BIOTA OF FRESHWATER ECOSYSTEMS

Identification Manual

II

FRESHWATER UNIONACEAN CLAMS (MOLLUSCA: PELECYPODA) OF NORTH AMERICA
Biota of Freshwater Ecosystems

Identification Manual No. 11

FRESHWATER UNIONACEAN CLAMS (MOLLUSCA: PELECYPODA) OF NORTH AMERICA

by

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"Freshwater Unionacean Clams (Mollusca: Pelecypoda) of North America" is the eleventh of a series of identification manuals for selected taxa of invertebrates occurring in freshwater systems. These documents, prepared by the Oceanography and Limnology Program, Smithsonian Institution for the Environmental Protection Agency, will contribute toward improving the quality of the data upon which environmental decisions are based.

Additional manuals will include but not necessarily be limited to, freshwater representatives of the following groups: dryopoid beetles, branchiuran crustaceans (*Argulus*), amphipod crustaceans (*Gammaridae*), isopod crustaceans (*Asellidae*), decapod crustaceans (*Astacidae*), leeches (*Hirudinea*), polychaete worms (*Polychaeta*), freshwater nematodes (*Nematoda*), freshwater planarians (*Turbellaria*), and freshwater clams (*Sphaeriacea*).
Bivalved mollusks of the superfamily Unionacea (Order Schizodonta) are represented in North America by three families, 46 genera, and, as treated in this key, 221 species. The primitive Margaritiferidae are represented by two genera and four species, the Amblemidae by eight genera and 25 species, and the very large family Unionidae by 36 genera and 192 species. Systematics are not well worked out in many groups, which makes a definitive listing of species somewhat arbitrary at this time. The present key in most instances reflects a conservative approach to the lower taxa and, although it omits many nominal species of doubtful validity, the key nevertheless represents most of the biological species.

Characters of soft anatomy are used to separate the families, subfamilies and, in a few cases, genera. Species are separated by shell characters. The main feature of this publication is an illustrated taxonomic key using both soft anatomy and shell characters for the identification of the North American Unionacea.
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SECTION I
INTRODUCTION

The richest unionacean fauna (freshwater mussels) in the world is found in North America and has been the subject of much species-naming since the time of C. S. Rafinesque in the early 19th century. However, indepth studies of these animals have been few, and investigations mainly have centered around faunal distributions and nomenclature. (A notable exception is the work of A. E. Ortmann.) Therefore, while distributions are rather well known for most of the nominal species, systematic relationships at all levels within the North American Unionacea are rather poorly understood. For that reason, systematics of our freshwater mussels have been the subject of considerable controversy in the past and at present, with much of the controversy still unresolved. Nevertheless, the taxonomy of unionacean clams of a few geographic regions has been rather thoroughly studied recently (e.g., see Johnson, 1970, 1972; Clarke, 1973), and those publications have been especially helpful in preparing the present key. But producing a finite, unified key for identification of freshwater mussels for all of North America is very difficult at this time. In spite of this, however, one may construct a workable key to the traditionally recognized taxa which probably represent most of the species. A more precise key must await further study, although it is improbable that many of our freshwater mussels will ever be adequately studied because of their extinction by pollution and the past and present destruction of their natural habitats by stream canalization and impoundments made by hydroelectric and other dams.

The Unionacea of North America (north of Mexico) as described in this publication consist of 221 species, grouped into 46 genera and 3 families. The systematic arrangement of the higher categories (i.e., the families and subfamilies) follows Heard and Guckert (1970) and reflects an interpretation of phylogenetic relationships based on reproductive features of the animals, rather than on shell characters. Such an organization rests largely on the highly regarded anatomical studies of A. E. Ortmann (see references), which are widely known and considered important by recent malacologists, but previous to Heard and Guckert's publication were either not used or interpreted only superficially. Following these latter authors, it seems logical "that a system based on aspects of reproduction, with parallelism in the shell features, more accurately reflects natural, evolutionary affinities than does a system which reverses the emphasis [i.e., one that is based only or mainly on shell characters]." But, to follow such a natural system with a group which shows parallel development of shell characters in several different major phylogenetic lines, means that a key to shells alone is extremely difficult to construct. For that reason, if one only has shells to be identified (without the soft parts), it may be necessary to try the specimens with the several individual keys of the different families (or in the case of the Unionidae, with the 4 subfamilies). Although such a procedure may require a little more time, nevertheless it should cause only a minor inconvenience.
Below is a list of the families, subfamilies and genera according to the taxonomic scheme used in this key. (The genera under each subfamily are arranged alphabetically. In the Lampsilinae (Unionidae), the genera are first arranged according to the marsupial characteristics of the gills, then alphabetically.)

Margaritiferidae

Margaritiferinae

Cumberlandinae

Amblemidae

Ambleminae

Gonideinae

Megalonaiadinae

Unionidae

Pleurobeminae

Popenaiadinae

Anodontinae

Lampsilinae (heterogenae)

Actinonaias

Carinolina

Dyeneomia

Ellipsaria

Glebula

Lampsilis

Lemioz

Leptodea

Ligurnia

Medionidus

Obovaria
LAMPSILINAE (continued) Proptera
Truncilla
Villosa

(mesogenae) Cyprogenia
Obliquaria

(eschatigenae) Dromus

(ptychogenae) Ptychobranchus
Fig. 1- Morphology of a freshwater mussel shell (*Cyclonaias tuberculata*) illustrating shell terminology: a- exterior of right valve; b- interior of left valve.
Characters of the shell of unionacean clams (freshwater mussels) are especially important in species recognition and often for generic placement. The shell consists of two halves or "valves" held together at the dorsal margin by a tough elastic ligament. The two valves are basically mirror images of each other and are articulated just below the ligament at the dorsal margin by a hinge, which in most cases is furnished with interlocking "teeth" (Fig. 1). These teeth or lamellae are projections in one valve which fit into corresponding depressions at the same point in the opposing valve (Fig. 2) and function in stabilizing the two valves against shearing forces. Those teeth immediately below or anterior to the beaks or umbos (the raised part of the dorsal margin of each valve) are called "pseudocardinal teeth", and those teeth posterior to the beaks are called "lateral teeth". The pseudocardinal teeth are usually short and jagged, and the lateral teeth are usually long and lamellar. In a few of the freshwater mussels (e.g., species of *Anodonta*), the hinge teeth are completely lacking, and in others (e.g., *Strophitus*) they are only rudimentary. In general, characteristics of the hinge teeth are rather uniform within each genus, and often differ from one genus to another. Therefore, in the taxonomic keys in the sections to follow, the hinge teeth are illustrated for at least one species of each genus.

![Diagram of shell articulation](image)

**Fig. 2- Articulation of hinge teeth as seen by a ventral view through the gaping valves (*Cyclonaias tuberculata*). (Modified from Clarke, 1973)**

The overall shape of the shell, as well as the shape or degree of development of particular regions of the shell, are widely used in identification. Related characters are those of shell dimensions, such as the ratio of length to height and the relative width. The more common shell shapes are shown in Figure 3. However, among the many species of freshwater clams are found various shapes intermediate to those shown here, and some common, wide-ranging species are rather polymorphic in shell shape.
Fig. 3- Shell shapes: a- rhomboidal; b- triangular; c- round; d- quadrare; e- oval; f- oval; g- elliptical; h- posterior ridge convex, i.e., bowed upward; i- posterior ridge concave, i.e., bowed downward.

On the exterior of the shell, the presence or absence of pustules or corrugations, the fine sculpture of the beaks (Fig. 4), the degree of development of the posterior ridge and posterior slope, and the color and glossiness of the periostracum are characters frequently used in classification. Characters of the inner surface of the valves useful in identification are color of the nacre, relative depth of the beak cavity, and especially characteristics of the hinge teeth.

Characters of the soft anatomy are important in classification, but are significant almost entirely at taxonomic levels above the species, i.e., subgenera (occasionally), genera, subfamilies and families. Of special importance is the basic structure and characteristics of the gills as they relate to the marsupial function in females (e.g., see Fig. 7). Color of the gills (in the living condition) is also sometimes significant. Characters of the posterior siphonal area can distinguish the
Fig. 4- Beak sculpture: a- concentric; b- double-looped; c- major ridges relatively fine; d- major ridges relatively coarse; Scale = 1 mm.

Fig. 5- Animal, with right valve and right mantle lobe folded back, exposing the foot, labial palp and demibranchs of the right gill.
Fig. 6- Mantle margins of freshwater mussels: a- *Margaritifera margaritifera*; b- *Amblema costata*.

*Margaritiferidae* from the other two North American unionacean families (Fig. 6), and peculiarities of the mantle margin around the incurrent opening will distinguish such genera as *Carunculina, Lampsilis* and *Villosa* (see Fig. 139).
Fig. 7- Cross sections of gravid female mussels (shell removed): a- all four demibranchs swollen and serving as marsupia (*Amblema costata* - Amblemidae); b- only outer two demibranchs swollen and serving as marsupia (*Elliptio* - Unionidae). (Modified from Heard, 1968)
SECTION II
SPECIES LIST AND RANGES

Family MARGARITIFERIDAE

Subfamily MARGARITIFERINAE

Genus Margaritifera Schumacher, 1817


*Margaritifera hembeli* (Conrad, 1838). Escambia River system in Alabama and in a tributary to Bayou Coccodrie, Louisiana.

*Margaritifera margaritifera* (Linnaeus, 1758). Widespread from Pennsylvania north to Newfoundland and Labrador in eastern North America.

Subfamily CUMBERLANDINAE

Genus Cumberlandia

*Cumberlandia monodonta* (Say, 1829). Cumberland and Tennessee River systems; Ohio, Illinois, Indiana and ?Nebraska.

Family AMBLEMIDAE

Subfamily AMBLEMINAE

Genus Amblema Ortmann, 1912

*Amblema costata* Rafinesque, 1820. Mississippi drainage from western New York to Minnesota, eastern Kansas and Texas. Alabama River drainage, the St. Lawrence drainage, Red River of the North, Saskatchewan River and Lake Winnipeg.

*Amblema neisleri* Lea, 1858. Apalachicola River system; Flint River, Georgia.

*Amblema perplicata* (Conrad, 1841). Gulf drainage rivers from central Texas to the Yellow River of Florida and north from Texas to river systems in Arkansas and Mississippi.

Genus Elliptoideus Frierson, 1927

*Elliptoideus sloatianus* (Lea, 1840). Apalachicola and Ochlockonee River systems.

Genus Fusconaia Simpson, 1900

*Fusconaia cee* (Conrad, 1834). Alabama River system and the Flint River, Georgia.

*Fusconaia cuneolus* (Lea, 1840). Tennessee River system.
Fusconaia ebenus (Lea, 1831). Mississippi drainage generally and the Alabama and Tombigbee Rivers.

Fusconaia flava flava (Rafinesque, 1820). In the Ohio-Mississippi River systems from Arkansas and Tennessee to North Dakota and Pennsylvania. Present in the Great Lakes system from Wisconsin to central New York and southern Ontario.

Fusconaia flava undata (Barnes, 1823). All of the Mississippi drainage; Coosa River in Alabama; Michigan and the upper St. Lawrence drainage.

Fusconaia subrotunda (Lea, 1831). Ohio, Cumberland and Tennessee River systems.

Fusconaia succissa (Lea, 1852). Choctawhatchee, Yellow and Escambia River systems (Florida west to Alabama).

Genus Plectomerus Conrad, 1853

Plectomerus dombeyanus (Valenciennes, 1833). Gulf drainage rivers and streams from Alabama River to eastern Texas and north in the Mississippi systems to northwest Tennessee.

Genus Quadrula Rafinesque, 1820

Quadrula archeri Frierson, 1905. Tallapoosa River, Alabama.

Quadrula aurea (Lea, 1859). Texas.

Quadrula cylindrica (Say, 1817). Ohio, Cumberland and Tennessee River systems west to Nebraska and south to Arkansas.

Quadrula intermedia (Conrad, 1836). Tennessee River system.

Quadrula metanevra Rafinesque 1820. Northern portion of the Mississippi drainage south to the Tennessee and Arkansas Rivers.

Quadrula nodulata (Say, 1834). All of the Ohio, Cumberland and Tennessee River systems; Mississippi; Mississippi drainages from southeastern Minnesota to Louisiana, west to southeastern Kansas and northeastern Texas.

Quadrula pustulosa (Lea, 1831). Mississippi drainage, Michigan and Lake Erie.

Quadrula quadrum (Rafinesque, 1820). Most tributaries of the Mississippi River, Great Lakes drainage, Alabama River system and some streams of eastern and central Texas.

Genus Quincuncina Ortmann, 1922

Quincuncina burkei (Walker, 1922). Choctawhatchee River system.

Quincuncina infuricata (Conrad, 1834). Suwannee River west to the Apalachicola River system.

Genus Tritogonia Agassiz, 1852

Tritogonia verrucosa (Rafinesque, 1820). Generally in the Mississippi drainage and in Gulf draining streams from the Alabama River system west to central Texas.
Subfamily GONIDEINAE

Genus *Gonidea* Conrad, 1857

*Gonidea angulata* (Lea, 1838). Central California north to British Columbia and east to Idaho.

Subfamily MEGALONAIADINAE

Genus *Megalonaias* Utterback, 1915

*Megalonaias giganteus* (Barnes, 1823). Throughout the Mississippi River system and the Tombigbee River of Alabama.

Family UNIONIDAE

Subfamily PLEUROBEMINAE

Genus *Cyclonaias* Pilsbry, 1922

*Cyclonaias tuberculata* (Rafinesque, 1820). Throughout the Mississippi drainage, Lake St. Clair drainage and Lake Erie and in the Ohio River drainage.

Genus *Elliptio* Rafinesque, 1820

Subgenus *Elliptio* s.s.

*Elliptio arctata* (Conrad, 1834). Alabama-Coosa, Escambia and Apalachicola River systems. Savannah River system of South Carolina, Catawba River and lower Cape Fear River system of North Carolina.

*Elliptio crassidens crassidens* (Lamarck, 1819). Generally in the Mississippi drainage, the Alabama-Coosa River system and the Amite River of Louisiana east to the St. Marys River system of Florida.

*Elliptio crassidens downiei* (Lea, 1858). Satilla River system of Georgia.


*Elliptio complanata* (Lightfoot, 1786). Apalachicola River system, Altamaha River system of Georgia north to St. Lawrence River system of Canada and in the Interior Basin west to Lake Superior and parts of the Hudson Bay drainage.

*Elliptio congaraea* (Lea, 1831). Ogeechee River system of Georgia north to the Cape Fear River system of North Carolina.

*Elliptio dariensis* (Lea, 1842). St. Johns River system and peninsular Florida and in the Altamaha River system of Georgia.

*Elliptio dilatata* (Rafinesque, 1820). Entire Mississippi drainage, St. Lawrence system, Alabama River system southeast into Florida and southwest to Guadalupe River, Texas.

*Elliptio fraterna* (Lea, 1852). Choctawhatchee River system of Florida, the upper Chattahoochee River, Georgia and the upper Savannah
River system of South Carolina.

