

A Revised List of the Freshwater Mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada

Authors: Williams, James D., Bogan, Arthur E., Butler, Robert S., Cummings, Kevin S., Garner, Jeffrey T., et al.

Source: Freshwater Mollusk Biology and Conservation, 20(2) : 33-58

Published By: Freshwater Mollusk Conservation Society

URL: <https://doi.org/10.31931/fmbc.v20i2.2017.33-58>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

REGULAR ARTICLE

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

James D. Williams^{1*}, Arthur E. Bogan², Robert S. Butler^{3,4}, Kevin S. Cummings⁵,
Jeffrey T. Garner⁶, John L. Harris⁷, Nathan A. Johnson⁸,
and G. Thomas Watters⁹

¹ Florida Museum of Natural History, Museum Road and Newell Drive, Gainesville, FL 32611 USA

² North Carolina Museum of Natural Sciences, MSC 1626, Raleigh, NC 27699 USA

³ U.S. Fish and Wildlife Service, 212 Mills Gap Road, Asheville, NC 28803 USA

⁴ Retired.

⁵ Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820 USA

⁶ Alabama Division of Wildlife and Freshwater Fisheries, 350 County Road 275, Florence, AL 35633 USA

⁷ Department of Biological Sciences, Arkansas State University, State University, AR 71753 USA

⁸ U.S. Geological Survey, Wetland and Aquatic Research Center, 7920 NW 71st Street, Gainesville, FL 32653 USA

⁹ Museum of Biological Diversity, The Ohio State University, 1315 Kinnear Road, Columbus, OH 43212 USA

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

*Corresponding Author: fishwilliams@gmail.com

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](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.

This work has been registered with ZooBank and a copy has been archived at Zenodo.org.

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

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

CLASS Bivalvia Linnaeus, 1758
 INFRAClass Heteroconchia Hertwig, 1895
 COHORT Unionomorpha 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
Amblesma 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
Elliptioideus Frierson, 1927
Eurynia Rafinesque, 1820
Fusconaia Simpson, 1900
Hemistena Rafinesque, 1820
Parvaspina Perkins, Gangloff, and Johnson, 2017
Plethobasus Simpson, 1900
Pleurobema Rafinesque, 1819
Pleuonaia Frierson, 1927

Quadrulini Ihering, 1901
Cyclonaias Pilsbry in Ortmann and Walker, 1922
Megalonaias Utterback, 1915
Quadrula Rafinesque, 1820
Theliderma Swainson, 1840
Tritogonia Agassiz, 1852
Uniomereus 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

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

Table 2, continued.

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

Table 2, continued.

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

Table 2, continued.

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

Table 2, continued.

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

Table 2, continued.

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

Table 2, continued.

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

Table 2, continued.

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

Table 2, continued.

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

Table 2, continued.

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

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

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 *Euryntia* (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

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.*

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. siliquoides* 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 fullerkeri*, 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

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 dolabelliformis*, 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.

Megaloniaias Utterback, 1915.—Turgeon et al. (1998) recognized one species, *Megaloniaias 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).

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 *Pleuonaia* (Campbell et al. 2005, 2008; Campbell and Lydeard 2012b; see *Parvaspina* and *Pleuonaia*). 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 atearni* 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.

Pleuonaia Frierson, 1927.—*Pleuonaia* 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 *Pleuonaia* to accommodate this group and reassignment of these three species to *Pleuonaia* as proposed previously (Williams et al. 2008; Campbell and Lydeard 2012a, 2012b). There are likely cryptic taxa of *Pleuonaia* in the upper Tennessee River drainage (Schilling 2015). We correct the gender agreement of the specific name of *Pleuonaia 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.

Ptychobranthus Simpson, 1900.—Turgeon et al. (1998) recognized five species. *Ptychobranthus foremanianus* was elevated from the synonymy of *Ptychobranthus 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 *Ptychobranthus 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*

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 Amblesinae (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

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 *Venustaconcha 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*

and *V. villosa* remaining in *Villosa* (Kuehn 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 (Kuehn 2009); based on this evidence, we recognize *V. umbrans*. There are several undescribed taxa within *Villosa* (Kuehn 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.

