

# Phylum Mollusca

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## Introduction to Mollusca

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### INTRODUCTION

The Mollusca is well represented in freshwaters by two classes of molluscs (or mollusks, depending on your preference): Gastropoda (meaning “stomach foot”) and Bivalvia (referring to “two valves” or shells). The freshwater Gastropoda of the Nearctic is divided into two major groups: (1) the pulmonates which evolved from terrestrial snails and still possess a mantle cavity modified as a pulmonary cavity or “lung;” and (2) caenogastropods (formerly called prosobranchs), which have a gill and evolved directly from marine snails. The Nearctic bivalves include the native order Unionoida (primarily the abundant pearly mussels) and one order of both native (seed and mussel clams) and invasive clams and mussels. The latter (Asian clams, zebra mussels, and quagga mussels) have caused major losses of native pearly mussels as well extensive economic damage.

All freshwater molluscs have one or two shells composed of a thin outer layer of proteinaceous periostracum and a strong inner layer of mostly crystalline calcium carbonate.

Molluscs are present in most Nearctic freshwater habitats other than hypersaline lakes, which are colonized by only a few snail species (*Assiminea* spp.). Their diversity tends to be lower in extremely soft waters, higher in lotic versus lentic habitats, and greatest in the southeastern USA. Some bivalves can survive outside of water (e.g., buried in a river bank until exposed by rising waters), and pulmonate snails regularly climb out of water on emergent vegetation or rocks to gain better access to oxygen or to avoid predators.

### LIMITATIONS

Identification of freshwater molluscs is primarily based on shell morphology and secondarily on color. Reliance on shell morphology may pose a serious problem, especially for snails, because the shape of the shell can be modified substantially by water currents (e.g., Britton & McMahon, 2004). Moreover, dried and preserved shells lose much of their identifying colors. Consequently, most taxonomic keys to extant

molluscs are based on shell morphology. Identification of specimens beyond a preliminary level within each class should be done by comparing your specimens with shells in museums or in other places where a highly trained specialist can provide identified conspecifics for comparison.

## MATERIAL PREPARATION AND PRESERVATION

When retrieving molluscs from any aquatic habitat, try to collect individuals from nearby macro- and microhabitats

with different current velocities. We recommend collecting recently dead molluscs (especially the bivalves) if possible. This will prevent killing an individual of one of the many threatened and endangered species. After gently cleaning the shell, allow the labeled shell to dry without any artificial coating. Store the soft tissue from any live specimens collected in labeled jars with the appropriate preservative (see recommendations later in this chapter). The preservatives may differ depending on whether molecular analysis will subsequently be performed.

## KEYS TO MOLLUSCA

### Mollusca: Classes

- 1 Single shell present which is coiled (snails) or uncoiled (freshwater “limpets”) ..... **Gastropoda [p. 192]**  
 1' Two shells (valves) present and connected by a ligament hinge; mussels and clams ..... **Bivalvia [p. 211]**

## REFERENCE

Britton, D.K. & R.F. McMahon. 2004. Environmentally and genetically induced shell-shape variation in the freshwater pond snail *Physa* (*Physella*) *virgata* (Gould, 1855). *American Malacological Bulletin* 19: 93–100.

## Class Gastropoda

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## INTRODUCTION

Strong et al. (2008) reported 585 native and invasive species of snails and limpets from the Nearctic, although controversy surrounds the taxonomy. Depending on the author, family, genus, and species definitions and numbers will vary greatly. Freshwater and amphibious gastropods may be found in any temporary or permanent aquatic habitats, except phytotelmata. Most are found on and around aquatic macrophytes or on rocks, but some live in soft muds. Several species are protected by environmental laws, some species are important vectors of wildlife disease, and others are invasive.

## LIMITATIONS

These keys are to adult freshwater gastropods. The Nearctic taxa are, for the most part, easily identified to family level. Much revisionary taxonomic work needs to be done in most gastropod groups. The extreme age and tremendous morphological plasticity of gastropods make the definition of most taxonomic categories difficult to

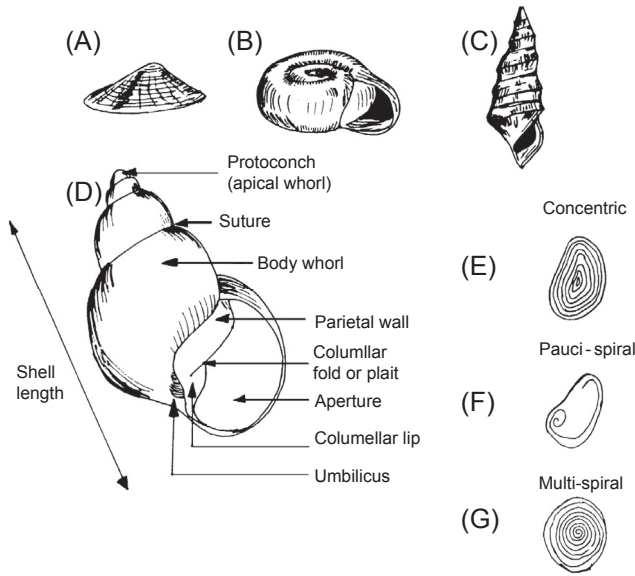
quantify. Particularly vexing is the strange confusion in the taxonomic literature, with many taxa accepted or rejected without explanation, and good quantitative taxonomic revisions ignored without explicit justifications. Because of this issue, the keys are taxonomically conservative, often terminating with species groups rather than species.

In Canada (Alberta, British Columbia, and Manitoba) and the USA (Alabama, Georgia, Idaho, New Mexico, Tennessee, and Utah) are several species that are protected under environmental law. Many species are protected at the state and province level in these countries.

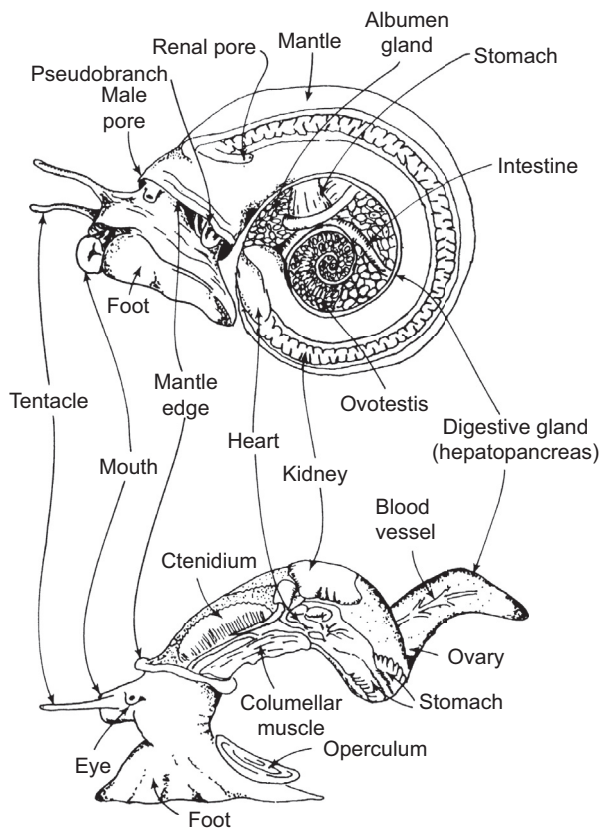
## TERMINOLOGY AND MORPHOLOGY

Defining characters are presented in Figs. 11.1–11.3<sup>1</sup>. Much of gastropod identification is dependent on shell structures; however, there is considerable overlap of shell characters,

1. Most figures in this chapter came from Brown & Lydeard (2010) or Cummings & Graf (2010). However, some figure legends have been changed to reflect current taxonomy.



**FIGURE 11.1** Basic anatomy of the shell, including shell architecture (conical, A; planispiral, B; spiral C, D), major features of the shell (D), and three types of opercula: (E)=concentric; (F)=paucispiral; and (G)=multispiral.



**FIGURE 11.2** Basic internal anatomy of a planorbid pulmonate (above, after Burch, 1989), and a pleurocerid prosobranch (below, after Pechenik, 1985).

so they cannot be used exclusively. The basic snail shell is a coiled tube. Each coil of the tube is called a whorl. The last 360 degrees of the coiled shell is called the body whorl and is the last whorl of the tube that does not have the shell

coiled completely around it. The dorsolateral surface of the whorl is the shoulder. The shell opening with the animal inside is the aperture. It may contain “teeth,” which are flattened lamellae, projecting from the inside surface.

In caenogastropods, this aperture can be sealed shut with a shell “door” called an operculum, which grows on the back of the animal’s foot. Operculae may grow spirally, concentrically, or paucispirally, wherein the successive whorls increase in size. If a shell is placed such that the spire is directed upward or away from the observer and the aperture is facing the observer, a shell with the aperture on the left and spiraling towards the right is sinistral in orientation, whereas a shell with the aperture on the right and spiraling to the left is dextral.

Because the shell is basically a tube, lines or grooves (called striae) that grow in the direction of the expanding tube are called spiral, while those that grow across the tube are called transverse. A shell may have a carina or ridgeline that follows the length of the tube, or one or more low lirae that are basically the same as a carina, only much smaller. If the ridges are transverse, they are called costae.

The entire coiled shell, other than the body whorl, is the spire. The line demarcating where one whorl is fused to the previous whorl is called the suture. The end of the spire is the apex. The structural point around which the shell spirals is called the columella. If this opens as a tube, it opens ventrally, and this opening is called the umbilicus. An open umbilicus is termed perforate, whereas a closed umbilicus is called imperforate. An aperture lip that reflects over the umbilicus is called a columellar lip.

Whorls may be rounded in cross section with deep sutures, or whorls may be flattened with shallow sutures. Flattened whorls give the shell a conical shape, while moderately rounded whorls give the shell a subglobose shape, and nearly spherical shells are globose in shape, and of course, a continuum exists between these three shell shapes. In the limpets, the tube is not coiled, but reduced to a conical cap, referred to as patelloid. Ramshorn snails typically coil as a disc, which form is referred to as planispiral.

The animal within the shell is composed of the eversible headfoot and mantle, and the non eversible visceral mass. The primary soft anatomy characters are within the headfoot and the mantle. The head portion contains one or more pairs of sensory tentacles, and generally, the eyes are placed at the bases of the primary pair. Anterior to the primary tentacle pair is the mouth, which may be flanked by a secondary tentacle pair. Inside the mouth is the radula, which is similar to a tongue. The radula is lined with transverse rows of radular teeth, which may each have one or more cusps for rasping periphyton from surfaces.

Most Nearctic freshwater gastropods are typically dioecious, with the males having an enlarged right tentacle as a copulatory organ or possess a penis or a specialized verge, or have no copulatory organ at all. Pulmonates, in contrast, are all monoecious. The basic components of the pulmonate reproductive system are shown in Fig. 11.3.

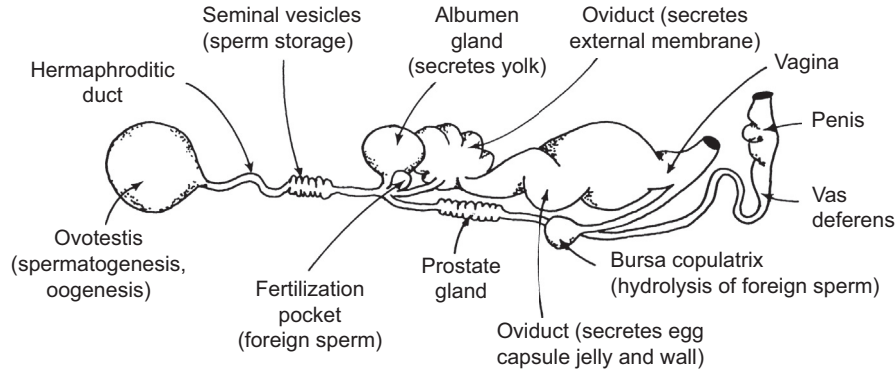


FIGURE 11.3 Anatomy of the reproductive system of the pulmonate snail *Physa* (from Brown & Lydeard, 2010).

Taxonomic diagnosis may require dissection of the genitalia. The penis or associated genitalic structures may have one or more obvious glands, often on projections. In the Physidae, the genitalic structures important for diagnosis are the preputium, the preputial gland and the penial sheath. The preputium is a tube that opens to the outside of the animal for releasing or receiving sperm. The preputium may or may not have a dorsal preputial gland. Posterior to the preputium is the penial sheath, which may be glandular or muscular, or both.

Empty shells can be kept dry. A bit of cotton stuffed carefully in the aperture and daubed with glue will hold the operculum in place. Shells that have had the animal removed should be cleaned with alcohol inside and let air dry to reduce odors.

Specimens where the animal needs to be extracted from the shell can be boiled in pure bleach for a few seconds or dipped in concentrated hydrochloric acid for a few seconds. Alternatively, the shell can be gently cracked with forceps and the shell pieces removed. The radula can be viewed by cutting open the top of the head and teasing the structure out with a needle, probe, or forceps.

The genitalia sit inside the headfoot just above and behind the eyes. Using a fine scalpel or a razor, gently cut the head open posteriorly between the eyes. The genitalic penial structures lie on the left side of the animal, behind and at the base of the left tentacle.

## MATERIAL PREPARATION AND PRESERVATION

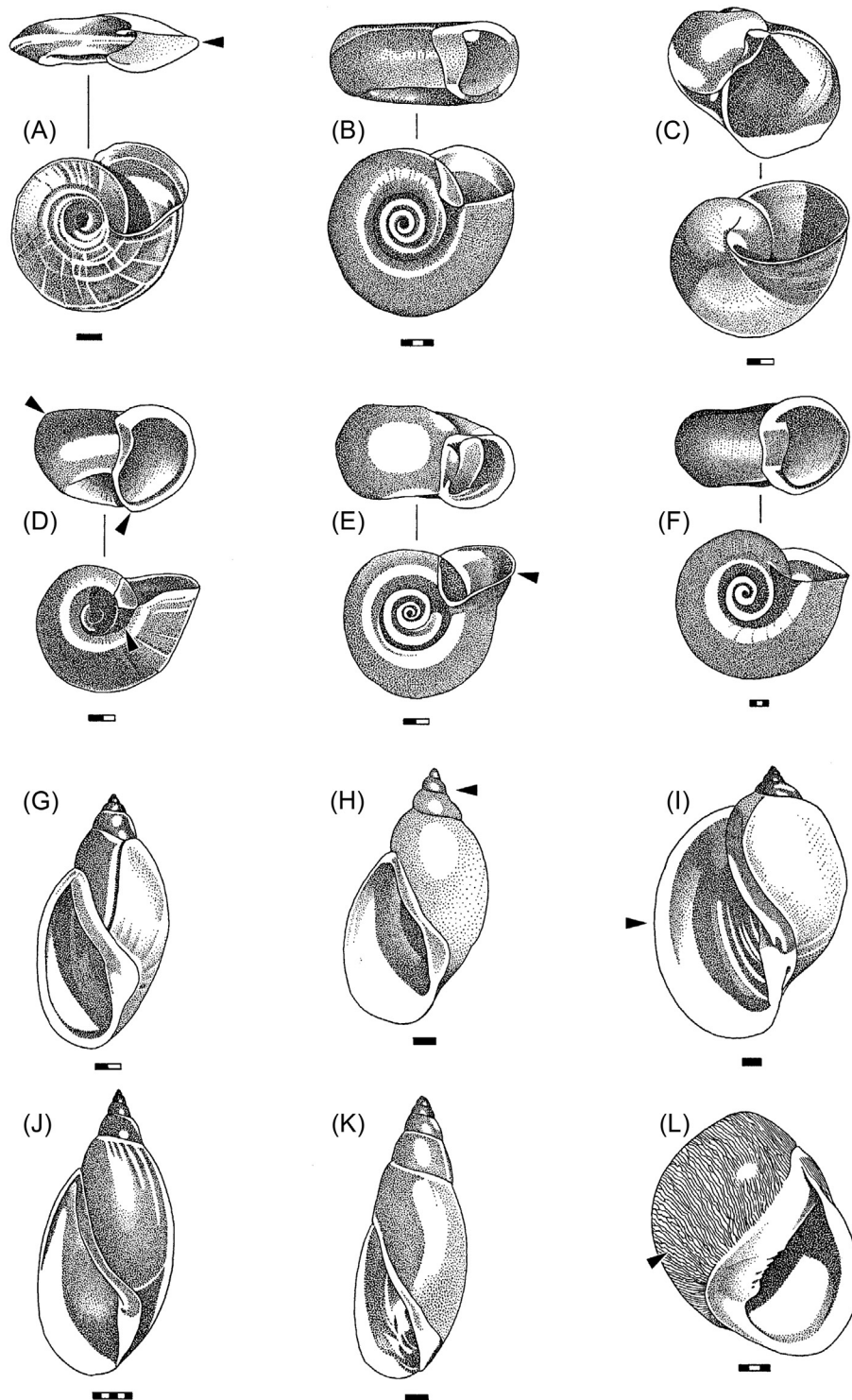
Whole animals can be preserved in ethyl or isopropyl alcohol. Formalin should never be used, as it will dissolve the shells.