Elliptio hopetonensis (Lea, 1838). Lower Altamaha River system of Georgia.

Elliptio icterina (Conrad, 1834). Escambia River system to the St. Marys River system of Georgia, peninsular Florida and the Altamaha River system of Georgia north to the White Oak River, North Carolina.

Elliptio jayensis (Lea, 1838). Suwannee River system, St. Marks River system and peninsular Florida.

Elliptio lanceolata (Lea, 1820). Discontinuous in the Escambia River system east to the Apalachicola River system, Satilla River system of Georgia and in Altamaha River system of Georgia north to the Juanita River of the Susquehanna River system of Pennsylvania.

Elliptio nigella (Lea, 1852). Apalachicola River system.

Elliptio sheparthina (Lea, 1834). Altamaha River system of Georgia.

Elliptio waccamawensis (Lea, 1863). Waccamaw River system of North Carolina.

Subgenus Canthyria Swainson 1840

Elliptio (Canthyria) spinosa (Lea, 1836). Altamaha River system of Georgia.

Genus Hemistena Rafinesque, 1820

Hemistena lata (Rafinesque, 1820). Ohio, Cumberland and Tennessee River systems.

Genus Plethobasus Simpson, 1900

Plethobasus cooperianus (Lea, 1834). Ohio, Cumberland and Tennessee River systems.

Plethobasus cyphus (Rafinesque, 1820). Ohio, Cumberland and Tennessee River systems and the Mississippi River system west to Iowa and north to Minnesota.

Genus Pleurobema Rafinesque, 1820

Subgenus Pleurobema s.s.

Pleurobema altum (Conrad, 1854). Alabama River system.

Pleurobema amabile (Lea, 1865). Butler, Taylor Co., Georgia.


Pleurobema bulbosum (Lea, 1857). Ocmulgee and Flint Rivers of Georgia.

Pleurobema chattanoeavense (Lea, 1858). Alabama River system.

Pleurobema clava (Lamarck, 1819). Ohio, Cumberland and Tennessee River systems; Maumee Basin; Iowa City, Iowa; St. Peter's River, Minnesota and Nebraska.

Pleurobema coradatum coccineum (Conrad, 1836). Upper Mississippi River
from southwestern New York to Kansas and Iowa, north to Wisconsin, south to Alabama and in the St. Lawrence River drainage.

*Pleurobema cordatum cordatum* (Rafinesque, 1820). Ohio, Cumberland and Tennessee River systems, Illinois west to the Mississippi River and at Claiborne, Alabama.

*Pleurobema cordatum papposulm* (Simpson, 1900). Lake Erie, Lake St. Clair and the Niagara River.

*Pleurobema cordatum pyramidalum* (Lea, 1834). Upper Mississippi River drainage from western Pennsylvania, north to upper Wisconsin, west to Kansas and Nebraska and south to Arkansas.

*Pleurobema curtum* (Lea, 1859). Tombigbee River, Mississippi.

*Pleurobema decisum* (Lea, 1831). Alabama and Tombigbee River systems.

*Pleurobema favosum* (Lea, 1856). Alabama River system.

*Pleurobema flavidulum* (Lea, 1861). Tombigbee River, Mississippi.

*Pleurobema furvum* (Conrad, 1834). Black Warrior River, Alabama.

*Pleurobema hagleri* Frierson, 1900. North and Black Warrior Rivers of Alabama.

*Pleurobema hanleyanum* (Lea, 1852). Coosa River drainage of Georgia and Alabama.


*Pleurobema irrasum* (Lea, 1861). Coosa River system.

*Pleurobema johannis* (Lea, 1859). Alabama River system.

*Pleurobema marshalli* Frierson, 1927. Tombigbee River, Alabama.

*Pleurobema meredithii* (Lea, 1858). Tennessee River system and the Black Warrior River, Alabama.

*Pleurobema modicum* (Lea, 1857). Chattahoochee River of Georgia.

*Pleurobema murrayense* (Lea, 1868). Coosa River system.

*Pleurobema nualeopsis* (Conrad, 1849). Coosa River system.

*Pleurobema nux* Lea, 1852. Alabama River system.

*Pleurobema oviforme* (Conrad, 1834). Tennessee.

*Pleurobema perovatum* (Conrad, 1834). Prairie Creek, Marengo Co., Alabama and small stream in Greene Co., Alabama.

*Pleurobema pyriforme* (Lea, 1857). Suwannee River west to the Apalachicola River system.

*Pleurobema realusum* (Wright, 1898). Ochlockonee River, Florida.

*Pleurobema rubellum* (Conrad, 1834). Black Warrior and Cahawba Rivers of Alabama.


*Pleurobema stabile* (Lea, 1861). Coosa River, Alabama.

*Pleurobema striatum* (Lea, 1840). Chattahoochee River of Georgia.

*Pleurobema strodeanum* (Wright, 1898). Choctawhatchee and Escambia Rivers of Florida and southern Alabama.

*Pleurobema tombigbeanum* Frierson, 1908. Tombigbee and Alabama Rivers.

*Pleurobema troschelianum* (Lea, 1852). Alabama River system.

Subgenus *Lexingtonia* Ortmann, 1914


*Pleurobema* (*Lexingtonia*) *dolabelloides* (Lea, 1840). Tennessee River drainage.

*Pleurobema* (*Lexingtonia*) *masoni* (Conrad, 1834). Ogeechee River system of Georgia north to the James River system of Virginia.

Genus *Uniomerus* Conrad, 1853

*Uniomerus* *tetrafasmus* (Say, 1831). Mississippi drainage north to the Ohio River. Alabama-Coosa River system and the Apalachicolan region east to the Suwannee River and peninsular Florida. Altamaha River system north to Chowan River system of North Carolina.

Subfamily *POPENAIADINAE*

Genus *Popenaias* Frierson, 1927

*Popenaias* *buckleyi* (Lea, 1843). Peninsular Florida.

*Popenaias* *popei* (Lea, 1857). Southern Texas and northeast Mexico.

Genus *Cyrtonaias* Crosse & Fischer, 1893

*Cyrtonaias* *berlandierii* (Lea). Southern Texas.

Subfamily *ANODONTINAE*

Genus *Alasmidonta* Say, 1818

Subgenus *Alasmidonta* s.s.

*Alasmidonta* *arcula* (Lea, 1836). Altamaha River system, Georgia.

*Alasmidonta* *calceolus* (Lea, 1830). Upper Mississippi drainage; Ohio, Cumberland, and Tennessee Rivers; Lower and Middle St. Lawrence system.

*Alasmidonta* *heterodon* (Lea, 1830). Atlantic draining rivers. Petitcadiac River system, New Brunswick, Canada south to the Neuse River system, North Carolina.

*Alasmidonta* *marginata* Say, 1819. In the Upper Mississippi drainage, the Ohio, Cumberland and Tennessee River systems, Michigan and the Upper St. Lawrence drainage.

*Alasmidonta* *radiatus* (Conrad, 1834). Small streams in southern Alabama.

*Alasmidonta* *raveneliana* (Lea, 1834). Tennessee and Cumberland River systems.

*Alasmidonta* *triangulata* (Lea, 1858). Apalachicola River system: Flint, Chattahoochee, Ogeechee and Savannah River drainages in Georgia; Apalachicola and Chipola drainages in Florida; Cooper-Santee River system in South Carolina.
Alasmidonta undulata (Say, 1817). Lower St. Lawrence drainage south to North Carolina.

Alasmidonta varicosa (Lamarck, 1819). Lower St. Lawrence drainage and Atlantic draining streams south to South Carolina.

Alasmidonta wrightiana (Walker, 1901). Restricted to the Ochlockonee River, Florida.

Subgenus Pegias Simpson, 1900

Alasmidonta (Pegias) fabula (Lea, 1836). Cumberland and Tennessee River systems.

Genus Anodonta Lamarck, 1799


Anodonta californiensis Lea, 1852. Rivers in California east to Utah and Arizona.

Anodonta cataracta Say, 1817. Alabama-Coosa River system; Choctawhatchee and upper Apalachicola River systems. Atlantic drainage: Altamaha River system of Georgia north to the St. Lawrence River system of Canada and westward to Michigan.

Anodonta couperiana Lea, 1842. Apalachicola, Ochlockonee and St. Marys River systems. Peninsular Florida and the Atlantic draining Altamaha River of Georgia north to the Cape Fear River system of North Carolina.

Anodonta dejecta Lewis, 1875. Southeastern California and northwestern Mexico; Arizona.

Anodonta gibbosa Say, 1824. Altamaha River system of Georgia.

Anodonta grandis corpulenta Cooper, 1834. Missouri River and the Upper Mississippi Drainage east to Indiana.

Anodonta grandis grandis Say, 1829. Throughout Mississippi-Missouri River drainage, the St. Lawrence drainage and Canadian Interior Basin from western Ontario to Alberta and in the Gulf drainages of Louisiana and Texas.

Anodonta grandis simpsoniana Lea, 1861. Hudson Bay drainage areas of Quebec, Ontario, northern Manitoba, Saskatchewan and Alberta and from the Arctic drainage area of northern Alberta and Northwest Territories in the Mackenzie River system north to the Mackenzie River Delta.

Anodonta implicata Say, 1829. St. Lawrence drainage north to New Brunswick and Nova Scotia, Canada and south to the Potomac River in Maryland.

Anodonta kennerlyi Lea, 1860. Oregon to British Columbia, Canada.

Anodonta oregonensis Lea, 1838. Washington, Oregon, northern California and eastward to the Great Salt Lake.


Anodonta suborbiculata Say, 1931. Mississippi drainage in Nebraska, Iowa, Illinois and south to Louisiana.
Anodonta wahlametensis Lea, 1838. Wahlamat River near the Columbia River junction.

Genus Anodontoides Simpson, 1898

Anodontoides ferussaciarius (Lea, 1834). Ohio-Mississippi River system. St. Lawrence River system and the Great Lakes, the Ottawa River, the Albany River and areas drained by the Nelson River.

Anodontoides radiatus (Conrad, 1834). Alabama-Coosa River system, Escambia River system and the Apalachicola River system.

Genus Arcidens Simpson, 1900

Arcidens confragosus (Say, 1829). In the Mississippi River drainage from southern Ohio west to eastern Kansas, north to southern Wisconsin and south to eastern Texas and into Louisiana.

Genus Arnansa Ortmann & Walker, 1912


Genus Lasmigona Rafinesque, 1831

Lasmigona complanata (Barnes, 1823). Upper Mississippi River drainage southwest to Arkansas, the Ohio River system, upper St. Lawrence system north to the Mackenzie River.

Lasmigona compressa (Lea, 1829). Interior Basin, Hudson Bay, Canada, the Upper Mississippi, Ohio and St. Lawrence River systems extending from Saskatchewan to Nebraska and eastward to Vermont and north on the Atlantic Slope to the Hudson River.

Lasmigona costata (Rafinesque, 1820). Generally in Mississippi River drainage, generally the St. Lawrence River system, Hudson Bay drainage in the Red and Winnipeg River systems and in the Tombigbee River of Mississippi.

Lasmigona subviridis (Conrad, 1835). New and Greenbrier Rivers, Virginia and West Virginia. Upper Savannah River system of South Carolina north to the Hudson River system and westward through Mohawk River, Erie Canal to the Genesee River of New York.

Genus Simpsoniconcha Frierson, 1914

Simpsoniconcha ambigua (Say, 1825). Ohio River system extending south to Arkansas, west to Iowa, north to Michigan and east to Tennessee.

Genus Strophitus Rafinesque, 1820

Strophitus subvexus (Conrad, 1834). Alabama-Coosa and Apalachicola River systems.
**Strophitus undalatus** (Say, 1817). Mississippi and Ohio River drainages, ranging from central Texas to Lake Winnipeg, Canada. Atlantic drainage, upper Savannah River tributary of South Carolina north to the St. Lawrence River system.

Subfamily LAMPSILINAE

Genus *Actinonaias* Crosse & Fischer, 1893

*Actinonaias carinata carinata* (Barnes, 1823). Ohio-Mississippi River drainage, St. Lawrence drainage in tributaries from Lake Michigan drainage; to Lake Ontario, New York and Minnesota to Arkansas.

*Actinonaias carinata gibba* (Simpson, 1900). Ohio River and southward.


*Actinonaias pectorosa* (Conrad, 1834). Tennessee and Cumberland River systems.

Genus *Carunculina* Simpson, 1898

*Carunculina parva* (Barnes, 1823). Throughout Mississippi drainage from western New York to Minnesota and south to Texas, Arkansas and Florida. On the Atlantic Slope it occurs in Black Creek, northern Florida.

*Carunculina pulla* (Conrad, 1838). Altamaha River of Georgia north to the Neuse River system of North Carolina.

Genus *Dysnomia* Agassiz, 1832

*Dysnomia arcaeformis* (Lea, 1831). Tennessee and Cumberland River systems.

*Dysnomia biemarginata* (Lea, 1857). Tennessee River drainage.

*Dysnomia brevidens* (Lea, 1834). Tennessee River drainage.

*Dysnomia capsaeformis* (Lea, 1834). Tennessee River drainage.

*Dysnomia flexuosa* (Rafinesque, 1820). Ohio River drainage.

*Dysnomia florentina* (Lea, 1857). Tennessee River drainage and the Cumberland River.

*Dysnomia haysiana* (Lea, 1833). Tennessee and Cumberland River drainage.


*Dysnomia metastriona* (Conrad, 1840). Black Warrior River and Woodville, Alabama.

*Dysnomia penita* (Conrad, 1834). Lower Alabama and Tombigbee River drainage.

*Dysnomia personata* (Say, 1829). Ohio River drainage.

*Dysnomia propinqua* (Lea, 1857). Tennessee and Cumberland River drainage.

*Dysnomia stewardsoni* (Lea, 1852). Tennessee River.

*Dysnomia sulcata* (Lea, 1830). Ohio River drainage.

*Dysnomia torulosa* (Rafinesque, 1820). Ohio River drainage and into Michigan.
*Dysnomia triquetra* (Rafinesque, 1820). Ohio River drainage, western New York to southern Ontario west to Wisconsin, Iowa and eastern Nebraska to Oklahoma and east to West Virginia, Tennessee and northern Alabama.

*Dysnomia turgidula* (Lea, 1858). Cumberland River, Alabama.

**Genus Ellipsaria** Rafinesque, 1820

*Ellipsaria lineolata* (Rafinesque, 1820). Mississippi River drainage south into Arkansas, west into eastern Iowa and Kansas and Texas and in the Tombigbee and Alabama River systems.

**Genus Glebula** Conrad, 1853

*Glebula rotundata* (Lamarck, 1819). Eastern Texas east to the Alabama-Coosa, Escambia and Apalachicola River systems.

**Genus Lampsilis** Rafinesque, 1820

*Lampsilis altilis* (Conrad, 1834). Alabama River drainage.

*Lampsilis anodontoides* (Lea, 1834). All of the Mississippi drainage north to eastern South Dakota. All of the Gulf drainage fromWithlacoochee River, Florida west to the Rio Grande and into Mexico.