ACKNOWLEDGMENTS

We thank the following individuals who were always very responsive to our questions regarding names of freshwater

mussels: John Alderman, Gerry Dinkins, Mike Gangloff, Dan Graf, Jordan Holcomb, Bob Howells, Sarina Jepsen, Paul Johnson, Stephen McMurray, Terry Myers, Charles Randklev, Kevin Roe, Tim Savidge, Daniel Schilling, Brian Watson, and Jason Wisniewski. We acknowledge Harry G. Lee (Jacksonville, Florida) for providing expert advice on the proper terminations for numerous species names. We also thank Sherry L. Bostick for assistance in preparation and review of several drafts of the manuscript. Although the individuals mentioned here provided assistance and input, we bear full responsibility for any errors. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of their agencies and institutions. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Ahlstedt, S. A., M. T. Fagg, R. S. Butler, J. F. Connell, and J. W. Jones. 2016. Quantitative monitoring of freshwater mussel populations from 1979–2004 in the Clinch and Powell Rivers of Tennessee and Virginia, with miscellaneous notes on the fauna. *Freshwater Mollusk Biology and Conservation* 19:1–18.
- Araujo, R., S. Schneider, K. J. Roe, D. Erpenbeck, and A. Machrodum. 2017. The origin and phylogeny of Margaritiferidae (Bivalvia, Unionoida): A synthesis of molecular and fossil data. *Zoologica Scripta* 46:289–307. doi: 10.1111/zsc.12217
- Arizona Game and Fish Department. 2017. Heritage data management system. *Anodonta californiensis*, California Floater. Available at http://www.azgfd.gov/pdfs/w_c/hdms/Invertebrates/Anodcali.fo.pdf (accessed June 15, 2017).
- Bequaert, J. C., and W. B. Miller. 1973. *The Mollusks of the Arid Southwest, with an Arizona Check List*. The University of Arizona Press, Tucson. 271 pp.
- Bieler, R., J. G. Carter, and E. V. Coan. 2010. Classification of bivalve families. Pages 113–133 in P. Bouchet, J.-P. Rocroi, Rüdiger Bieler, J. G. Carter, and E. V. Coan, editors. *Nomenclator of Bivalve Families with a Classification of Bivalve Families*. *Malacologia* 52:1–184.
- Bogan, A. E., J. Bowers-Altman, and M. E. Raley. 2011a. A new threat to conservation of North American freshwater mussels: Chinese Pond Mussel *Sinanodonta woodiana* in the United States. *Tentacle* 19:39–40.
- Bogan, A. E., J. Bowers-Altman, and M. E. Raley. 2011b. The first confirmed record of the Chinese Pond Mussel (*Sinanodonta woodiana*) (Bivalvia: Unionidae) in the United States. *The Nautilus* 125:41–43.
- Bogan, A. E., and M. E. Raley. 2013. Taxonomic status of the Cumberland Papershell, *Anodontoides argenteus* (Lea, 1840) [formerly *Anodontoides denigrata* (Lea, 1852)] (Mollusca: Bivalvia: Unionidae). Unpublished report submitted to U.S. Fish and Wildlife Service, Frankfort, Kentucky. 32 pp.
- Bogan, A. E., M. Raley, and J. Levine. 2003. Determination of the systematic position and relationships of the Atlantic Pigtoe, *Fusconaia masoni* (Conrad, 1834) (Mollusca: Bivalvia: Unionidae) with distributions in Virginia, North and South Carolina, and Georgia. Unpublished report submitted to U.S. Fish and Wildlife Service, Asheville, North Carolina. 14 pp.
- Bolotov, I. N., Y. V. Bespalaya, I. V. Vikhrev, O. V. Aksenova, P. E. Aspholm, M. Y. Gofarov, O. K. Klishko, Y. S. Kolosova, A. V. Kondakov, A. A. Lyubas, I. S. Paltser, E. S. Konopleva, S. Tumpeesuwan, N. N. Bolotov, and I. S. Voroshilova. 2015. Taxonomy