## KEYS TO GASTROPODA

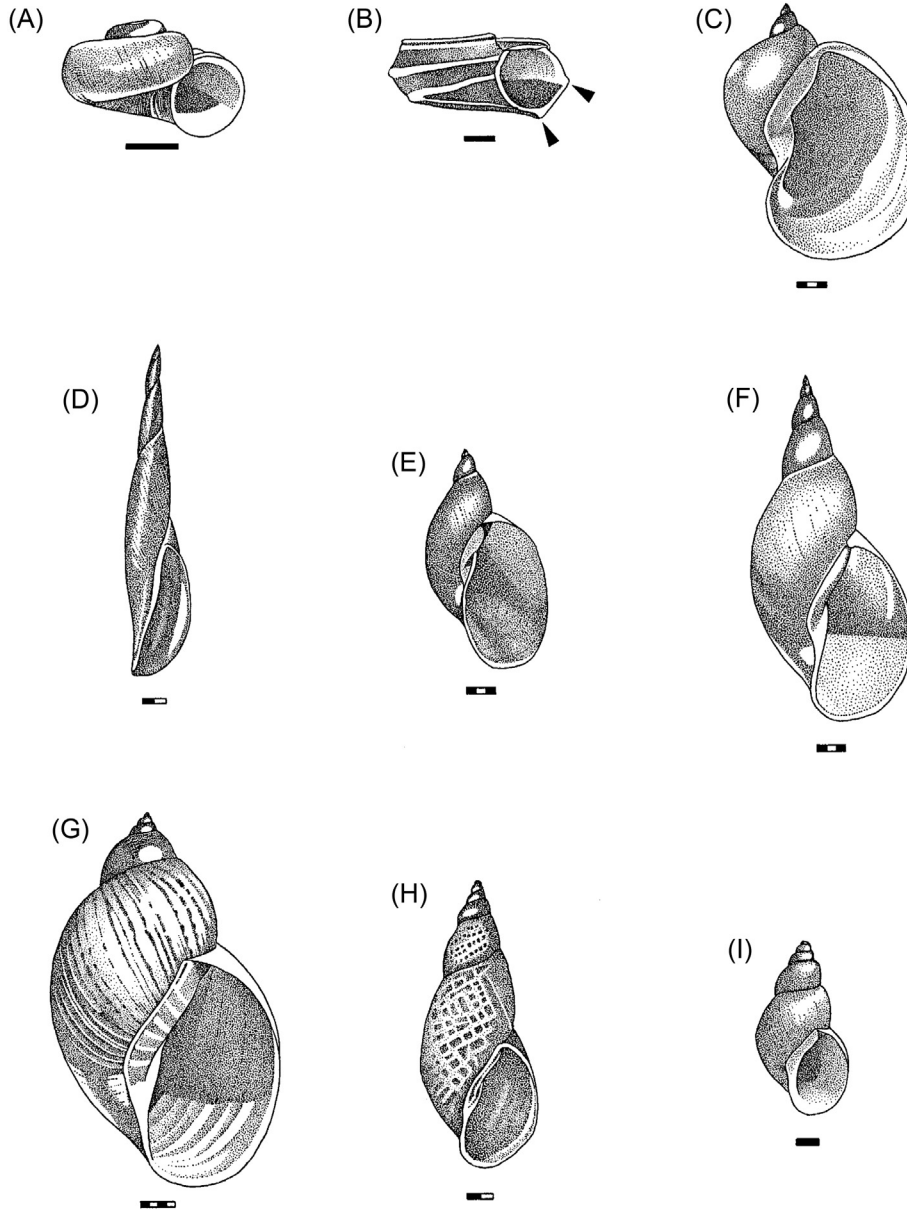
### Gastropoda: Superfamilies

1	Operculum present (Fig. 11.1) .....	2
1'	Operculum absent .....	7
2(1)	Shell rough, or if smooth, not globose; spire prominent or shell patelliform; columella rarely produced as a flat septum; operculum without internal processes .....	3
2'	Shell globose, smooth, like porcelain or a marble; spire reduced, rounded; columella transverse, projecting as a septum (shelf like); operculum calcareous with small digitiform projections along the lower margin (Fig. 11.4 L) .....	Neritoidea, one family: Neritidae; one genus: <i>Neritina</i> [p. 198]
3(2)	Operculum oval and concentric, paucispiral, or multispiral (Fig. 11.1 E–G).....	4
3'	Operculum circular and spiral; plumose gill extends outside of shell (Fig. 11.5 A, B) .....	Valvatoidea, one family: Valvatidae; one genus: <i>Valvata</i>
	[Widespread. Genus in need of revision, 8–12 species. Not keyed further.]	
4(3)	Operculum concentric, corneous (Fig. 11.1 E).....	5
4'	Operculum paucispiral, or multispiral; operculum calcareous or corneous (Fig. 11.1 F, G) .....	6
5(4)	Aperture broader than spire is long; shell with short spire or planispiral in form; oral tentacles present (Fig. 11.6 A, B) .....	Ampullaroidea, one family: <b>Ampullariidae</b> [p. 198]
5'	Aperture narrower or subequal to length of spire; oral tentacles always absent (Fig. 11.6 C–G) .....	Viviparoidea, one family: <b>Viviparidae</b> [p. 198]



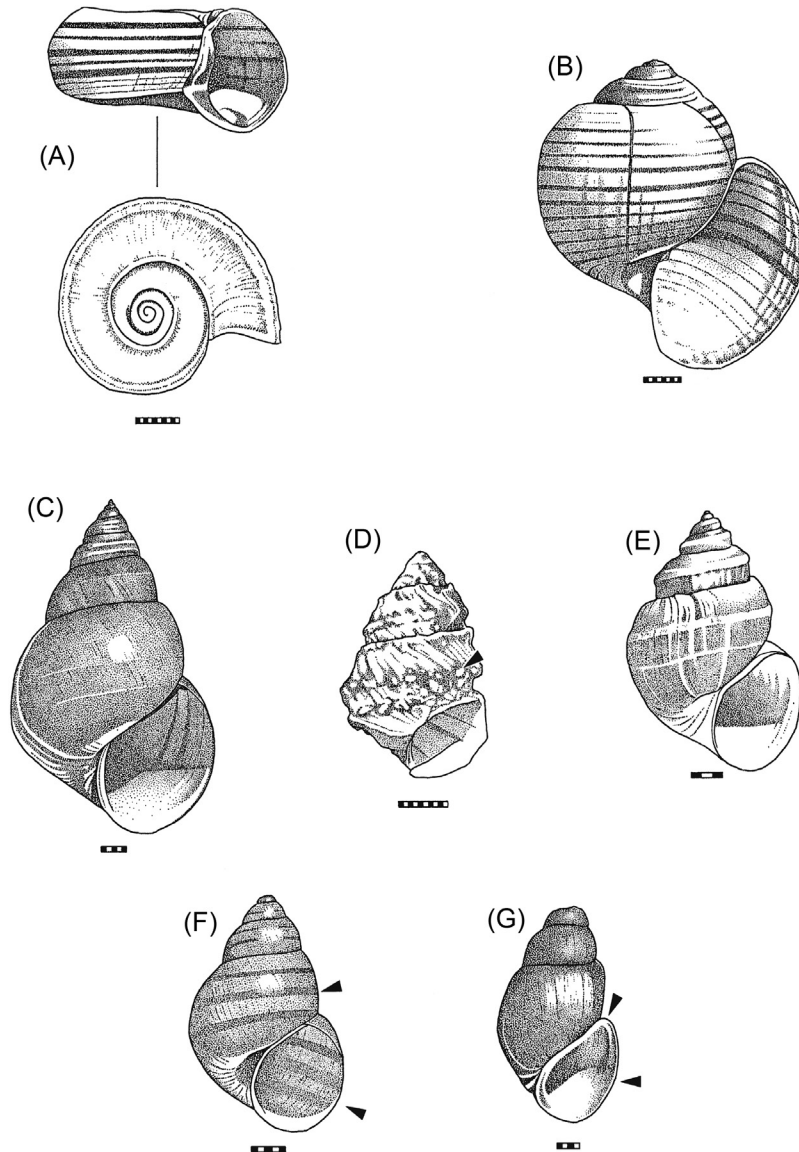


**FIGURE 11.4** Representative physids and planorbids and neritiniids. (A) *Promenetus exacuus* (note flared body whorl and carina); (B) *Biomphalaria glabrata*; (C) *Vorticifex effusa*; (D) *Helisoma anceps* (note strong growth lines and carina); (E) *Helisoma companulata* (sometimes called *companulatum*, note flared lip of aperture); (F) *Helisoma trivolvis* (this species reaches 20 mm in diameter and is extremely common); (G) *Physa gyrina*; (H) *Physa integra*; (I) *Physa* sp.; (J) *Physa* sp.; (K) *Aplexa elongata* (note the bullet shape and lustrous black shell); (L) *Neritina reclinata* (note markings on shell and teeth on parietal wall). The scale bars equal 1 mm. Figures A–I after Burch, 1989.

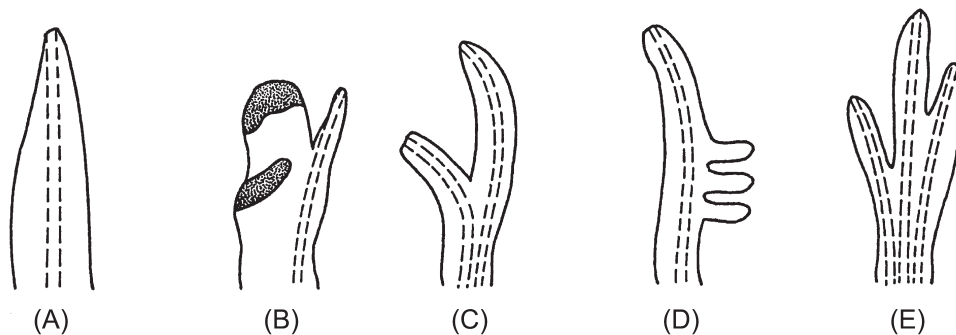


**FIGURE 11.5** Representative valvatids and lymnaeids. (A) *Valvata sincera* (note multispiral operculum); (B) *Valvata tricarinata* (note carina); (C) *Radix auricularia* (note expanded body whorl); (D) *Lymnaea haldemani* (note extremely narrow shell); (E) *Lymnaea columella* (note thin, transparent shell and amphibious habit); (F) *Lymnaea stagnalis* (note large and fragile shell) (G) *Lymnaea megaloma* (note thick, large shell); (H) *Lymnaea elodes* (note malleations sometimes present); (I) *Lymnaea humilis* (note small size). Scale bars equal 1 mm. Figures A–I after Burch, 1989.

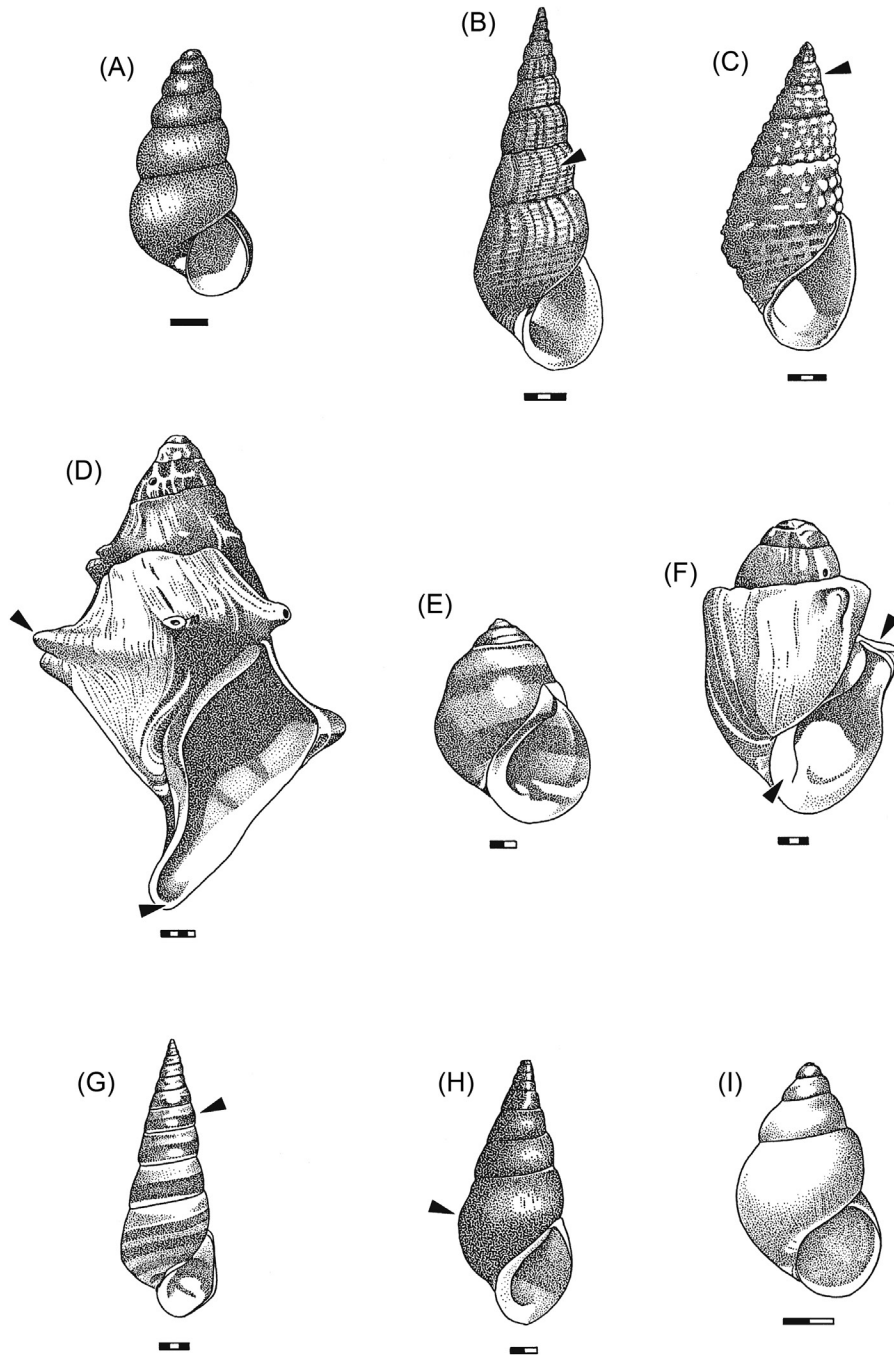
6(4)	Males if present with a penis; adult often under 10 mm, but may reach 15 mm; shell rarely with any sculpturing (Fig. 11.7 A–E) .....	Rissooidea [p. 199]
6'	Males if present without a verge; adults typically 15 to 75 mm; shell typically with strong sculpturing (Fig. 11.8 B–I) .....	Cerithioidea [p. 202]
7(1)	Shell not patelliform, or if patelliform, then spire sinistral (apex centered or to right of midline) and blunt, with adult patelliform shell larger than 7 mm (Fig. 11.9 A, B, D–G) .....	8
7'	Shell patelliform with spire dextral (apex to left of midline), acute; adult shell less than 7 mm in length (Fig. 11.9 C) .....	Acroloxidea, one family; Acroloxidae: <i>Acroloxus coloradensis</i> (Henderson, 1939) [Canada: Alberta, British Columbia. USA: Idaho, Colorado, Montana]
8(7)	Tentacles narrow, filiform .....	9



**FIGURE 11.6** Representative ampullarids and viviparids. (A) *Marisa cornuarietis* (note large, planospiral shell); (B) *Pomacea paludosa* (large “apple” snail common in Florida); (C) *Bellamya japonica* (introduced but now widespread species in North America); (D) *Tulothoma magnifica* (note tubercles which may be absent in some morphs or species, recently rediscovered in Alabama rivers); (E) *Lioplax subcarinata*; (F) *Viviparus georgianus* (note circular operculum, and bands which may disappear in adults, common throughout eastern U. S.); (G) *Campeloma decisum* (sometimes referred to as *decisa*; note operculum is longer than it is wide and shouldered junction of aperture and body whorl, quite common in rivers and lakes in eastern states). Scale bars equal 1 mm. Figures A–G after Burch, 1989.