*Lampsilis australis* Simpson, 1900. Choctawhatchee and Escambia River systems.

*Lampsilis binominata* (Simpson, 1900). Chattahoochee and Flint Rivers of Georgia (upper Apalachicola River system).


*Lampsilis carioea* (Say, 1817). Atlantic drainage from Georgia to the lower St. Lawrence system.

*Lampsilis dolabraeformis* (Lea, 1838). Altamaha River system of Georgia.

*Lampsilis excavata* Lea, 1857. Extends from the Escambia River system of Alabama and western Florida to the Pearl River of Mississippi.


*Lampsilis hydiana* (Lea, 1838). Eastern Texas, Oklahoma, Arkansas and east to Alabama.

*Lampsilis jonesi* van der Schalie, 1934. In the Choctawhatchee River system of Alabama and Florida.

*Lampsilis ochracea* (Say, 1817). Atlantic drainage from Nova Scotia south to the Savannah River system of Georgia.

*Lampsilis orbiculata* (Hildreth, 1828). Ohio and Cumberland Rivers west to the Mississippi River.

*Lampsilis ovata ovata* (Say, 1817). Interior Basin, Ohio and Mississippi drainages, St. Lawrence drainage, Hudson Bay drainage and introduced into the Potomac River system in Maryland.

*Lampsilis ovata ventricosa* (Barnes, 1823). All of the Mississippi drainage, the St. Lawrence system and the Hudson Bay drainages.
Lampsilis perpasta (Lea, 1861). Coosa River of Alabama and the Swamp Creek, Georgia.

Lampsilis radiata radiata (Gmelin, 1792). St. Lawrence drainage, Manitoba, Atlantic Slope south to South Carolina.

Lampsilis radiata siliquoides (Barnes, 1823). All of the Mississippi valley and all of Canada east of the Rocky Mountains.

Lampsilis splendida (Lea, 1838). Altamaha River system of Georgia north to the Cooper-Santee River system of South Carolina.

Lampsilis straminea (Conrad, 1834). Southern Alabama and southern Mississippi.

Lampsilis streckeri Frierson, 1927. Little Red River, Arkansas and in Travis Co., Texas.

Lampsilis subangulata (Lea, 1840). Ochlockonee River of Georgia west to the Choctawhatchee River of Alabama.

Genus Lemiox Rafinesque, 1831

Lemiox caelata (Conrad, 1834). Tennessee River drainage.

Genus Leptodea Rafinesque, 1820

Leptodea amphichaena Frierson, 1898. Saline River, Texas.

Leptodea fragilis (Rafinesque, 1820). All of the Mississippi drainage. New York to Kansas and south to Texas, Mississippi and Alabama, north to Wisconsin and Minnesota. In the St. Lawrence River drainage and the Hudson River.

Leptodea laevissima (Lea, 1830). Entire Mississippi drainage from New York to Minnesota and south to eastern Texas and Louisiana.

Leptodea leptodon (Rafinesque, 1820). Upper Mississippi River drainage south to the Tennessee River; Buffalo, New York; southern Michigan and the Souris River, Manitoba.

Genus Ligumia

Ligumia nasuta (Say, 1817). James River of Virginia north to the St. Lawrence River system, west to Lake Erie, Ohio and Michigan.

Ligumia recta (Lamarck, 1819). Throughout Mississippi drainage; Alabama River drainage, north to Minnesota and Manitoba and the St. Lawrence system.

Genus Medionidus Simpson, 1900

Medionidus acutissimus (Lea, 1831). Alabama River system.

Medionidus conradi (Lea, 1834). Tennessee River drainage and the Alabama River system.

Medionidus megamamiae van der Schalie, 1939. Tombigbee River.

Medionidus penicillatus (Lea, 1857). From the Suwannee River of Florida west to the Chipola River, Alabama.
Genus *Obovaria* Rafinesque, 1819

*Obovaria jacksoniana* Frierson, 1912. Pearl and Yalabusha Rivers of Mississippi.

*Obovaria olivaria* (Rafinesque, 1820). Western Pennsylvania and New York to Missouri, Iowa and Kansas, south to Alabama and Arkansas and north to Minnesota, Michigan, Ontario and Quebec.

*Obovaria retusa* (Lamarck, 1819). Ohio, Cumberland and Tennessee River systems.

*Obovaria rotulata* (Wright, 1899). Escambia River, Florida.

*Obovaria subrotunda* (Rafinesque, 1820). Ohio, Tennessee and Cumberland River systems, southeastern Louisiana and the Tombigbee drainage, north to Michigan and the St. Lawrence drainage.

*Obovaria unicolor* (Lea, 1845). Gulf flowing streams of Mississippi and Alabama.

Genus *Proptera* Rafinesque, 1819

*Proptera alata* (Say, 1817). Throughout the Mississippi drainage south to Arkansas; Tennessee and northern Alabama in the St. Lawrence drainage and in parts of the Red River of the North and Winnipeg River.

*Proptera capax* (Green, 1832). Lower Ohio River drainage south to St. Francis River in Arkansas and north to eastern Iowa.

*Proptera purpureata* (Lamarck, 1819). Eastern Texas north to Kansas and southern Missouri, western Tennessee to the Alabama River drainage.

Genus *TrunciZla* Rafinesque, 1819

*TrunciZla donaciformis* (Lea, 1828). Generally in the Mississippi drainage from western Pennsylvania to eastern Kansas, north to Minnesota and south to eastern Texas and east to Louisiana and Alabama.

*TrunciZla macrodon* (Lea, 1859). Eastern Texas northward into Oklahoma.

*TrunciZla truncata* Rafinesque, 1820. Throughout the Mississippi River drainage from western Pennsylvania to Michigan and Minnesota, south to Iowa, eastern Kansas and Texas, northern Alabama and Tennessee.

Genus *VilZosa* Frierson, 1927

*VilZosa concestator* (Lea, 1857). North Carolina to Louisiana and Texas.

*VilZosa constricta* (Conrad, 1838). James River system of Virginia south to the Catawba River, North Carolina.

*VilZosa delumbis* (Conrad, 1834). Altamaha River system of Georgia north to the Neuse River system of North Carolina.

*VilZosa fabalis* (Lea, 1831). Ohio River drainage and the Rouge River in Michigan.

*VilZosa iris* (Lea, 1830). St. Lawrence River system in the Lake Huron to Lake Ontario drainages and in Ohio, Tennessee and upper Mississippi River systems.

*VilZosa lienzosa* (Conrad, 1834). Alabama-Coosa River system to the Apalachicola region; in the lower Mississippi River drainage north to
the lower Ohio and Wabash Rivers and east to southwest Georgia and
peninsular Florida.

*Villosa nebulosa* (Conrad, 1834). Cumberland and Tennessee River systems,
Green River of Kentucky, the Tombigbee and Alabama River systems and
at Columbus, Georgia and Wolfville, North Carolina.

*Villosa ortmanni* (Walker, 1925). Green and Barren Rivers and probably
other streams in Kentucky.

*Villosa picta* (Conrad, 1834). Tennessee and Duck Rivers and the upper
Cumberland Basin.

*Villosa propria* (Lea, 1865). Found in Walker Co., Georgia and the Clinch
River of Virginia.

*Villosa trabalis* (Conrad, 1834). In streams of the upper Cumberland
Basin and in the Clinch River of Virginia.

*Villosa vanuxemensis* (Lea, 1838). Cumberland and Tennessee River systems
and headwaters of the Coosa River.

*Villosa vibex* (Conrad, 1834). Alabama-Coosa River system and Apalachi­
colan region. The Pearl River system of Mississippi east to the
Suwannee River system of Florida. Altamaha River system of Georgia
north to the Cape Fear River system of North Carolina.

*Villosa villosa* (Wright, 1898). Apalachicola River system east to the
St. Marys River system of Georgia and in peninsular Florida.

Genus *Cyprogenia* Agassiz, 1852

*Cyprogenia aberti* (Conrad, 1850). Southeastern Kansas, southern Missouri,
eastern Oklahoma and Arkansas.

*Cyprogenia irrorata* (Lea, 1830). Ohio, Cumberland and Tennessee River
systems.

Genus *Obliquaria* Rafinesque, 1820

*Obliquaria reflexa* Rafinesque, 1820. Entire Mississippi drainage from
western Pennsylvania north into Ontario, Canada, southwest to east­
ern Kansas and Oklahoma and east into Georgia.

Genus *Dromus* Simpson, 1900

*Dromus dromus* (Lea, 1834). Tennessee and Cumberland River systems.

Genus *Ptychobranchus* Simpson, 1900

*Ptychobranchus fasciolare* (Rafinesque, 1820). Ohio, Tennessee and Cumber­
land River systems, lower Michigan, Kansas, Arkansas, Oklahoma
and Louisiana.

*Ptychobranchus foremanianum* (Lea, 1842) Coosa River, Alabama.

*Ptychobranchus greeni* (Conrad, 1834). Black Warrior River, Alabama.

*Ptychobranchus occidentalis* (Conrad, 1836). Current and Little Red
Rivers, Arkansas.

*Ptychobranchus subtentum* (Say, 1825). Tennessee and Cumberland River
systems.
The key below for separating the three families of North American Unionacea (Margaritiferidae, Amblemidae and Unionidae) is based on characters of the animal following Heard and Guckert (1970), rather than on characters of the shell. As these authors point out, as well as others before them, such features of the soft anatomy seem more liable to accurately reflect natural, evolutionary taxonomic units than does a system based on the shell. Inasmuch as many specimens for identification will consist of only shells, it may be necessary initially to do some scanning of pictures, or to actually try identification of the specimens with the keys to each of the three families. However, since the Margaritiferidae are represented by only several species, this reduces the preliminary keying procedure to essentially only two families, the Amblemidae (with eight genera) and the very large Unionidae (with 36 genera).

1 Posterior mantle margins not united dorsally to form separate anal opening; posterior medial mantle margins not thickened or exhibiting any tendency toward forming distinct siphons (Fig. 6a): MARGARITIFERIDAE (page 26)

Posterior mantle margin forming one or more separate openings (supra-anal openings) dorsally; mantle border area thickened at point between branchial (incurrent) opening and anal (excurrent) opening, indicating tendency to form distinct siphons (Fig. 6b) 2

2(1) All 4 demibranchs serve as marsupia, i.e., appear swollen in gravid females (Fig. 7a): AMBLEMIDAE (page 29)

Only the 2 outer demibranchs serve as marsupia and appear swollen in the gravid female condition (Fig. 7b): UNIONIDAE (page 44)
KEY TO SPECIES OF MARGARITIFERIDAE

1 Shell thin and fragile, narrow dorsoventrally; pseudocardinal teeth greatly reduced, that of right valve pointed, nearly picklike (Fig. 8):

   Cumberlandia monodonta

Shell more sturdy, deeper dorsoventrally; pseudocardinal teeth broad, well-developed. Genus Margaritifera .......... 2

Fig. 8- Cumberlandia monodonta: a- right valve; b- hinge plate of right valve (arrow points to pseudocardinal tooth); c- hinge of left valve. Scale = 1 cm.
2(1) Posterior slope corrugated (Fig. 9): \textit{Margaritifera hembeli}
Posterior slope smooth ................................. 3

3(2) East of the Continental Divide; nacre white, except in headwaters of Missouri, where specimens have purple nacre; pseudocardinal teeth of left valve have well-developed anterior and posterior cusps, although they occasionally may be unequal in size; sexes separate (Fig. 10a):
\textit{Margaritifera margaritifera}
Pacific drainage; nacre typically or usually purple, sometimes salmon or pink, rarely white; pseudocardinal teeth of left valve with anterior cusp usually very much reduced in size or obsolete; hermaphroditic. (Fig. 10b)
\textit{Margaritifera falcata}

Fig. 9- \textit{Margaritifera hembeli}: right valve. Scale = 1 cm.
Fig. 10- *Margaritifera*: a- *M. margaritifera*, right valve and hinge plate of left valve; b- *M. falcata*. Scale = 1 cm
KEY TO SPECIES OF AMBLEMIDAE

1  Hinge teeth well-developed ............................................. 2
Hinge teeth lacking. Restricted to Pacific Coast drainage
(Fig. 11):  

Gonidea angulata

2 (1)  Shell surface with distinct corrugations on posterior
slope ................................................................. 3
Shell surface without distinct corrugations on posterior
slope ................................................................. 12

3 (2)  Shell surface with distinct pustules, usually covering a
considerable area ................................................... 4
Shell surface without distinct pustules .......................... 6

4 (3)  Shell round or roundly-oval (Fig. 12):  Quadrula intermedia
Shell elongate, rhomboidal ........................................... 5

Fig. 11- Gonidia angulata: right valve and hinge plate
of left valve. Scale = 1 cm.
5(4) Posterior ridge well-developed; shell without diagonal row of large pustules; nacre purple or purplish-pink (Fig. 13a): *Tritogonia verrucosa*

Posterior ridge low; shell with diagonal row of large pustules anterior and ventral to posterior ridge; nacre white (Fig. 13b): *Quadrula cylindrica*

6(5) Shell elongate, rhomboidal, with truncate posterior end; nacre purple, especially in lower half of shell. Con­fined to the Ochlockonee and Apalachicola River systems in Georgia and Florida (Fig. 14): *Elliptoideus sloatianus*

Shell elongate, oval or round; nacre white ................. 7

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Fig. 12- *Quadrula intermedia*: right valve.
Scale = 1 cm.
Fig. 13a- *Tritogonia verrucosa*, right valve and hinge plate of left valve; b- *Quadrula cylindrica*, right valve. Scale = 1 cm.
7(6) Shell small (usually less than 6 cm); shell corrugations relatively fine. Conflined to Gulf drainage from Suwannee to Choctawhatchee River, Florida. Genus Quinuncina .................................................. 8

Shell large (often up to 13 cm in length and sometimes 18 cm), corrugations heavy ............................ 9

8(7) Shell nearly as high as long, truncately oval in outline (Fig. 15a): Quinuncina infuscata
Shell elongate (Fig. 15b): Quinuncina burkei

Fig. 14- Elliptoideus sloatianus: right valve and hinge plate of left valve. Scale = 1 cm.
Fig. 15- Quincuncina: a- Q. infuscata, right valve and hinge plate of left valve; b- Q. burkei, right valves. Scale = 1 cm.
9(7) Shell sculpture extending anterior to beaks (Fig. 16): *Megaloniaias giganteus*

Shell sculpture not extending anterior to beaks. Genus *Amblema* .................................................. 10

10(9) Large, equal-sized, parallel undulations extended across posterior ridge; shell very inflated (Fig. 17): *Amblema neisleri*

Large, but not necessarily equal-sized undulations fan out from beak to shell margins; undulations on posterior ridge more or less follow ridge, rather than crossing it; shell moderately inflated or flattened ....................... 11

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Fig. 16- *Megaloniaias giganteus*: right valve of a rather young adult, and hinge plate of left valve. Scale = 1 cm.
Fig. 17- *Amblema neislerii*: right valve, hinge plate of left valve and outline of medial cross-section. Scale = 1 cm.
11(10) Shell round or roundly-oval, moderately inflated, its ventral margin typically rounded (Fig. 18a): *Amblema perplicata*