- and distribution of the freshwater pearl mussels (Unionoida: Margaritiferidae) in the Far East of Russia. *PLoS ONE* 10:e0122408. doi: 10.1371/journal.pone.0122408
- Bolotov, I. N., I. V. Vikhrev, Y. V. Bespalaya, M. Y. Gofarov, A. V. Kondakov, E. S. Konopleva, N. N. Bolotov, and A. A. Lyubas. 2016. Multi-locus fossil-calibrated phylogeny, biogeography and a subgeneric revision of the Margaritiferidae (Mollusca: Bivalvia: Unionoida). *Molecular Phylogenetics and Evolution* 103:104–121.
- Brim Box, J., and J. D. Williams. 2000. Unionid mollusks of the Apalachicola Basin in Alabama, Florida, and Georgia. *Alabama Museum of Natural History Bulletin* 21:1–143.
- Burch, J. B. 1973. Freshwater unionacean clams (Mollusca: Pelecypoda) of North America. *Biota of Freshwater Ecosystems. Identification Manual* 11, U.S. Environmental Protection Agency, Washington, D.C. 176 pp.
- Burch, J. B. 1975. Freshwater unionacean clams (Mollusca: Pelecypoda) of North America. Revised edition. Malacological Publications, Hamburg, Michigan. 204 pp.
- Burlakova, L. E., D. Campbell, A. Y. Karatayev, and D. Barclay. 2012. Distribution, genetic analysis and conservation priorities for rare Texas freshwater molluscs in the genera *Fusconaia* and *Pleurobema* (Bivalvia: Unionidae). *Aquatic Biosystems* 8:1–15.
- Campbell, D. C., P. D. Johnson, J. D. Williams, A. K. Rindsberg, J. M. Serb, K. K. Small, and C. Lydeard. 2008. Identification of ‘extinct’ freshwater mussel species using DNA barcoding. *Molecular Ecology Resources* 8:711–724. doi: 10.1111/j.1755-0998.2008.02108.x
- Campbell, D. C., and C. Lydeard. 2012a. Molecular systematics of *Fusconaia* (Bivalvia: Unionidae: Ambleminae). *American Malacological Bulletin* 30:1–17.
- Campbell, D. C., and C. Lydeard. 2012b. The genera of *Pleurobemini* (Bivalvia: Unionidae: Ambleminae). *American Malacological Bulletin* 30:19–38.
- Campbell, D. C., J. M. Serb, J. E. Buhay, K. J. Roe, R. L. Minton, and C. Lydeard. 2005. Phylogeny of North American amblemines (Bivalvia, Unionoida): Prodigious polyphyly proves pervasive across genera. *Invertebrate Biology* 124:131–164.
- Carter, J. G., C. R. Altaba, L. C. Anderson, R. Araujo, A. S. Biakov, A. E. Bogan, D. C. Campbell, M. Campbell, C. Jin-hua, J. C. W. Cope, G. Delvene, H. H. Dijkstra, F. Zong-jie, R. N. Gardner, V. A. Gavrilo, I. A. Goncharova, P. J. Harries, J. H. Hartman, M. Hautmann, W. R. Hoeh, J. Hylleberg, J. Bao-yu, P. Johnston, L. Kirkendale, K. Kleemann, J. Koppka, J. Kříž, D. Machado, N. Malchus, A. Márquez-Aliaga, J.-P. Masse, C. A. McRoberts, P. U. Middelfart, S. Mitchell, L. A. Nevesskaja, S. Özer, J. Pojeta, Jr., I. V. Polubotko, J. M. Pons, S. Popov, T. Sánchez, A. F. Sartori, R. W. Scott, I. I. Sey, J. H. Signorelli, V. V. Silantiev, P. W. Skelton, T. Steuber, J. B. Waterhouse, G. L. Wingard, and T. Yancey. 2011. A synoptical classification of the Bivalvia (Mollusca). *Paleontological Contributions No. 4*. Kansas University Paleontological Institute. The University of Kansas, Lawrence. 47 pp.
- Chong, J. P., J. C. Brim Box, J. K. Howard, D. Wolf, T. L. Myers, and K. E. Mock. 2008. Three deeply divided lineages of the freshwater mussel genus *Anodonta* in western North America. *Conservation Genetics* 9:1303–1309.
- Chong, J. P., J. L. Harris, and K. J. Roe. 2016. Incongruence between mtDNA and nuclear data in the freshwater mussel genus *Cyprogenia* (Bivalvia: Unionidae) and its impact on species delineation. *Ecology and Evolution* 6:2439–2452. doi: 10.1002/ece3.2071
- Cicerello, R. R., and G. A. Schuster. 2003. A guide to the freshwater mussels of Kentucky. Kentucky State Nature Preserves Commission, Scientific and Technical Series, No. 7. 62 pp.
- Clarke, A. H. 1981. The tribe Alasmidontini (Unionidae: Anodontinae). Part I: *Pegias*, *Alasmidonta*, and *Arcidens*. *Smithsonian Contributions to Zoology*, No. 326. 101 pp.