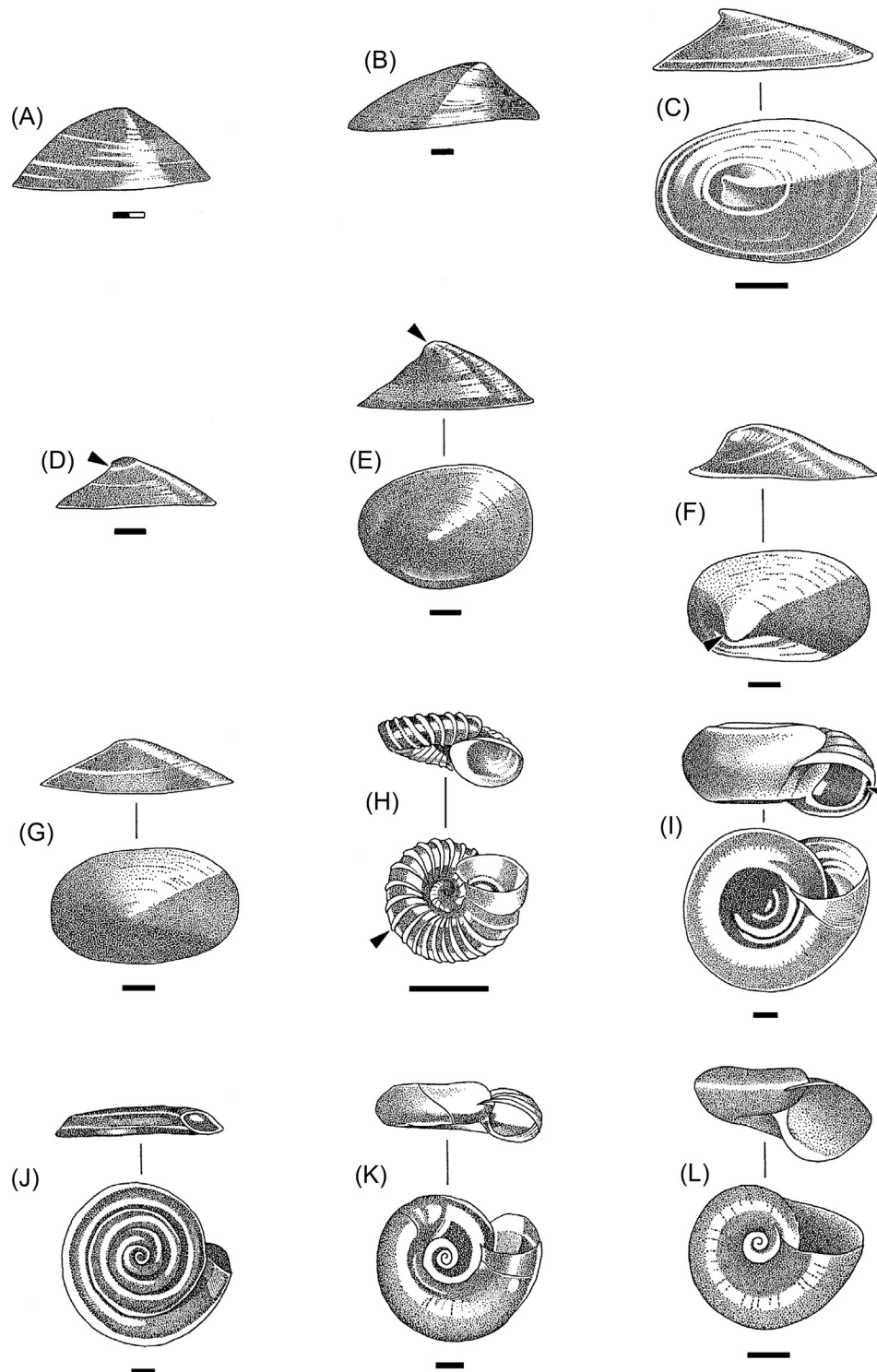
**FIGURE 11.7** Structure of the penis (verge) in various hydrobiids. (A) simple penis in Lithoglyphidae; (B) glandular crests of penis in subfamily Nymphophilinae; (C) two-ducted penis in Amnicolidae; (D) penis with accessory lobes in Hydrobiinae; and (E) three ducted penis of hydrobiid subfamily Fontigentinae. Figures A–E after Burch, 1989.



**FIGURE 11.8** Representative Potamiopsids, thiarids and pleurocerids. (A) *Pomatiopsis lapidaria* (note paucispiral operculum); (B) *Melanoides tuberculata* (note costae and lirae); (C) *Thiara granifera* (note tubercles and flattened whorls near apex); (D) *Io fluviatilis* (length of spines variable); (E) *Leptoxis carinata*; (F) *Lithasia/Pleurocera* (note thickened anterior aperture lip); (G) *Lithasia/Pleurocera* (note acute angle on anterior aperture); (H) *Lithasia/Pleurocera* (note there is tremendous variation in shell sculpture in this genus). (I) *Bithynia tentaculata*. Figures A–I after Burch, 1989.

- 8' Tentacles, broad, flat, triangular; haemoglobin absent; coiled shell always dextral, patelliform shell with apex central or sinistral; never planospiral (Fig. 11.5 C–I) ..... Lymnaeioidea, one family: **Lymnaeidae** [p. 203]
- 9(8) Aperture with three teeth on columella only; shell elongate; haemoglobin absent from blood ..... Ellobioidea, one family: Ellobiidae: *Myosotella myosotis* (Draparnaud, 1801)  
[Palaeartic. USA: Invasive in California, Oregon]
- 9' Aperture without teeth, or with teeth set back, inside aperture, never on columella; shell elongate, patelliform, planospiral, fusiform or succiniform; if patelliform, then shell apex central or sinistral; coiled shell dextral or sinistral (Figs. 11.9 D–L and 11.4 A–K); haemoglobin present in blood or not ..... **Planorbioidea** [p. 205]





**FIGURE 11.9** Representative limpets and planorbids: (A) lymaeid limpet *Lanx patelloides* (note large size, west coast distribution); (B) limpet *Fisherola nutalli*; (C) *Acroloxus*; (D) limpet *Rhodacmea rhodacme* (note notched depression and southeastern distribution); (E) limpet *Ferrissia rivularis* (note elevated shell, may possess posterior “shelf” in shell, wide distribution); (F) limpet *Hebetancylus excentricus* (note depressed apex to the right of midline, colorless tentacles, and southern distribution); (G) *Laevapex fuscus* (note obtuse apex near midline of shell, black pigmented tentacles, and widespread distribution in eastern backwaters and southern, slow flowing streams); (H) *Gyraulus crista* (note costae); (I) *Planorbula armigera* (note teeth in aperture); (J) *Drepanotrema kermatoides*; (K) *Gyraulus deflectus*; (L) *Menetus dilatatus*. Figures A–L after Burch, 1989.

**Gastropoda: Neritoidea: Neritidae: *Neritina* Species**

- 1 Shell black with scattered white triangular spots ..... *Neritina clenchi* Russel, 1940  
[USA: Florida. Neotropics]
- 1' Shell olive green with thin black transverse lines ..... *Neritina usnea* (Röding, 1798)  
[USA: Alabama, Florida, Louisiana, Mississippi, Texas. Mexico: Gulf coast. Neotropics]

**Gastropoda: Ampullaroidea: Ampullariidae: Genera**

- 1 Shell not planospiral (Fig. 11.6 B) ..... *Pomacea* [p. 198]
- 1' Shell planospiral (Fig. 11.6 A) ..... *Marisa cornuarietis* (Linnaeus, 1758)  
[Invasive, native to Neotropics. USA: California, Colorado, Idaho, Florida, Nevada]

**Gastropoda: Ampullariidae: *Pomacea*: Species**

- 1 Sutures and whorls normal, not deeply impressed ..... 2
- 1' Sutures deeply impressed forming a channel around the spire ..... *Pomacea maculata* (Perry, 1810)  
[Neotropical. Invasive in USA: Alabama, Arizona, California, Colorado, Idaho, Indiana, Florida, Nevada]
- 2(1) Shell whorl shoulders angular, flattened ..... *Pomacea bridgesii* (Reeve, 1856)  
[Neotropical. Invasive in USA: California, Florida]
- 2' Shell whorl shoulders rounded ..... *Pomacea paludosa* (Say, 1829)  
[USA: Florida. Neotropical. Invasive in USA: California, Florida, Georgia, Louisiana, Nevada, Oklahoma]

**Gastropoda: Viviparoidea: Viviparidae: Genera**

- 1 Operculum concentric ..... 2
- 1' Operculum concentric with nucleus spiral (Fig. 11.6 E) ..... *Lioplax* [p. 198]
- 2(1) Whorls with a distinct shoulder (Fig. 11.6 D, F, G) ..... 3
- 2' Whorls rounded, shoulder lacking (Fig. 11.6 C) ..... *Bellamyia* [p. 199]  
[Oriental and Palearctic. Invasive in Nearctic. Canada: southern border. USA: Widespread. Mexico(?)]
- 3(2) Carinae absent or present, but never tuberculate (Fig. 11.6 F, G) ..... 4
- 3' Carinae broken up into tubercles, may be partially obliterated (Fig. 11.6 D) .....  
..... *Tulotoma magnifica* (Conrad, 1834)  
[USA: Alabama.]
- 4(3) Operculum circular, aperture subcircular (Fig. 11.6 F) ..... *Viviparus* [p. 199]
- 4' Operculum and aperture oval (Fig. 11.6 G) ..... *Campeloma*  
[In need of revision, not keyed further. Canada: Great Lakes region. USA: east of the Mississippi to the Atlantic, Great Lakes/St. Lawrence River, to Gulf Coast]

**Gastropoda: Viviparoidea: Viviparidae: *Lioplax*: Species**

- 1 Shell form subcylindrical ..... 2
- 1' Shell form subglobose ..... 3
- 2(1) Body whorl with shoulder rounded ..... *Lioplax cyclostomaformis* (Lea, 1841)  
[USA: Alabama, Georgia]
- 2' Body whorl with shoulder angulate ..... *Lioplax talquinensis* Vail, 1979  
[USA: Alabama, Florida]
- 3(1) Shoulder subcarinate or smooth ..... 4
- 3' Shoulder strongly carinate ..... *Lioplax subcarinata* (Say, 1816)  
[USA: Atlantic drainages from New York to South Carolina]

- 4(3) Shell dark green/brown to black, length to 30 mm ..... *Lioplax pilsbryi* Walker, 1905  
[USA: Alabama, Florida, Georgia]
- 4' Shell brown to fawn or dark green, length less than 25 mm ..... *Lioplax sulculosa* (Menke, 1827)  
[USA: Arkansas, Illinois, Indiana, Iowa, Kentucky, Minnesota, Missouri, Ohio, Wisconsin]

### Gastropoda: Viviparoidea: Viviparidae: *Bellamya*: Species

- 1 Whorls malleate; whorls lacking spiral striae; spire obtuse ..... *Bellamya chinensis* (Reeve, 1863)  
[Canada: southern border regions. USA: (invasive) widespread. Native to China]
- 1' Whorls not malleate; whorls with spiral striae; spire acute ..... *Bellamya japonica* (von Martens, 1861)  
[USA: (invasive) widespread. Native to Japan]

### Gastropoda: Viviparoidea: Viviparidae: *Viviparus*: Species

- 1 Whorls rounded, but not globose; broad spiral banding present or absent ..... 2
- 1' Whorls broadly rounded; broad spiral banding absent ..... *Viviparus intertextus* (Say, 1829)  
[USA: Alabama, Georgia, Louisiana, Mississippi, South Carolina, Texas]
- 2(1) Shell yellowish to olive green; typically four color bands (if present) ..... *Viviparus georgianus* (Lea, 1834)  
[Canada: Quebec. USA: Gulf Coast to Great Lakes and New England]
- 2' Shell yellowish to greenish brown; three color bands (if present) ..... *Viviparus subpurpureus* (Say, 1829)  
[USA: Arkansas, Illinois, Iowa, Kentucky, Louisiana, Mississippi, Missouri, Tennessee, Texas]

### Gastropoda: Rissoidae: Families

Most families are very difficult to separate, and there are many undescribed taxa. Use caution in identifying these animals. The key below follows the taxonomy of [Wilke et al., 2013](#).