Shell elongated, typically flattened, sometimes moderately inflated; ventral margin of shell typically nearly straight and more or less parallel to dorsal margin (Fig. 18b):

*Amblema costata*

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Fig. 18- *Amblema*: a- *A. perplicata*, right valve; b- *A. costata*, right valve and hinge plate of left valve. Scale = 1 cm.
12(2) Shell rhomboidal, with raised and relatively sharp posterior ridge (Fig. 19): *Plectomerus dombeyanus*
Shell round, oval or triangular ................................ 13

13(12) Shell surface pustulose. Genus *Quadrula* in part .......... 14
Shell surface smooth .... Genus *Fusconaia* ......................... 21

14(13) Shell twice as long as high (Fig. 13b): *Quadrula cylindrica*
Shell less than twice as long as high ................................ 15

15(14) Shell with green chevron-shaped markings ................... 16
Shell lacking chevron-shaped color markings ......................... 17

16(15) Shell moderately inflated; posterior ridge high and usually having 3-5 very large swellings or raised pustules (Fig. 20a): *Quadrula metanevra*
Shell compressed; posterior ridge low and rounded and with pustules similar to those found on other parts of shell (Fig. 12): *Quadrula intermedia*

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Fig. 19- *Plectomerus dombeyanus*: right valve and hinge plate of left valve. Scale = 1 cm.
17(15) Shell with median sulcus on surface which extends from umbo to ventral margin; shell usually moderately to heavily pustulose, but pustules occasionally may be lacking (Fig. 20b):

\[ Quadrula \quad quadrula \]

Shell lacking median sulcus on disc and umbonal region; shell with or without pustules .......................... 18

18(17) Umbonal region highly inflated, with beak extending well above hinge plate; commonly pustulose ...................... 19

Umbonal region only slightly inflated; beak does not extend noticeably above hinge plate; commonly lacking pustules . 20

Fig. 20- Quadrula: a- Q. metanevra, right valve; b- Q. quadrula, right valve and hinge plate of left valve. Scale = 1 cm.
19(18) Pustules on disc arranged in 2 divergent rows; shell without green rays on umbonal region (Fig. 21a): *Quadrula nodulata*

Pustules on disc more evenly scattered over shell surface; umbonal region commonly with wide green ray (Fig. 21b): *Quadrula pustulosa*

20(18) Shell nearly circular in outline; shell nearly as high as long (Fig. 22a): *Quadrula aroheri*

Shell rectangular to broadly elliptical in outline; shell clearly longer than high (Fig. 22b) *Quadrula aurea*

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Fig. 21- *Quadrula*, right valves: a- *Q. nodulata*; b- *Q. pustulosa*. 
Scale = 1 cm.
21(13) Beaks very high; the umbonal region extremely inflated, continuing full, high and round onto disc below the umbo ........................................ 22
Beaks not especially high; umbonal region not extremely inflated ........................................ 24

22(21) Posterior ridge angular (Fig. 23): Fusoonata flavo undata
Posterior ridge angular and smooth ............................. 23

Fig. 22- Quadrula, right valves: a- Q. archeri; b- Q. aurea. Scale = 1 cm.
23(22) Disc inflated from umbo down to ventral margin of shell (Fig. 24a):
   *Fusconaia ebenus*
   Disc inflated only on upper half of shell valve (Fig. 24b):
   *Fusconaia subrotunda*

24(21) Shell as high as long, or very nearly so ..... 25
Shell length exceeds height ............... 26

Fig. 23- *Fusconaia flavafusca undata:* right valve. Scale = 1 cm.

Fig. 24- *Fusconaia,* right valves: a- *F. ebenus,* b- *F. subrotunda.* Scale. = 1 cm.
25(24) Shell with median sulcus; shell typically with many dark green rays (Fig. 25a):

Fusconaia cor

Median sulcus absent; shell without color rays (Fig. 25b):

Fusconaia succissa

Fig. 25- Fusconaia, right valves: a- F. cor; b- F. succissa. Scale = 1 cm.

Fig. 26- Median sulcus on right valves:

a- sulcus extending up onto umbonal region;
b- sulcus not extending into sulcus region.
26(24) Shell's posterior slope from posterior ridge to dorsal-posterior margin, short and steep; shell with median sulcus .................................................. 27
Shell's posterior slope long and gently descending; shell without median sulcus (Fig. 25b): Fusconaia succissa

27(26) Wide shallow median sulcus on disc extends up onto umbonal region (Fig. 26a), giving umbonal region flattened appearance (Fig. 27a): Fusconaia cuneolus
Wide shallow median sulcus of disc does not extend into umbonal region (Fig. 26b), leaving umbonal region with full round appearance (Fig. 27b): Fusconaia flava flava

Fig. 27- Fusconaia: a- F. cuneolus, right valve; b- F. flava flava, right valve and hinge plate of left valve. Scale = 1 cm.
KEY TO SUBFAMILIES OF UNIONIDAE

1 In gills of gravid females, secondary septa which are more or less perpendicular to primary septa (except in \textit{Strophitus}) divide each water tube into 3 tubes (Fig. 28a) (glochidia contained only in middle tube of each set); glochidia with hooks: ANODONTINAE (page 72)

In gills septa and water tubes undivided; glochidia without hooks (except in \textit{Proptera}, which has axehead-shaped glochidia) ..... 2

2(1) Marsupium filling entire outer pair of gills, forming smooth pads (Fig. 28b); shell not sexually dimorphic .................. 3

Marsupium confined to restricted regions of outer demibranchs (Fig. 28c,d,e,f); marsupia not forming smooth pads but marked externally by sulci; shell generally exhibiting sexual dimorphism: LAMPSILINAE (page 93)

3(2) Animals bradytictic, i.e., long-term breeders, retaining developing glochidial larvae in their gills except in Nearctic summer: POPENAIADINAE (page 70)

Animals tachytictic, i.e., short-term breeders, carrying glochidia in their gills only during Nearctic summer: PLEUROBEMINAE (page 45)

Fig. 28 - Marsupial gills in gravid female unionid clams: a- cross-section of gill of \textit{Lasmigona} (glochidia shown in only one main water tube); b- \textit{Elliptio dilatata}; c- \textit{Psychobranchus fasciolare} (ptychogenae); d- \textit{Obliquaria reflexa} (mesogenae); e- \textit{Dromus dromus} (eschatigenae); f- \textit{Lampsilis fasciola} (heterogenae). f = foot; id = inner demibranch; lm = left mantle lobe; lb = labial palp; mwt = main water tube; od = outer demibranch; P = placenta; ps = primary septum; rm = right mantle lobe, folded back to expose gills; ss = secondary septum; swt = secondary water tube.
1 Shell surface sculptured with pustules .................. 2
Shell surface without pustules ............................. 4

2(1) Shell rounded in shape; nacre purple (Fig. 29):

*Cyclonaias tuberculata*

Shell irregularly oval in shape; nacre white, sometimes with slight pinkish tinge. Genus *Plethobasus* ................. 3

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Fig. 29- *Cyclonaias tuberculata*: right valve and hinge plate of left valve. Scale = 1 cm.
3(2) Pustules over entire posterior half of shell surface
(Fig. 30a) *Plethobasus cooperianus*
Pustules arranged in central median row, absent from anterior
and posterior shell surface (Fig. 30b): *Plethobasus cyphyus*

Fig. 30 - *Plethobasus*: a - *P. cooperianus*, right valve; b - *P. cyphyus*, right valve and hinge plate of left valve. Scale = 1 cm.
(1) Pseudocardinal teeth rather poorly developed to obsolete ... 5
Pseudocardinal teeth well developed .......................... 6

(4) Pseudocardinal teeth present, although poorly developed
(Fig. 31): Uniomerus tetralasmus
Pseudocardinal teeth rudimentary or absent (Fig. 32):
Hemistena lata

Fig. 31- Uniomerus tetralasmus: right valve and hinge plate of left valve. Scale = 1 cm.
6(4) Shell generally high, triangular, high-oval, roundly oval, or occasionally elliptical; beaks generally high and generally arched forward; nacre white or occasionally pinkish. Genus *Pleurobema* ........................................... 7

Shell elongate, rhomboidal (or if low-triangular, broadly elliptical, or somewhat oval, nacre purple); beaks low, not arched; nacre purple (usually), pink or iridescent. Genus *Elliptio* .................................................. 22

7(6) Placentae in gravid females deep orange or red. Subgenus *Lexingtonia* ..................................................... 8

Placentae in gravid females grayish-white to pale brown. Subgenus *Pleurobema* s.s. ..................................... 11

8(7) Shell with spines on posterior ridge and slope (Fig. 33a) *Pleurobema* (*Lexingtonia*) *collina*

Shell without spines .................................................. 9

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Fig. 32 - *Hemistena lata*: right valve and hinge plate of left valve. Scale = 1 cm.
Fig. 33- *Pleurobema (Lexingtonia) collina*: a- dorsal view of both valves (anterior end to right) of a specimen with spines (after Boss and Clench, 1967); b- right valve of a specimen without spines. Scale = 1 cm.
9(8) Shell high, especially in adults; beaks prominent and arched forward; color rays on shell especially prominent (Fig. 34): *Pleurobema (Lexingtonia) dolabelloides*

Shell more elongate; beaks less prominent and not noticeably arched forward; color rays, when present, not prominent

10(9) Periostracum smooth and yellowish, without color rays or with only slightest hint of some very narrow brownish rays (Fig. 33b): *Pleurobema (Lexingtonia) collina*

Periostracum rougher, satiny, due to fine periostracal growth ridges; brownish to dark olive-green with dark green or brown color rays (Fig. 35): *Pleurobema (Lexingtonia) masoni*

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Fig. 34- *Pleurobema (Lexingtonia) dolabelloides*: right valves and hinge plate of left valve. Scale = 1 cm.
Fig. 35- *Pleurobema (Lexingtonia) masoni*: right valves and hinge plate of left valve. Scale = 1 cm.
11(8) Shell distinctly higher than long .......................... 12
      Shell height and width similar, or shell length exceeds height ........................................ 14

12(11) Height of shell and prominence of beaks greatly accentuated;
      shell especially inflated in area below beaks (Fig. 36a);
      beak cavities relatively deep (Fig. 36b):
      *Pleurobema cordatum pyramidatum*
      Height of shell and beaks not as pronounced; beak cavities shallow ........................................ 13

13(1) Shell nearly round to roundly oval (Fig. 37a):
      *Pleurobema marshalli*
      Shell triangularly oval (Fig. 37b):
      *Pleurobema altum*

14(11) Shell height and length nearly equal ....................... 15
      Shell distinctly longer than high .......................... 17

15(14) Beak cavities very deep (Fig. 38):
      *Pleurobema cordatum cordatum*
      Beak cavities shallow ........................................ 16

Fig. 36- *Pleurobema cordatum pyramidatum*: a- anterior end showing both valves; b- right valve. Scale = 1 cm.
Fig. 37- *Pleurobema*, right valves: a- *P. marshalli*; b- *P. altum*. Scale = 1 cm.

Fig. 38- *Pleurobema cordatum cordatum*: right valve and hinge plate of left valve. Scale = 1 cm.
16(15) Shell brown, dark brown or green-brown, especially dark on
disc below beaks (Fig. 39a): \textit{Pleurobema showalterii}
Shell tan or straw-yellow (Fig. 39b): \textit{Pleurobema altum}

17(13) Shell strongly arched, beaks at extreme dorsal anterior
end .................................................. 18
Shell not strongly arched, beaks may be far anterior, but
not at extreme dorsal anterior end ...................... 21

18(17) Shell with distinct lateral dorsoventral median sulcus
(Fig. 40a): \textit{Pleurobema clava}
Shell without a distinct lateral dorsoventral median
sulcus .................................................. 19

\textbf{Fig. 39-} \textit{Pleurobema}, right valves: a- \textit{P. showalterii}; b- \textit{P. altum}.
Scale = 1 cm.
19(18) Adult shell small, 4 cm or less in length, dark olive-brown to green-black in color (Fig. 40b): *Pleurobema curtum*

Adult shell larger, 5 cm or more in length, dark tan to straw-yellow in color

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Fig. 40- *Pleurobema*, right valves: a- *P. clava*; b- *P. curtum*. Scale = 1 cm.
20(19) Beaks high and prominent; shell deeply but narrowly inflated just below the beaks (Fig. 41a):

*Pleurobema decisum*

Beaks lower, not as high and prominent; shell broadly inflated below beaks (Fig. 41b):

*Pleurobema chattanogaense*

21(17) Shell high, rounded, triangular or subtriangular (Fig. 42a-d; 43):

*Pleurobema ssp.*

Shell lower, oval, ovate-triangular, elliptical or sub-rhomboidal (Fig. 42e-i; 44):

*Pleurobema ssp.*

(No thorough study has been made of the genus *Pleurobema* on a broad basis. The systematic status of many or most of the nominal species is unknown or confused. Therefore, a workable key at this time is impossible to construct. Figures 42, 43 and 44 illustrate many of the named forms. Their distributions, as far as known, are given in the preceding section "Species List and Ranges".)

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Fig. 41- *Pleurobema*, right valves: a- *P. decisum*; b- *P. chattanogaense*. Scale = 1 cm.
Fig. 42- *Pleurobema*, right valves: a- *P. cordatum pauperculum*; b-*P. cordatum coccineum*; c- *P. oviforme*; d-*P. verum*; e,f-*P. irrasum*; g-*P. nux*; h-*P. perovatum*; i-*P. reclusum*. Scale = 1 cm.
Fig. 43- Outlines of shells of various nominal species of *Pleurobema* which are high, rounded-triangular or subtriangular in outline. Scale = 1 cm.
Fig. 44: Outlines of shells of various nominal species of *Pleurobema* which are low, oval, ovate-triangular, elliptical or subrhomboidal in outline. Scale = 1 cm.
22(6) Shell with spines (Fig. 45): *Elliptio (Canthyria) spinosa*
Shell without spines. Subgenus *Elliptio s.s.* .......................... 23

23(22) Shell extremely elongate, length/height ratio 3.5 or greater (Fig. 46): *Elliptio shepardiana*
Shell elongate (but length/height ratio less than 3) to relatively stubby ................................................. 24

24(23) Shell subtriangular to subrhomboidal, rather heavy, generally relatively high, somewhat arched forward ..................... 25
Shell generally more elongate, elliptical to rhomboidal, of varying thickness (often thin) but not especially heavy, usually no or little indication of being arched forward .... 26

25(24) Shell especially heavy (Fig. 47a): *Elliptio crassidens crassidens*
Shell lighter, usually more elongate, and with more anteriorly placed beaks. Restricted to Satilla River system of Georgia (Fig. 47b): *Elliptio crassidens downiei*

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Fig. 45- *Elliptio (Canthyria) spinosa*: right valve. Scale = 1 cm.

