lea, 1857)**	Texas Hornshell	
***Potamilus* Rafinesque, 1818**		
***Potamilus alatus* (Say, 1817)**	Pink Heelsplitter	
***Potamilus amphichaenus* (Frierson, 1898)**	Texas Heelsplitter	
***Potamilus capax* (Green, 1832)**	Fat Pocketbook	
***Potamilus inflatus* (Lea, 1831)**	Inflated Heelsplitter	Common name changed from Alabama Heelsplitter
***Potamilus metnecktayi* Johnson, 1998**	Salina Mucket	Described as new species
***Potamilus ohiensis* (Rafinesque, 1820)**	Pink Papershell	
***Potamilus purpuratus* (Lamarck, 1819)**	Bleufer	
***Ptychobranchus* Simpson, 1900**		
***Ptychobranchus fasciolaris* (Rafinesque, 1820)**	Kidneyshell	
***Ptychobranchus foremanianus* (Lea, 1842)**	Rayed Kidneyshell	Elevated from synonymy
***Ptychobranchus greenii* (Conrad, 1834)**	Triangular Kidneyshell	
***Ptychobranchus jonesi* (van der Schalie, 1934)**	Southern Kidneyshell	
***Ptychobranchus occidentalis* (Conrad, 1836)**	Ouachita Kidneyshell	
**Ptychobranchus subtentum* (Say, 1825)	Fluted Kidneyshell	Incorrect spelling of species name
***Ptychobranchus subtentus* (Say, 1825)**	Fluted Kidneyshell	Spelling correction of species name
***Pyganodon* Crosse and Fischer, 1894**		
***Pyganodon cataracta* (Say, 1817)**	Eastern Floater	
***Pyganodon fragilis* (Lamarck, 1819)**	Newfoundland Floater	
***Pyganodon gibbosa* (Say, 1824)**	Inflated Floater	
***Pyganodon grandis* (Say, 1829)**	Giant Floater	
***Pyganodon lacustris* (Lea, 1857)**	Lake Floater	Publication date corrected

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Quadrula* Rafinesque, 1820**		
***Quadrula apiculata* (Say, 1829)**	Southern Mapleleaf	
**Quadrula asperata* (Lea, 1861)	Alabama Orb	Reassigned to *Cyclonaias*
**Quadrula aurea* (Lea, 1859)	Golden Orb	Reassigned to *Cyclonaias*
***Quadrula couchiana* (Lea, 1860)**	Rio Grande Monkeyface	
**Quadrula cylindrica cylindrica* (Say, 1817)	Rabbitsfoot	Nominotypical subspecies not required; reassigned to *Theliderma*
**Quadrula cylindrica strigillata* (Wright, 1898)	Rough Rabbitsfoot	Subspecies no longer recognized
***Quadrula fragosa* (Conrad, 1835)**	Winged Mapleleaf	
**Quadrula houstonensis* (Lea, 1859)	Smooth Pimpleback	Reassigned to *Cyclonaias*
**Quadrula intermedia* (Conrad, 1836)	Cumberland Monkeyface	Reassigned to *Theliderma*
**Quadrula kieneriana* (Lea, 1852)	Coosa Orb	Reassigned to *Cyclonaias*
**Quadrula metanevra* (Rafinesque, 1820)	Monkeyface	Reassigned to *Theliderma*
***Quadrula nobilis* (Conrad, 1854)**	Gulf Mapleleaf	Elevated from synonymy
**Quadrula nodulata* (Rafinesque, 1820)	Wartyback	Reassigned to *Cyclonaias*
**Quadrula petrina* (Gould, 1855)	Texas Pimpleback	Reassigned to *Cyclonaias*
**Quadrula pustulosa mortoni* (Conrad, 1835)	Western Pimpleback	Subspecies elevated to species; reassigned to *Cyclonaias*
**Quadrula pustulosa pustulosa* (Lea, 1831)	Pimpleback	Nominotypical subspecies not required; reassigned to *Cyclonaias*
***Quadrula quadrula* (Rafinesque, 1820)**	Mapleleaf	
**Quadrula refulgens* (Lea, 1868)	Purple Pimpleback	Reassigned to *Cyclonaias*
***Quadrula rumphiana* (Lea, 1852)**	Ridged Mapleleaf	
**Quadrula sparsa* (Lea, 1841)	Appalachian Monkeyface	Reassigned to *Theliderma*
**Quadrula stapes* (Lea, 1831)	Stirrupshell	Reassigned to *Theliderma*
**Quadrula tuberosa* (Lea, 1840)	Rough Rockshell	Synonym of *Theliderma metanevra*
**Quincuncina* Ortmann, 1922		Synonym of *Fusconaia*
**Quincuncina burkei* Walker, 1922	Tapered Pigtoe	Reassigned to *Fusconaia*
**Quincuncina infucata* (Conrad, 1834)	Sculptured Pigtoe	Reassigned to *Cyclonaias*
**Quincuncina mitchelli* (Simpson, 1895)	False Spike	Reassigned to *Fusconaia*
***Reginaia* Campbell and Lydeard, 2012**		Described as new genus
***Reginaia apalachicola* (Williams and Fradkin, 1999)**	Apalachicola Ebonyshell	Described as new species; reassigned from *Fusconaia*
***Reginaia ebenus* (Lea, 1831)**	Ebonyshell	Reassigned from *Fusconaia*; spelling correction of species name
***Reginaia rotulata* (Wright, 1899)**	Round Ebonyshell	Reassigned from *Obovaria*
***Simpsonaias* Frierson, 1914**		
***Simpsonaias ambigua* (Say, 1825)**	Salamander Mussel	
***Sinanodonta* Modell, 1945**		Not previously reported from North America
***Sinanodonta beringiana* (Middendorff, 1851)**	Yukon Floater	Reassigned from *Anodonta*
***Sinanodonta woodiana* (Lea, 1834)**	Chinese Pondmussel	Introduced and established in New Jersey
***Strophitus* Rafinesque, 1820**		
***Strophitus connasaugaensis* (Lea, 1858)**	Alabama Creekmussel	
***Strophitus subvexus* (Conrad, 1834)**	Southern Creekmussel	
***Strophitus undulatus* (Say, 1817)**	Creeper	
***Theliderma* Swainson, 1840**		Elevated from synonymy
***Theliderma cylindrica* (Say, 1817)**	Rabbitsfoot	Reassigned from *Quadrula*
***Theliderma intermedia* (Conrad, 1836)**	Cumberland Monkeyface	Reassigned from *Quadrula*
***Theliderma metanevra* (Rafinesque, 1820)**	Monkeyface	Reassigned from *Quadrula*
***Theliderma sparsa* (Lea, 1841)**	Appalachian Monkeyface	Reassigned from *Quadrula*
***Theliderma stapes* (Lea, 1831)**	Stirrupshell	Reassigned from *Quadrula*