- 1 Operculum multispiral or paucispiral (Fig. 11.1 F, G) ..... 2
- 1' Operculum concentric (Fig. 11.1 E) ..... Bithyniidae, one species *Bithynia tentaculata* (L., 1758)  
[Canada, USA: Great Lakes region, mid-Atlantic states]
- 2(1) Operculum without a calcareous white smear; separate sexes ..... 3
- 2' Operculum with a calcareous white smear; almost always females only, males extremely rare .....  
..... Tateidae, one species: *Potamopyrgus antipodarum* (Gray, 1853)  
[Invasive exotic species. Canada: Ontario. USA: Great Lakes region and scattered localities in the western states, expanding]
- 3(2) Omniphoric groove absent; tentacles normal ..... 4
- 3' Omniphoric groove present; tentacles very short to absent ..... Assimineidae; one genus: *Assiminea* [p. 200]  
[Estuarine and saline spring habitats]
- 4(3) Tentacles with sides gradually converging distally, with or without penal lobes or internal tubular glands (Fig. 11.7 A, C–E); operculum variable ..... 5
- 4' Tentacles with sides parallel; penis with a single medial or basal lobe, and an internal tubular gland that extends back into the head (Fig. 11.7 C); operculum paucispiral ..... **Ammicolidae** [p. 200]
- 5(4) Radula with marginal teeth bearing larger cusps on inner margin; outer marginal teeth with cusps on both sides ..... 6
- 5' Radula with marginal teeth with cusps subequal; outer marginal teeth with cusps on inner side (Fig. 11.8 A) .....  
..... Pomatiopsidae, one genus: **Pomatiopsis** [p. 200]
- 6(5) Penis with external glands, often on lobes or crests (Fig. 11.7 B, C) ..... 7
- 6' Penis lacking external glands (Fig. 11.7 A) ..... **Lithoglyptidae** [p. 201]
- 7(6) Penis with narrow glandular fields, sometimes ridged, or large circular glandular areas sometimes borne on crests ..... Hydrobiidae  
[Widespread, numerous genera, many in need of revision, and with many undescribed taxa]
- 7' Penis papillate and/or with several gland types present, often with glands on stalks ..... Cochliopidae  
[Widespread, numerous genera, many in need of revision and with many undescribed taxa]

**Gastropoda: Rissooidea: Assimineidae: Assiminea: Species**

1	Estuarine species .....	2
1'	Desert spring species .....	3
2(1)	Pacific estuaries .....	<i>Assiminea californica</i> (Tryon, 1865)
	[Canada: British Columbia. USA: California, Oregon, Washington. Mexico: Baja California]	
2'	Atlantic estuaries .....	<i>Assiminea succinea</i> (Pfeiffer, 1840)
	[USA: Massachusetts, south along Atlantic and Gulf coasts. Mexico: Gulf coast. Neotropics]	
3(1)	From Death Valley, California .....	<i>Assiminea infima</i> Berry, 1947
	[USA]	
3'	From New Mexico and Texas .....	<i>Assiminea pecos</i> Taylor, 1987
	[USA]	

**Gastropoda: Rissooidea: Amnicolidae: Genera**

1	Animal lacking eyes and pigment; subterranean .....	2
1'	Animal with eyes and pigment; protoconch with weak spiral lines .....	3
2(1)	Protoconch transversely fimbriate .....	<i>Dasyscias franzi</i> Thompson & Hershler, 1991
	[USA: Florida]	
2'	Protoconch wrinkled or pustulate, with spiral grooves .....	<i>Antroselates spiralis</i> Hubricht, 1971
	[USA: Indiana, Kentucky]	
3(1)	Shell 2.9 to 4.8 mm in length; female with one large seminal receptacles .....	4
3'	Shell 1.3 to 3.3 mm in length; female with two small seminal receptacles .....	<i>Colligyryus</i> [p. 200]
	[USA: northern Great Basin springs]	
4(3)	Mantle with bands of pigment .....	<i>Amnicola</i>
	[Many undescribed species. Canada: southern regions. USA: widespread]	
4'	Mantle with pigment pattern diffuse .....	<i>Lyogyryus</i>
	[Many undescribed species. Canada: southern regions. USA: widespread]	

**Gastropoda: Rissooidea: Amnicolidae: Colligyryus: Species**

1	Shell globose to depressed conic .....	2
1'	Shell conical .....	<i>Colligyryus greggi</i> (Pilsbry, 1935)
	[USA: Idaho, Utah]	
2(1)	Aperture sinuate; teleoconch sutures deeply impressed .....	<i>Colligyryus convexus</i> Hershler, Frest, Liu & Johannes, 2003
	[USA: California]	
2'	Aperture simple; teleoconch sutures normal .....	<i>Colligyryus depressus</i> Hershler, 1999
	[USA: Oregon]	

**Gastropoda: Rissooidea: Pomatiopsidae: Pomatiopsis: Species**Modified from [Burch \(1982\)](#)

1	Distribution west of the continental divide .....	2
1'	Distribution east of the continental divide .....	4
2(1)	Umbilicus open .....	3
2'	Umbilicus imperforate; adult shell 3 mm in length .....	<i>Pomatiopsis binneyi</i> Tryon, 1863
	[USA: California]	
3(2)	Shell chestnut brown .....	<i>Pomatiopsis californica</i> Pilsbry, 1899
	[USA: California]	
3'	Shell olive brown .....	<i>Pomatiopsis chacei</i> Pilsbry, 1937
	[USA: California]	



4(1)	Aperture oval; whorls flattened; shell elongate .....	5
4'	Aperture round; whorls rounded, shell broadly conical ..... <i>Pomatiopsis cincinnatiensis</i> (Lea, 1840) [USA: Illinois, Iowa, Michigan, Tennessee, Virginia, Wisconsin]	
5(4)	Umbilicus broadly open; teleoconch narrow, subacute, spire up to five whorls; length at least twice body whorl width .....	
	..... <i>Pomatiopsis lapidaria</i> (Say, 1817) [Canada: Ontario, Quebec. USA: east of Continental Divide, except northern Great Plains]	
5'	Umbilicus narrow; spire up to four whorls, obtuse; length approximately 1.5 times the width of body whorl .....	
	..... <i>Pomatiopsis lapidaria</i> (Say, 1817)	

### Gastropoda: Rissooidea: *Lithoglyphidae*: Genera

1	Eyes and pigment present .....	2
1'	Eyes and pigment absent; adults minute; occurring in ground water ..... <i>Phreatodrobia</i> [p. 201] [USA: Texas]	
2(1)	Shell not neritiform, columella never produced as a septum .....	3
2'	Shell neritiform; spire reduced, rounded; columella transverse, projecting as a septum (shelf-like) .....	
	..... <i>Lepyrium showalteri</i> (Lea, 1861) [USA: Alabama]	
3(2)	Umbilicus closed or very narrow .....	4
3'	Umbilicus open, broad .....	
	..... <i>Clappia</i> [USA: Alabama, possibly extinct. Two poorly defined species]	
4(3)	Shell aperture margin thick .....	
	..... <i>Fluminicola</i> [Large genus in need of revision, many undescribed species. Canada: British Columbia. USA: California, Idaho, Nevada, Oregon, Utah, Washington, Wyoming]	
4'	Shell aperture thin .....	
	..... <i>Gillia atilis</i> (Lea, 1841) [USA: Mid-Atlantic States]	

### Gastropoda: Rissooidea: *Lithoglyptidae*: *Phreatodrobia*: Species

1	Protoconch normal .....	2
1'	Protoconch with apex uncoiled and protruding distally ..... <i>Phreatodrobia coronae</i> Hershler & Longley, 1987 [USA: Texas]	
2(1)	Distal body whorl thickened, appearing whitish and opaque .....	3
2'	Body whorl simple .....	4
3(2)	Shell trochoid to planospiral or low conical; aperture flared, may touch body whorl .....	
	..... <i>Phreatodrobia nugax nugax</i> (Pilsbry & Ferriss, 1906) [USA: Texas]	
3'	Shell globose; aperture fused to body whorl, and flared only at fusion point .....	
	..... <i>Phreatodrobia nugax inclinata</i> Hershler & Longley, 1986 [USA: Texas]	
4(2)	Shell planospiral .....	5
4'	Shell conical .....	7
5(4)	Operculum without striae; aperture not emarginate in dorsal view .....	6
5'	Operculum with short, deep striae across the growth lines; aperture in dorsal view broadly emarginate.....	
	..... <i>Phreatodrobia rotunda</i> Hershler & Longley, 1986 [USA: Texas]	
6(5)	Aperture simple, circular; operculum circular; body whorl with weak axial growth lines .....	
	..... <i>Phreatodrobia micra</i> (Pilsbry & Ferriss, 1906) [USA: Texas]	
6'	Aperture flared apically, transverse to narrowly oval; operculum broader than wide; body whorl with thick, wrinkled colabrial lines .....	
	..... <i>Phreatodrobia plana</i> Hershler & Longley, 1986 [USA: Texas]	

- 7(4) Operculum flared ..... 8
- 7' Operculum simple; teleoconch with numerous short ridges ..... *Phreatodrobia conica* Hershler & Longley, 1986  
[USA: Texas]
- 8(7) Operculum as long as wide; teleoconch with collabral costae and spiral lines ..... *Phreatodrobia imitata* Hershler & Longley, 1986  
[USA: Texas]
- 8' Operculum broader than wide; teleoconch punctate ..... *Phreatodrobia punctata* Hershler & Longley, 1986  
[USA: Texas]

### Gastropoda: Cerithoidea: Families

- 1 Mantle margin smooth; separate sexes, males common; females deposit eggs; female foot with right side bearing an egg-laying sinus ... 2
- 1' Mantle margin papillate; parthenogenic, with males extremely rare or absent; females brood eggs and hatchlings in a brood pouch dorso-posteriorly to the head ..... **Thiaridae** [p. 202]
- 2(1) Female with egg laying sinus a deep, "H"-shaped lumen, seminal receptacle absent; alimentary system smooth ..... **Pleuroceridae** [p. 202]  
[Canada: Ontario, Quebec. USA: east of Continental Divide]
- 2' Female with egg-laying sinus a shallow, simple, flattened lumen, seminal receptacle present; alimentary system bearing dorsally with deep folds and clefts ..... Semisulcospiridae, one genus: *Juga* [p. 202]  
[Genus in need of revision. Canada: British Columbia. USA: west of Continental Divide]

### Gastropoda: Cerithoidea: Thiaridae: Genera

- 1 Shell whorls flattened; whorl spiral sculpture of transverse tubercle rows (Fig. 11.8 C) ..... *Tarebia granifera* (Lamarck, 1816)  
[Oriental and Pacific islands. Invasive in USA: California (?), Florida, Idaho, Texas]
- 1' Shell whorls rounded; whorls bearing spiral grooves and fine ridges, and bearing transverse lines that may develop into costae in older animals; groove/ridge intersections with transverse costae may give a tuberculate appearance (Fig. 11.8 B) ..... *Melanoides tuberculata* (Müller, 1774)  
[Afrotropical, Palaearctic, Oriental. Invasive in Nearctic. USA: southern US and California, Colorado, Idaho, Montana, Nevada, North Carolina, spreading. Mexico: widespread, spreading]

### Gastropoda: Cerithoidea: Pleuroceridae: Genera

The key is partially based on Burch (1982), and no attempt was made to resolve the species. Taxonomy in part follows Dillon (2011) and is conservative. The family needs revision, and the genera and many species are difficult to distinguish (Hoznagel & Lydeard, 2000; Lydeard et al., 2002; Ó Foighil et al., 2009; Dillon, 2011, 2014).

- 1 Aperture with an anterior canal present or absent, if present, never produced anteriorly; aperture rounded or quadrate ..... 2
- 1' Aperture with an anterior canal present and produced anteriorly; aperture fusiform; whorls generally with a single row of large projecting spines (Fig. 11.8 D) ..... *Io fluviatilis* (Say, 1825)  
[USA: Alabama (extinct), Tennessee, West Virginia]
- 2(1) Body whorl posterior suture margin without a long slit ..... 3
- 2' Body whorl posterior suture margin with a long slit ..... *Gyrotoma*  
[Probably extinct due to impoundments. USA: Alabama]
- 3(2) Radula lateral teeth with median cusps narrow, pointed, triangular or cordate/hastate; shell elongate or narrowly conic to broadly conic, ovate or cylindrical (Fig. 11.8 F–H) ..... *Pleurocer/Lithasia*
- 3' Radula lateral teeth with median cusps broadly rounded, blunt; shell globose to subglobose, ovate, or broadly conic (Fig. 11.8 E) ..... *Leptoxis*  
[USA: Atlantic, Gulf, and lower Mississippi River Drainages]

### Gastropoda: Cerithoidea: Semisulcospiridae: *Juga*: Species

This genus needs revision (Strong & Kohler, 2009). There are possible undescribed species. *Juga acutifilosa* and *J. occata* are in the subgenus *Calibasis*, which may represent a separate genus (Strong & Frest, 2007).

1	Adult shell smooth .....	2
1'	Adult shell with sculpture, sometimes fine, sometimes limited to early whorls .....	4
2(1)	Shell whorls with shoulder rounded; shell greenish-brown to brown to black .....	3
2'	Shell whorls with shoulder flattened; shell black; montane headwater streams and rivers .....	<i>Juga nigrina</i> (Lea, 1856)
	[USA: California, Oregon]	
3(2)	Shell color uniformly brown to black; Great Basin Desert springs .....	<i>Juga laurae</i> (Goodrich, 1944)
	[USA: California, Nevada]	
3'	Shell light to dark greenish-brown, sometimes with yellow, and often with darker bands of color .....	<i>Juga bulbosa</i> (Gould, 1847)
	[USA: California, Oregon, Washington]	
4(1)	Shell with spiral ridges on all whorls, costae present or not .....	5
4'	Shell with costae, and bearing spiral ridges on early whorls only .....	<i>Juga hemphilli</i> (Henderson, 1935)
	[USA: Oregon, Washington]	
5(4)	Shell with costae transverse to the spiral ridges .....	6
5'	Shell without costae .....	8
6(5)	Shell with costae on all whorls .....	7
6'	Shell with costae limited to early whorls .....	<i>Juga silicula</i> (Gould, 1847)
	[USA: Oregon, Washington]	
7(6)	Shell with spire low and rounded, usually not more than three whorls; spiral ridges large, lamellar, generally projecting beyond and partially obscuring costae .....	<i>Juga occata</i> (Hinds, 1844)
	[USA: California]	
7'	Shell with spire long, usually composed of four or more whorls; spiral ridges small, flat, never projecting beyond costae; costae never obscured .....	<i>Juga plicifera</i> (Lea, 1838)
	[USA: Oregon, Washington]	
8(5)	Shell with spiral ridges fine, discontinuous and unevenly spaced on body whorl, and only apparent under low magnification; Great Basin Desert springs .....	<i>Juga interioris</i> (Goodrich, 1944)
	[USA: Nevada]	
8'	Shell with spiral ridges large, obvious without magnification; mountain springs and rivers .....	<i>Juga acutifilosa</i> (Stearns, 1890)
	[USA: California]	

## Gastropoda: Lymnaeoidea: Lymnaeidae: Genera

Taxonomy follows [Hubendick \(1951\)](#) and [Correa et al. \(2010\)](#).

1	Shell patelliform (limpets) ( <a href="#">Fig. 11.9 A, B</a> ) .....	2
1'	Shell spiral ( <a href="#">Fig. 11.5 C–I</a> ) .....	3
2(1)	Shell apex eccentric ( <a href="#">Fig. 11.9 B</a> ) .....	<i>Fisherola nuttalli</i> (Haldeman, 1841)
	[USA: Idaho, Oregon, Washington]	
2'	Shell apex subcentral ( <a href="#">Fig. 11.9 A</a> ) .....	<i>Lanx</i> [p. 203]
	[USA: California, Oregon]	
3(1)	Adult shell lacking spiral striae; body whorl globose; spire very short ( <a href="#">Fig. 11.5 C</a> ) .....	<i>Radix auricularia</i> (Linnaeus, 1758)
	[Holarctic, widespread]	
3'	Adult shell lacking spiral striae; body whorl globose or not ( <a href="#">Fig. 11.5 D–I</a> ) .....	<i>Lymnaea</i> [p. 204]
	[Taxonomy confused, genus needs revision]	

## Gastropoda: Lymnaeoidea: Lymnaeidae: *Lanx*: Species

1	Shell not depressed, margin not flared, shell height in lateral view one-third or more shell height .....	2
1'	Shell depressed, flattened, margin flared, shell height in lateral view one-third or less shell width .....	<i>Lanx klamathensis</i> Hannibal, 1912
	[USA: Oregon, California (?)]	

- 2(1) Adult shell robust ..... 3
- 2' Adult shell thin, fragile ..... *Lanx subrotundata* (Tryon, 1865)  
[USA: California, Oregon]
- 3(2) Shell red to brown ..... 4
- 3' Shell mostly black, often with margin reddish to brown, sometimes with scattered, small green dots ..... *Lanx patelloides* (Lea, 1856)  
[USA: California]
- 4(3) Klamath River system ..... *Lanx alta* (Tryon, 1865)  
[USA: California, Oregon]
- 4' Snake River system ..... *Lanx* sp.  
[Typically undescribed species are not considered in this series. However, this undescribed species, the "Banbury Lanx," is federally listed under the U.S. Endangered Species Act.]