Fig. 46- *Elliptio shepardiana*: right valve. Scale = 1 cm.
Fig. 47- *Elliptio*: a- *E. crassidens crassidens*, right valve and hinge plate of left valve; b- *E. crassidens downiei*, right valve. Scale = 1 cm.
26(24) Shell flattened (Fig. 48a) ........................................... 27
Shell inflated (Fig. 48b) .................................................. 34

27(26) Posterior ridge relatively close to dorsal margin and bowed
upward (Fig. 49a)  
_Elliptio dilatata_ 
Posterior ridge more median in position and nearly straight . 28

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Fig. 48- Shells of _Elliptio_ in anterior end view: a- flattened
shell; b- inflated shell.

Fig. 49- _Elliptio_, right valves: a- _E. dilatata_; 
b- _E. fratera_. Scale
= 1 cm.
28(27) Posterior slope usually sculptured with wrinkles that radiate dorsally from posterior ridge (Fig. 49b): *Elliptio fraterna*
Posterior slope usually without wrinkles .......................... 29

29(28) Shell considerably higher posteriorly than anteriorly.
Apalachicola River system of Florida, Alabama and Georgia.
(Fig. 50a): *Elliptio nigella*
Shell height nearly same in posterior and anterior regions .. 30

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**Fig. 50** - *Elliptio*, right valves: a- *E. nigella*; b- *E. arctata*.
Scale = 1 cm.
30(29) Shell arcuate, i.e., bowed upwards medially, with ventral margin curved concavely upward (Fig. 50b): *Elliptio arctata*
Shell not arcuate, ventral margin straight or convexly curved downward .................................. 31

31(30) Shell lanceolate, i.e., especially elongated and usually pointed posteriorly near midline (Fig. 51a): *Elliptio lanceolata*
Shell rhomboidal to subelliptical .................................. 32

32(31) Shell subelliptical, ventral margin curved downward.
Apalachicola River system. (Fig. 51b): *Elliptio chipolaensis*
Shell rhomboidal, ventral margin usually straight or only slightly curved ................................. 33

Fig. 51- *Elliptio*, right valves: a- *E. lanceolata*; b- *E. chipolaensis*. Scale = 1 cm.
33(32) Shell rather uniformly trapezoidal, disc flattened; periostracum not usually shiny, often rayed, yellowish-green to black (Johnson, 1970) (Fig. 52a): *Elliptio complanata*

Shell subrhomboidal, often somewhat pointed, very variable as to shape and degree of inflation; periostracum usually subshiny to shiny, often rayed, yellowish to brownish (Johnson, 1970) (Fig. 52b): *Elliptio icterina*

34(26) Shell elongate, subelliptical or lanceolate; length/height ratio nearly 2 or greater .................................................. 35

Shell shorter, rhomboidal to sub-ovate; length/height ratio 1.75 or less ................................................................. 36

Fig. 52- *Elliptio*: a- *E. complanata*, right valve and hinge plate of left valve; b- *E. icterina*. Scale = 1 cm.
Shell generally dark and usually with numerous fine dark green rays. St. Marks and Suwannee River systems and peninsular Florida. (Fig. 53a; 54b): *Elliptio jayensis*

Shell greenish-yellow or olive (except very old specimens which are dark), often with greenish color rays, but not as numerous and fine as above. Atlantic slope, from Susquehanna River system of Pennsylvania to Satilla River system of Georgia; Apalachicola region (Escambia River system, east to Apalachicola River system) (Fig. 51a): *Elliptio lanceolata*

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Fig. 53- *Elliptio*, right valves: a- *E. jayensis*; b- *E. hopetonensis*. Scale = 1 cm.
36(34) Posterior end broadly and bluntly truncate; dorsal margin very long, joining posterior margin at an acute angle. Lower Altamaha River system only. (Fig. 53b): *Elliptio hopetonensis*

Posterior end not broadly truncate; dorsal margin shortened, joining posterior margin at a wider angle ............. 37

37(36) Shell subovate to subelliptical .................................. 38
Shell rhomboidal, subrhomboidal, subtriangular or quadrate . 39

38(37) Shell epidermis chestnut brown, without color rays. Apalachicola River system (Fig. 54a): *Elliptio chipolaensis* Shell epidermis dark or light green, or yellow-green, usually with numerous fine dark green rays. St. Marks and Suwannee River systems and peninsular Florida (Fig. 53a; 54b): *Elliptio jayense*

Fig. 54- *Elliptio*, right valves: a- *E. chipolaensis*; b- *E. jayense*. Scale = 1 cm.
39(37) Shell subtriangular or quadrate, moderately heavy. Southern Atlantic drainage, from Cape Fear River system of North Carolina to Ogeechee River system of Georgia. (Fig. 55):

Elliptio congaraea

Shell rhomboidal or subrhomboidal ........................................ 40

40(39) Posterior ridge rounded or subangular. St. Marks and Suwannee River systems and peninsular Florida. (Fig. 53a; 54b):

Elliptio jayensis

Posterior ridge usually acutely angular .................................. 41

41(40) Shell small, usually less than 6 cm in length. Restricted to Waccamaw River system of North Carolina. (Fig. 56):

Elliptio waccamawensis

Shell large, up to or exceeding 13 cm in length. Altamaha River system of Georgia and peninsular Florida. (Fig. 57):

Elliptio dariensis

Fig. 55- Elliptio congaraea: right valve. Scale = 1 cm.
Fig. 56- *Elliptio waccamawensis*: right valve. Scale = 1 cm.

Fig. 57- *Elliptio dariensis*: right valves. Scale = 1 cm.
KEY TO SPECIES OF POPENAIADINAE

1 Shell elongate, length/height ratio 1.8 or greater. Genus Popenaias ............................................. 2
2 Shell high, length/height ratio 1.4 or less: Genus Cyrtonaias (Fig. 58): Cyrtonaias berlandierii

2(1) Shell flattened; posterior slope broad and shallow; periostracum dull (Fig. 59a): Popenaias popei
Shell inflated; posterior slope steep; periostracum glossy (Fig. 59b): Popenaias buckleyi

Fig. 58- Cyrtonaias berlandierii: right valve and hinge plate of left valve. Scale = 1 cm.
Fig. 59- Popenaias: a- *P. popei*; b- *P. buckleyi*, right valve and hinge plate of left valve. Scale = 1 cm.
KEY TO SPECIES OF ANODONTINAE

1  Hinge entirely without teeth, or teeth very reduced with only pseudocardinal teeth present, and these represented only by small rudiment; shell thin, fragile ............... 2
   Hinge teeth quite distinct, even though they may be rather poorly developed in some species; shell of moderate thickness, or if thin, not particularly fragile ............... 30

2(1) Pseudocardinal teeth absent. Genus *Anodonta*, *Anodontoides*
in part, *Strophitus* in part .................................. 3
   Pseudocardinal teeth present, but rudimentary .......... 24

3(2) Species east of Continental Divide ...................... 4
   Species in Pacific Drainage ............................... 17

4(3) Umbos do not extend above dorsal margin ............... 5
   Umbos extend above dorsal margin ....................... 8

5(4) Shell very flat, high, nearly round in outline (Fig. 60):

   *Anodonta suborbiculata*
   Shell more elongate, not especially flattened, often quite inflated ........................................... 6

6(5) Shell more elongate, length/height ratio approximately 2.0
   (Fig. 61):  *Anodonta imbecillus*
   Shell higher, length/height ratio approximately 1.5 ......... 7

7(6) Shell height greatest in posterior half; color pattern: straw-yellow on blue-green background (Fig. 62a)  *Anodonta peggyae*
   Shell height greatest in median portion; color pattern: blue-green on straw-yellow background (Fig. 62b)  *Anodonta couperiana*

Fig. 60- *Anodonta suborbiculata*: right valve. Scale = 1 cm.
Fig. 61- Anodonta imbecillus: right valve. Scale = 1 cm.

Fig. 62- Anodonta, right valves: a- A. peggae; b- A. couperiana. Scale = 1 cm.
8(4) Shell high, length/height ratio 1.6 or less ................. 9
Shell elongate, length/height ratio greater than 1.6 ......... 10

9(8) Shell strikingly inflated in posterior region of disc and posterior ridge, being inflated down to ventral shell margin; nacre usually iridescent or white (Fig. 63a):

*Anodonta gibbosa*

Shell more evenly inflated, not being noticeably more inflated in posterior region; nacre often coppery-pink or salmon pink (Fig. 63b):

*Anodonta grandis corpulenta*

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Fig. 63- *Anodonta*, right valves: a- *A. gibbosa*; b- *A. grandis corpulenta*. Scale = 1 cm.
10(8) Shell strikingly inflated in posterior region of disc and posterior ridge, being inflated down to ventral shell margin (Fig. 63a): *Anodonta gibbosa*
Shell more evenly inflated, not being noticeably more inflated in posterior region ........................................ 11

11(10) Beak sculpture double-looped and nodulous (Fig. 64): *Anodonta grandis grandis*
Beak sculpture single- or double-looped, but not nodulous (i.e., each ridge of sculpture rather uniform in height).. 12

12(11) Beak sculpture with 7-10 ridges. East of Continental Divide this species is known only from western Alberta, Canada (Fig. 65): *Anodonta kennerlyi*
Beak sculpture with 3-6 ridges ........................................ 13

13(12) Beak sculpture single-looped, or only faintly double-looped . 14
Beak sculpture double-looped, usually distinctly so ........ 16

Fig. 64- *Anodonta grandis grandis*: right valve. Scale = 1 cm.

Fig. 65- *Anodonta kennerlyi*: right valve. Scale = 1 cm.
Fig. 66a- beak sculpture coarse; b- beak sculpture fine; c- Strophitus undulatus, right valve; d- S. undulatus, hinge plate of left valve. Scale = 1 cm.

Fig. 67a- Anodontoides ferussacianus, right valve; b- Anodonta grandis simpsoniana, right valve. Scale = 1 cm.
14(13) Major ridges of beak sculpture (Fig. 66a) relatively coarse
(Fig. 66c): \textit{Strophitus undulatus}
Major ridges of beak sculpture relatively fine (Fig. 66b)...

15(14) Ridges of beak sculpture are not parallel to concentric
growth lines of beak, but cross them obliquely (Fig.
67a): \textit{Anodontoides ferussacianus}
Ridges of beak sculpture run parallel to concentric growth
lines of beak; Hudson Bay drainage of Canada (Fig. 67b):
\textit{Anodonta grandis simpeoniana}

16(13) Anterior ventral portion of shell below pallial line is
noticeably thickened; nacre often coppery-pink to salmon
pink (Fig. 68a): \textit{Anodonta implicata}
Anterior ventral portion of shell below pallial line is not
thickened; nacre white or iridescent, never pink (Fig.
68b): \textit{Anodonta cataracta}

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Fig. 68- \textit{Anodonta}: a- \textit{A. implicata}, right valve; b- \textit{A. cataracta},
right valve and hinge plate of left valve. Scale = 1 cm.
Fig. 69. *Anodonta dejecta*: right valve. Scale = 1 cm.

Fig. 70. *Anodonta*, right valves: a- *A. wahlametensis*; b- *A. californiensis*. Scale = 1 cm.
17(3) Height of posterior half of shell greater than height of anterior half ................................................. 18
Height of posterior half of shell nearly equal to height of anterior half ........................................... 20

18(17) Shell length/height ratio is 2 or greater; shell nearly rhomboidal in outline (Fig. 69): Anodonta dejecta
Shell length/height ratio is 1.5 or less; shell broadly ovate in outline ............................................. 19

19(18) Shell with high conspicuous wing (Fig. 70a): Anodonta wahlametensis
Shell with wing of only moderate height (Fig. 70b): Anodonta californiensis

20(17) Shell inflated only over anterior half of shell (Fig. 71): Anodonta beringiana
Shell inflated over median and/or posterior portion ........ 21

21(20) Bars of beak sculpture uneven in height, making beak bumpy or tuberculose (Fig. 64): Anodonta grandis grandis
Bars of beak sculpture even in height ............................. 22

22(21) Posterior end of shell truncate (Fig. 69): Anodonta dejecta
Posterior end of shell pointed .................................................. 23

Fig. 71- Anodonta beringiana: right valve.
Scale = 1 cm.
Fig. 72- *Anodonta oregonensis*: right valve. Scale = 1 cm.

Fig. 73a- *Alasmidonta varicosa*, right valve; b- *Anodontoides radiatus*, right valve and hinge plate of right valve. Scale = 1 cm.
23(22) Shell narrowly elliptical, length/height ratio 2, shell inflated primarily along posterior ridge (Fig. 65): \( \textit{Anodonta kennerleyi} \)

Shell typically less narrowly elliptical, length/height ratio usually less than 2, shell inflated primarily over median portion (Fig. 72): \( \textit{Anodonta oregonensis} \)

24(2) Pseudocardinal teeth very thin, blade-like .......................... 25
Pseudocardinal teeth tubercular ......................................... 26

25(24) Shell rhomboidal; posterior ridge prominent; posterior slope with rather fine corrugated sculpture (Fig. 73a): \( \textit{Alasmidonta varicosa} \)

Shell long-ovate; posterior ridge absent; anterior slope smooth (Fig. 73b): \( \textit{Anodontoides radiatus} \)

26(24) Posterior slope with corrugated sculpture. Genus \( \textit{Alasmidonta} \) 27
Posterior slope lacking corrugated sculpture ........................... 29

27(26) Posterior ridge angular (Fig. 74a): \( \textit{Alasmidonta marginata} \)
Posterior ridge rounded .................................................. 28

Fig. 74- \( \textit{Alasmidonta} \), right valves. a- \( \textit{A. marginata} \); b- \( \textit{A. raveneliana} \). Scale = 1 cm.
28(27) Shell surface relatively smooth, except for periodic rest marks; ventral margin of shell typically without broad, shallow indentation (Fig. 74b): *Alasmidonta raveneliana*

Shell surface with irregular undulations, giving it rough appearance; ventral margin of shell typically with broad, shallow indentation (Fig. 73a): *Alasmidonta varicosa*

29(26) Shell elongate, length/height ratio about 2; posterior ridge low, rounded, hardly noticeable (Fig. 75a): *Simpsoniconcha ambiguа*

Shell less elongate, length/height ratio 1.6 or less; posterior ridge well developed (Fig. 75b): *Strophitus subvexus*

![Fig. 75a- Simpsoniconcha ambiguа, right valve and hinge plate of left valve; b- Strophitus subvexus, right valve. Scale = 1 cm.](image-url)
30(1) Shell with large corrugations on disc and posterior slope, or on both ......................................................... 31
Shell without large corrugations on either disc or posterior slope ......................................................... 32

31(30) Tubercles of beak sculpture extending beyond beaks; pseudo-cardinal teeth compressed, laminate (Fig. 76):

*Arcidens confragosus*

Tubercles of beak sculpture restricted to first 3 or 4 mm of beaks; pseudocardinal teeth large and triangular, not compressed (Fig. 77):

*Arkansia wheeleri*

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Fig. 76 - *Arcidens confragosus*: right valve and hinge plate of left valve. Scale = 1 cm.
32(30) Beak sculpture concentric (see Fig. 4). Genus Alasmidonta .. 33
Beak sculpture double-looped (see Fig. 4). Genus Laemigona .. 43

33(32) Posterior end broadly truncate, with truncate slope running anterioventrally; posterior end sometimes bifurcate at shell margin (Fig. 78): Alasmidonta (Pegias) fabula
Posterior end rounded or pointed, or if truncate, truncate slope runs anteriodorsally. Subgenus Alasmidonta s.s.... 34

34(33) Shell short and high, length/height ratio less than 1.5 ..... 35
Shell elongate, length/height ratio more than 1.5 ............. 38

35(34) Shell very high; posterior slope extremely steep, at an angle of nearly 90° to disc (Fig. 79): Alasmidonta arcuata
Shell height lower; posterior slope not so steep ............... 36

Fig. 77- Arkansia wheeleri: right valve and hinge plate of left valve. Scale = 1 cm.
Fig. 78- *Alasmidonta (Pegias) fabula*: right valve and hinge plate of left valve. Scale = 1 cm.