- Clarke, A. H. 1992. Brief communications. *Malacology Data Net* 3:98.
- Clench, W. J., and R. D. Turner. 1956. Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River. *Bulletin of the Florida State Museum, Biological Sciences* 1:97–239, plates 1–9.
- Combosch, D. J., T. M. Collins, E. A. Glover, D. L. Graf, E. M. Harper, J. M. Healy, G. Y. Kawauchi, S. Lemer, E. McIntyre, E. E. Strong, J. D. Taylor, J. D. Zardus, P. M. Mikkelsen, G. Giribet, and R. Bieler. 2017. A family-level Tree of Life for bivalves based on a Sanger-sequencing approach. *Molecular Phylogenetics and Evolution* 107:191–208.
- Cummings, K. S., and J. M. K. Berlocher. 1990. The naiades or freshwater mussels (Bivalvia: Unionidae) of the Tippecanoe River, Indiana. *Malacological Review* 23:83–98.
- Cummings, K. S., and D. L. Graf. 2010. Mollusca: Bivalvia. Pages 309–384 in J. H. Thorp and A. P. Covich, editors. *Ecology and Classification of North American Freshwater Invertebrates*. 3rd ed. Elsevier, Amsterdam, The Netherlands.
- Davis, G. M., and S. L. H. Fuller. 1981. Genetic relationships among Recent Unionacea (Bivalvia) of North America. *Malacologia* 20:217–253.
- Davis, G. M., and P. Mulvey. 1993. Species status of Mill Creek *Elliptio*. Savannah River Plant National Environment Research Park, SRO–NERP 22:4–58.
- Doucet-Beaupré, H., P. U. Blier, E. G. Chapman, H. Piontkivska, F. Dufresne, B. E. Sietman, R. S. Mulcrone, and W. R. Hoeh. 2012. *Pyganodon* (Bivalvia: Unionoida: Unionidae) phylogenetics: A male- and female-transmitted mitochondrial DNA perspective. *Molecular Phylogenetics and Evolution* 63:430–444.
- Elderkin, C. L., A. D. Christian, J. L. Metcalfe-Smith, and D. J. Berg. 2008. Population genetics and phylogeography of freshwater mussels in North America, *Elliptio dilatata* and *Actinonaias ligamentina* (Bivalvia: Unionidae). *Molecular Ecology* 17:2149–2163.
- Frierson, L. S. 1927. A Classification and Annotated Check List of the North American Naiades. Baylor University Press, Waco, Texas. 111 pp. Errata et Corrigenda.
- Gangloff, M. M., B. A. Hamstead, E. F. Abernethy, and P. D. Hartfield. 2013. Genetic distinctiveness of *Ligumia recta*, the Black Sandshell, in the Mobile River Basin and implications for its conservation. *Conservation Genetics* 14:913–916. doi: 10.1007/s10592-013-0480-0
- Gangloff, M. M., J. D. Williams, and J. W. Feminella. 2006. A new species of freshwater mussel (Bivalvia: Unionidae), *Pleurobema atearni*, from the Coosa River drainage of Alabama, USA. *Zootaxa* 1118:43–56.
- Gilbert, C. R. 1961. Hybridization versus intergradation: An inquiry into the relationship of two cyprinid fishes. *Copeia* 1961:181–192.
- Gordon, M. E. 1995. *Venustaconcha sima* (Lea), an overlooked freshwater mussel (Bivalvia: Unionoidea) from the Cumberland River basin of central Tennessee. *The Nautilus* 108:55–60.
- Graf, D. L. 2002. Molecular phylogenetic analysis of two problematic freshwater mussel genera (*Unio* and *Gonidea*) and a re-evaluation of the classification of Nearctic Unionidae (Bivalvia: Palaeoheterodonta: Unionoida). *Journal of Molluscan Studies* 68:65–71.
- Graf, D. L., and K. S. Cummings. 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies* 73:291–314.
- Graf, D. L., and K. S. Cummings. 2017. The freshwater mussels (Unionoida) of the world (and other less consequential bivalves). MUSSELp database. Available at <http://mussel-project.uwsp.edu/db/> (accessed March 25, 2017).
- Graf, D. L., and D. Ó Foighill. 2000. The evolution of brooding characters among the freshwater pearly mussels (Bivalvia: Unionoidea) of North America. *Journal of Molluscan Studies* 66:157–170.
- Grobler, J. P., J. W. Jones, N. A. Johnson, R. J. Neves, and E. M. Hallerman. 2011. Homogeneity at nuclear microsatellite loci masks mitochondrial