### Gastropoda: Lymnaeoidea: Lymnaeidae: *Lymnaea*: Species

This genus was revised by Hubendick (1951). Although most recent authors have ignored that work, a recent molecular assessment by Correa et al. (2010) supported Hubendick (1951), at least as far as genus level treatments are concerned, and their work is followed here.

- 1 Entire shell never attenuated, although spire may be, aperture width generally one-half or more length; body whorl shoulders rounded ..... 2
- 1' Shell strongly attenuated, extremely narrow, aperture width one-third or less length; body whorl shoulders flattened; spire long (Fig. 11.5 D) ..... *Lymnaea haldemani* Binney, 1867  
[Canada, USA: Great Lakes region]
- 2(1) Shell not translucent, not thin and fragile; shell periostracum not sculptured with microscopic spiral threads ..... 3
- 2' Shell translucent or nearly transparent, thin and fragile; shell periostracum sculptured with microscopic spiral threads (Fig. 11.5 E) ..... *Lymnaea columella* Say, 1817  
[Widespread]
- 3(2) Columella not projecting ..... 4
- 3' Columella with a large projecting fold, nearly a tooth; penis and penal sheath very short and pyriform ..... *Lymnaea arctica* Lea, 1864  
[Canada, USA: arctic and subarctic]
- 4(3) Adult shell of variable length, but if greater than 35 mm, the spire longer than aperture ..... 5
- 4' Adult shell length greater than 35 mm, with spire shorter than aperture length; umbilicus imperforate (Fig. 11.5 G) ..... *Lymnaea megasoma* Say, 1824  
[Canada: Manitoba, Northwest Territories, Nova Scotia, Ontario, Quebec. USA: Great Lakes Region]
- 5(4) Spire not attenuated ..... 6
- 5' Spire narrow, attenuate; aperture flared; umbilicus generally imperforate (Fig. 11.5 F) ..... *Lymnaea stagnalis* Linnaeus, 1758  
[Canada: widespread except Arctic. USA: northern states]
- 6(5) Body whorl usually lacking distinct transverse ridges, but if present then umbilicus barely open; spiral striae present or absent ..... 7
- 6' Body whorl with distinct transverse ridges and spiral striae; umbilicus imperforate ..... *Lymnaea palustris* (Müller, 1774)  
[Canada: widespread except arctic. USA: northern and western states]
- 7(6) Umbilicus imperforate to barely open ..... 8
- 7' Umbilicus open ..... *Lymnaea bulimoides* Lea, 1841
- 8(7) Columella with an obvious twist or plait; spiral sculpture very fine to microscopic, but present (Fig. 11.5 I) ..... 9
- 8' Columella generally without a twist or plait; spiral sculpture weak, obscured, or absent (Fig. 11.5 H) ..... *Lymnaea catascopium* Say, 1817 species group  
[This group contains *L. eleodes*, *L. emarginata*, *L. gabbi*, and *L. utahensis*, which cannot be reliably and consistently separated. Canada: widespread. USA: northern and western states]



- 9(8) Radula with lateral teeth with three large and obvious cusps ..... *Lymnaea truncatula* (Müller, 1774)/*Lymnaea humilis* Say, 1822  
[Canada: southern provinces. USA: widespread. Mexico: Chihuahua, Coahuila, Nuevo Leon, Tamaulipas]
- 9' Radula with lateral teeth with two large and obvious cusps ..... *Lymnaea cubensis* Pfeiffer, 1839  
[USA: Florida, Louisiana, Texas. Mexico: widespread. Neotropics]

### Gastropoda: Planorbiodea: Families

- 1 Pseudobranch absent; shell obviously sinistral (coiling to the left), with an acute, posteriorly directed spire; mantle margin generally with digitate or serrate lobes; blood clear, lacking haemoglobin (Fig. 11.4 G–K) ..... **Physidae [p. 205]**
- 1' Pseudobranch present as a cup-like lobe projecting from under the mantle posteriolaterally on the left side; shell patelliform (limpets), discoidal (ram's horn snails), or if with a projecting spire, then appearing dextral (spiraling to the right); blood red with haemoglobin (Figs. 11.4 A–F and 11.9 D–L) ..... **Planorbidae [p. 206]**

### Gastropoda: Planorbiodea: Physidae: Genera

- 1 Shell elongated, glossy, shiny, and smooth; spire conical; aperture no more than half the total shell length; mantle never with lobes (Fig. 11.4 K) ..... *Aplexa elongata* (Say, 1821)  
[Canada: Alberta, British Columbia, Manitoba, Ontario, Saskatchewan. USA: Alaska, Idaho, Montana, North Dakota, South Dakota, Utah, Washington, Wyoming, Great Lakes region, and New England states]
- 1' Shell variable; aperture length more than half the total shell length; mantle usually with digitate or serrate lobes (Fig. 11.4 G–J) ..... ***Physa* [p. 205]**

### Gastropoda: Planorbiodea: Physidae: *Physa*: Species

Follows Wethington & Lydeard (2007) and Wethington et al. (2009). Shell morphology is highly variable (reviewed in Rogers & Wethington, 2007).

- 1 Aperture length at most 75% of total shell length, aperture not as wide as widest shell width; animal not adapted as below (Fig. 11.4 G, H, J) ..... 2
- 1' Aperture length nearly as long as total shell length, aperture width equal to widest shell width; foot very broad, adapted for living on vertical cliffs under a thin water film; animal very black (Fig. 11.4 I) ..... *Physa zionis* Pilsbry, 1926  
[USA: Utah]
- 2(1) Penis preputium with a large and obvious preputial gland; mantle variable ..... 3
- 2' Penis preputium without a large and obvious preputial gland; mantle extending around much of body whorl ..... *Physa marmorata* Guilding, 1828  
[USA: Texas. Mexico: Gulf Coast and tropics. Neotropical]
- 3(2) Penal sheath entirely glandular ..... 4
- 3' Penal sheath either partially glandular distally, or not glandular at all ..... 6
- 4(2) Mantle not extending externally around most of body whorl ..... 5
- 4' Mantle extending externally around most of body whorl ..... *Physa megalochlamys* Taylor, 1988  
[Canada: Saskatchewan. USA: Colorado, Idaho, Oregon, Utah, Wyoming]
- 5(4) Arctic ..... *Physa jennessi* Dall, 1919  
[Canada: Arctic. USA: Alaska. Palaeartic]
- 5' Not found in arctic habitats ..... *Physa vernalis* Taylor & Jokinen, 1984  
[Canada: Great Lakes Region, Newfoundland. USA: Great Lakes region, New England]
- 6(3) Penal sheath or not glandular at all; spire acute ..... 7
- 6' Penal sheath glandular in distal one half to one fourth; spire subacute to rounded ..... 8
- 7(6) Surface waters (Fig. 11.4 H) ..... *Physa acuta* Draparnaud, 1805  
[Cosmopolitan]

- 7' Subterranean ..... *Physa spelunca* Turner & Clench, 1974  
[USA: Wyoming]
- 8(6) Penal sheath glandular in distal fourth ..... *Physa pomilia* Conrad, 1834 species group  
[USA: eastern states and California]
- 8' Penal sheath glandular in distal half (Fig. 11.4 G, J) ..... *Physa gyrina* Say, 1821 species group  
[Nearctic]

## Gastropoda: Planorbiodea: Planorbidae: Genera

Taxonomy follows [Walther et al. \(2006\)](#), [Albrecht et al. \(2006\)](#), and [Dillon & Herman \(2009\)](#).

- 1 Shell patelliform (limpets) (Fig. 11.9 D–G) ..... 2
- 1' Shell spiral (Figs. 11.4 A–F and 11.9 H–L) ..... 5
- 2(1) Three or more adductor muscles, or adductor muscle scars in shell ..... 3
- 2' One crescent shaped adductor muscle scar nearly circling the inside of the shell (Fig. 11.9 D) ..... *Rhodacmea* [p. 207]
- 3(2) Three primary adductor muscle scars (two anterior, one posterior) with a smaller secondary adductor muscle scar between the anterior two, and one between the right anterior and the posterior primary scars ..... 4
- 3' Three primary adductor muscle scars (two anterior, one posterior) with no smaller secondary scars (Fig. 11.9 E) ..... *Ferrissia* [p. 207]
- 4(3) Shell apex at or just to right of shell midline, and just posterior of center; tentacles with prominent pigment cores (Fig. 11.9 G) .....  
..... *Laevapex fuscus* (Adams, 1841)  
[Canada, USA: east of the Great Plains]
- 4' Shell apex far to right of midline, and in posterior fourth of shell; tentacles without a pigmented core (Fig. 11.9 F) .....  
..... *Hebetancylus excentricus* (Morelet, 1851)  
[USA: Florida, Georgia, Texas. Mexico: Gulf states. Neotropics]
- 5(1) Shell with body whorl and aperture greatly and abruptly larger than preceding whorl; aperture length greater than one-half the shell width (Fig. 11.4 C) ..... 6
- 5' Shell with whorls gradually and uniformly increasing in size (Figs. 11.9 H–L and 11.4 A, B, D–F) ..... 8
- 6(5) Aperture length more than one-half, but less than two-thirds body whorl width ..... 7
- 6' Aperture length greater than two-thirds body whorl width; adult shell 2 mm in diameter ..... *Amphigyra alabamensis* Pilsbry, 1906  
[USA: Alabama (possibly extinct)]
- 7(6) Adult shell 2 mm in diameter ..... *Neoplanorbis* [p. 207]  
[USA: Alabama]
- 7' Adult shell more than 8 mm in diameter ..... *Vorticifex* [p. 207]  
[USA: California, Nevada, Oregon]
- 8(5) Aperture without teeth ..... 9
- 8' Aperture with teeth set back from aperture (aperture may need to be broken to view this character) (Fig. 11.9 I) ..... *Planorbula* [p. 208]
- 9(8) Shell aperture width less than one-half shell diameter ..... 10
- 9' Shell aperture width greater than one-half shell diameter ..... 13
- 10(9) Adult shell greater than 8 mm in diameter; adult shell with four or five whorls, never with numerous low spiral striae (Fig. 11.4 B, D–F) ..  
..... 11
- 10' Adult shell less than 8 mm in diameter; adult shell with five or six whorls, if only four or five, then bearing numerous low spiral striae (Fig. 11.9 J) ..... *Drepanotrema* [p. 208]
- 11(10) Shell thick, not easily crushed ..... 12
- 11' Shell thin, fragile (Fig. 11.4 B) ..... *Biomphalaria* [p. 208]
- 12(11) Shell shoulder with a carina; spire always present ..... *Carinifex*  
[In need of revision. USA: California, Nevada, Oregon, Utah, Wyoming]
- 12' Shell shoulder lacking a carina; spire rarely present, shell generally discoidal (Fig. 11.4 D–F) ..... *Helisoma*  
[Nearctic: widespread. Large genus in great need of revision. Many “species” cannot be reliably separated from each other]
- 13(12) Shell whorls without large transverse ridges ..... 14
- 13' Shell costate, i.e., whorls with large transverse ridges (Fig. 11.9 H) ..... *Gyraulus* (in part) [p. 208]

- 14(13) Shell with umbilicus deep and narrow, body whorl on opposite side of shell from aperture slightly wider than umbilicus; shoulder carinate or not ..... 15
- 14' Shell with umbilicus shallow and wide, body whorl on opposite side of shell from aperture slightly narrower than umbilicus; shoulder not carinate (Fig. 11.9 K) ..... *Gyraulus* (in part) [p. 208]
- 15(14) Mantle with a large, well defined lobe anterior of the anal pore and pseudobranch; shell with shoulder angular, and bearing a carina between midpoint and shoulder (Fig. 11.9 L) ..... *Menetus*  
[Genus in need of revision. Canada: widespread, except Arctic. USA: widespread]
- 15' Mantle without a well defined lobe anterior of the anal pore and pseudobranch; shell with body whorl rounded or carinate medially (Fig. 11.4 A) ..... *Promenetus* [p. 208]

### Gastropoda: Planorbiodea: Planorbidae: *Rhodacmea*: Species

Genus needs revision. Modified from Burch (1982).

- 1 Shell smooth ..... *Rhodacmea elatior* (Anthony, 1855)/*Rhodacmea hinkleyi* (Walker, 1908)  
[USA: Alabama, Tennessee]
- 1' Shell ribbed ..... *Rhodacmea filosa* (Conrad, 1834)  
[USA: Alabama, Tennessee (?)]

### Gastropoda: Planorbiodea: Planorbidae: *Ferrissia*: Species

Follows Walther et al. (2010).

- 1 Shell apex on midline ..... *Ferrissia rivularis* (Say, 1817)  
[Widespread except in Arctic and subarctic]
- 1' Shell apex to right of midline ..... *Ferrissia fragilis* (Tryon, 1863)  
[USA: southern Atlantic drainages]

### Gastropoda: Planorbiodea: Planorbidae: *Neoplanorbis*: Species

Modified from Burch (1982). This genus needs to be revised (it may only represent one or two variable species). It is only known from the Coosa River in Alabama and is probably extinct.

- 1 Umbilicus closed; columella without teeth ..... 2
- 1' Umbilicus open; columella with teeth ..... 3
- 2(1) Shell with spiral striae; shoulder with a carina ..... *Neoplanorbis tantillus* Pilsbry, 1906  
[USA: Alabama]
- 2' Shell without spiral striae; shoulder rounded ..... *Neoplanorbis smithi* Walker, 1908  
[USA: Alabama]
- 3(1) Shoulder with a carina ..... *Neoplanorbis carinatus* Walker, 1908  
[USA: Alabama]
- 2' Shoulder rounded ..... *Neoplanorbis umbilicatus* Walker, 1908  
[USA: Alabama]

### Gastropoda: Planorbiodea: Planorbidae: *Vorticifex*: Species

Modified from Burch (1982). This genus needs to be revised.

- 1 Body whorl with a ventral carina or angle around the umbilicus ..... *Vorticifex solida* (Dall, 1870)  
[USA: California, Nevada]
- 1' Body whorl lacking carinae ..... *Vorticifex effusa* (Lea, 1856)  
[USA: California, Oregon]

**Gastropoda: Planorbiodea: Planorbidae: *Planorbula*: Species**

- 1 Shell thin, fragile, up to 20 mm in diameter; low teeth present inside aperture on outer whorl wall ..... *Planorbula campestris* (Dawson, 1875)  
[Canada: Alberta, British Columbia, Manitoba, Saskatchewan. USA: western states]
- 1' Shell solid, up to 8 mm in diameter; aperture teeth on all sides ..... *Planorbula armigera* (Say, 1821)  
[Canada: widespread, except southwest. USA: east of Great Plains]

**Gastropoda: Planorbiodea: Planorbidae: *Drepanotrema*: Species**

Modified from Burch (1982).

- 1 Adult shell extremely flattened, bearing four or five whorls, lacking spiral striae ..... 2
- 1' Adult shell not extremely flattened, bearing five or six whorls, bearing deep, obvious spiral striae ..... *Drepanotrema aeruginosum* (Morelet, 1851)  
[USA: Arizona, Texas. Mexico: widespread. Neotropics]
- 2(1) Adult shell shoulder with an obvious and strong keel ..... *Drepanotrema kermatoides* (d'Orbigny, 1835)  
[USA: Florida, Texas. Mexico: widespread. Neotropics]
- 2' Adult shell shoulder rounded or angular ..... *Drepanotrema cimex* (Moricand, 1839)  
[USA: Texas. Mexico: widespread. Neotropical]

**Gastropoda: Planorbiodea: Planorbidae: *Biomphalaria*: Species**

Modified from Burch (1982).