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Toxolasma* Rafinesque, 1831**		
***Toxolasma corvunculus* (Lea, 1868)**	Southern Purple Lilliput	
***Toxolasma cylindrellus* (Lea, 1868)**	Pale Lilliput	
***Toxolasma lividum* Rafinesque, 1831**	Purple Lilliput	Spelling correction of species name; parentheses unnecessary
**Toxolasma lividus* (Rafinesque, 1831)	Purple Lilliput	Incorrect spelling of species name
**Toxolasma mearnsi* (Simpson, 1900)	Western Lilliput	Synonym of *Toxolasma texasiense*
***Toxolasma parvum* (Barnes, 1823)**	Lilliput	Spelling correction of species name
**Toxolasma parvus* (Barnes, 1823)	Lilliput	Incorrect spelling of species name
***Toxolasma paulum* (Lea, 1840)**	Iridescent Lilliput	Spelling correction of species name
**Toxolasma paulus* (Lea, 1840)	Iridescent Lilliput	Incorrect spelling of species name
***Toxolasma pullus* (Conrad, 1838)**	Savannah Lilliput	
***Toxolasma texasiense* (Lea, 1857)**	Texas Lilliput	Spelling correction of species name
**Toxolasma texasiensis* (Lea, 1857)	Texas Lilliput	Incorrect spelling of species name
***Tritogonia* Agassiz, 1852**		
***Tritogonia verrucosa* (Rafinesque, 1820)**	Pistolgrip	
***Truncilla* Rafinesque, 1819**		
***Truncilla cognata* (Lea, 1860)**	Mexican Fawnsfoot	
***Truncilla donaciformis* (Lea, 1828)**	Fawnsfoot	
***Truncilla macrodon* (Lea, 1859)**	Texas Fawnsfoot	
***Truncilla truncata* Rafinesque, 1820**	Deertoe	
***Uniomerus* Conrad, 1853**		
***Uniomerus carolinianus* (Bosc, 1801)**	Eastern Pondhorn	Common name changed from Florida Pondhorn
***Uniomerus columbensis* (Lea, 1857)**	Apalachicola Pondhorn	Elevated from synonymy
***Uniomerus declivis* (Say, 1831)**	Tapered Pondhorn	
***Uniomerus tetralasmus* (Say, 1831)**	Pondhorn	
***Utterbackia* Baker, 1927**		
***Utterbackia imbecillis* (Say, 1829)**	Paper Pondshell	
***Utterbackia peggyae* (Johnson, 1965)**	Florida Floater	
***Utterbackia peninsularis* Bogan and Hoeh, 1995**	Peninsular Floater	
***Utterbackiana* Frierson, 1927**		Elevated from synonymy
***Utterbackiana couperiana* (Lea, 1840)**	Barrel Floater	Reassigned from *Anodonta*
***Utterbackiana hartfieldorum* (Williams, Bogan, and Garner, 2009)**	Cypress Floater	Described as new species; reassigned from *Anodonta*
***Utterbackiana heardi* (Gordon and Hoeh, 1995)**	Apalachicola Floater	Reassigned from *Anodonta*
***Utterbackiana implicata* (Say, 1829)**	Alewife Floater	Reassigned from *Anodonta*
***Utterbackiana suborbiculata* (Say, 1831)**	Flat Floater	Reassigned from *Anodonta*
***Venustaconcha* Frierson, 1927**		
***Venustaconcha ellipsiformis* (Conrad, 1836)**	Ellipse	
***Venustaconcha pleasii* (Marsh, 1891)**	Bleedingtooth Mussel	
***Venustaconcha trabalis* (Conrad, 1834)**	Tennessee Bean	Reassigned from *Villosa*; common name changed from Cumberland Bean
***Venustaconcha troostensis* (Lea, 1834)**	Cumberland Bean	Elevated from synonymy
***Villosa* Frierson, 1927**		
**Villosa amygdala* (Lea, 1843)	Florida Rainbow	Incorrect spelling of species name
***Villosa amygdalum* (Lea, 1843)**	Florida Rainbow	Spelling correction of species name
**Villosa arkansasensis* (Lea, 1862)	Ouachita Creekshell	Reassigned to *Obovaria*
**Villosa choctawensis* Athearn, 1964	Choctaw Bean	Reassigned to *Obovaria*
***Villosa constricta* (Conrad, 1838)**	Notched Rainbow	
***Villosa delumbis* (Conrad, 1834)**	Eastern Creekshell	
***Villosa fabalis* (Lea, 1831)**	Rayed Bean	

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Table 2, continued.

Scientific Name	Common Name	Changes in Scientific and Common Names
***Villosa iris* (Lea, 1829)**	Rainbow	
***Villosa lienosa* (Conrad, 1834)**	Little Spectaclecase	
***Villosa nebulosa* (Conrad, 1834)**	Alabama Rainbow	
***Villosa ortmanni* (Walker, 1925)**	Kentucky Creekshell	
**Villosa perpurpurea* (Lea, 1861)	Purple Bean	Synonym of *Venustaconcha trabalis*
***Villosa sima* (Lea, 1838)**	Caney Fork Rainbow	Elevated from synonymy
***Villosa taeniata* (Conrad, 1834)**	Painted Creekshell	
**Villosa trabalis* (Conrad, 1834)	Cumberland Bean	Reassigned to *Venustaconcha*
***Villosa umbrans* (Lea, 1857)**	Coosa Creekshell	Species elevated from subspecies
**Villosa vanuxemensis umbrans* (Lea, 1857)	Coosa Creekshell	Subspecies elevated to species
***Villosa vanuxemensis* (Lea, 1838)**	Mountain Creekshell	
**Villosa vanuxemensis vanuxemensis* (Lea, 1838)	Mountain Creekshell	Nominotypical subspecies not required
***Villosa vaughaniana* (Lea, 1838)**	Carolina Creekshell	
***Villosa vibex* (Conrad, 1834)**	Southern Rainbow	
***Villosa villosa* (Wright, 1898)**	Downy Rainbow	

genus, species, and subspecies levels relative to previous lists. We recognize in total 298 freshwater mussel species from the United States and Canada. These comprise the families Margaritiferidae with one genus and five species and Unionidae with 54 genera and 293 species (Table 2). Turgeon et al. (1998) recognized in total 304 taxa: Margaritiferidae with two genera and five species and Unionidae with 49 genera, 286 species, and 13 subspecies. We summarize our changes to Turgeon et al. (1998) as follows. We recognize eight additional genera, including three recently described (*Hamiota*, *Parvaspina*, and *Reginaia*), four elevated from synonymy (*Eurynia*, *Pleuronaia*, *Theliderma*, and *Utterbackiana*), and one newly reported from North America (*Sinanodonta*). We place in synonymy four genera, including one in the Margaritiferidae (*Cumberlandia*) and three in the Unionidae (*Arkansia*, *Lexingtonia*, and *Quincuncina*). We recognize 25 additional species (all Unionidae), including four newly described species and 21 species elevated from synonymy. We place in synonymy 29 species and consider *Pleurobema altum* a nomen dubium, and we reassigned 41 species to other genera. We corrected the specific epithet spelling for eight species, corrected the date of publication for four, and changed the common names of five. Last, we recognized no subspecies, elevating 10 subspecies to species status and subsuming four subspecies into their nominal species (see Methods).

Margaritiferidae Henderson, 1929

Turgeon et al. (1998) recognized two genera in Margaritiferidae, *Cumberlandia* (one species) and *Margaritifera* (four species). On the basis of shell morphology and soft anatomy, Smith (2001) placed *Cumberlandia* in *Margaritanopsis* and *Margaritifera* (in part) in *Pseudunio*, but this classification was not widely accepted. In a molecular phylogenetic analysis, Huff et al. (2004) considered *Cumberlandia* a junior synonym of *Margaritifera*, and this classification was followed by some subsequent authors (e.g., Graf and Cummings 2007, 2017; Cummings and Graf 2010), but others continued to recognize the genus as valid (e.g., Williams et al. 2008; Watters et al. 2009; Haag 2012). A more comprehensive phylogeny of the Margaritiferidae that included eight of 13 currently recognized species (three from North America) retained the use of *Cumberlandia* (Bolotov et al. 2015). However, based on more recent evidence (Bolotov et al. 2016; Araujo et al. 2017), we consider *Cumberlandia* a junior synonym of *Margaritifera*.

Cumberlandia *Ortmann, 1912*.—Turgeon et al. (1998) recognized one species, *Cumberlandia monodonta*. We place *Cumberlandia* in the synonymy of *Margaritifera* (see Margaritiferidae).

Margaritifera *Schumacher, 1816*.—Turgeon et al. (1998) recognized four species of *Margaritifera*. Placement of *Cumberlandia* in the synonymy of *Margaritifera* brings the number of recognized species to five (see Margaritiferidae).

Unionidae Rafinesque, 1820

Turgeon et al. (1998) recognized 49 genera, 286 species, and 13 subspecies in Unionidae. We recognize 54 genera, 293 species, and no subspecies. We provide support for and discussion of these changes in the following assessments of genera.

Actinonaias *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized two species, *Actinonaias ligamentina* and *Actinonaias pectorosa*. Molecular analyses (e.g., Campbell et al. 2005; Zanatta and Murphy 2006) found that the two species of *Actinonaias* together did not represent a monophyletic grouping, but the position of each of these lineages within the Lampsilini was unresolved. The type locality for *Actinonaias* is central Mexico, and 10 recognized species are restricted to this region (Graf and Cummings 2017), but no species

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attributable to *Actinonaias* occur between Mexico and the range of *ligamentina* and *pectorosa* in the central United States and southern Canada. No phylogenetic research has examined relationships among Mexican *Actinonaias* and *ligamentina* and *pectorosa*, but it is unlikely they are closely related considering the disjunct distribution and lack of precedent for such a geographical pattern in other freshwater taxa (e.g., Miller et al. 2005). *Actinonaias ligamentina* and *pectorosa* require placement in two different genera, but at this time we retain these two species in the genus *Actinonaias* pending the outcome of further phylogenetic research.

Alasmidonta *Say, 1818*.—Turgeon et al. (1998) recognized 12 species, and recent evidence supports no changes to this classification.

Amblema *Rafinesque, 1820*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification.