- haplotype diversity in the endangered Fanshell Pearlymussel (*Cyprogenia stegaria*). *Journal of Heredity* 102:196–206.
- Haag, W. R. 2012. *North American Freshwater Mussels: Natural History, Ecology, and Conservation*. Cambridge University Press, New York. 505 pp.
- Haag, W. R., and R. R. Cicerello. 2016. A distributional atlas of the freshwater mussels of Kentucky. Scientific and Technical Series 8. Kentucky State Nature Preserves Commission, Frankfort. 299 pp.
- Harris, J. L., W. R. Hoeh, A. D. Christian, J. Walker, J. L. Farris, R. L. Johnson, and M. E. Gordon. 2004. Species limits and phylogeography of Lampsilinae (Bivalvia; Unionoida) in Arkansas with emphasis on species of *Lampsilis*. Unpublished final report to Arkansas Game and Fish Commission and U.S. Fish and Wildlife Service. 70 pp, 10 plates.
- Harris, J. L., W. R. Posey, 2nd, C. L. Davidson, J. L. Farris, S. R. Oetker, J. N. Stoeckel, M. G. Crump, S. Barnett, H. C. Martin, J. H. Seagraves, N. J. Wentz, R. Winterringer, C. Osborne, and A. D. Christian. 2009. Unionoida (Mollusca: Margaritiferidae, Unionidae) in Arkansas, third status review. *Journal of the Arkansas Academy of Science* 63:50–86.
- Heard, W. H., and R. H. Guckert. 1971. A re-evaluation of the Recent Unionacea (Pelecypoda) of North America. *Malacologia* 10:333–355.
- Herrmannsen, A. N. 1848. Indicis generum Malacozoorum primordia. Nomina subgenerum, familiarum, tribuum, ordinum, classium; adjectis auctoribus, temporibus, locis systematicis atque literariis, etymis, synonymis. *Praeterrmittuntur Cirripedia, Tunicata et Rhizopoda*. 2:353–492.
- Hewitt, T. L., J. L. Bergner, D. A. Woolnough, and D. T. Zanatta. 2016. Phylogeography of the freshwater mussel species *Lasmigona costata*: Testing post-glacial colonization hypotheses. *Hydrobiologia*. doi: 10.1007/s10750-016-2834-3
- Hoeh, W. R., A. E. Bogan, K. S. Cummings, and S. I. Guttman. 2002. Evolutionary relationships among the higher taxa of freshwater mussels (Bivalvia: Unionoida): Inferences on phylogeny and character evolution from analyses of DNA sequence data. *Malacological Review* 31–32:123–141.
- Hoeh, W. R., A. E. Bogan, and W. H. Heard. 2001. A phylogenetic perspective on the evolution of morphological and reproductive characteristics in the Unionoida. Pages 257–280 in G. Bauer and K. Wächtler, editors. *Ecology and Evolution of the Freshwater Mussels Unionoida*. Ecological Studies, Vol. 145. Springer-Verlag, Berlin.
- Hoeh, W. R., A. E. Bogan, W. H. Heard, and E. G. Chapman. 2009. Palaeoheterodont phylogeny, character evolution, diversity and phylogenetic classification: A reflection on methods of analysis. *Malacologia* 51:307–317.
- Howells, R. G., R. W. Neck, and H. D. Murray. 1996. *Freshwater Mussels of Texas*. Texas Parks and Wildlife Department, Inland Fisheries Division, Austin. 218 pp.
- Huang, J., and L. L. Knowles. 2016. The species versus subspecies conundrum: Quantitative delimitation from integrating multiple data types within a single Bayesian approach in Hercules Beetles. *Systematic Biology* 65:685–699.
- Huff, S. W., D. Campbell, D. L. Gustafson, C. Lydeard, C. R. Altaba, and G. Giribet. 2004. Investigations into the phylogenetic relationships of freshwater pearl mussels (Bivalvia: Margaritiferidae) based on molecular data: Implications for their taxonomy and biogeography. *Journal of Molluscan Studies* 70:379–388.
- Inoue, K., D. M. Hayes, J. L. Harris, and A. D. Christian. 2013. Phylogenetic and morphometric analyses reveal ecophenotypic plasticity in freshwater mussels *Obovaria jacksoniana* and *Villosa arkansasensis* (Bivalvia: Unionidae). *Ecology and Evolution* 3:2670–2683.
- Inoue, K., A. L. McQueen, J. L. Harris, and D. J. Berg. 2014. Molecular phylogenetics and morphological variation reveal recent speciation in freshwater mussels of the genera *Arcidens* and *Arkansia* (Bivalvia: Unionidae). *Biological Journal of the Linnean Society* 112:535–545.