- 1 Adult shell (five or more whorls) 15 mm in diameter or larger ..... *Biomphalaria glabrata* (Say, 1818)  
[Invasive. USA: Florida. Neotropics]
- 1' Adult shell (five or more whorls) 10 mm in diameter or smaller ..... *Biomphalaria havanensis* (Pfeiffer, 1839)  
[USA: Arizona, Florida, Louisiana, Texas. Mexico: widespread. Neotropics]

**Gastropoda: Planorbiodea: Planorbidae: *Gyraulus*: Species**

- 1 Shell with umbilicus deep and narrow, body whorl on opposite side of shell from aperture slightly wider than umbilicus; shoulder carinate or not ..... 2
- 1' Shell with umbilicus shallow and wide, body whorl on opposite side of shell from aperture slightly narrower than umbilicus; shoulder not carinate ..... *Gyraulus crista* (Linnaeus, 1758)  
[Holarctic]
- 2(1) Periostracum glabrous; shoulder rounded to subangular ..... 3
- 2' Periostracum hirsute on at least the youngest whorls; shoulder flattened obliquely ..... *Gyraulus deflectus* (Say, 1824)
- 3(2) Shell in lateral view, with aperture one-third or more shell width ..... 4
- 3' Shell in lateral view, with aperture one-fourth or less shell width; shell with spire and umbilicus nearly identical in general appearance ....  
..... *Gyraulus circumstriatus* (Tryon, 1866)  
[Canada: widespread, except Arctic. USA: northern states, and Rocky Mountains to New Mexico]
- 4(3) Aperture width and length subequal ..... *Gyraulus hornensis* Baker, 1934  
[Canada: Manitoba, Northwest Territories, Ontario, Saskatchewan. USA: North Dakota, Wisconsin]
- 4' Aperture width subequal to half its length ..... *Gyraulus parvus* (Say, 1817)

**Gastropoda: Planorbiodea: Planorbidae: *Promenetus*: Species**

- 1 Shell body whorl peripherally carinate ..... *Promenetus exacuouus* (Say, 1821)  
[Canada: widespread, except Arctic. USA: Alaska, and east of the Continental Divide]
- 1' Shell body whorl with shoulder rounded, no carina ..... *Promenetus umbilicatellus* (Cockerell, 1877)  
[Canada: Alberta, British Columbia, Manitoba, Saskatchewan. USA: Alaska, Oregon, Utah, Washington, northern central states]



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## Class Bivalvia

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*Kansas Biological Survey and The Biodiversity Institute, Kansas University, Lawrence, KS, USA*INTRODUCTION<sup>2</sup>

The Nearctic bivalve molluscs (or mollusks) consist of five families in two orders: Unionoida (Margartiferidae

2. The prekey material in this section is based on various sources, especially Cummings & Graf (2010).

and Unionidae) and Veneroida (Sphaeriidae, Corbiculidae, and Dreissenidae) (Turgeon et al., 1998; Strayer, 1999; Grigorovich et al., 2000).

The vast majority of species in these families are in the Unionidae with its nearly 300 Nearctic species, compared to about 837 species worldwide (Graf & Cummings, 2002).

The distribution of Nearctic unionids is shown in Fig. 19.38 of Volume I of this edition. Most occur in rivers of the southeastern USA. These are known as pearly mussels, naiads, or unionids. Another major center of unionid diversity is China.

The Margaritiferidae bear a close resemblance to some unionids, but they lack a posterior mantle fusion. These “pearl mussels” are represented by one genus and five Nearctic species.

The small bivalves of Sphaeriidae (fingernail, pea, pill, or seed clams) are divided into four genera and about 40 species in the Nearctic: *Eupera*, *Pisidium*, *Sphaerium*, and *Musculium*, with about 200 species worldwide in 4–5 genera. The sphaeriids are most abundant in the Nearctic within the Rocky Mountains (where unionoid mussel diversity is low) and in the formerly glaciated regions of the continent.

The Dreissenidae contains only a few freshwater forms. In the Nearctic, there is one species native to the Nearctic and two invasive species from the Palearctic.

## LIMITATIONS

Freshwater bivalve molluscs are generally identified by shell characteristics. Unfortunately, shell shape can be variable within a taxon depending on environmental conditions (e.g., see Fig. 19.6 in Vol. I), and the external sculpture can be eroded or otherwise obscured, especially for animals living in turbulent streams or poorly buffered waters of low alkalinity (i.e., with little calcium carbonate for shell formation). Color patterns can also be an element of identification of mussels, but these may not survive drying or preservation. Therefore, the best way to identify bivalves is to consult a specialist and view a variety of shells of the likely taxa and similar ones known from the same locality.

## TERMINOLOGY AND MORPHOLOGY

The bivalve shell is composed of two separate halves called valves. The oldest portion of the valve (the juvenile shell) is the umbo or beak, which lies on the dorsal surface of the shell. A diagram defining the anterior, posterior, and right and left sides of the animal is presented in Fig. 11.10. If the soft tissues are still present and attached to the shell, then the incurrent and excurrent apertures exit posteriorly, that is to the right side of the right valve (or left side of the left valve).

Shells in which the umbo is in the middle of each valve are called “equilateral” (equal size right and left valves are termed “equivalve”). The overall outline of a valve is often important. A valve may be rhomboidal, triangular (or trigonal), round, quadrate, oval (or ovoid) or elliptical.

The two valves are connected by a hinge that extends from the beak towards the posterior end of the animal. The hinge is connected by a ligament, which is a flexible

structure joining the two valves. This ligament may be internal (inside the hinge) or external (outside the hinge).

Inside the hinge line, on the interior surface of the valve, one or more longitudinal ridges or grooves may be present. These are the lateral teeth. One or more transverse, rounded projections, termed pseudocardinal teeth, may be present just below and sometimes slightly anterior of the umbo. These teeth and the ligament lie on a surface called the umbo cavity.

On the interior surface of each valve are muscle scars. At the anterior end, there may be a large anterior adductor scar and a smaller protractor scar. At the posterior end are the large posterior adductor scar and smaller posterior retractor scar. These scars appear as round to oblong polygons. A long pallial line runs in an arc inside the valve, from the anterior to the posterior muscle scars. The substance making up the inside of the shell is called nacre.

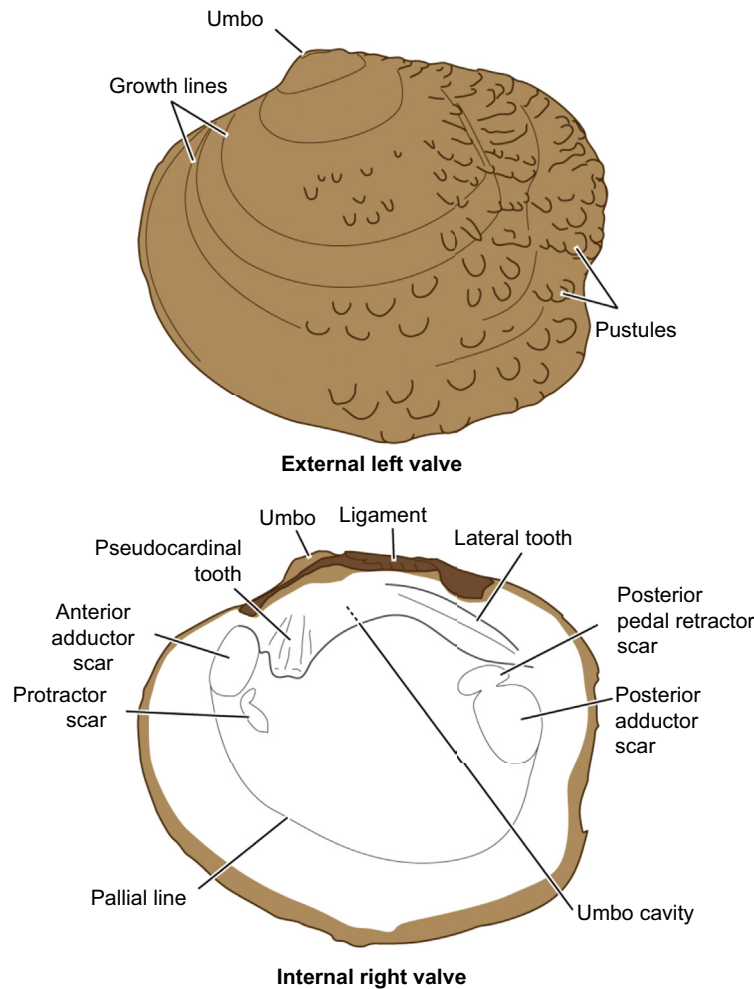
The external shell surface sculpture is important for diagnosis. The external surface of the valves is covered in a thin layer called the periostracum. Most shells have a series of growth lines, which run parallel to and generally mirror the valve margins. The shell may bear transverse or radial ridges, a secondary ridge that runs from the umbo to the posterior margin called a posterior ridge, rounded bumps called pustules, or a flattened flange extending dorsally from the hinge line, called a wing.

Sometimes confusion arises between small juvenile mussels, sphaeriid clams, and small *Corbicula*, but the presence of both posterior and anterior lateral teeth easily identifies all clams. Asian clams (*Corbicula*) grow much larger and thicker than sphaeriids. The external surface of sphaeriids is always smooth or with finely striated ridges, whereas *Corbicula* has evenly spaced, thicker, elevated ridges on the shell surface.

## MATERIAL PREPARATION AND PRESERVATION

Detailed methods for collecting, curation, and rearing bivalve molluscs are discussed in Cummings & Graf (2014) in Chapter 19 of Volume I. Sturm et al. (2006) published a guide to collecting and preserving mussels. The following section is a summary of Cummings & Graf (2014).

Focus wherever possible on collecting the shells from recently dead animals to avoid collecting live molluscs, many of which are threatened or endangered in nature. Clean the shell of all specimens with a toothbrush, vegetable brush, or a nylon scrub pad (but not wire brushes or harsh scrub pads) to reveal characters used in identification. Avoid all harsh cleaning agents that may damage the shell, and do not coat the shell with any substances, including paraffin, oil (baby, linseed, etc.), or petroleum jelly. Keep dry shells in cabinets out of direct light in a temperature and humidity controlled environment wherever possible. Catalog number should be written



**FIGURE 11.10** Gross anatomy of the exterior and interior of a valve (shell) of the freshwater unionid mussel *Theliderma intermedia*. From Cummings & Graf, 2010.

on the inside shell surface with India ink or other permanent marker, such that the internal characters are not obscured; this eliminates the problem of losing tags over the years.

For anatomical studies of live collected specimens, narcotize and relax the specimens before fixing them by using agents such as MS-222, chloroform, menthol crystals, and phenobarbital. Preserve soft tissue (with or without the shells) in 10% buffered formalin (except when planning

genetic analyses). If the whole animals are to be preserved, first freeze live animals with the shell slightly open (wedged open slightly with a wooden peg) and then transfer the specimens afterward into formalin. After a few days in formalin, soak the specimens in freshwater with several rinses over a few days, and then transfer the whole animal or soft parts into 70% ethanol for long term storage. For molecular genetic studies, fix and store the animal in 95% ethanol.

## KEYS TO BIVALVIA

As described in Cummings & Graf (2010), many state or regional monographs are available, but many are dated, unavailable, or in need of revision. Williams et al. (1993) provides a listing by U.S. states of nearly 200 references on freshwater mussels. Regional monographs on mussels published after 1993 include: Florida (in part) (Williams & Butler, 1994), Vermont (Fichtel & Smith, 1995), Texas (Howells et al., 1996),

Maine (Martin, 1997; Nedeau et al., 2000), Minnesota (Graf, 1997), New York (Strayer & Jirka, 1997), Tennessee (Parmalee & Bogan, 1998), Kansas (Bleam et al., 1999), the Apalachicola River and Rio Grande drainages (Johnson, 1999; Brim Box & Williams, 2000), and others (Ohio and Alabama) are in preparation or press. The essential references for tracking freshwater mussel nomenclature through the ages are Simpson (1900, 1914), Frierson (1927), Haas (1969a,b), and Burch (1975) (Cummings & Graf, 2010).

**Bivalvia: Orders**

- 1 Anterior and posterior lateral teeth present on inside of valves ..... **Veneroida [p. 212]**  
 1' Anterior pseudocardinal tooth and posterior lateral tooth present on valves ..... **Unionoida [p. 213]**

**Bivalvia: Veneroida: Families**

- 1 Shell hinge external; hinge teeth present or absent; shell not triangular in cross section ..... 2  
 1' Shell hinge internal; hinge teeth absent; shell triangular to somewhat oval in cross section; stripes often present on exterior of shell .....  
 ..... **Dreissenidae [p. 212]**  
 2(1) Lateral teeth serrate; external surface with raised concentric ridges; thick shell yellow to brown, often with a purple stripe on umbo; adults generally >2.5 cm (Fig. 11.11 D) ..... Corbiculidae, one genus: *Corbicula*  
 [Nearctic: invasive. Palaearctic, Oriental]  
 2' Lateral teeth smooth; external shell smooth or with fine, concentric striae; thin shell; adults generally <2.5 cm ..... **Sphaeriidae [p. 212]**

**Bivalvia: Veneroida: Dreissenidae: Genera**

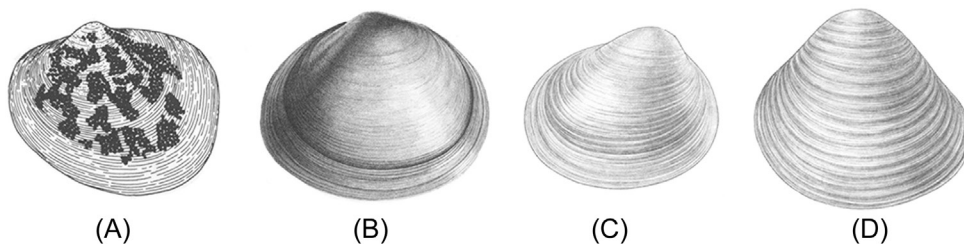
- 1 Myopore plate (internal plate at the base of the umbo) lacking a tooth projecting ventrally into the internal shell cavity; umbo pointed ..... ***Dreissena* [p. 212]**  
 1' Myopore plate (internal plate at the base of the umbo) bearing a triangular tooth projecting ventrally into the internal shell cavity; shell umbo rounded ..... *Mytilopsis leucophaeata* (Conrad, 1831)  
 [USA, Mexico: Gulf Coast rivers and estuaries; Invasive in Canada and USA along the Atlantic coast, in the Great Lakes, and in the Mississippi drainage]

**Bivalvia: Veneroida: Dreissenidae: *Dreissena*: Species**

- 1 Shell ventral margin flat to concave and flattened; ventrolateral shoulder with a ridge; shell triangular in cross section; variable colors but often with prominent stripes; zebra mussel ..... *Dreissena polymorpha* (Pallas, 1771)  
 1' Shell ventral margin rounded, convex, never flattened; ventrolateral shoulder without a ridge; color pale (especially near hinge) but may have dark concentric rings; quagga mussel ..... *Dreissena rostriformis bugensis* (Andrusov, 1897)

**Bivalvia: Veneroida: Sphaeriidae: Genera**

- 1 Umbo anterior ..... 2  
 1' Umbo distinctly posterior; generally small (0.5–10 mm) (Fig. 11.11 C) ..... *Pisidium*  
 [Nearctic]  
 2(1) Two cardinal teeth in one valve and one in opposing valve; shell not mottled (Fig. 11.11 B) .....  
 ..... *Sphaerium/Musculium*  
 [Recent studies show extreme overlap in genus and species level characters. Nearctic: widespread]  
 2 One cardinal tooth per valve; shell interior usually mottled and sometimes visible to exterior (Fig. 11.11 A) .....  
 ..... *Eupera cubensis* (Prime, 1865)  
 [USA: Atlantic and Gulf Coastal Plain. Neotropical]



**FIGURE 11.11** External view of shells of: (A) *Eupera*, (B) *Sphaerium*, (C) *Pisidium*; and (D) *Corbicula*. After Burch, 1975.