Anodonta *Lamarck, 1799*.—Turgeon et al. (1998) recognized 10 species. Mock et al. (2004) and Zanatta et al. (2007) found *Anodonta* to be polyphyletic, with eastern North American species forming a monophyletic clade distinct from the one that includes the type species (*Anodonta cygnea*, which occurs in Eurasia) and western North American *Anodonta*. Without discussion, Graf and Cummings (2007) and Cummings and Graf (2010) placed *Anodonta couperiana*, *A. heardi*, and *A. suborbiculata* in *Utterbackia*, and *A. implicata* in *Pyganodon*. Because no supporting evidence was provided, we do not recognize these changes. The next available genus for the eastern North American clade (*A. couperiana*, *A. heardi*, *A. suborbiculata*, and *A. implicata*) identified as distinct by Mock et al. (2004) is *Utterbackiana*. *Anodonta hartfieldorum* Williams, Bogan, and Garner, 2009, was described subsequently and also belongs to *Utterbackiana* (see *Utterbackiana*).

In a phylogenetic analysis of western North American *Anodonta*, Chong et al. (2008) found *A. beringiana* to be more closely related to the Asian species *Sinanodonta woodiana* than to North American species. Based on this evidence, we reassign *beringiana* to *Sinanodonta* (see *Sinanodonta*).

We retain the remaining four western North American species within *Anodonta* (*A. californiensis*, *A. kennerlyi*, *A. nuttalliana*, and *A. oregonensis*) based on their phylogenetic affinity to Eurasian *Anodonta* (Mock et al. 2004; Zanatta et al. 2007; Chong et al. 2008). *Anodonta dejecta* was recognized by Turgeon et al. (1998), Graf and Cummings (2007), and Cummings and Graf (2010). This species is treated as a synonym of *A. californiensis* by Bequaert and Miller (1973) and the Arizona Game and Fish Department (2017). We do not recognize *A. dejecta*, which is here placed in synonymy of *A. californiensis*.

Anodontoides *Simpson in Baker, 1898*.—Turgeon et al. (1998) recognized two species. One additional species, *Anodontoides denigrata*, was recognized without discussion by Neves et al. (1997) and Cicerello and Schuster (2003). Haag and Cicerello (2016) recognized *A. denigrata* on the basis of molecular data showing that upper Cumberland River drainage populations were distinct from *A. ferussacianus* (Bogan and Raley 2013), and we recognize this species for the same reason. Bogan and Raley (2013) referred to *A. denigrata* as *A. argenteus* (Lea, 1840), for which the type locality is Stones River, Tennessee. The Stones River is a tributary of the middle Cumberland River and well downstream of the putative distribution of *A. denigrata* and other species considered endemic to the upper Cumberland River drainage upstream of the hypothesized original location of Cumberland Falls (Haag and Cicerello 2016). Until further research delineates this species' distribution more precisely, we use *A. denigrata*, for which the type locality is in the upper Cumberland River drainage (Clear Fork, Campbell County, Tennessee; see Ortmann 1918). Ahlstedt et al. (2016) reported a possibly distinct *Anodontoides* species from the Powell River, Virginia, but further work is needed to determine its validity and taxonomy.

Arcidens *Simpson, 1900*.—Turgeon et al. (1998) recognized one species, *Arcidens confragosus*. Clarke (1981) considered *Arkansia* (see *Arkansia*) a junior synonym of *Arcidens* (see also Graf and Cummings 2007), and this classification was supported by morphological and molecular data (Inoue et al. 2014). We recognize two species of *Arcidens*.

Arkansia *Ortmann and Walker, 1912*.—*Arkansia* was described as a monotypic genus including *A. wheeleri*, which was recognized by Turgeon et al. (1998). We place *Arkansia* in the synonymy of *Arcidens* (see *Arcidens*).

Cyclonaias *Pilsbry in Ortmann and Walker, 1922*.—Turgeon et al. (1998) recognized *Cyclonaias*, which has long been considered a monotypic genus for *C. tuberculata*. *Cyclonaias tuberculata* has been aligned with the Quadrulini based on morphological (e.g., Frierson 1927; Modell 1964) and protein polymorphism data (Davis and Fuller 1981). Heard and Guckert (1971) placed *Cyclonaias* in the Pleurobemini based on its ectobranchous brooding (see also Graf and Cummings 2007). However, it appears that ectobranchy arose multiple times (Davis and Fuller 1981; Graf 2002; Roe and Hoeh 2003), meaning that this trait does not necessarily exclude *Cyclonaias* from the Quadrulini, and some female *C. tuberculata* brood glochidia in all four gills (Frierson 1927).

Recent molecular studies consistently supported inclusion of *Cyclonaias* in the Quadrulini, but they further show that it is a member of a monophyletic clade including *Q. pustulosa* and related species (Campbell et al. 2005; Campbell and Lydeard 2012b). Serb et al. (2003) did not support this relationship, but these results were later attributed to an error in sample labeling (Campbell and Lydeard 2012b). However, Serb et al. (2003) as well as Campbell et al. (2005) and Campbell and Lydeard (2012b) support the monophyly of the *Quadrula pustulosa* clade and its distinctiveness from other species of *Quadrula* (see *Quadrula* and *Theliderma*). In addition to *Cyclonaias tuberculata*, the *Quadrula pustulosa* clade identified by these studies includes the following species recognized by Turgeon et al. (1998): *Q. asperata*, *Q. aurea*, *Q. houstonensis*, *Q. nodulata*, *Q. petrina*, *Q. pustulosa*, and *Q. refulgens*, as well

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as *Fusconaia succissa* and *Quincuncina infucata* (see *Fusconaia* and *Quincuncina*).

The name *Quadrula* is not available for the *Q. pustulosa* clade because the type species, *Q. quadrula*, is a member of another distinct, monophyletic clade (see *Quadrula*). Graf and Cummings (2007) elevated the generic name *Amphinaias* Crosse and Fischer, 1894, for the *Q. pustulosa* clade. The type species for *Amphinaias* (by original designation) is *Unio couchianus* Lea, 1860, which has a quadrate shell and sulcus (but lacks pustules) similar to the *Q. quadrula* clade. This morphology is very different from the rounded, pustulose shells of the *Q. pustulosa* clade. *Quadrula couchiana* is considered extinct and genetic data are unavailable; however, we do not consider *Amphinaias* an available name for the *Q. pustulosa* clade because of the strongly divergent morphology of the type species. Campbell and Lydeard (2012b) proposed *Rotundaria* Rafinesque, 1820, as a name for the *Q. pustulosa* clade, presuming its availability based on statements in Valenciennes (1827). However, Valenciennes noted that Rafinesque had confused two species, one for which he kept Rafinesque's name *Unio verrucosa* and named the other *Unio tuberculosa* [sic]. As such, Valenciennes's statement cannot be accepted as a subsequent designation of *Obliquaria tuberculata* Rafinesque, 1820, as the type species of *Rotundaria* (P. Bouchet, Muséum National d'Histoire Naturelle, Paris, personal communication), and Herrmannsen (1848) later designated *Obliquaria subrotunda* Rafinesque, 1820, as the type species of *Rotundaria*. Rafinesque did not select a type species for *Rotundaria* and because more than one species was included by him in the genus, the type species cannot be fixed by monotypy. Therefore, *Rotundaria* is not available for the *Q. pustulosa* clade. Frierson (1927) erected the subgenus *Bullata* for *Q. pustulosa* but realized this was preoccupied and created the replacement name *Pustulosa* with the same type species. Thus, *Cyclonaias* becomes the oldest available name for this group.

Of the 10 species discussed above as members of *Cyclonaias*, three were not recognized by Turgeon et al. (1998) (*C. archeri*, *C. kieneriana*, and *C. kleiniana*), and one was considered a subspecies (*C. mortoni*, as *Quadrula pustulosa mortoni*). Graf and Cummings (2007) elevated *Q. archeri* from synonymy with *Q. asperata*, but they provided no justification for this change. The distinctiveness of *C. archeri* was recognized by Williams et al. (2008) based on its morphology, absence of intergrades, and isolated and restricted distribution. We recognize *C. archeri*. The distinctiveness of *C. kieneriana* was recognized by Williams et al. (2008) based on shell morphology; however, it was not supported by molecular data (Serb et al. 2003), but that study included only one specimen of this putative taxon. We recognize *C. kieneriana* until additional information becomes available (see Williams et al. 2008). *Cyclonaias kleiniana* was synonymized under *Quincuncina infucata* by Clench and Turner (1956), but molecular studies supported the distinctiveness of these species and their inclusion in *Cyclonaias* (Lydeard et al. 2000; Campbell and Lydeard 2012b). Molecular data supported the distinctiveness of *C. mortoni* from *C. pustulosa* (Serb et al. 2003). In summary, we recognize *Cyclonaias* as including 14 species: *C. tuberculata*, seven species recognized by Turgeon et al. (1998) under *Quadrula*, one subspecies recognized by Turgeon et al. (1998) but now elevated to species status (*C. mortoni*), two species recognized by Turgeon et al. (1998) in different genera (*C. infucata* and *C. succissa*), and three species elevated from synonymy (*C. archeri*, *C. kieneriana*, and *C. kleiniana*).