Fig. 79- *Alasmidonta armula*: right valve. Scale = 1 cm.
36(35) Posterior end flatly truncate; ventral margin of shell nearly straight; growth lines sharp, giving periostracum rough appearance (Fig. 80): *Alasmidonta calceolus*

Posterior end pointed or rounded; ventral margin of shell rounded; periostracum may be irregular in places, but basically smooth .................................................. 37

37(36) Posterior slope strongly and rather coarsely corrugated; beaks near center of shell (Fig. 81a): *Alasmidonta wrightiana*

Posterior slope either without corrugations, or if they are present, they are minor and rather fine; beaks near forward end of shell (Fig. 81b): *Alasmidonta triangulata*

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Fig. 80- *Alasmidonta calceolus*: right valve and hinge plates of left valve. Scale = 1 cm.
Fig. 81- *Alasmidonta*: a- *A. wrightiana*; b- *A. triangulata*. Scale = 1 cm.
38(34) Right valve contains 2 lateral teeth (Fig. 82): *Ajasmidonta heterodon*
Right valve contains only 1 lateral tooth, which is often rudimentary ................................................. 39

39(38) Posterior ridge angular (Fig. 74a): *Ajasmidonta marginata*
Posterior ridge rounded .................................................. 40

40(39) Pseudocardinal teeth well-developed; tooth surface typically rough, with ridges or bumps ......................... 41
Pseudocardinal teeth rather rudimentary; tooth surface smooth .......................................................... 42

41(40) Pseudocardinal teeth large; ridges on beak large and heavy; periostracum may be irregular in places, but basically smooth (Fig. 83): *Ajasmidonta undulata*
Pseudocardinal teeth relatively smaller; ridges on beak of moderate size; growth lines sharp, giving periostracum rough appearance (Fig. 80): *Ajasmidonta calceolus*

Fig. 82- *Ajasmidonta heterodon*: right valve and hinge plate of left valve. Scale = 1 cm.
42(40) Ventral margin of shell gently rounded convexly when viewed laterally; shell surface relatively smooth, except for periodic rest marks (Fig. 74b): *Alasmidonta raveneliana*

Ventral margin rounded concavely when viewed laterally; shell surface with irregular undulations, making surface rough (Fig. 73a): *Alasmidonta varicosa*

43(32) Posterior ridge with undulations; hinge teeth heavy and rough ........................................ 44
Posterior ridge without undulations; hinge teeth smooth or more delicate ........................................ 45

Fig. 83- *Alasmidonta undulata*: right valve and hinge plate of left valve. Scale = 1 cm.
44(43) Shell roundly oval to nearly round, with prominent wing; undulations on posterior slope gentle, not coarse corrugation (Fig. 84a): *Lasmigona complanata*

Shell elongate, without wing; posterior slope strongly corrugated (Fig. 84b): *Lasmigona costata*

45(43) Shell roundly oval to nearly round (Fig. 84a): *Lasmigona complanata*

Shell elongate ............................................. 46

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Fig. 84 - *Lasmigona*: a- *L. complanata*, right valve and hinge plate of left valve; b- *L. costata*, right valve. Scale = 1 cm.
Lateral teeth rudimentary (Fig. 85a):

Laemigona holstonia

Lateral teeth clearly developed

Fig. 85- Laemigona: a- L. holstonia, right valve; b- L. compressa, right valve and hinge plate of left valve. Scale = 1 cm.
Major cusps of pseudocardinal teeth in left valve directly below or posterior of beaks (Fig. 85b): *Lasmigona compressa*

Major cusps of pseudocardinal teeth in left valve anterior of beaks (Fig. 86): *Lasmigona subviridis*

Fig. 86 - *Lasmigona subviridis*: right valve and hinge plate of left valve. Scale = 1 cm.
**KEY TO SPECIES OF LAMPSILINAE**

1. Entire ventral part of outer gill demibranch serving as marsupium, its ventral edge folded (Fig. 28c). Genus *Ptychobranchus* ................................................................. 2  
   (The shells of this genus are elongated, flattened and with very low beaks which generally do not rise much above the hinge line. The shells are straw-yellow in color, with radiating green rays. Because of the coloring and general shape of their shells, species of *Ptychobranchus* can be confused with certain species of *Actinonaias* (e.g., *A. ellipsiformis*), but the lateral teeth in *Ptychobranchus* are shorter, directed downward, and are somewhat swollen posteriorly (see Fig. 88.).)  
   Marsupium confined to either central or posterior part of outer gill demibranch (Fig. 28d,e,f) ......................... 6

2(1) Posterior slope corrugated (Fig. 87): *Ptychobranchus subtentum*  
   Posterior slope not corrugated ........................................... 3

3(2) Green rays on shell wide, broken into rectangular spots .... 4  
   Green rays on shell of fine continuous lines ....................... 5

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**Fig. 87-** *Ptychobranchus subtentum*: right valve.  
Scale = 1 cm.
Fig. 88- Ptychobranchus: a- P. foremanianum, right valve; b- P. faesiolare, right valve and hinge plate of left valve. Scale = 1 cm.
4(3) Color rays restricted mainly to upper half of shell; posterior ridge straight (Fig. 88a): *Ptychobranchus foremanianum*
Color rays usually well represented on lower half of shell; posterior ridge arched upward (Fig. 88b).

5(3) Posterior ridge straight or bowed downward; posterior ridge on beak angular (Fig. 89a): *Ptychobranchus greenii*
Posterior ridge arched upward; posterior ridge on beak rounded (Fig. 89b): *Ptychobranchus occidentalis*

6(1) Marsupium confined to central part of outer gill demibranch (Fig. 28d) ........................................ 7
Marsupium confined to posterior part of outer gill demibranch (Fig. 28e, f) ........................................ 9

Fig. 89. *Ptychobranchus*, right valves: a - *P. greenii*; b - *P. occidentalis*. Scale = 1 cm.
Shell with single median row of large tubercles (Fig. 90): *Obliquaria reflexa*

Shell surface sculptured with numerous tubercles or nodules of varying sizes or with radiating wrinkles, but without single median row of large tubercles. Genus *Cyprogenia*.

Shell more triangular in outline, often with irregular swellings on disc and posterior slope, but lacking high round pustules (Fig. 91a): *Cyprogenia aberti*

Shell nearly round in outline, sculptured with round, high pustules, usually abundant and distributed over nearly entire shell surface (Fig. 91b): *Cyprogenia irrorata*

Fig. 90- *Obliquaria reflexa*: right valve and hinge plate of left valve. Scale = 1 cm.
Fig. 91- Cyprogenia: a- C. aberti, right valve; b- C. irrorata, right valve and hinge plate of left valve. Scale = 1 cm.
Marsupium confined to lower part of posterior outer gill demibranch (Figs 28e, 92):  

\[ \textit{Dromus dromus} \]

Marsupium contained in both upper and lower halves of posterior part of gill demibranch (Fig. 28f) (characteristic of most of subfamily Lampsilinae, i.e. 15 genera) ........ 10

Fig. 92- \textit{Dromus dromus}: right valve and hinge plate of left valve. Scale = 1 cm.
10(9) Posterior slope transversely corrugated .......................... 11
Posterior slope smooth, or if corrugated, with radiating
corrugations only .......................................................... 15

11(10) Shell relatively high; sculpture on posterior half of disc
consisting of radiating grooves, which run to ventral
shell margin (Fig. 93):

\[ \textit{Lemiox caelata} \]

Shell elongate; not sculptured with radiating grooves.
Genus \textit{Medionidus} ......................................................... 12

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Fig. 93- \textit{Lemiox caelata}: right valve and hinge
plate of left valve. Scale = 1 cm.
12(11) The posterior shell margin meets dorsal margin at sharp angle, forming wing (Fig. 94a): Medionidus magle
Shell without wing ..................................................

13(12) Shell shorter, length/height ratio 1.8 or less; disc below umbo full and round (Fig. 94b): Medionidus penicill
Shell longer, length/height ratio 2.0 or greater; disc below umbo flattened ..............................................

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Fig. 94- Medionidus: a- M. maglamereae, right valve; b- M. penicilli, right valve and hinge plate of left valve. Scale = 1 cm.
Rays on shell mostly continuous occurring on anterior third of shell as abundantly as on median and posterior portions; periostracum has satiny appearance due to closely spaced microscopic ridges (Fig. 95a): **Medionidus conradicus**

Rays on shell broken mostly into streaks, blotches or chevron designs, typically less abundant on anterior third of shell; periostracum glossy (Fig. 95b): **Medionidus acutissimus**

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**Fig. 95- Medionidus, right valves: a- M. conradicus; b- M. acutissimus. Scale = 1 cm.**
15(10) Posterior half of pseudocardinal teeth divided into series of parallel, vertical, rough, deeply divided lamellae (Fig. 96): *Glebula rotundata*

Posterior half of pseudocardinal teeth may be rough, but they are not deeply lamellate

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Fig. 96- *Glebula rotundata*: right valve, hinge plate of left valve and enlargement of pseudocardinal tooth in left valve. Scale = 1 cm.
16(15) Shell high, arced, flattened; posterior transverse slope short, without trace of wing, and at 90° angle to disc; hinge teeth very large and heavy (Fig. 97): *Ellipsaria lineolata*

Shells without above combination of characters; if shell is high it is generally not arced, and if so, it is inflated, not flattened, and has less acute posterior slope .................................................... 17

Fig. 97- *Ellipsaria lineolata*: right valve and hinge plate of left valve. Scale = 1 cm.
Fig. 98- Carunculina: a- *C. parva*, right valve and hinge plate of left valve; b- *C. pulla*, right valves. Scale = 1 cm.
17(16) Females with well-developed caruncle on inner edge of each side of mantle in front of branchial opening (see Fig. 139c); adults small, usually less than 40 mm in length:

Genus Carunculina (Fig. 98)

(A number of nominal species have been placed in the genus Carunculina. However, the systematics have not been well worked out, although Johnson (1967) has spent the most time analyzing Carunculina shell characters and their variation. He recognizes two species, C. parva (Barnes) and C. pulla (Conrad). According to Johnson, C. pulla is restricted to the Altamaha River system of Georgia north to the Neuse River system in North Carolina. Carunculina is not found north of the Neuse River on the Atlantic slope. C. parva is a very variable species which is found throughout the Interior Basin, from western New York to Minnesota, to Texas, Arkansas and Florida (Johnson, 1967). It is found in the Atlantic drainage in northern Florida in Black Creek.)

Females lack caruncles on inner edge of each side of mantle in front of branchial opening; adults larger, usually more than 40 mm in length ........................................ 18

18(17) Shell elongate, length/height ratio 2.0 or greater ............ 19
Shell shorter, length/height ratio less than 2.0 ................... 23

19(18) Posterior ridge high, near dorsal margin, and ending posteriorly in point above dorsoventral midline (Fig. 99):

Lampsilis anodontoides

Posterior ridge lower, further from dorsal margin, and ending posteriorly at or below dorsoventral midline ...... 20

Fig. 99- Lampsilis anodontoides: right valve.
Scale = 1 cm.
20(19) Posterior ridge concave (see Fig. 3), i.e. bowed downward  
(Fig. 100a):  \textit{Lampsilis subangulata}  
Posterior ridge straight or slightly convex (see Fig. 3): \textit{21}

21(20) Posterior end of shell truncate (Fig. 100b):  \textit{Lampsilis jonesi}  
Posterior end of shell bluntly pointed. Genus \textit{Ligumia} \textbf{... 22}

22(21) Posterior ridge extends to posterior margin of shell, and  
is often angular near umbo; posterior slope typically  
concave; posterior margin meets dorsal margin at angle,  
forming low wing (Fig. 101a):  \textit{Ligumia nasuta}  
Posterior ridge indistinct near posterior margin of shell,  
and is broadly rounded near umbo; posterior slope  
usually not concave; without wing where posterior and  
dorsal margins meet (Fig. 101b):  \textit{Ligumia recta}

\textbf{Fig. 100-} \textit{Lampsilis}, right valves:  \textit{a- L. subangulata}; \textit{b- L. jonesi}.  
Scale = 1 cm.
23(18) Shell round, or high-oval; teeth heavy. Genus Obovaria ...... 24
Shell elongate or oval (if oval, teeth are not heavy) ........ 30

24(23) Beaks of shell high and arched strongly anteriorly .......... 25
Beaks of shell lower and not strongly arched anteriorly ...... 26

Fig. 101- Ligumia: a- L. nasuta, right valve and hinge plates of left valve; b- L. recta, right valve and hinge plates of left valves. Scale = 1 cm.
Fig. 102- *Obovaria*, right valves: a- *O. retusa*; b- *O. olivaria*. Scale = 1 cm.

Fig. 103- *Obovaria subrotunda*: right valve and hinge plate of left valve. Scale = 1 cm.
25(24) Nacre purple; typically rayless (Fig. 102a): \textit{Obovaria retusa}
Nacre white; upper 1/3 of shell with green rays (Fig. 102b): \textit{Obovaria olivaria}

26(24) Beaks central, or nearly so ................................. 27
Beaks located anteriorly ............................................... 29

27(26) Periostracum light-colored, often with color rays, especially on disc (Fig. 103): \textit{Obovaria subrotunda}
Periostracum dark brown or black; color rays, if present, limited to posterior slope ................................. 28

28(27) Shell almost circular in outline. Distribution limited to Escambia River of Alabama and Florida (Fig. 104a): \textit{Obovaria rotulata}
Shell roundly elliptical or roundly ovate. Distribution limited to the Alabama-Coosa River system (Fig. 104b): \textit{Obovaria unicolor}

Fig. 104- \textit{Obovaria}, right valves: a- \textit{O. rotulata}; b- \textit{O. unicolor}.
Scale = 1 cm.
29(26) Shell ovate, nearly as high as long (Fig. 102b): Obovaria olivaria
Shell elliptical, clearly longer than high (Fig. 105):
Obovaria jacksoniana

30(23) Shell showing strong sexual dimorphism. Genus Dysnomia .... 31
Shells of males and females only slightly sexually dimorphic, if at all................................. 61

31(30) Shell 3-pronged in outline (Fig. 106), strongly so in females, due to greatly protruding posterior and median ridges ...................................................... 32
Female shell not 3-pronged in outline; although shells of males may be weakly 3-pronged in 3 species (D. biemarginata, D. florintina and D. torulosa) ....................... 34

32(31) Median ridge greatly raised on at least half of disc, with large swelling just prior to rest period lines (Fig. 107):
Dysnomia flexuosa
Median ridge not particularly raised on disc, swellings before rest period lines are confined to protruding portion of shell which projects beyond normal ventral margin ..................................................... 33

Fig. 105- Obovaria jacksoniana: right valve.
Scale = 1 cm.
Fig. 106- *Dysnomia*: right valves showing 3-pronged condition in female (left) and male (right).