**Bivalvia: Unionoida: Families**Modified from [Burch \(1975\)](#).

- 1 Midinterior scars present; mantle not dorsally united to form a separate opening; posteriomedial mantle margins not forming distinct siphons; pseudocardinal and lateral teeth present, at least in juveniles; shell typically thick, dark, and shell elliptical (elongate) with brown or black and relatively thick; umbo displaced anteriorly ..... Margaritiferidae, one genus: *Margaritifera* [p. 213]
- 1' Midinterior scars absent; mantle united posteriorly to form incurrent and excurrent siphons; pseudocardinal and lateral teeth present or not; shells various; umbo central or displaced anteriorly ([Fig. 11.13](#)) ..... **Unionidae** [p. 213]

**Bivalvia: Unionoida: Margaritiferidae: *Margaritifera*: Species**

- 1 Lateral teeth reduced or absent in adults; shell sculpturing absent ..... 2
- 1' Lateral teeth always present in the adult; shell posteriodorsal surface at least faintly sculptured and plicate ..... 4
- 2(1) Pseudocardinal teeth broad; shell thick ..... 3
- 2' Pseudocardinal teeth reduced, pseudocardinal tooth in right valve subacute; shell thin ..... *Margaritifera monodonta* (Say, 1829)  
[USA: Upper Mississippi River system]
- 3(2) East of Continental Divide ..... *Margaritifera margaritifera* (Linnaeus, 1758)  
[Canada: New Brunswick, Newfoundland and Labrador, Nova Scotia, Prince Edward Island, Quebec. USA: New England]
- 3' West of Continental Divide ..... *Margaritifera falcata* (Gould, 1850)  
[Canada: British Columbia. USA: Alaska, California, Idaho, Montana, Nevada, Oregon, Utah, Washington, Wyoming]
- 4(1) Ventral margin arcuate ..... *Margaritifera hembeli* (Conrad, 1838)  
[USA: Arkansas, Louisiana]
- 4' Ventral margin straight or slightly curved ..... *Margaritifera marrianae* Johnson, 1983  
[USA: Alabama]

**Bivalvia: Unionoida: Unionidae: Genera<sup>3</sup>****Kevin S. Cummings***Illinois Natural History Survey, Center for Biodiversity, Champaign, IL, USA***Daniel L. Graf***Biology Department, University of Wisconsin-Stevens Point, Stevens Point, WI, USA*The following keys are divided by subregions within the Nearctic. A map of these subregions is shown in [Fig. 11.12](#).**Pacific Subregion**

- 1 Shell angular, with a strongly developed posterior ridge, reduced lateral teeth ..... *Gonidea angulate* (Lea, 1838)  
[Canada: British Columbia. USA: California, Idaho, Nevada, Oregon, Washington]
- 1' Shell not angular, without well-developed posterior ridge, lateral teeth completely absent ..... *Anodonta*  
[Canada: British Columbia. USA: Alaska, California, Idaho, Nevada, Oregon, Washington]

**Atlantic Subregion**

- 1 Shell with pseudocardinal and lateral teeth absent or greatly reduced ..... 2
- 1' Shell with pseudocardinal teeth present, lateral teeth may be absent or greatly reduced ..... 5
- 2(1) Umbo projecting above the hinge line ..... 3

3. This section was edited by Thorp &amp; Rogers from the original text appearing in the third edition (2010).



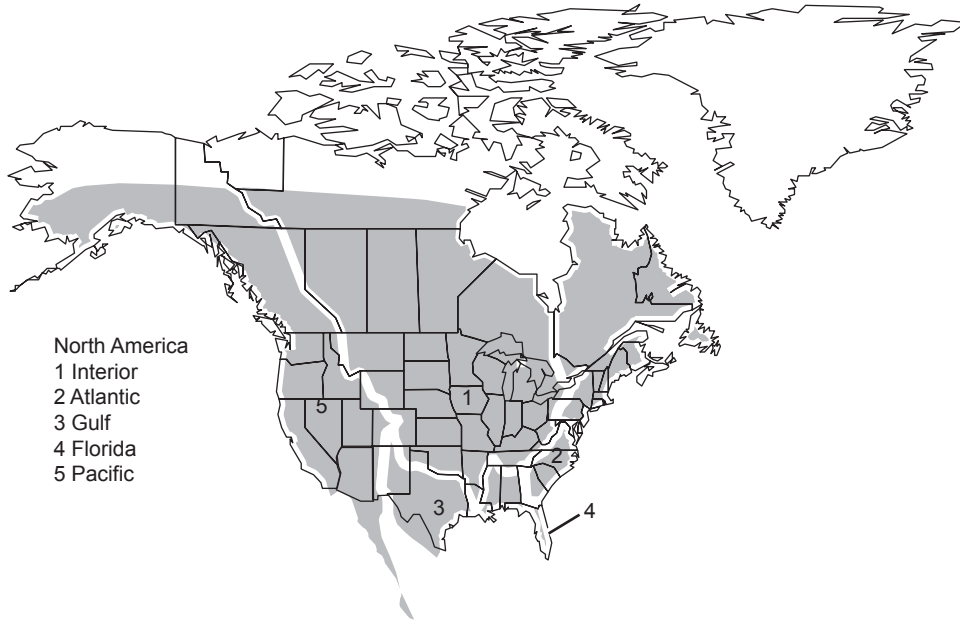


FIGURE 11.12 Map of geographic areas covered in the key (original elements of the map rendered by Jerry Graf).

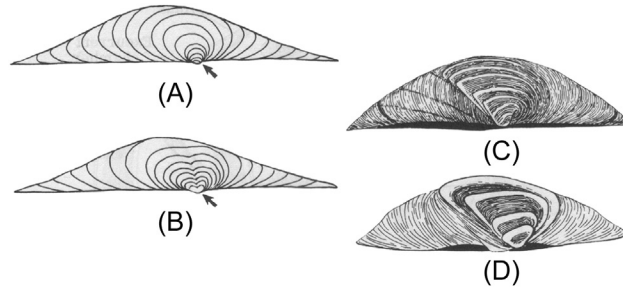


FIGURE 11.13 Beak sculpture of freshwater bivalves: (A) single-looped concentric ridges; (B) double-looped concentric ridges; (C) fine concentric ridges; and (D) coarse concentric ridges. From Burch, 1975.

2'	Umbo not projecting above the hinge line .....	<i>Utterbackia</i>
3(2)	Umbo sculpture consists of concentric bars (Fig. 11.13) .....	5
3'	Umbo sculpture double looped (Fig. 11.13 B), shell thin .....	<i>Pyganodon</i>
4(3)	Nacre usually orange or salmon colored; pseudocardinal and lateral teeth reduced to a thickened ridge; umbo sculpture prominent or pronounced .....	<i>Strophitus</i>
4'	Nacre bluish or white; pseudocardinal and lateral teeth completely absent; umbo sculpture fine .....	<i>Anodontoides</i>
5(3)	Shell truncated, with well-developed lateral teeth in left valve .....	6
5'	Right valve with two lateral teeth or lateral teeth absent or reduced and not interlocking .....	<i>Alasmidonta</i>
6(5)	Shell with spines .....	7
6'	Shell without spines .....	8
7(6)	Shell thick and often large .....	<i>Elliptio</i>
7'	Shell and spines small .....	<i>Pleurobema collina</i> Conrad, 1837
8(6)	Left valve without extra interdental tooth .....	9
8'	Left valve hinge line with an additional small interdental or accessory tooth, giving the appearance of three pseudocardinal teeth, shell more or less compressed, rhomboid, periostracum dark green with numerous green rays, umbo sculpture with heavy bars .....	<i>Lasmigona</i> (in part)

9(8)	Shell shape broadly triangular .....	10
9'	Shell shape oval, round, or rhomboid .....	11
10(9)	From the James River .....	<i>Lexingtonia</i>
10'	From an area extending from the Roanoke River south to the headwaters of the Savannah River Basin .....	<i>Fusconaia masoni</i> (Conrad, 1834)
11(10)	Shell shape rhomboid or rectangular .....	12
11'	Shell shape oval or round .....	15
12(11)	Shell usually more than twice as long as broad .....	13
12'	Shell usually less than twice as long as broad; periostracum light in color with numerous green rays; shell relatively small and thin, oval to elongate oval; blade-like pseudocardinal teeth .....	<i>Villosa</i>
13(12)	Nacre color white, shell inflated .....	14
13'	Nacre color typically some shade of purple, but ranges from salmon to purple .....	<i>Elliptio</i> (in part)
14(13)	Periostracum not rayed and mat or dull, shell moderately thick and slightly rectangular, posterior end angled with two grooves running along the posterior slope .....	<i>Unio</i>
14'	Periostracum not mat and often rayed, particularly in juveniles, posterior end tapered to a sharp point .....	<i>Ligumia</i>
15(13)	Adult shell typically >40 mm in length, with a smooth periostracum .....	16
15'	Adult shell typically <40 mm in length, with a dark cloth-like or mat periostracum .....	<i>Toxolasma</i>
16(15)	Shell relatively large, oval to elongate oval in shape, periostracum very shiny to mat with rays .....	<i>Lampsilis</i>
16'	Shell thin and oval in shape, periostracum dull yellow, rayless or with very fine rays all over the shell found in or near the tidewater, nacre often salmon colored .....	<i>Leptodea ochracea</i> Say, 1817

## Interior Subregion

1	Shell without lateral teeth or all pseudocardinal teeth .....	3
2'	Shell with both pseudocardinal and lateral teeth present .....	9
3(2)	Shell with pseudocardinal teeth, but lacking lateral teeth .....	4
3'	Shell with greatly reduced or completely lacking both pseudocardinal and lateral teeth .....	5
4 (3)	Shell <25 mm, periostracum often eroded, umbo sculpture consists of heavy bars .....	<i>Pegias fabula</i> (Lea, 1838)
	[Upper Cumberland and Tennessee River basins.]	
4'	Shell relatively large >25 mm, umbo sculpture consists of heavy bars .....	<i>Lasmigona</i>
	[Widespread in Mississippi River basin; also found in the Tennessee River drainage.]	
5(3)	Hinge teeth completely absent .....	6
5'	Shell with pseudocardinal tooth consisting of a swelling or knob, lateral teeth reduced to a thickened ridge, umbo sculpture heavy "v"-shaped ridges .....	<i>Strophitus undulates</i> Say, 1817
6(5)	Umbo projects above the hinge line .....	7
6'	Umbo even with or below the hinge line .....	<i>Utterbackia imbecillis</i> (Say, 1829)
7(6)	Umbo projecting only slightly above the hinge line .....	8
7'	Umbo projects well above the hinge line .....	<i>Pyganodon grandis</i> (Say, 1829)
8(7)	Umbo projecting only slightly above the hinge line, shell elongate, umbo sculpture consists of faint "v"-shaped ridges .....	<i>Anodontioides ferussacianus</i> (Lea, 1834)
8'	Umbo barely above the hinge line, shell rounded in shape, umbo sculpture with double looped ridges .....	<i>Utterbackia suborbiculata</i> Say, 1831
9(2)	Shell with external surface sculpture (plications, pustules, ridges) .....	10
9'	Shell without surface sculpture .....	27
10(9)	Shell with prominent external surface pustules, knobs or bumps and/or plications or ridges .....	11
10'	Shell lacking plicae .....	19
11(10)	Shell with prominent plications or ridges but lacking pustules, knobs, or bumps .....	12
11'	Shell with prominent plications or ridges and pustules, knobs or bumps on the anterior part of the shell .....	17

12(11)	Shell with prominent plications or ridges confined to the posterior slope .....	13
12'	Shell with prominent plications or ridges not confined to the posterior slope .....	14
13(12)	Shell elongate, inflated, with bluegreen nacre color .....	<i>Medionidus conradicus</i> (Lea, 1834)
	[Restricted to the Cumberland and Tennessee River basins.]	
13'	Shell elongate, inflated, nacre not as above, posterior slope and ridge rounded .....	<i>Ptychobranthus subtentum</i> Say, 1825
	[Restricted to the Cumberland and Tennessee River basins.]	
14(12)	Shell without a distinct posterior ridge; nacre white .....	15
14'	Shell shape rectangular with a distinct posterior ridge; nacre purplish .....	<i>Plectomerus dombeyanus</i> (Humboldt & Bonpland, 1827)
	[Lower Ohio and Mississippi River basins]	
15(14)	Shell not as below .....	16
15'	Shell thick, small <50 mm, with many low plications all over the posterior surface of the shell .....	<i>Lemiox rimosus</i> (Rafinesque, 1831)
16(15)	Shell laterally compressed to inflated, round to quadrate in shape; heavy pseudocardinal teeth, well-developed lateral teeth; deep umbo cavity, shell surface typically with three prominent, well-developed ridges .....	<i>Amblema plicata</i> (Say, 1817)
	[Widespread in the Mississippi River basin.]	
16'	Shell inflated and somewhat thin, rounded, approaching oval, pseudocardinal teeth curved, surface with indistinct undulations or ridges ..	<i>Arcidens wheeleri</i> (Ortmann & Walker, 1912)
	[Confined to the Red and Ouachita River basins.]	
17(11)	Shell not elongate, quadrate or rounded in shape and the pustules less numerous or confined to the anterior part of the shell .....	18
17'	Shell elongate with numerous small pustules over surface .....	<i>Tritogonia verrucosa</i> (Rafinesque, 1820)
18(17)	Shell large and quadrate in shape with the pustules confined to the anterior part of the shell .....	<i>Megaloniais nervosa</i> (Rafinesque, 1820)
18'	Shell more or less rounded in shape with indistinct undulations on the surface; lateral teeth poorly developed .....	<i>Arcidens confragosus</i> (Say, 1829)
19(10)	Shell surface with generally distributed pustules .....	20
19'	Shell with pustules restricted to a single or double row .....	23
20(19)	Shell rounded, compressed to slightly inflated; pustules covering most of the shell; nacre white; umbo cavity deep .....	21
20'	Shell rounded, compressed to slightly inflated, pustules covering most of the shell, nacre purple, umbo cavity deep .....	<i>Cycloniais tuberculata</i> (Rafinesque, 1820)
21(20)	Shell rounded; pustules generally variable in shape .....	22
21'	Shell rounded, pustules small and covering most of the shell; elevated ridges at the growth lines; nacre white; umbo cavity deep .....	<i>Cyprogenia</i>
22(21)	Shell rounded, compressed to slightly inflated; pustules covering most of the shell; nacre white; umbo cavity deep; a conspicuous green stripe always present on the umbo .....	<i>Amphinaias pustulosa</i> (Lea, 1831)
22'	Shell rounded; pustules covering most of shell; nacre white, pink or salmon; umbo cavity deep; green stripe absent; periostracum reddish chestnut in color .....	<i>Plethobasus cooperianus</i> (Lea, 1834)
23(19)	Pustules forming two distinct rows .....	24
23'	Pustules forming a single row .....	25
24(23)	Shell rounded to quadrate; two rows of pustules, with one row on the posterior ridge, a sulcus or shallow depression may be present between the rows of pustule .....	<i>Quadrula</i> (in part)
24'	Shell rounded to quadrate in shape; two rows of paired pustules, with one row on the posterior ridge, sulcus absent .....	<i>Amphinaias nodulata</i> (Rafinesque, 1820)
25(23)	Valve with a single median row of large pustules .....	26
25'	Shell quadrate to elongate and rectangular in shape, often with chevron markings; posterior ridge with a single row of pustules or small pustules spread across surface .....	<i>Theliderma</i>
26(25)	A single row of three large pustules running down the center of the valve which alternate on each valve .....	<i>Obliquaria reflexa</i> Rafinesque, 1820
26'	A single row of numerous large pustules running down the center of the valve which do not alternate between the valves .....	<i>Dromus/Plethobasus</i>
27(9)	Shell with a well-developed dorsal wing projecting above the hinge line, usually found posterior to the umbo but a small wing may also be present anterior to the umbo .....	28