Cyprogenia *Agassiz, 1852*.—Turgeon et al. (1998) recognized two species. Subsequent molecular data suggested cryptic species diversity in the genus (Serb and Barnhart 2008; Grobler et al. 2011). The most recent molecular analysis of *Cyprogenia* identified three independent evolutionary lineages: *C. aberti* in the Ozark drainages of Arkansas, Missouri, and Kansas; *C. stegaria* in the Ohio River Basin; and a third lineage in the Ouachita River drainage in Arkansas (Chong et al. 2016). Confusion regarding the type locality of *Unio lamarckianus* Lea, 1852, requires resolution to determine whether that name is available for the Ouachita River drainage population. We recognize the distinctiveness of this species but defer including it in our list until a specific epithet can be designated.

Cyrtonaias *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized one species, *Cyrtonaias tampicoensis*, and recent evidence supports no changes to this classification. Five other species are recognized, all of which occur in Mexico or Central America (Graf and Cummings 2017).

Disconaias *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized one species, *Disconaias salinasensis* Simpson in Dall, 1908, which was subsequently placed in the synonymy of *Disconaias fimbriata* by Graf and Cummings (2007). Five other species are recognized, all of which occur in Mexico (Graf and Cummings 2017). We recognize *Disconaias fimbriata* as the only species of the genus occurring in the United States (Rio Grande drainage).

Dromus *Simpson, 1900*.—Turgeon et al. (1998) recognized one species, *Dromus dromas*, and recent evidence supports no changes to this classification.

Ellipsaria *Rafinesque, 1820*.—Turgeon et al. (1998) recognized one species, *Ellipsaria lineolata*, and recent evidence supports no changes to this classification.

Elliptio *Rafinesque, 1819*.—Turgeon et al. (1998) recognized 36 species, making it the largest unionid genus in the United States and Canada, but species concepts within this group remain mostly untested, and their highly variable shell morphology precludes traditional approaches for species diagnosis. Recent molecular studies have largely supported the monophyly of *Elliptio* with two exceptions (Campbell et al. 2005; Campbell and Lydeard 2012b; Perkins et al. 2017). *Elliptio dilatata*, which is morphologically and anatomically similar to many *Elliptio*, is not a member of this group; we recognize reassignment of this species to *Eurynia* (Campbell and Lydeard 2012b). We also recognize reassignment of *Elliptio steinstansana* to *Parvaspina* based on molecular data (Perkins et al. 2017). It is important to note that phylogenetic

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affinities remain unknown for most species that we currently recognize under *Elliptio* and some may prove to be members of other genera (e.g., *Eurynia*; Elderkin et al. 2008; Campbell and Lydeard 2012b).

Because of our poor understanding of species diversity within *Elliptio*, we largely retain the classification of Turgeon et al. (1998) with the following exceptions. We stress that this classification is provisional and meant to provide a stable, working hypothesis for diversity within the genus. We elevate from synonymy four species of *Elliptio*: *E. fumata* (from *E. complanata*), *E. occulta* and *E. pullata* (from *E. icterina*), and *E. purpurella* (from *E. arctata* and *E. strigosa*); these changes are based primarily on differences in shell morphology (Brim Box and Williams 2000; Williams et al. 2008, 2011, 2014). We place eight species into synonymy. Four Atlantic Slope species (*E. errans*, *E. hepatica*, *E. lugubris*, and *E. raveneli*) were recognized by Turgeon et al. (1998) based on Davis and Mulvey (1993). The research by Davis and Mulvey (1993) was confined almost exclusively to the Savannah River drainage and has no context within the greater Atlantic Coast region. The validity of these species has not been evaluated further. We return these species to synonymy following Johnson (1970) as follows: *E. errans* is synonymized under *E. complanata*; and *E. hepatica*, *E. lugubris*, and *E. raveneli* are synonymized under *E. icterina*. We place *Elliptio waccamawensis* into the synonymy of *E. congaraea* based on molecular data (McCartney et al. 2016). We place the following species into synonymy based on examination of shell type material by Clarke (1992) and Williams et al. (2011, 2014): *E. waltoni* (synonymized under *E. ahenea*), *E. judithae* (synonymized under *E. roanokensis*), and *E. buckleyi* (synonymized under *E. jayensis*). After these changes, we recognize 30 species of *Elliptio*, and it remains the largest unionid genus in the United States and Canada.

Turgeon et al. (1998) listed the common names Flat Spike and Florida Shiny Spike for *Elliptio jayensis* and *E. buckleyi*, respectively. We follow the recommendation of Williams et al. (2014) that the common name of *E. jayensis* be changed to Florida Spike because the species is largely endemic to that state and is neither consistently flat nor shiny.

Elliptoideus *Frierson, 1927*.—Turgeon et al. (1998) recognized one species, *Elliptoideus sloatianus*, and recent evidence supports no changes to this classification.

Epioblasma *Rafinesque, 1831*.—Turgeon et al. (1998) recognized 20 species and five subspecies. Our changes to this classification involve recognition of two newly described cryptic species, elevating one species from synonymy, and elevating subspecies to species status. We recognize *Epioblasma ahlstedti* Jones and Neves, 2010, a cryptic species formerly included within *E. capsaeformis*, and we recognize and elevate to species status *Epioblasma aureola* Jones and Neves, 2010, formerly identified as *E. florentina walkeri* but described as *E. florentina aureola* Jones and Neves, 2010.

Epioblasma cincinnatiensis was not recognized by Turgeon et al. (1998), and it has been considered a synonym (e.g., Parmalee and Bogan 1998) or a subspecies (e.g., Morrison 1942) of *Epioblasma torulosa*. Williams et al. (2008) elevated this species from synonymy based on examination of shell type material. Watters et al. (2009) also recognized this taxon but placed it in the synonymy of *Epioblasma phillipsii* (Conrad, 1835). However, *E. phillipsii* is considered a synonym of *Obliquaria reflexa* (see Williams et al. 2008). We follow Williams et al. (2008) in recognizing *E. cincinnatiensis*.

Turgeon et al. (1998) recognized eight subspecies of *Epioblasma* in three nominal species: *florentina* (three), *obliquata* (two), and *torulosa* (three). A conclusive assessment of the taxonomic status of these taxa may be impossible at this time because half are considered extinct (*E. florentina florentina*, *E. f. curtisii*, *E. torulosa torulosa*, and *E. t. gubernaculum*). Cummings and Berlocher (1990) found no evidence of intergradation between *E. t. torulosa* and *E. t. rangiana* and both taxa co-occurred at many sites; based on this evidence, we elevate these subspecies to species status. *Epioblasma aureola* and *E. walkeri* represent morphologically and genetically distinct sister taxa (Jones and Neves 2010, as *E. florentina aureola* and *E. florentina walkeri*). These taxa appear to be restricted to two different river systems (Tennessee and Cumberland, respectively); based on the low probability of exchange between these populations and their distinctiveness, we recognize and elevate to full species status *E. aureola* and *E. walkeri*. There is little information with which to assess the taxonomic status of *E. florentina florentina*, *E. florentina curtisii*, *E. obliquata obliquata*, *E. obliquata perobliqua*, and *E. torulosa gubernaculum*, but all have distinctive shell morphology or occupy distinct geographical regions and we recognize all these taxa as distinct species (see Methods).

We recognize 28 *Epioblasma* species, making it the second largest unionid genus in the United States and Canada.

Eurynia *Rafinesque, 1820*.—*Eurynia* was not recognized in Turgeon et al. (1998). *Eurynia* was elevated from synonymy by Campbell and Lydeard (2012b) to accommodate *Elliptio dilatata*, which consistently falls outside the *Elliptio* clade in molecular analyses (see also Perkins et al. 2017). We consider *Eurynia* monotypic at this time, but more inclusive molecular studies may identify other species that belong to this genus, including some now assigned to *Elliptio* (Elderkin et al. 2008; Campbell and Lydeard 2012b).