- Johnson, R. I. 1970. The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the southern Atlantic Slope Region. *Bulletin of the Museum of Comparative Zoology* 140:263–449.
- Johnson, R. I. 1998. A new mussel, *Potamilis metnecktai* (Bivalvia: Unionidae), from the Rio Grande system, Mexico and Texas with notes on Mexican *Disconaias*. *Occasional Papers on Mollusks* 5:427–455, plates 22–27.
- Jones, J. W., and R. J. Neves. 2010. Descriptions of a new species and a new subspecies of freshwater mussels, *Epioblasma ahlstedti* and *Epioblasma florentina aureola* (Bivalvia: Unionidae), in the Tennessee River drainage, USA. *The Nautilus* 124:77–92.
- Jones, J. W., R. J. Neves, S. A. Ahlstedt, and E. M. Hallerman. 2006. A holistic approach to taxonomic evaluation of two closely related endangered freshwater mussel species, the Oyster Mussel *Epioblasma capsaeformis* and Tan Riffleshell *Epioblasma florentina walkeri* (Bivalvia: Unionidae). *Journal of Molluscan Studies* 72:267–283. doi: 10.1093/mollus/ey1004
- King, T. L., M. S. Eackles, B. Gjetvaj, and W. R. Hoeh. 1999. Intraspecific phylogeography of *Lasmigona subviridis* (Bivalvia: Unionidae): Conservation implications of range discontinuity. *Molecular Ecology* 8:S65–S78.
- Kuehnl, K. F. 2009. Exploring levels of genetic variation in the freshwater mussel genus *Villosa* (Bivalvia: Unionidae) at different spatial and systematic scales: Implications for biogeography, taxonomy, and conservation. Doctoral dissertation, The Ohio State University, Columbus.
- Lane, T. W., E. M. Hallerman, and J. W. Jones. 2016. Phylogenetic and taxonomic assessment of the endangered Cumberland Bean, *Villosa trabalis* and Purple Bean, *Villosa perpurpurea* (Bivalvia: Unionidae). *Conservation Genetics* 17:1109–1124. doi: 10.1007/s10592-016-0847-0
- Layzer, J. B., M. E. Gordon, and R. M. Anderson. 1993. Mussels: The forgotten fauna of regulated rivers. A case study of the Caney Fork River. *Regulated Rivers: Research and Management* 8:63–71.
- Lee, H. G. 2006. Musings on a local specimen of *Toxolasma paulum* (I. Lea, 1840), the Iridescent Lilliput. *Shell-O-Gram* 47:3–6.
- Lee, H. G. 2008. Book review: *Freshwater Mussels of Alabama and the Mobile Basin in Georgia, Mississippi and Tennessee*. *The Nautilus* 122:261–263.
- Lopes-Lima, M., E. Froufe, V. T. Do, M. Ghamizi, K. E. Mock, U. Kebapci, O. Klishko, S. Kovitvadhii, U. Kovitvadhii, O. S. Paul, J. M. Pfeiffer, 3rd, M. Raley, N. Riccardi, H. Sereffisan, R. Sousa, A. Teixeira, S. Varandas, X. P. Wu, D. T. Zanatta, A. Zieritz, and A. E. Bogan. 2017. Phylogeny of the most species rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): Defining modern subfamilies and tribes. *Molecular Phylogeny and Evolution* 106:174–191. Available at <http://dx.doi.org/10.1016/j.ympev.2016.08.021>
- Lydeard, C., R. L. Minton, and J. D. Williams. 2000. Prodigious polyphyly in imperiled freshwater pearly-mussels (Bivalvia: Unionidae): A phylogenetic test of species and generic designations. Pages 145–158 in E. M. Harper, J. D. Taylor, and J. A. Crane, editors. *The Evolutionary Biology of the Bivalvia*. Geological Society Special Publication, No. 177.
- Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. *Methods and Principles of Systematic Zoology*. McGraw-Hill, New York. 336 pp.
- McCartney, M. A., A. E. Bogan, K. M. Sommer, and A. E. Wilbur. 2016. Phylogenetic analysis of Lake Waccamaw freshwater mussel species. *American Malacological Bulletin* 34:109–120.
- McMurray, S. E., J. S. Faiman, A. Roberts, B. Simmons, and M. C. Barnhart. 2012. *A guide to Missouri's freshwater mussels*. Missouri Department of Conservation, Jefferson City. 94 pp.
- Miller, R. R., W. L. Minckley, and S. M. Norris. 2005. *Freshwater Fishes of México*. University of Chicago Press, Chicago, Illinois. 490 pp.
- Mock, K. E., J. C. Brim Box, M. P. Miller, M. E. Downing, and W. R. Hoeh. 2004. Genetic diversity and divergence among freshwater mussel