Fig. 107- *Dysnomia flexuosa*, right valves: a- female; b- male; c- hinge plate of left valve. Scale = 1 cm.
Fig. 108- *Dysnomia lewisii*, right valves: a- female; b- male. Scale = 1 cm.
Rays inconspicuous on posterior ridge, typically obscured on that portion of median ridge which protrudes beyond normal ventral margin (Fig. 108): *Dysnomia lewisi*

Rays noticeable on posterior ridge, typically also on that portion of median ridge which protrudes beyond normal ventral margin (Fig. 109): *Dysnomia stewardsoni*

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Fig. 109- *Dysnomia stewardsoni*, right valves: a- female; b- male. 
Scale = 1 cm.
Fig. 110- *Dysonomia torulosa*, right valves: a- female; b- male. Scale = 1 cm.
34(33) Median ridge present on shell as well as posterior ridge; with large swellings between rest period lines, making high round knobs along median ridge (Fig. 110):

\[Dysnomia\ \text{torulosa}\]

Median ridge either present or absent; knobs absent on disc ............................................. 35

35(34) Rays discontinuous, especially on posterior ridge, giving shell spotted, streaked or chevroned appearance ............ 36

Rays continuous ................................................. 38

36(35) Rays easily seen to be chevroned; posterior ridge very angular; posterior slope steep (Fig. 111):

\[Dysnomia\ \text{triquetra}\]

Rays not chevroned, or only minutely chevroned on small local areas; posterior ridge not angular; posterior slope not steep ............................................. 37

Fig. 111- \[Dysnomia\ \text{triquetra}\], right valves: a- female; b- male. Scale = 1 cm.
37(36) Rays typically conspicuous, appearing streaked on disc, but becoming dot-like on posterior ridge and posterior slope; disc immediately below umbo typically low and flattened; shell typically ovate-elliptical; length/height ratio 1.5 or greater (Fig. 112):

*Dysnomia brevidens*

Rays typically inconspicuous; disc immediately below umbo typically high and rounded; shell often short and high; length/height ratio 1.3 or less (Fig. 113):

*Dysnomia metastriata*

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Fig. 112- *Dysnomia brevidens*, right valves: a- female; b- male. Scale = 1 cm.
38(35) Shell usually with color rays primarily on posterior ridge and immediately adjacent areas, although immature shells may be rayed occasionally over median portion of valve as well ................................. 39
Color rays on shell not limited to region of posterior ridge ............................................. 44

Fig. 113—Dysnomia metastriata, right valves: a- female; b- male. Scale = 1 cm.
39(38) Shell typically pale ashy-green; shell elongate-elliptical and small, rarely exceeding 3.75 cm in length (Fig. 114):

*Dysomia lenior*

Shell not pale ashy-green, but rather yellow, brown, green or olive  

40

Fig. 114- *Dysomia lenior*, right valves: a-female; b-male. Scale = 1 cm.
Dysnomia penita

Upper margin of shell very broad and humped; color rays on shell consisting of very fine, dark brown lines, arranged very close together; minute chevroned spots often occur between rays; posterior ridge occasionally furrowed along rays (Fig. 115):

Upper margin of shell narrower and not especially humped; color rays on shell are broader and spaced wider apart ...

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Fig. 115- Dysnomia penita, right valves: a- female; b- male. Scale = 1 cm.
41(40) Posterior ridge usually furrowed; periostracum glossy; nacre usually lavender-purple (Fig. 116): *Dysnomia haysiana*

Posterior ridge not furrowed, or only rarely furrowed close to ventral margin on females; nacre usually white.. 42

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Fig. 116—*Dysnomia haysiana*, right valves: a—female; b—male. Scale 1 cm.
42(41) Periostracum very glossy; shell 2.5 cm in length or less
(Fig. 116):  
\textit{Dysnomia haysiana} (juvenile)
Periostracum dull or with only low gloss .................. 43

43(42) Shell high and inflated, especially in male; marsupial
extension on female shell is relatively narrow (Fig. 117):
\textit{Dysnomia sulcata}

Shell only slightly inflated; marsupial extension on
female shell is relatively broad (Fig. 118): \textit{Dysnomia turgidula}

Fig. 117- \textit{Dysnomia sulcata}, right valves: a- female; b- male. Scale = 1 cm.
44(43) Shell greatly inflated; posterior ridge sharply angled; posterior slope very steep and often with 1 or 2 minor ridges. (Fig. 119): *Dysnomia archaeformis*

Shell not greatly inflated; posterior ridge round (except in *D. biemarginata* and some specimens of *D. flexuosa*).... 45

Fig. 118- *Dysnomia turgidula*, right valves: a- female; b- male. Scale = 1 cm.
Fig. 119 - *Dysnomia archaiformis*, right valves: a - female; b - male. Scale = 1 cm.
47(46) Depression between median and posterior ridge on male wide; on females marsupial extension is narrow and centrally located (Fig. 107): *Dysnomia flexuosa*
Depression between median and posterior ridge relatively narrow; on females marsupial extension is broad and located posteriorly (Fig. 120): *Dysnomia biemarginata*

48(46) Posterior margin of shell long and curved, giving shell characteristic shape; beaks greatly displaced anteriorly (Fig. 121): *Dysnomia propinqua*
Posterior margin of shell shorter and more acutely curved; beaks not greatly displaced anteriorly .................... 49

Fig. 120- *Dysnomia biemarginata*, right valves: a- female; b- male.
Scale = 1 cm.
Fig. 121 - *Dysnomia propinqua*, right valves: a- female; b- male. Scale = 1 cm.

Fig. 122 - *Dysnomia personata*, right valves: a- female; b- male. Scale = 1 cm.
49(48) Umbos flattened, due to extension of depression between posterior ridge and median ridge up onto umbo; shell rather evenly colored over entire surface; rays obscure (Fig. 107): *Dysnomia flexuosa*

Umbos round and full, depression between posterior and median ridge not extending up onto umbo. Shell often with bright green rays (Fig. 110): *Dysnomia torulosa*

50(45) Median ridge low and smooth or absent ............................................. 51
Median ridge absent .............................................................................. 54

51(50) Umbos low and flattened due to depression between posterior and median ridges extend up onto umbo (Fig. 109): *Dysnomia stewardsoni*

Umbos round and full, depression between posterior and median ridges not extending up onto umbo ............................................. 52

52(51) Shell as high as long, or nearly so ....................................................... 53
Shell clearly longer than high (Fig. 110): *Dysnomia torulosa*

53(52) Umbos centrally placed, or nearly so (Fig. 122): *Dysnomia personata*
Umbos anteriorly placed (Fig. 117): *Dysnomia sulcata*

54(50) Shell as high as long, or nearly so ....................................................... 55
Shell clearly longer than high ................................................................. 56

55(54) Umbos centrally placed, or nearly so (Fig. 122): *Dysnomia personata*
Umbos anteriorly placed (Fig. 117): *Dysnomia sulcata*

56(54) Shell rayless, yellow and small (not exceeding 3 cm in length) (Fig. 113): *Dysnomia metastriata* (immature)
Shell with rays .................................................................................... 57

57(56) On left valve, interdentum clearly discernable as flat ledge of about 2 mm width; pseudocardinal and lateral teeth large and heavy; shell obscurely rayed (Fig. 108): *Dysnomia lewisi*

On left valve interdentum inconspicuous; pseudocardinal and lateral teeth not large and heavy (except in *D. sulcata*); Shell typically distinctly rayed with dark green, but occasionally obscurely rayed ............................................. 58

58(57) Beak greatly displaced anteriorly; nacre often purple or pink (although sometimes white); female shell with narrow marsupial extension (Fig. 117): *Dysnomia sulcata*
Beak not greatly displaced anteriorly; nacre typically white; female shell with broad marsupial extension ....................... 59

126
59(58) Shell elliptical in outline, not inflated (Fig. 123):

Dysnomia capsaeformis

Shell typically short and inflated ....................... 60

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Fig. 123- Dysnomia capsaeformis, right valves: a- female; b- male.
Scale = 1 cm.
60(59) Beaks low (Fig. 124): *Dysomia florentina*
Beaks higher, clearly extending well above upper anterior
and posterior margins (Fig. 118): *Dysomia turgida*

61(31) Posterior ridge angular. Genera *Truncilla, Lampsilis* (in
part) ................................................................. 62
Posterior ridge rounded or absent ................................ 70

Fig. 124- *Dysomia florentina*, right valves: a- female; b- male.
Scale = 1 cm.
62(61) Shell flattened laterally; beak cavities shallow; color rays on shell with or without v-shaped markings. Genus *Truncilla* ....... 63

Shell inflated; beak cavities deep; color rays present (without v-shaped markings) or absent. Genus *Lampeilis* (in part) ................. 65

63(62) Shell high, oval to subtriangular; posterior ridge sharp, distinct down to ventral margin of shell; posterior slope very short and very steep (Fig. 125): *Truncilla truncata*

Shell elongate, elliptical (juveniles sometimes oval); posterior ridge angular, but becoming round and fading out near ventral margin of shell ...................... 64

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Fig. 125- *Truncilla truncata*: right valve and hinge plate of left valve. Scale = 1 cm.

129
Fig. 126 - *Truncilla*, right valves: a - *T. macrodon*; b - *T. donaciformis*. Scale = 1 cm.

Fig. 127 - *Lampsilis*: a - *L. dolabraeformis*, right valve; b - shell inflated to ventral margin; c - shell inflated to upper half only. Scale = 1 cm.
64(63) Color rays on shell generally narrow; shell typically quite flattened; beak cavity generally very shallow (Fig. 126a):

Truncilla macrodon

Color rays on shell generally broad; shell somewhat inflated; beak cavity shallow, but clearly discernable (Fig. 126b):

Truncilla donaciformis

65(62) Shell high, length/height ratio 1.4 or less .................. 66
Shell more elongate, length/height ratio 1.5 or more ............ 68

66(65) Posterior end rounded (Fig. 127a): Lampsilis dolabraeformis
Posterior end pointed ........................................ 67

67(66) Shell inflated down to ventral margin (Fig. 127b; 128a):

Lampsilis excavata

Shell well inflated in upper half, but not down to ventral margin (Fig. 127c; 128b):

Lampsilis ovata ovata

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Fig. 128- Lampsilis, right valves: a- L. excavata; b- L. ovata ovata.
Scale = 1 cm.
Fig. 129 - *Lampsilis* perpasta: right valve. Scale = 1 cm.

Fig. 130 - *Lampsilis*, right valves: a - *L. binominata*; b - *L. splendida*. Scale = 1 cm.
68(65) Shell without color rays; posterior ridge convex (Fig. 129): 
   Lampsilis perpasta

Shell with color rays; posterior ridge straight or concave .. 69

69(68) Shell with only a few narrow (but sharply defined) color 
   rays (Fig. 130a): 
   Lampsilis binominata

Shell with many color rays (Fig. 130b): 
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70(61) Pseudocardinal teeth poorly developed. Genus Leptodea ...... 71

Pseudocardinal teeth well developed ........................... 75

71(70) Shell elongate (length/height ratio 1.5 or more), with poorly 
   to only moderately developed wing ............................ 72

Shell higher (length/height ratio less than 1.5), with well 
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Fig. 131- Leptodea shells, anterior view: 
   a- shell very flattened; b- shell inflated.
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Shell inflated (Fig. 131b); wing absent or at most low and poorly developed (Fig. 132b): *Leptodes amphichaena*

73(72) Ground color of periostracum straw-yellow to grey or grey-brown; nacre white on adults, silvery and iridescent on juveniles (Fig. 133a): *Leptodea fragilis*
Ground color of periostracum greenish-grey; nacre coppery-pink on adults, silvery and iridescent on juveniles (Fig. 133b): *Leptodes laevissima*

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Fig. 133 - *Leptodea*: a - *L. fragilis*, right valve and hinge plate of left valve; b - *L. laevissima*. Scale = 1 cm.
Fig. 134- *Proptera alata*: right valve and hinge plate of left valve. Scale = 1 cm.

Fig. 135a- extremely inflated shell, anterior end view; b- fine beak sculpture (e.g., *Proptera capax*); c- coarse beak sculpture (e.g., *Lampsilis ovata ventricosa*). Scale = 1 cm.
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<td>Wing usually lacking, but if present is very low and poorly developed</td>
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<td>Shell without purple nacre, nacre usually white, or if pinkish-purple, shell is small (less than 6 cm)</td>
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Fig. 136- *Proptera*, right valves: a - *P. capax*; b - *P. purpurata*. Scale = 1 cm.
77(76) Posterior mantle margin without papillate or ribbon-like projections. Genus *Actinonaias* ............................ 78
    Posterior mantle margin area in front of branchial opening modified to form extensions, either papillate projections or ribbon-like flaps ........................................ 81

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    Color rays on shell more or less of continuous intensity ... 79

79(78) Periostracum rather dull, not glossy; shell elongate; posterior half of shell generally not higher than shell anterior to beaks (Fig. 137b):  *Actinonaias ellipsiformis*
    Periostracum glossy; shell higher; posterior half of shell higher than shell anterior to beaks ...................... 80

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Fig. 137- *Actinonaias*, right valves:  a- *A. pectorosa*; b- *A. ellipsiformis*. Scale = 1 cm.
Fig. 138—*Astinonaias*: a- *A. carinata carinata*, right valve and hinge plate of left valve; b- *A. carinata gibba*. Scale = 1 cm.
Posterior mantle margins with long papillate projections (Fig. 139a). Genus *Villosa* ........................................ 82

(There are many nominal species that should be placed in the genus *Villosa*. However, how many of these represent distinct biological species and which are synonyms has not been adequately studied. According to Johnson (1970) it is not yet possible to tell how many species there are in *Villosa*. Therefore, the key below is only to species complexes.)

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84(83) Posterior end of shell truncate or very broadly rounded; shell more or less rhomboidal in outline: *V. fabalis* complex (This group includes the species *V. fabalis*, *V. lienosa* (Fig. 141a) and *V. propria*.)