Fusconaia *Simpson, 1900*.—Turgeon et al. (1998) recognized 13 species. Several studies showed that the genus *Fusconaia* as portrayed by Turgeon et al. (1998) was polyphyletic (Lydeard et al. 2000; Serb et al. 2003; Campbell et al. 2005; Campbell and Lydeard 2012a, 2012b; Pfeiffer et al. 2016). Based on these results, we reassign three species recognized by Turgeon et al. (1998) to other genera: *F. succissa* to *Cyclonaias*, *F. barnesiana* to *Pleuronaia*, and *F. ebenus* to *Reginaia*. *Pleuronaia* was resurrected to accommodate *F. barnesiana*, along with two other species in the clade (Williams et al. 2008; Campbell and Lydeard 2012a, 2012b; see *Pleuronaia*). *Reginaia* was described to accommodate *F.*

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ebenus and two other species (Campbell and Lydeard 2012a; see *Reginaia*).

These studies also showed that several species assigned to other genera belonged in *Fusconaia*. Based on these results, *Quincuncina* is a junior synonym of *Fusconaia*, and we reassign *Q. burkei* and *Q. mitchelli* to *Fusconaia* (Lydeard et al. 2000; Serb et al. 2003; Campbell et al. 2005; Pfeiffer et al. 2016; see *Cyclonaias*, *Quadrula*, and *Quincuncina*). *Lexingtonia* was placed in the synonymy of *Fusconaia* when its type species, *L. subplana*, was determined a junior synonym of *Fusconaia masoni* based on molecular data (Bogan et al. 2003).

Fusconaia chunii was not recognized by Turgeon et al. (1998), but they recognized two other *Fusconaia* from Texas: *F. askewi* and *F. lananensis*. Subsequent molecular data showed that all *Fusconaia* in Texas drainages from the Sabine River west belonged to a single species (Burlakova et al. 2012). However, *Unio chunii* Lea, 1861, has priority over *Unio askewi* Marsh, 1896, and *Quadrula lananensis* Frierson, 1901, so we place *F. askewi* and *F. lananensis* in the synonymy of *F. chunii*.

We adopt the former common name for *F. askewi*, Texas Pigtoe, for *F. chunii* because it is descriptive of the species' range. Turgeon et al. (1988) listed the common name Gulf Pigtoe for *Fusconaia cerina*, but it was changed to Southern Pigtoe in Turgeon et al. (1998) without comment. However, Turgeon et al. (1998) also used Southern Pigtoe as the common name of *Pleurobema georgianum*. We designate the common name Gulf Pigtoe for *F. cerina*.

In summary, we recognize 11 species of *Fusconaia*, including eight species recognized by Turgeon et al. (1998) under *Fusconaia*, two species recognized by Turgeon et al. (1998) in other genera, and one species elevated from synonymy.

Glebula *Conrad, 1853*.—Turgeon et al. (1998) recognized one species, *Glebula rotundata*, and recent evidence supports no changes to this classification.

Gonidea *Conrad, 1857*.—Turgeon et al. (1998) recognized one species, *Gonidea angulata*, and recent evidence supports no changes to this classification.

Hamiota *Roe and Hartfield, 2005*.—*Hamiota* was described subsequent to Turgeon et al. (1998) to accommodate a monophyletic clade of four species that produce superconglutinates (Roe et al. 2001). They were previously recognized under *Lampsilis*: *L. altilis*, *L. australis*, *L. perovalis*, and *L. subangulata* (Roe and Hartfield 2005). We recognize all four of these species under *Hamiota*.

Hemistena *Rafinesque, 1820*.—Turgeon et al. (1998) recognized one species, *Hemistena lata*, and recent evidence supports no changes to this classification.

Lampsilis *Rafinesque, 1820*.—Turgeon et al. (1998) recognized 28 species and four subspecies. Molecular data indicated that *Lampsilis*, as presented by Turgeon et al. (1998), is polyphyletic (Graf and Ó Foighil 2000; Campbell et al. 2005). There are likely unrecognized taxa in the genus *Lampsilis* (e.g., in Arkansas; Harris et al. 2009). The genus *Hamiota* was described to accommodate a monophyletic clade of four species, *Lampsilis altilis*, *L. australis*, *L. perovalis*, and *L. subangulata* (Roe and Hartfield 2005), and we recognize reassignment of these species from *Lampsilis* to *Hamiota*. We also recognize reassignment of *Lampsilis haddletoni* to *Obovaria* (Williams et al. 2008; see *Obovaria*). In addition to *Hamiota*, molecular data suggested the existence of at least two other paraphyletic clades within *Lampsilis* as recognized by Turgeon et al. (1998). *Lampsilis cardium*, *L. ornata*, and *L. ovata* formed a monophyletic clade sister to *Hamiota*, and *L. siliquoidea* and *L. teres* were members of a clade sister to the latter two groups; however, these groupings were not consistently or strongly supported, and the analyses did not include other species of putative *Lampsilis* (Campbell et al. 2005). Additional generic-level changes regarding *Lampsilis* will likely occur in the future, but we retain traditional use of this genus for all species except those reassigned to *Hamiota* and *Obovaria*.

Lampsilis floridensis was not recognized by Turgeon et al. (1998), and formerly it was recognized as a subspecies (Clench and Turner 1956) or synonym (Burch 1975) of *Lampsilis teres*. We recognize *L. floridensis* as a full species based on shell morphology, unpublished molecular data, and its allopatric distribution (Williams et al. 2008).

Turgeon et al. (1998) recognized nominal *Lampsilis reeveiana* along with two subspecies, *L. r. brevicula* and *L. r. brittsi*. Molecular data showed that *brittsi* populations from the Missouri River drainage formed a well-supported monophyletic clade separate from nominal *reeveiana*, but there was no morphological or genetic distinction between nominal *L. reeveiana* and *L. r. brevicula* (Harris et al. 2004). Based on these data, we follow McMurray et al. (2012) in recognizing *L. brittsi* and *L. reeveiana* as species and placing *L. reeveiana brevicula* into the synonymy of *L. reeveiana*.

Turgeon et al. (1998) recognized nominal *Lampsilis radiata* and one subspecies, *L. r. conspicua*. However, molecular and shell morphology data did not support the distinctiveness of *L. r. conspicua* (Stiven and Alderman 1992), and we place this taxon into the synonymy of *Lampsilis radiata*. Turgeon et al. (1998) also recognized *Lampsilis fullerkati*, but we recognize placement of that species into the synonymy of *L. radiata* based on molecular data (McCartney et al. 2016).

Turgeon et al. (1998) recognized nominal *Lampsilis straminea* and one subspecies, *L. s. claibornensis*. *Lampsilis straminea straminea* is restricted to the Black Belt Prairie region of Alabama and Mississippi and is characterized by a profusion of fine, concentric ridges on the shell, which are absent in *L. s. claibornensis*. However, concentric ridges are present in some other mussels inhabiting streams in the Black Belt Prairie region and are most likely environmentally induced and not due to genetic differences (Williams et al. 2008). We do not recognize the taxonomic validity of these shell forms and place *L. s. claibornensis* in the synonymy of *Lampsilis straminea*. The common name of *Lampsilis s. straminea*, Rough Fatmucket (Turgeon et al. 1998), is

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descriptive of individuals in only a small portion of its range (i.e., the Black Belt Prairie). Therefore, we retain the common name for *L. straminea claibornensis*, Southern Fatmucket, for *L. straminea*.

In summary, we recognize 24 species of *Lampsilis* including one species elevated from synonymy and two species elevated from subspecies. *Lampsilis* is the third largest genus in the family Unionidae following *Elliptio* (30) and *Epioblasma* (28).

Lasmigona *Rafinesque, 1831*.—Turgeon et al. (1998) recognized six species and one subspecies. Williams et al. (2008) elevated *Lasmigona complanata alabamensis* to species status based on examination of museum shell material, and molecular data supported the distinctiveness of this taxon (King et al. 1999). Williams et al. (2008) also recognized Mobile Basin populations of *Lasmigona holstonia* as a distinct species based on unpublished molecular data and the occurrence of these populations in two different river systems. They resurrected from synonymy *Lasmigona etowaensis* to refer to Mobile Basin populations and retained *L. holstonia* to refer to Tennessee and Ohio River drainage populations. We recognize all three of these species.

Molecular studies showed that *Lasmigona* is polyphyletic: *L. alabamensis*, *L. complanata*, and *L. costata* formed a monophyletic clade, and *L. compressa* and *L. subviridis* represented another monophyletic clade more closely related to *Alasmidonta* (King et al. 1999). However, this study did not include all species of *Lasmigona*, and a broader study within the context of the tribe Anodontini is needed to clarify these relationships. Populations of *Lasmigona costata* in the Ozark Highlands represented a monophyletic clade strongly differentiated from populations east of the Mississippi River, suggesting the presence of at least one cryptic species within this taxon; additional investigation across the range of *L. costata* is needed to better understand these patterns (Hewitt et al. 2016). An endemic form of *Lasmigona* in the Barrens region of the upper Caney Fork drainage in Tennessee was recognized by Layzer et al. (1993), but the status of this putative taxon has not been evaluated further.