- (*Anodonta*) populations in the Bonneville Basin of Utah. *Molecular Ecology* 13:1085–1098.
- Modell, H. 1964. Das natürliche system der Najaden. 3. Archiv für Molluskenkunde 93:71–126.
- Morrison, J. P. E. 1942. Preliminary report on mollusks found in the shell mounds of the Pickwick Landing Basin in the Tennessee River Valley. Pages 337–392 in W. S. Webb and D. L. DeJarnette, editors. An archaeological survey of Pickwick Basin in the adjacent portions of the states of Alabama, Mississippi and Tennessee. Bureau of American Ethnology, Bulletin 129.
- Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: A downward spiral of diversity. Pages 43–85 in G. A. Benz and D. E. Collins, editors. *Aquatic Fauna in Peril: The Southeastern Perspective*. Special Publication No. 1, Southeast Aquatic Research Institute. Lenox Design & Communications, Decatur, Georgia.
- Ortmann, A. E. 1918. The nayades (freshwater mussels) of the upper Tennessee drainage. With notes on synonymy and distribution. *Proceedings of the American Philosophical Society* 57:521–626.
- Ortmann, A. E. 1920. Correlation of shape and station in freshwater mussels (Naiades). *Proceedings of the American Philosophical Society* 59:269–312.
- Parmalee, P. W., and A. E. Bogan. 1998. *The Freshwater Mussels of Tennessee*. The University of Tennessee Press, Knoxville. 328 pp.
- Perkins, M. A., N. A. Johnson, and M. M. Gangloff. 2017. Molecular systematics of the critically-endangered North American spinymussels (Unionidae: *Elliptio* and *Pleurobema*) and description of *Parvaspina* gen. nov. *Conservation Genetics* 18:745–757. doi: 10.1007/s10592-017-0924-z
- Pfeiffer, J. M., 3rd, N. A. Johnson, C. R. Randklev, R. G. Howells, and J. D. Williams. 2016. Generic reclassification and species boundaries in the rediscovered freshwater mussel “*Quadrula*” *mitchelli* (Simpson in Dall, 1896). *Conservation Genetics* 17:279–292. doi: 0.1007/s10592-015-0780-7
- Raley, M. E., A. E. Bogan, C. B. Eads, and J. F. Levine. 2007. Molecular evidence for a novel placement of the Carolina Creekshell, *Villosa vaughaniana* (Lea, 1836). Page 41 in *Freshwater Mollusk Conservation Society Symposium*, Little Rock, Arkansas.
- Roe, K. J. 2013. Molecular phylogenetics and zoogeography of the freshwater mussel genus *Ptychobranchus* (Bivalvia: Unionidae). *Bulletin of the American Malacological Society* 31:257–265.
- Roe, K. J., and P. D. Hartfield. 2005. *Hamiota*, a new genus of freshwater mussel (Bivalvia: Unionidae) from the Gulf of Mexico drainages of the southeastern United States. *The Nautilus* 119:1–10.
- Roe, K. J., P. D. Hartfield, and C. Lydeard. 2001. Phylogenetic analysis of the threatened and endangered superconglutinate-producing mussels of the genus *Lampsilis* (Bivalvia: Unionidae). *Molecular Ecology* 10:2225–2234.
- Roe, K. J., and W. R. Hoeh. 2003. Systematics of freshwater mussels (Bivalvia: Unionoida). Pages 91–122 in C. Lydeard and D. R. Lindberg, editors. *Molecular Systematics and Phylogeography of Mollusks*. Smithsonian Books, Washington, D.C.
- Roe, K. J., and C. Lydeard. 1998. Species delineation and the identification of evolutionarily significant units: Lessons from the freshwater mussel genus *Potamilus* (Bivalvia: Unionidae). *Journal of Shellfish Research* 17:1359–1363.
- Schilling, D. E. 2015. Assessment of morphological and molecular genetic variation of freshwater mussel species belonging to the genera *Fusconia*, *Pleurobema*, and *Pleuronaia* in the upper Tennessee River basin. Master’s thesis, Virginia Polytechnic Institute and State University, Blacksburg.
- Serb, J. M., and M. C. Barnhart. 2008. Congruence and conflict between molecular and reproductive characters when assessing biological diversity in the Western Fanshell *Cyprogenia aberti* (Bivalvia, Unionidae). *Annals of the Missouri Botanical Garden* 95:248–261.
- Serb, J. M., J. E. Buhay, and C. Lydeard. 2003. Molecular systematics of the North American freshwater bivalve genus *Quadrula* (Unionidae: Ambloeminae) based on mitochondrial ND1 sequences. *Molecular Phylogenetics and Evolution* 28:1–11.