27'	Shell without a prominent dorsal wing .....	29
28(27)	Shell and hinge teeth thin, pseudocardinal teeth compressed; periostracum dull and typically yellow; nacre white with suffusions of pink .....	<i>Leptodea</i>
28'	Shell and hinge teeth thin, pseudocardinal teeth compressed; periostracum shiny and typically olive, brown, or black; nacre evenly colored light or dark purple .....	<i>Potamilus</i>
29(27)	Shell shape round .....	30
29'	Shell shape not round .....	36
30(29)	Shell inflated or various shaped .....	31
30'	Shell compressed and thick, usually triangular in shape with a sharp posterior ridge; yellow in color with "v"-shaped rays .....	<i>Ellipsaria lineolata</i> (Rafinesque, 1820)
31(30)	Umbo nearly central .....	32
31'	Umbos located anteriorly .....	34
32(31)	Shell without raised ridge or hump .....	33
32'	Shell with a raised ridge or hump located near the middle running parallel with the growth lines .....	<i>Dromus dromas</i> (Lea, 1834) [Restricted to the Cumberland and Tennessee River basins.]
33(32)	Shell surface smooth, round, without a sulcus .....	<i>Obovaria</i>
33'	Shell with a broad shallow sulcus; fine green rays; shallow umbo cavity; females with a swollen, broadly expanded posteroventral margin .....	<i>Epioblasma</i>
34(33)	Umbo cavity relatively shallow .....	35
34'	Umbo cavity deep and compressed; a shallow sulcus present in some species, nacre white .....	<i>Fusconaia</i>
35(34)	Shell yellowish with green rays near the umbo; thick, well-developed lateral teeth .....	<i>Lexingtonia dolabelloides</i> (Lea, 1840) [Restricted to the Tennessee River basin.]
35'	Shell rounded or quadrate; umbo cavity relatively shallow, without a sulcus; nacre white to pink or salmon .....	<i>Pleurobema</i>
36(29)	Shell shape not oval .....	37
36'	Shell shape oval to oblong .....	51
37(36)	Shell shape rectangular, triangular, or quadrate with sulcus .....	38
37'	Shell shape elongate, two to four times as long as high .....	41
38(37)	Umbo cavity deep .....	39
38'	Umbo cavity shallow .....	40
39(38)	Shell shape rectangular or slightly rounded; umbo with green rays .....	<i>Fusconaia</i>
39'	Shell shape triangular .....	<i>Pleurobema</i>
40(38)	Posterior slope angled; periostracum highly variable in color and may be green, brown, or yellow with chevron markings; nacre variable from white to pink .....	<i>Truncilla</i>
40'	Shell rectangular, thick; nacre white with purple .....	<i>Elliptio crassidens</i> (Lamarck, 1819)
41(37)	Shell thin .....	42
41'	Shell thick .....	45
42(41)	Shell inflated .....	43
42'	Shell compressed, thin; periostracum yellow with green rays; nacre white with suffusions of pink .....	<i>Hemistena lata</i> (Rafinesque, 1820)
43(42)	Adult shell >50 mm; periostracum usually with rays .....	44
43	Adult shell small <50 mm; hinge teeth thin; periostracum light brown and rayless .....	<i>Simpsonaias ambigua</i> (Say, 1825)
44(43)	Adult shell relatively small <70 mm; hinge teeth typically thin; periostracum rayed .....	<i>Villosa</i>
44'	Adult shell relatively small <70 mm; hinge teeth thin; periostracum yellow and rayed or rayless .....	<i>Lampsilis</i>
45(41)	Shell compressed .....	46
45'	Shell inflated .....	48
46(45)	Adult shell small >40 mm .....	47
46'	Adult shell small <40 mm; periostracum rayed .....	<i>Villosa fabalis</i> (Lea, 1831)
47(46)	Shell thick; hinge teeth stout and curved; nacre white, periostracum yellow with green rays .....	<i>Ptychobranchus</i>

47'	Shell thick; hinge teeth large, straight or slightly curved; nacre white or purple; periostracum dark brown or black and rayless; umbo sculpture consists of heavy bars .....	<i>Elliptio dilatata</i> (Rafinesque, 1820)
48(45)	Adult shell length <55 mm .....	49
48'	Adult shell length >55 mm .....	50
49(48)	Periostracum olive green with numerous dark green rays .....	<i>Villosa</i> [Restricted to the Tennessee River basin.]
49'	Periostracum ranges from greenish to dark brown and rayless, nacre white to purple .....	<i>Toxolasma</i>
50(48)	Shell inflated, periostracum rayless, umbo sculpture consists of heavy "v"-shaped ridges .....	<i>Unio merus tetralasmus</i> (Say, 1831)
50'	Shell inflated, periostracum dark green with faint rays in juveniles and rayless in adults, umbo sculpture consists of numerous wavy w-shaped ridges, nacre white or pink to light purple .....	<i>Ligumia</i>
51(36)	Shell shape oval .....	52
51'	Shell shape oblong .....	53
53(52)	Shell thin to thick; posterior ridge rounded to angular; periostracum usually yellow with green rays, nacre varies from white to pink .....	<i>Lampsilis</i>
53'	Shell elongate oval .....	<i>Villosa</i>
53(51)	Shell oblong, not inflated, thick .....	54
53'	Shell oblong, inflated, thin, rayless; hinge line sinuate .....	<i>Potamilus capax</i> (Green, 1832)
54(53)	Adult shell length <70 mm; shell elliptical, thick; nacre white; hinge teeth stout; periostracum dark yellow to greenish with wavy rays on the posterior end .....	<i>Venustaconcha</i>
55'	Adult shell length >70 mm; shell oval, thick; nacre white; hinge teeth stout; periostracum dark yellow without wavy rays on the posterior end .....	<i>Actinonaias</i>

## Gulf Coast and Florida Subregion

1	Shell with pseudocardinal and lateral teeth reduced or absent .....	2
1'	Shell with both pseudocardinal and lateral teeth present .....	5
2(1)	Shell with pseudocardinal and lateral teeth present but greatly reduced .....	3
2'	Shell completely lacking both pseudocardinal and lateral teeth .....	4
3(2)	Shell with pseudocardinal tooth consisting of a swelling or knob, lateral teeth reduced to a thickened ridge; umbo sculpture heavy "v"-shaped ridges .....	<i>Strophitus</i>
3'	Shell with pseudocardinal tooth thin, reduced and compressed; umbo projecting only slightly above the hinge line; shell elongate, umbo sculpture very fine "v"-shaped ridges .....	<i>Anodontioides radiata</i> (Conrad, 1834)
4(2)	Umbo projects well above the hinge line; shell thin, large, "w"-shaped umbo sculpture .....	<i>Pyganodon</i>
4'	Umbo even with or below the hinge line .....	<i>Utterbackia</i>
5(1)	Shell surface with sculpture (plications, pustules, ridges) .....	6
5'	Shell surface without sculpture .....	18
6(5)	Shell surface with prominent pustules, knobs or bumps and/or plications or ridges .....	7
6'	Shell with only prominent pustules, knobs, or bumps .....	14
7(6)	Shell with prominent plications or ridges but not pustules, knobs or bumps .....	8
7'	Shell anteriorly with prominent plications or ridges and pustules, knobs or bumps .....	12
8(7)	Shell with prominent plications or ridges confined to the posterior slope .....	9
8'	Shell with prominent plications or ridges not confined to the posterior slope .....	10
9(8)	Shell round or oval, compressed; periostracum dark brown or black; posterior wing may be present .....	<i>Lasmigona complanata</i> (Barnes, 1823)
9'	Shell small, elongate, slightly inflated; nacre bluegreen .....	<i>Medionidus</i>
10(8)	Shell round to rectangular without a distinct posterior ridge; nacre white .....	11
10'	Shell thick, rectangular with a distinct posterior ridge; nacre purplish .....	<i>Plectomerus dombeyanus</i> (Valenciennes, 1827)
11(10)	Shell thick, elongate rectangular; posterior slope with plications or wrinkles; nacre white with purple around the distal half .....	<i>Elliptioideus sloatianus</i> (Lea, 1840)



11'	Shell laterally compressed to inflated; round to quadrate in shape; heavy pseudocardinal teeth, well-developed lateral teeth; deep umbo cavity; shell surface typically with three prominent well-developed ridges .....	<i>Amblema</i>
12(7)	Shell not elongate, quadrate or rounded in shape; pustules less numerous or confined to the shell anterior .....	13
12'	Shell elongate with numerous small pustules all over the surface of the shell .....	<i>Tritogonia verrucosa</i> (Rafinesque, 1820)
13(12)	Shell large and quadrate in shape; pustules confined to the anterior part of the shell .....	<i>Megalonaias</i>
13'	Shell surface more or less rounded in shape with indistinct corrugations; lateral teeth poorly developed .....	<i>Arcidens confragosus</i> (Say, 1829)
14(6)	Shell surface with pustules .....	15
14'	Shell with pustules restricted to a single or double row .....	16
15(14)	Shell <60mm; rounded, compressed to slightly inflated; chevron-shaped pustules covering most of the shell; nacre purple; umbo cavity deep .....	<i>Quincuncina</i>
15'	Shell >60mm; rounded, slightly inflated; pustules covering most of the shell; nacre white to slightly pink; umbo cavity deep .....	<i>Amphinaias</i>
16(14)	Pustules forming two distinct rows, especially near the umbo .....	17
16'	Pustules large, usually three in number, forming a single row down the center of the shell which alternate on each valve .....	<i>Obliquaria reflexa</i> (Rafinesque, 1820)
17(16)	Shell rounded to quadrate in shape; two rows of pustules, with one row on the posterior ridge .....	<i>Quadrula</i> (in part)
17'	Shell rounded to quadrate in shape; two rows of pustules, with one row on the posterior ridge, a sulcus or shallow depression may be present between the rows of pustules; nacre purple .....	<i>Amphinaias refulgens</i> (Lea, 1868)
18(5)	Shell without a prominent dorsal wing .....	19
18'	Shell with a well-developed dorsal wing projecting above the hinge line (occasionally absent) usually found posterior to the umbo, but a small wing may also be present anterior to the umbo .....	<i>Leptodea fragilis</i> (Rafinesque, 1820)
19(18)	Shell shape round .....	20
19'	Shell shape not round .....	25
20(19)	Shell inflated, not compressed round to oval .....	21
20'	Shell thick, compressed, round to triangular in shape; sharp posterior ridge; yellow in color with "v"-shaped rays .....	<i>Ellipsaria lineolata</i> (Rafinesque, 1820)
21(20)	Umbo nearly central .....	22
21'	Umbos anterior .....	24
22 (21)	No broad green ray on the umbo .....	23
22'	Shell with a broad green ray on the umbo; without pustules .....	<i>Amphinaias asperata</i> (Lea, 1861)
23(22)	Shell surface smooth, round, without a sulcus .....	<i>Obovaria</i>
23'	Shell with a broad shallow sulcus and fine green rays; umbo cavity shallow; females with a swollen, broadly expanded posteroventral margin .....	<i>Epioblasma</i>
24(21)	Umbo cavity deep and compressed; a shallow sulcus present in some species; nacre white .....	<i>Fusconaia</i>
24'	Umbo cavity relatively shallow; shell wedge-shaped to triangular or quadrate, without a Sulcus; nacre white to pink or salmon .....	<i>Pleurobema</i> (in part)
25(19)	Shell shape not oval .....	26
25'	Shell shape oval to oblong .....	38
26(25)	Shell shape rectangular, triangular, or quadrate with sulcus .....	27
26'	Shell shape elongate, two to four times as long as high .....	31
27(26)	Umbo cavity deep .....	28
27'	Umbo cavity shallow or broad and open .....	29
28(27)	Shell shape rectangular, with green rays on the umbo .....	<i>Fusconaia cerina</i> (Conrad, 1838)
28'	Shell shape triangular .....	<i>Pleurobema</i> (in part)
29(27)	Posterior ridge very sharp, posterior slope steep .....	30
29'	Posterior slope angled; periostracum highly variable in color and may be green, brown, or yellow with chevron markings; nacre also variable from white to pink .....	<i>Truncilla</i>
30(29)	Shell thin, inflated, abruptly truncate posteriorly .....	<i>Alasmidonta</i>
30'	Shell rectangular, thin to thick, inflated posterior end; nacre ranges from salmon to purple .....	<i>Elliptio crassidens</i> (Lamarck, 1819)

31(26)	Shell thin .....	32
31'	Shell thick .....	34
32(31)	Shell slightly inflated .....	33
32'	Shell compressed, thin, elongate to rectangular; periostracum yellowish with green rays; nacre white to light purple .....	<i>Popenaias popei</i> (Lea, 1857)
33(32)	Adult shell relatively small <70 mm; hinge teeth thin; periostracum rayed .....	<i>Villosa</i>
33'	Adult shell relatively large >70 mm; rounded to oval in shape; hinge teeth not thin; periostracum yellow, rayed or rayless .....	<i>Lampsilis/Hamiota</i> spp.
34(31)	Shell compressed .....	35
34'	Shell slightly inflated .....	36
35(31)	Shell thick; hinge teeth stout and curved; nacre white; periostracum yellow or brown, with or without green rays .....	<i>Ptychobranchus</i>
35'	Shell thick; hinge teeth large, straight or slightly curved; nacre white or purple; periostracum dark brown or black and rayless; umbo sculpture consists of heavy bars .....	<i>Elliptio</i>
36(34)	Shell rayless .....	37
36'	Shell elongate, inflated; periostracum dark green with faint rays in juveniles and rayless in adults; umbo sculpture consists of numerous wavy "w"-shaped ridges; nacre white or pink to light purple .....	<i>Ligumia recta</i> (Lamarck, 1819)
37(36)	Shell inflated; posterior end pointed; umbo sculpture consists of heavy "v"-shaped ridges .....	<i>Unionomerus</i>
37'	Adult shell relatively small <50 mm; periostracum ranges from greenish to dark brown .....	<i>Toxolasma</i>
38(25)	Shell shape oval .....	39
38'	Shell shape oblong .....	41
39(38)	Pseudocardinal tooth not divided as below .....	40
39'	Posterior half of the pseudocardinal tooth divided into several parallel vertical ridges; shell thick, inflated; periostracum cloth-like and light to dark brown and rayless .....	<i>Glebula rodundata</i> (Lamarck, 1819)
40(39)	Shell thin to thick; posterior ridge rounded to angular; periostracum usually yellow with green rays; nacre varies from white to pink .....	<i>Lampsilis</i>
40'	Shell shape elongate oval .....	<i>Villosa</i>
41(38)	Shell shape oblong, not inflated or globose .....	42
41'	Shell shape oblong, inflated to globose; unrayed .....	<i>Potamilus</i>
42(41)	Shell shape elongate oval; relatively thin, compressed; pseudocardinal teeth compressed; periostracum tan to brown, with dark green rays .....	<i>Disconaias</i>
42'	Shell shape oval; relatively thick, moderately inflated; periostracum brown with very faint green rays in juveniles .....	<i>Cyrtonaias</i>

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