Lemiox *Rafinesque, 1831*.—Turgeon et al. (1998) recognized one species, *Lemiox rimosus*, and recent evidence supports no changes to this classification.

Leptodea *Rafinesque, 1820*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification. Smith (2000) proposed moving *Leptodea ochracea* into the genus *Ligumia* based on mantle margin pigment and size of glochidia. We do not accept this proposal due to the limited number of taxa (four species in two genera) in that analysis, and we retain *ochracea* in *Leptodea*.

Lexingtonia *Ortmann, 1914*.—Turgeon et al. (1998) recognized two species. However, the type species, *Lexingtonia subplana*, was subsequently relegated to the synonymy of *Fusconaia masoni* based on Johnson (1970) and Bogan et al. (2003). As such, *Lexingtonia* is a junior synonym of *Fusconaia*. The other species recognized by Turgeon et al. (1998), *Lexingtonia dolabelloides*, did not group with *Fusconaia* in molecular analyses but formed a monophyletic clade with two other species (Campbell et al. 2005; Campbell and Lydeard 2012a, 2012b). *Pleuronaia* was resurrected by Williams et al. (2008) to accommodate this clade (see *Pleuronaia*).

Ligumia *Swainson, 1840*.—Turgeon et al. (1998) recognized three species. Subsequent molecular studies indicated the genus is not monophyletic, but further research is needed to fully elucidate these patterns (Campbell et al. 2005; Kuehnl 2009). We retain the classification of Turgeon et al. (1998), but as additional information becomes available taxa assigned to this genus will likely change (see Raley et al. 2007). Gangloff et al. (2013) identified a genetically divergent clade of *Ligumia recta* from the Mobile Basin that may warrant recognition as a distinct taxon.

Medionidus *Simpson, 1900*.—Turgeon et al. (1998) recognized seven species. We no longer recognize *Medionidus mcglameriae*, which was placed in the synonymy of *Leptodea fragilis* based on examination of the type specimen (Williams et al. 2008). Campbell et al. (2005) found some evidence for polyphyly of *Medionidus*, but this evidence was not conclusive and we make no other changes to this genus.

Megalonaias *Utterback, 1915*.—Turgeon et al. (1998) recognized one species, *Megalonaias nervosa*, and recent evidence supports no changes to this classification.

Obliquaria *Rafinesque, 1820*.—Turgeon et al. (1998) recognized one species, *Obliquaria reflexa*, and recent evidence supports no changes to this classification.

Obovaria *Rafinesque, 1819*.—Turgeon et al. (1998) recognized six species. Molecular data showed that *Obovaria* as depicted by Turgeon et al. (1998) is polyphyletic (Campbell et al. 2005). Notably, *Obovaria rotulata* was not a member of this group, and it was later reassigned to *Reginaia* (Campbell and Lydeard 2012b); we recognize this reassignment. In an analysis by Campbell et al. (2005), *O. olivaria* fell outside the clade containing other *Obovaria* and *Epioblasma*, but this conclusion was not consistently supported. We retain *olivaria* within *Obovaria*, but further work on this species is needed to resolve its generic assignment.

Evidence also supports reassignment to *Obovaria* of species recognized by Turgeon et al. (1998) under other genera. We reassign *Villosa arkansasensis* and *V. choctawensis* to *Obovaria* based on molecular data (Kuehnl 2009; Inoue et al. 2013) and marsupial morphology (Williams et al. 2011, for *choctawensis*). We also recognize reassignment of *Lampsilis haddletoni* to *Obovaria* based on shell morphology of the type lot (Williams et al. 2008, 2011), but this species is considered extinct and there are no available soft parts for anatomical or molecular study. *Obovaria jacksoniana* was recognized in Turgeon et al. (1998) but is synonymous with *Villosa arkansasensis* (Inoue et al. 2013). *Unio jacksoniana* Frierson, 1912, is a junior synonym of *Unio arkansasensis* Lea, 1862, and we place *O. jacksoniana* in the synonymy of *Obovaria arkansasensis*. There is also potential for unrecognized taxa within *O. arkansasensis* in central Gulf Slope drainages (Inoue et al. 2013).

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In summary, we recognize seven species of *Obovaria*, including four species recognized by Turgeon et al. (1998) and three species reassigned from other genera, one from *Lampsilis* and two from *Villosa*.

Parvaspina *Perkins, Gangloff, and Johnson, 2017*.—*Parvaspina* was described subsequent to Turgeon et al. (1998) to accommodate a monophyletic clade of two species previously recognized as *Elliptio steinstansana* and *Pleurobema collina* (Perkins et al. 2017). We recognize these species as *Parvaspina steinstansana* and *Parvaspina collina*.

Pegias *Simpson, 1900*.—Turgeon et al. (1998) recognized one species, *Pegias fabula*, and recent evidence supports no changes to this classification.

Plectomerus *Conrad, 1853*.—Turgeon et al. (1998) recognized one species, *Plectomerus dombeyanus*, and recent evidence supports no changes to this classification.

Plethobasus *Simpson, 1900*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification.

Pleurobema *Rafinesque, 1819*.—Turgeon et al. (1998) recognized 32 species, making it one of the largest unionid genera. Molecular data largely support the monophyly of *Pleurobema* as depicted by Turgeon et al. (1998) with two exceptions (Campbell et al. 2005, 2008; Campbell and Lydeard 2012b). These studies support reassignment of *P. collina* to *Parvaspina* and *P. gibberum* to *Pleuronaia* (Campbell et al. 2005, 2008; Campbell and Lydeard 2012b; see *Parvaspina* and *Pleuronaia*). However, Campbell et al. (2008) and Campbell and Lydeard (2012b) provided evidence that *Pleurobema* includes two distinct lineages, one including *P. sintoxia*, *P. cordatum*, *P. plenum*, *P. riddellii*, and *P. rubrum* and the other including all other species. Further research is needed to elucidate these relationships; we retain traditional use of *Pleurobema*.

Pleurobema rivals *Elliptio* in its large number of described species and the intractability of many species concepts, particularly in the Mobile Basin, but these problems are compounded for *Pleurobema* because many putative taxa are considered extinct. Based on a comprehensive comparison of shell type specimens and other available material, Williams et al. (2008) placed into synonymy nine species of Mobile Basin *Pleurobema* recognized by Turgeon et al. (1998): *P. chattanoogaense* (into *P. decisum*); *P. murrayense* (into *P. stabile*); *P. nucleopsis* and *P. troschelianum* (into *P. georgianum*); *P. flavidulum* and *P. johannis* (into *P. perovatum*); and *P. avellanum*, *P. furvum*, and *P. hagleri* (into *P. rubellum*). Some of these synonyms are further supported by molecular data (e.g., *P. chattanoogaense*, *P. furvum*; Campbell et al. 2008), and we recognize all of these changes. We do not recognize *Pleurobema altum* since it was deemed a nomen dubium because it is not identifiable due to incomplete description, vague type locality, and lack of type material (Williams et al. 2008). One Ohio River drainage species, *Pleurobema bournianum*, was placed into the synonymy of *Pleurobema clava* based on shell morphology (Watters et al. 2009), and we recognize this change.

We recognize four additional Mobile Basin species of *Pleurobema* not recognized by Turgeon et al. (1998). Williams et al. (2008) recognized three species based on examination of shell type specimens: *P. fibuloides*, *P. hartmanianum*, and *P. stabile*. We correct the spelling of *P. stabilis* as used by Williams et al. (2008) to *stabile* based on Lee (2008). *Pleurobema athearni* Gangloff, Williams, and Feminella, 2006, was described subsequent to Turgeon et al. (1998) based on morphological data (Gangloff et al. 2006). In addition, preliminary findings identified an undescribed species in the upper Tennessee River drainage (Schilling 2015).

In summary, we recognize 23 species of *Pleurobema*, including 19 species recognized by Turgeon et al. (1998), three species elevated from synonymy, and one newly described species.