- Sietman, B. E., J. M. Davis, and M. C. Hove. 2012. Mantle display and glochidia release behaviors of five quadruline freshwater mussel species (Bivalvia: Unionidae). *American Malacological Bulletin* 30:39–46.
- Smith, D. G. 2000. On the taxonomic placement of *Unio ochraceus* Say, 1817 in the genus *Ligumia* (Bivalvia: Unionidae). *The Nautilus* 114:115–160.
- Smith, D. G. 2001. Systematics and distribution of the recent Margaritiferidae. Pages 33–49 in G. Bauer and K. Wächtler, editors. *Ecology and Evolution of Freshwater Mussels Unionoida*. Ecological Studies, Vol. 145. Springer-Verlag, Berlin.
- Sproules, J., P. Grobler, N. Johnson, J. W. Jones, R. J. Neves, and E. M. Hallerman. 2006. Genetic analysis of selected populations of the Rabbitsfoot Pearlymussel (*Quadrula cylindrica cylindrica*) (Bivalvia: Unionidae). Unpublished final report submitted to U.S. Fish and Wildlife Service, Frankfort, Kentucky. 16 pp.
- Stiven, A. E., and J. Alderman. 1992. Genetic similarities among certain freshwater mussel populations of the *Lampsilis* genus in North Carolina. *Malacologia* 34:355–369.
- Turgeon, D. D., A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, C. F. E. Roper, A. Scheltema, F. G. Thompson, and J. D. Williams. 1988. *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks*. American Fisheries Society, Special Publication 16. 277 pp., 12 plates.
- Turgeon, D. D., J. F. Quinn, A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks*, 2nd ed. American Fisheries Society, Special Publication 26. 526 pp.
- Valenciennes, A. 1827. Coquilles fluviatiles bivalves du Nouveau-Continent, recueillies pendant le voyage de MM. De Humboldt et Bonpland. In A. von Humboldt and A. J. A. Bonpland, editors. *Recueil d’observations de zoologie et d’anatomie compare, faites dans l’océan Atlantique, dans l’intérieur du nouveau continent et dans la mer du sud pendant les années 1799, 1800, 1801, 1802 et 1803*; par Al. de Humboldt et A. Bonpland. J. Smith and Gide, Paris, 2:225–237, colored plates 48, 50, 53, 54.
- Walker, J. M., J. P. Curole, D. E. Wade, E. G. Chapman, A. E. Bogan, G. T. Watters, and W. R. Hoeh. 2006. Taxonomic distribution and phylogenetic utility of gender-associated mitochondrial genomes in the Unionoida (Bivalvia). *Malacologia* 48:265–282.
- Watters, G. T., M. A. Hoggarth, and D. H. Stansbery. 2009. *The Freshwater Mussels of Ohio*. The Ohio State University Press, Columbus. 421 pp.
- Williams, J. D., A. E. Bogan, and J. T. Garner. 2008. *The Freshwater Mussels of Alabama and the Mobile Basin of Georgia, Mississippi, and Tennessee*. University of Alabama Press, Tuscaloosa. 908 pp.
- Williams, J. D., A. E. Bogan, and J. T. Garner. 2009. A new species of freshwater mussel, *Anodonta hartfieldorum* (Bivalvia: Unionidae), from the Gulf Coastal Plain drainages of Alabama, Florida, Louisiana and Mississippi, USA. *The Nautilus* 123:25–33.
- Williams, J. D., R. S. Butler, G. L. Warren, and N. A. Johnson. 2014. *Freshwater Mussels of Florida*. University of Alabama Press, Tuscaloosa. 498 pp.
- Williams, J. D., R. S. Butler, and J. M. Wisniewski. 2011. Annotated synonymy of the recent freshwater mussel taxa of the families Margaritiferidae and Unionidae described from Florida and drainages contiguous with Alabama and Georgia. *Bulletin of the Florida Museum of Natural History* 51:1–84.

- Williams, J. D., and A. Fradkin. 1999. *Fusconaia apalachicola*, a new species of freshwater mussel (Bivalvia: Unionidae) from pre-Columbian archaeological sites in the Apalachicola basin of Alabama, Florida, and Georgia. *Tulane Studies in Zoology* 31:51–62.
- Williams, J. D., M. L. Warren, Jr., K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of the freshwater mussels of the United States and Canada. *Fisheries* 18:6–22.
- Zanatta, D. T., and R. W. Murphy. 2006. Evolution of active host-attraction strategies in the freshwater mussel tribe Lampsilini (Bivalvia: Unionidae). *Molecular Phylogenetics and Evolution* 41:195–208. doi: 10.1016/j.ympev.2006.05.030
- Zanatta, D. T., A. Ngo, and J. Lindell. 2007. Reassessment of the phylogenetic relationships among *Anodonta*, *Pyganodon*, and *Utterbackia* (Bivalvia: Unionoida) using mutation coding of allozyme data. *Proceedings of the Academy of Natural Sciences of Philadelphia* 156:211–216.