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86(85) Posterior ridge high, terminating in rather sharp point well above midline of shell (Fig. 142a): *Lampsilis anodontoides*
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Fig. 145- *Lampsilis*, right valves: a- L. altilis; b- L. bracteata.
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Fig. 146- *Lampsilis*: a- *L. australis*, right valve; b- *L. radiata siliquoidea*, right valve and hinge plate of left valve. Scale = 1 cm.
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Fig. 147- Lampsilis, right valves: a- L. hydiana; b- L. radiata radiata. Scale = 1 cm.
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102(101) Shell with high protruding umbos (Fig. 151a) ............... 103  
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Fig. 154- *Lampsilis*, right valves: a- *L. binominata*; b- *L. ochracea*. Scale = 1 cm.
SECTION IV

ACKNOWLEDGEMENTS

I wish to thank Mr John L. Tottenham for preparing most of the illustrations, Ms P. A. Ayers for providing technical assistance, and Dr W. H. Heard for advice regarding some of the key anatomical characters.
The bibliography below is not intended to be complete, but to bring to
the attention of the interested reader some of the more important publi-
cations dealing with North American freshwater mussels, as well as to
provide a good cross-section of the workers who have published on
unionid clams in the northern part of the Western Hemisphere. A complete
bibliography of the Unionacea of North America would take many pages,
and for those interested can be assembled from the references given in
the works cited below.

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Alate - Having a "wing", i.e., a dorsal, thin, flat projection, as the extension of the posterior slope of some freshwater mussels.

Anal opening or siphon - The dorsal posterior opening or siphon located near the anus through which water leaves the mantle cavity of a mollusk such as a freshwater mussel. Through it are carried excretory products of the alimentary and renal systems. Also called the excurrent opening or siphon.

Angular - Having an angle or having the tendency to form an angle, in contrast to being round.

Anterior end - The shorter end of the shell (from the beaks) in freshwater mussels. The foot of the animal is directed toward this end.

Arched - In the form of an arch or curve; bending in a curved manner in a particular direction.

Beak - The raised part on the dorsal margin of each of the bivalved shell valves. The beaks are formed by the embryonic shell, around which the later shell develops distally in a concentric manner. Also called umbo (pl. umbos).

Beak cavity - The cavity on the inside of each valve of a mussel shell going into the beak. In some species the cavity is quite deep, in others it is so shallow as to be hardly more than a weak depression.

Beak sculpture - The natural surface markings, other than those of color, found on the beaks or umbos of mussel shells. Such markings are in some cases characteristically different in the various taxa, and thereby provide means of identification. They are sometimes considered important in indicating phylogenetic relations between genera and higher taxonomic groups.

Biangular - Having two angles or corners.

Bifurcate - Divided into two branches.

Bivalve - A common or popular name referring to a member of the molluscan class Pelecypoda or Bivalvia. The name refers to the possession by the animal of two apposing plates or valves composed mainly of calcium carbonate which enclose and protect the soft body of the mollusk.
Bradytictic - Refers to mussels that are long-term breeders, i.e., that retain developing glochidial larvae in their gills throughout the year, except in the Nearctic summer.

Branchial opening or siphon - The ventral posterior opening or siphon through which water enters the mantle cavity of a mollusk such as a freshwater mussel. After entering the mantle cavity the water flows over and through the branchiae or gills, providing oxygen, and in filter-feeders such as freshwater mussels, bringing microorganisms that are trapped as food by the gill surface. Also called the incumbent opening or siphon.

Caruncle - A fleshy elevation or outgrowth; a characteristic protuberance on the inner edge of each side of the mantle in front of the branchial opening of members of the lamsiline genus Carunculina.

Chevron-shaped - Shaped like a wide-angled V, normally positioned or inverted.

Clam - A common or popular name for a bivalved mollusk of the class Pelecypoda or Bivalvia.

Color ray - A more or less straight band of color, continuous or discontinuous, contrasted to the ground color of the shell and radiating from the umbonal area distally toward or to the peripheral margins of the valve.

Concentric - Having the same center, e.g., the umbo, and expanding outward in parallel (i.e., equidistant) lines, as in the lines of growth of a mussel shell.

Compressed - Flattened or pressed together laterally, such as the appearance of some freshwater mussels.

Corrugated - Wrinkled by alternating ridges and furrows.

Cusp - The highest elevations of the lateral and pseudocardinal teeth.

Demibranch - One-half of one of the paired gills of a lamellibranch pelecypod; i.e., the two apposing rows of gill filaments on one side of the gill; a half-gill. A vertical cross-section of one of the paired lamellibranch gills is like a W pressed together. One-half of the W is the demibranch. This peculiar type of ctenidium found in lamellibranchs apparently evolved by the elongation of the gill filaments on each side of the gill axis, forming and inverted V, followed by the bending back on itself of each filament forming a W.

Disc - The middle, central or main portion of the exterior of the valve of a mussel as distinct from the posterior slope and other areas immediately adjacent to the marginal peripheries.
Double-looped - Being in the form of two adjacent semicircles, i.e., end to end with the openings oriented in the same direction. This is usually contrasted to single-looped, in which case there is only one semicircle. In regard to freshwater mussels, both terms refer to the sculpturing of the umbo or beak of the shell.

Elliptical - Having the form of an ellipse.

Elongate - Lengthened; extending length-wise; especially longer than high.

Excurrent opening or siphon - The dorsal posterior opening or siphon through which water leaves the mantle cavity of a mollusk such as a freshwater mussel. This opening or siphon is located near the anus and nephridopores, and so also serves as an exit for excretory products. Also called the anal opening or siphon.

Furrowed - Grooved or channelled.

Gill (Branchia) - The platelike or filamentous outgrowth, usually located within the mantle cavity, serving as the respiratory organ of aquatic mollusks. In lamellibranch mollusks the gills are greatly enlarged, serving not only the function of respiratory gaseous exchange, but also in food gathering ("filter-feeding"). The basic structure of the molluscan gill is characteristic throughout the phylum and is referred to as a "ctenidium".

Gill filament - One of the leaflets of the gill.

Glochidium - The bivalved larva of freshwater mussels, generally parasitic on fish during this early stage in the life history.

Glossy - Smooth and shining; highly polished.

Gravid female - A female with marsupium filled with young embryos.

Ground color - The basic or background color of a shell, against which any additional color markings are contrasted.

Growth lines - Minute lines on the outer shell surface indicating a minor rest period during growth. Not to be confused with the major "rest marks", caused by prolonged growth arrest (as during winter).

Hinge - The stabilizing lamellae (pseudocardinal and lateral teeth) in the dorsal part of each valve of a mussel shell. The opposing single lamella in one valve articulates with a pair of complementary lamellae in the opposing valve.

Hinge plate - That part of the dorsal margin of the shell between and including the pseudocardinal and lateral teeth.
Incurrent opening or siphon - The ventral posterior opening or siphon through which water enters the mantle cavity of a mollusk such as a freshwater mussel. Also called the branchial opening or siphon. Water flows through this opening to the gills or branchia, where oxygen-carbon dioxide exchange occurs, and in filter-feeders such as freshwater mussels, where microorganisms are trapped as food.

Inf1ated - Swollen; expanded; distented.

Interdentum - The space on the hinge plate between the pseudocardinal and lateral teeth.

Interlamellar connections - Connections of tissue joining the two lamellae of a demibranch. Together with the interfilamental connections (and at right angles to them) they are responsible for the formation of ascending water tubes within the gill demibranch. Water enters the water tubes by ostia in the interfilamental connections and flows upward to the exhalent space at the top of the gill, and thence to the outside of the animal via the exhalant opening or siphon.

Iridescent - Prismatic coloration; exhibiting colors like the rainbow.

Lamella - A small thin plate, blade or scalelike structure.

Lamellate (Lamellar) - Formed in thin plates, composed of thin plates or covered with them.

Lamina - A thin layer, blade or platelike extension.

Laminate - Consisting of plates or layers, one over another.

Lateral teeth - The elongated lamellae on the posterior half of the hinge-plate.

Left valve - The shell half on the left side when the shell is placed with the hinge up and the anterior end forward.

Length/height ratio - The number or quotient obtained by dividing the greatest length of a clam shell by its greatest height. The more elongate the clam, the higher will be the quotient; the shorter and higher the shell, the lower will be the quotient.

Mantle - An extension of the dorsal body wall of mollusks as one or a pair of folds, which usually secretes a shell and encloses a mantle cavity, typically containing gills.

Mantle margin - The edge of the mantle or pallium, the characteristic soft outer fold of integument covering the body of mollusks. In gastropods, the mantle margin is adjacent to the shell aperture. In pelecypods, the mantle margin is adjacent to the distal edge of the shell. The mantle margin functions in shell deposition during new growth, and in pelecypods it also serves a sensory function.
Marsupial extension (on shell) - The bulge or ventral extension of the shell on some female unionacean clams caused by new shell material being laid down by the protruding mantle covering the swollen gravid gills during shell growth. The marsupial extension on females results in sexual dimorphism.

Marsupium - The pouch used to contain young. In unionacean clams, internal spaces in the gills perform this service, and the type of modification of the gills to perform this protective function is important in higher classification within the superfamily.

Median ridge - A dorsoventral ridge on the shell running from the region of the umbos toward or to the ventral margin in some bivalves.

Mussel - A common or popular name for a bivalved mollusk of the class Pelecypoda or Bivalvia.

Nacre - The white or iridescent inner layer of shell in many mollusks, lying next to the mantle and often characteristically colored in many unionacean clams.

Nodule - A small knot, lump or irregularly shaped mass, such as the projections occurring on the shell surface of some freshwater mussels.

Nodulose (Nodular, Nodulate) - Having small knobs, nodules or projections.

Oblique - Slanting, as some ridges which are not parallel to the concentric growth lines.

Obsolete - Obscure; not distinct; very rudimentary.

Oval - In the shape of the longitudinal section of a hen's egg, i.e., oblong and curvilinear, with one end narrower than than the other.

Pallial line - On the inside surface of a bivalved shell that line of attachment of the mantle to the shell, often marked by a depression or scar.

Papillate - Having many small papillae or bumps on the surface.

Parallel - Spaced the same relative distance apart throughout the length, even though the objects may be in the form of a curve, circle or spiral.

Periostracum - The thin proteinaceous external layer covering most mollusk shells.

Placenta - A name by which the branchial brood pouches (marsupia) of unionacean clams are sometimes called.
Posterior end - The longer end of the shell (from the beaks). This is the end containing the siphonal (inhalant and exhalant) openings through which water passes into and out of the mantle cavity. In most unionid clams, this is the end sticking above the substratum in which the animal is buried.

Posterior ridge - A ridge on the external surface of many mussel shells, extending from the umbos posterovertrally toward or to the shell margin. It is often used as a diagnostic character for species discrimination.

Posterior slope - The area on the external surface of a mussel shell between the posterior ridge and the dorsal margin of the shell.

Pseudocardinal teeth - The usually compact lamellae on the anterior part of the hinge plate.

Pustule - A blisterlike prominence, such as the projections found on the shell surface of some freshwater mussels.

Pustulose (Pustular, Pustulate) - Having prominences resembling blisters.

Radiating - Proceeding outwardly (as, for example, lines) from a central point, as color rays on a mussel shell.

Ray - A streak or linear mark. It may be continuous or interrupted at intervals.

Rest mark - A darker or thicker part of the shell characteristically formed during a major rest period in growth.

Rhomboidal - Having the shape of a rhomboid, i.e., quadrilateral with opposite sides and angles equal, but neither equilateral nor equiangular.

Right valve - The shell half on the right side when the shell is placed with the hinge up and the anterior end forward.

Rounded - Having a more or less evenly curved contour, in contrast to being angular.

Rudimentary - Vestigial; not or barely functional in one species as contrasted to being developed in others.

Sculpture - The natural surface markings, other than those of color, usually found on mussel shells, and often furnishing identifying marks for species recognition.

Septa - Partitions (formed by the interlamellar connections) separating spaces occurring between the two lamellae of a eulamellibranch demibranch.
Sexually dimorphic - Males and females of the same species being morphologically different. In unionacean clams sexual dimorphism is usually indicated by the marsupial extension on the shell. This extension is caused by new shell material being laid down by the protruding mantle covering the swollen gravid gills during shell growth.

Single-looped - Being in the form of one loop or semicircle, as contrasted to being double-looped, i.e., consisting on two semicircles facing the same direction and joined end-to-end. Refers to the condition of the ridges on the umbo or beak of a mussel shell.

Siphon - A tubular or siphonlike structure formed by the opposing posterior mantle margins in mussels; a pair are commonly present on bivalves, providing restricted incurrent and excurrent openings to the mantle cavity.

Sulcus - A groove, furrow or channel.

Supra-anal opening - A dorso-posterior opening in the fused right and left mantle margin in the anal region above the excurrent siphonal opening. Present in the Amblemidae and Unionidae, but absent in the Margaritiferidae.

Tachytictic - Refers to mussels that are short-term breeders, i.e., that carry glochidial larvae in their gills only during the Nearctic summer.

Teeth - The opposing lamellae on the hinge plates of bivalved mollusks which serve to stabilize the two valves against shearing forces. In the Unionacea the anterior lamellae are called pseudocardinal teeth and the posterior lamellae are called lateral teeth.

Transverse - In the same direction (i.e., parallel to) the growth lines in a mussel shell; at right angles to radiating lines, which originate at the beaks and run distally toward the shell periphery.

Truncate - Having the end cut off more or less squarely.

Tubercle - A nodule or small eminence, such as a solid elevation occurring on the shell surface of some freshwater mussels.

Tuberculate (Tuberculose, Tubercled, Tubercular) - Covered with tubercles or rounded knobs.

Umbo - The oldest part of the bivalved shell valve, formed by the embryonic shell and around which the later shell is laid down distally in a semi-concentric manner. The umbos can readily be identified as the raised parts on the dorsal margin of each of the shell valves. Also called "beak".

Undulation - A wavy form, resembling that of a wave or waves.
Unionacea (Unionoidea) - A superfamilies of bivalved mollusks (class Pelecypoda or Bivalvia, subclass Lamellibranchia, order Schizodonta) living in freshwater and characterized by a schizodont hinge, the mantle divided into two almost entirely separate flaps, a hatchet-shaped foot and large leaflike gills behind the foot, which are used as marsupia to brood eggs and larval young.

Valve - The single undivided shell of non-pelecypod mollusks, or one of the opposing halves of the divided shell of a pelecypod mollusk. In bivalved mollusks the two shell halves are held together at one margin by an elastic ligament.

Wing - The dorsal, thin, flat extension of the posterior slope of some freshwater mussels.
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Bivalved mollusks of the superfamily Unionacea (Order Schizodonta) are represented in North America by three families, 46 genera, and, as treated in this key, 221 species. The primitive Margaritiferidae are represented by two genera and four species, the Amblemidae by eight genera and 25 species, and the very large family Unionidae by 36 genera and 192 species. Systematics are not well worked out in many groups, which makes a definitive listing of species somewhat arbitrary at this time. The present key in most instances reflects a conservative approach to the lower taxa and, although it omits many nominal species of doubtful validity, the key nevertheless represents most of the biological species.

Characters of soft anatomy are used to separate the families, subfamilies and, in a few cases, genera. Species are separated by shell characters. The main feature of this publication is an illustrated taxonomic key using both soft anatomy and shell characters for the identification of the North American Unionacea.