Pleuronaia *Frierson, 1927*.—*Pleuronaia* was not included in Turgeon et al. (1998). This was the senior available name for a monophyletic clade of three species—*Fusconaia barnesiana*, *Lexingtonia dolabelloides*, and *Pleurobema gibberum*—identified in a molecular study by Campbell et al. (2005). We recognize resurrection of *Pleuronaia* to accommodate this group and reassignment of these three species to *Pleuronaia* as proposed previously (Williams et al. 2008; Campbell and Lydeard 2012a, 2012b). There are likely cryptic taxa of *Pleuronaia* in the upper Tennessee River drainage (Schilling 2015). We correct the gender agreement of the specific name of *Pleuronaia gibberum* to *gibber* (H. Lee, Jacksonville, Florida, personal communication).

Popenais *Frierson, 1927*.—Turgeon et al. (1998) recognized one species, *Popenais popeii*, and recent evidence supports no changes to this classification.

Potamilus *Rafinesque, 1818*.—Turgeon et al. (1998) recognized six species. One additional species, *Potamilus metnecktayi* Johnson, 1998, was described subsequently, and we recognize this species. *Potamilus inflatus* was referred to as the Inflated Heelsplitter by Turgeon et al. (1988) but was changed to Alabama Heelsplitter by Turgeon et al. (1998) without comment. Alabama Heelsplitter is the established common name for *Lasmigona alabamensis*, and we adopt the original common name Inflated Heelsplitter for *P. inflatus*. Roe and Lydeard (1998) found the Amite River population of *P. inflatus* to be genetically divergent, and it may warrant recognition as a distinct taxon.

Ptychobranchus *Simpson, 1900*.—Turgeon et al. (1998) recognized five species. *Ptychobranchus foremanianus* was elevated from the synonymy of *Ptychobranchus greenii* (in part) by Williams et al. (2008) based on shell morphology and periostracum color. A molecular analysis of this genus included insufficient material to resolve the relationship between these two taxa (Roe 2013), but we recognize both species. We correct the gender agreement of *Ptychobranchus subtentum* to *P. subtentus* following Lee (2008).

Pyganodon *Crosse and Fischer, 1894*.—Turgeon et al. (1998) recognized five species. Graf and Cummings (2007) without comment moved *Anodonta implicata* to *Pyganodon*

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and omitted *P. fragilis* and *P. lacustris*. However, molecular data demonstrated the validity of *P. fragilis* and *P. lacustris* (Doucet-Beaupré et al. 2012). Based on these results and the lack of justification for movement of *A. implicata* to *Pyganodon*, we retain the classification of Turgeon et al. (1998) for *Pyganodon*.

Quadrula *Rafinesque, 1820*.—Turgeon et al. (1998) recognized 18 species and two subspecies. Molecular studies generally supported the monophyly of *Quadrula* as depicted by Turgeon et al. (1998), but they also showed that it is composed of three deeply divergent monophyletic clades plus *Tritogonia verrucosa*, each of which warranted generic recognition (Serb et al. 2003; Campbell et al. 2005; Campbell and Lydeard 2012b). The type species for *Quadrula* is *Q. quadrula*, and the clade containing this species also includes *Q. apiculata*, *Q. fragosa*, *Q. nobilis*, and *Q. rumphiana*. *Quadrula nobilis* was elevated from synonymy based on shell morphology and unspecified genetic data (Howells et al. 1996) but not recognized by Turgeon et al. (1998). Relationships among species in the *Q. quadrula* group were not clearly resolved by Serb et al. (2003), but we recognize all five species. We also recognize within this group *Q. couchiana* on the basis of its shell morphology, which is similar to that of *Q. quadrula* (see *Cyclonaias*).

Based on molecular data, we reassign to *Cyclonaias* 10 taxa recognized by Turgeon et al. (1998) under *Quadrula*, and we reassign 5 species to *Theliderma* (Serb et al. 2003; Campbell et al. 2005; Campbell and Lydeard 2012b; see also Graf and Cummings 2007). We also synonymize two taxa recognized by Turgeon et al. (1998) under *Quadrula* (see *Theliderma*). In summary, we recognize six species of *Quadrula*, including five recognized under this genus by Turgeon et al. (1998) and one elevated from synonymy (*Q. nobilis*).

Quincuncina *Ortmann, 1922*.—Turgeon et al. (1998) recognized three species. Molecular data showed that the type species, *Quincuncina burkei*, belongs in *Fusconaia* (Lydeard et al. 2000; Serb et al. 2003; Campbell et al. 2005). As such, *Quincuncina* is a junior synonym of *Fusconaia*, and we reassign to this genus *Q. burkei* and *Q. mitchelli* (see also Pfeiffer et al. 2016). Based on these findings, we also reassign *Q. infucata* to *Cyclonaias* (see *Cyclonaias*).

Reginaia *Campbell and Lydeard, 2012*.—*Reginaia* was described subsequent to Turgeon et al. (1998) to accommodate a monophyletic clade of two species identified in a phylogenetic analysis of Ambleminae (Campbell and Lydeard 2012b). The two *Reginaia* species were included in Turgeon et al. (1998) as *Fusconaia ebena* and *Obovaria rotulata* (Campbell and Lydeard 2012b); we recognize assignment of these species to *Reginaia*. We follow Watters et al. (2009) in correcting the spelling of the species name *ebena* to *ebenus*. A third species, *Fusconaia apalachicola* Williams and Fradkin, 1999, was described subsequent to Turgeon et al. (1998) from archaeological material; we reassign this species to *Reginaia* based on its shell characters, which are similar to those of *R. ebenus* and *R. rotulata*.

Simpsonaias *Frierson, 1914*.—Turgeon et al. (1998) recognized one species, *Simpsonaias ambigua*, and recent evidence supports no changes to this classification.

Sinanodonta *Modell, 1945*.—*Sinanodonta* was not included in Turgeon et al. (1998). This genus was previously considered to be confined to Asia and not part of the North America fauna. Molecular data showed that *A. beringiana* is more closely related to the Asian species *Sinanodonta woodiana* than to other western North American *Anodonta* (Chong et al. 2008; see *Anodonta*). Based on this evidence, we reassign *beringiana* to *Sinanodonta*. In 2010 *S. woodiana*, Chinese Pondmussel, was found in Wickecheoke Creek, a tributary of the Delaware River, New Jersey (Bogan et al. 2011a). Several known glochidial host fishes, native and introduced species, occur in the watershed (Bogan et al. 2011b). The species appears to have become established in that stream despite eradication efforts (J. Bowers-Altman, New Jersey Division of Fish and Wildlife, personal communication). We recognize *S. woodiana* as established in New Jersey (Table 2). This is the only nonindigenous unionid mussel known to have become established in the United States or Canada.

Strophitus *Rafinesque, 1820*.—Turgeon et al. (1998) recognized three species, and recent evidence supports no changes to this classification. *Strophitus undulatus*, one of the most wide-ranging species in the United States and Canada, likely contains unrecognized cryptic taxa (Watters et al. 2009).

Theliderma *Swainson, 1840*.—*Theliderma* was not recognized by Turgeon et al. (1998). This genus was resurrected from synonymy by Graf and Cummings (2007) to accommodate a monophyletic clade of five species recognized by Turgeon et al. (1998) under *Quadrula* (*Q. cylindrica*, *Q. intermedia*, *Q. metanevra*, *Q. sparsa*, and *Q. stapes*; see Serb et al. 2003). *Theliderma* is the oldest available name for this clade and has *T. metanevra* as its type species. We recognize placement of all five of these species in *Theliderma*. No molecular data are available for *Theliderma stapes*, but its shell morphology is very similar to that of other *Theliderma*, and we include it in this genus following Graf and Cummings (2007).

Turgeon et al. (1998) recognized *Quadrula tuberosa*, but we place this taxon in the synonymy of *Theliderma metanevra* following Parmalee and Bogan (1998, as *Q. metanevra*). However, the relationship of *tuberosa* to other species is uncertain, and if it represents a valid species, it is considered extinct (see Haag and Cicerello 2016). *Quadrula cylindrica* was recognized in Turgeon et al. (1998) as containing two subspecies, *Theliderma cylindrica cylindrica* and *T. cylindrica strigillata*. These subspecies traditionally were distinguished from each other based on shell morphology and distribution, with *strigillata* being confined mainly to the upper Tennessee River system in Tennessee and Virginia (Parmalee and Bogan 1998). However, the distributional limits of *strigillata* have never been clearly defined as it grades into typical *T. c. cylindrica* in larger streams, suggesting that the shell forms represent ecophenotypic variation (Ortmann 1920), and

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molecular data provide no support for recognition of *T. c. strigillata* (Serb et al. 2003; Sproules et al. 2006). Based on this evidence, we do not recognize subspecies within *T. cylindrica*. Both *T. c. cylindrica* (threatened) and *T. c. strigillata* (endangered) are federally protected taxa. Synonymizing *strigillata* under *T. cylindrica* will not remove the protection provided by the Endangered Species Act but may impact the status of populations formerly recognized as *strigillata*.

Toxolasma *Rafinesque, 1831*.—Turgeon et al. (1998) recognized eight species. Recent evidence supports no changes at the genus level, but species boundaries within *Toxolasma* remain uncertain. Howells et al. (1996) placed *Toxolasma mearnsi* in the synonymy of *Toxolasma texasiense* based on electrophoretic analysis, a change overlooked by Turgeon et al. (1998); we recognize placement of *T. mearnsi* in the synonymy of *T. texasiense*. Undescribed species of *Toxolasma* have been recognized (e.g., Gulf Lilliput) but have yet to be formerly described (Williams et al. 2008, 2014).

Lee (2006) concluded that *Toxolasma* has a neuter gender, which necessitates correction of spellings from *lividus* to *lividum*, *parvus* to *parvum*, and *paulus* to *paulum*, without change to *corvunculus*, *cylindrellus*, or *pullus*; we recognize these spelling changes. Lee (2006) provided an incorrect spelling of *Toxolasma texasiense* (as *texasense*), but we correct it based on the spelling presented in the original description.

Tritogonia *Agassiz, 1852*.—Turgeon et al. (1998) recognized one species, *Tritogonia verrucosa*. Molecular data clearly supported inclusion of *T. verrucosa* within the tribe Quadrulini, but its placement within that group was unresolved, and Serb et al. (2003) recommended its placement within *Quadrula* (*sensu lato*) until relationships were better understood (e.g., see Williams et al. 2008; Haag and Cicerello 2016). Regardless of its relationship to other clades within the Quadrulini, *Tritogonia* represents a deeply divergent lineage (Serb et al. 2003; Campbell et al. 2012b), and our recognition of three other genera within this tribe (*Cyclonaias*, *Theliderma*, and *Quadrula* sensu stricto) warrants retention of *Tritogonia* as a monotypic genus (e.g., see Watters et al. 2009; Sietman et al. 2012).

Truncilla *Rafinesque, 1819*.—Turgeon et al. (1998) recognized four species, and recent evidence supports no changes to this classification.

Uniomerus *Conrad, 1853*.—Turgeon et al. (1998) recognized three species. Recent evidence supports no changes at the genus level, but species concepts within *Uniomerus* are uncertain (see Williams et al. 2008). *Uniomerus columbensis* was not recognized by Turgeon et al. (1998) but was elevated from synonymy by Williams et al. (2008) based on unpublished molecular data and shell morphology; we recognize this change. Species boundaries for other taxa (e.g., *Uniomerus declivis*) remain unresolved.

The inappropriate and misleading common name for *Uniomerus carolinianus*, Florida Pondhorn, was changed to Eastern Pondhorn by Williams et al. (2014) because the species occurs not only in Florida but northward along the Atlantic Coast; we recognize this change.

Utterbackia *Baker, 1927*.—Turgeon et al. (1998) recognized three species and recent evidence supports no changes to this classification.

Utterbackiana *Frierson, 1927*.—*Utterbackiana* was not recognized by Turgeon et al. (1998). We resurrect this genus as the senior available name for a monophyletic clade of four eastern North American species included in Turgeon et al. (1998) under *Anodonta* (*A. couperiana*, *A. heardi*, *A. implicata*, and *A. suborbiculata*; Mock et al. 2004; Zanatta et al. 2007; see *Anodonta*). The type species for the genus is *Anodonta suborbiculata* Say, 1831. In addition to the four taxa mentioned above, a new species was described subsequent to Turgeon et al. (1998), *Anodonta hartfieldorum* (Williams et al. 2009). We also place this species in *Utterbackiana* because it appears closely related to *U. suborbiculata* and was formerly associated with that species.

Venustaconcha *Frierson, 1927*.—Turgeon et al. (1998) recognized two species. Molecular data showed that *Villosa perpurpurea* and *Villosa trabalis* also are members of *Venustaconcha* (Kuehnl 2009; Lane et al. 2016). Molecular data further showed that *Venustaconcha perpurpurea* is a junior synonym of *Venustaconcha trabalis*, and populations of this species in the Tennessee River drainage are genetically and morphologically distinct from those in the Cumberland River drainage (Lane et al. 2016). Based on the type locality of *trabalis*, Flint River, Alabama, this name is applicable to the Tennessee River drainage species. *Unio troostensis* Lea, 1834, is the oldest available name for the Cumberland drainage species (type locality is Stones River, Tennessee), and we recognize this species as *Venustaconcha troostensis* (see Haag and Cicerello 2016; Lane et al. 2016). Cumberland Bean was the common name used for *V. trabalis* by Turgeon et al. (1998), but Lane et al. (2016) proposed Tennessee Bean for *Venustaconcha trabalis* and Cumberland Bean for *Venustaconcha troostensis*; we follow this use. *Venustaconcha sima* was not included in Turgeon et al. (1998) but was elevated from synonymy by Gordon (1995) based on shell coloration and conchological characters, and its distinctiveness is supported by molecular data (Kuehnl 2009). This species was synonymized under *Villosa iris* by Parmalee and Bogan (1998), and molecular data support its relationship to *Villosa* (Kuehnl 2009). We recognize *sima* as a species of *Villosa*.

Villosa *Frierson, 1927*.—Turgeon et al. (1998) recognized 17 species and one subspecies. Molecular data show that *Villosa*, as depicted by Turgeon et al. (1998), is wildly polyphyletic, with species occurring in as many as seven different clades within the Lampsilini (Kuehnl 2009). These and other data support reassignment of *Villosa trabalis* to *Venustaconcha*, synonymization of *Villosa perpurpurea* under *Venustachoncha trabalis* (see *Venustaconcha*), and reassignment of *Villosa choctawensis* and *V. arkansasensis* to *Obovaria* (see *Obovaria*). Most other species will require reassignment to existing genera (e.g., *V. vaughniana* to *Ligumia*; Raley et al. 2007; Kuehnl 2009) or resurrected or newly described genera, potentially with only *Villosa amygdala*

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and *V. villosa* remaining in *Villosa* (Kuehnl 2009). However, these relationships are not fully understood, and currently synonymized or newly described generic names have not been proposed. With the exception of *Villosa trabalis*, *V. perpurpurea*, *V. choctawensis*, and *V. arkansasensis*, we retain all other species recognized by Turgeon et al. (1998) in *Villosa*.

Villosa vanuxemensis umbrans was elevated to species status by Williams et al. (2008) based on shell characters and preliminary molecular data, and subsequent molecular data support this change (Kuehnl 2009); based on this evidence, we recognize *V. umbrans*. There are several undescribed taxa within *Villosa* (Kuehnl 2009; Harris et al. 2009). We recognize correction of gender agreement for *Villosa amygdala*, as given by Turgeon et al. (1998), to *Villosa amygdalum* following Williams et al. (2011, 2014). We recognize fifteen species of *Villosa*.

DISCUSSION

Changes in mussel taxonomy compared to Turgeon et al. (1998) reflect our better understanding of mussel phylogenetic relationships obtained mainly from molecular genetic data (e.g., Serb et al. 2003; Campbell and Lydeard 2012a, 2012b; Inoue et al. 2013, 2014; Pfeiffer et al. 2016). Molecular genetics continues to be one of the most important tools for understanding unionoid relationships and taxonomy, but other data sets (e.g., life history, host use, soft anatomy, shell morphology, zoogeography) are informative and should not be overlooked when constructing phylogenies and conducting taxonomic studies (e.g., Roe et al. 2001; Jones and Neves 2010; Lane et al. 2016).

We recognize a larger number of genera than Turgeon et al. (1998; 56 vs. 49), but the number of currently recognized species is similar. However, recent studies show that considerable cryptic biodiversity exists in the Unionidae (e.g., *Cyprogenia*, *Lampsilis*, *Villosa*). Most of this biodiversity remains to be discovered, and its future recognition may result in increased numbers of species in the United States and Canada (see Haag 2012). Currently unrecognized species may be narrowly distributed (e.g., one river system) and in need of conservation measures. Development of additional molecular markers, more inclusive taxon sampling, advancements in phylogenetic analyses, and other techniques for species delineation are facilitating taxonomic recognition of species. More thorough understanding of life histories with improved husbandry techniques should also help facilitate species recognition.

Future research will most likely reveal unrecognized taxa. Conversely, additional synonymy may be warranted for some currently recognized species. Much more research is needed to delineate true diversity of the mussels of the United States and Canada.

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