

10

MOLLUSCA: GASTROPODA

Kenneth M. Brown

*Department of Biological Sciences
Louisiana State University
Baton Rouge, Louisiana 70803*

- I. Introduction
- II. Anatomy and Physiology
 - A. External and Internal Morphology
 - B. Organ System Function
 - C. Environmental Physiology
- III. Ecology and Evolution
 - A. Diversity and Distribution
 - B. Reproduction and Life History
 - C. Ecological Interactions
- D. Evolutionary Relationships
- IV. Collecting and Culturing Freshwater Gastropods
- V. Identification of the Freshwater Gastropods of North America
 - A. Taxonomic Key to Families and Selected Genera of Freshwater Gastropods
- Literature Cited

I. INTRODUCTION

Gastropods are the most diverse class of the phylum Mollusca, with anywhere from 40,000 to 100,000 species, depending on the authority (Bieler, 1992; Ponder and Lindberg, 1997). In North America, there are 14 families, 88 genera and 659 species of freshwater snails (Bogan, 1999). Snails are common organisms along the margins of lakes and streams. They feed on detritus, graze on the periphyton covering of macrophytes or cobble, or even float upside down at the water surface, supported by the surface tension, and feed on algae trapped in the same fashion (Fig. 1). In fact, gastropods often control the amount and composition of periphyton in both lotic and lentic environments. They are also the basis of food chains dominated by sport fish. Predators, by controlling snail populations, may indirectly facilitate algal producers. Freshwater snails also have extensive intraspecific variation in life histories, productivity, morphology and feeding habits that adapt them to live in uncertain freshwater habitats. There is increasing concern, however, that many riverine gastropod populations in the southeastern United States are currently endangered because of habitat alterations such as impoundments.

Snails are soft bodied, unsegmented animals, with a body organized into a muscular foot, a head, a visceral mass containing most of the organ systems, and a fleshy mantle which secretes the calcareous shell. Gastropods have a univalve shell and possess a filelike radula used in feeding on the periphyton coverings of rocks or plants. Traditionally, gastropods were divided into three subclasses: Prosobranchia (including 53% of modern species), Opisthobranchia (4%), and Pulmonata (43%). Prosobranch snails possess a gill (ctenidium) and a horny (flexible) or calcareous operculum, or "trap door," which is pulled in after the foot to protect the animal. Pulmonates have secondarily re-invaded freshwaters from the terrestrial habitats used by their ancestors, use a modified portion of the mantle cavity as a lung, and lack an operculum.

Later authors divided the prosobranchs into the ancestral archeogastropods, the mesogastropods, and most-derived neogastropods, with a trend toward reduction in number of gills, auricles, and kidneys. Cox (1960) combined the meso- and neogastropods into the Caenogastropoda. More recent authors have also considered the valvatids to be more closely allied to the opisthobranchs and pulmonates than to the prosobranch groups, and they have suggested combining the three



FIGURE 1 An adult *Lymnaea stagnalis* (length about 5 cm), supported by the surface tension, is foraging upside down at the water surface.

former groups into the Heterogastropoda (Kosuge, 1966). Cephalopods are thought to be the closest sister group to the gastropods, and patellid limpets (a marine, intertidal group) are thought to be the most primitive gastropods (Ponder and Lindberg, 1997). More details on the time line of gastropod evolution are given by Bandel (1997).

The first gastropods are thought to have had coiled shells, and several trends have occurred throughout gastropod evolution (Ponder and Lindberg, 1997). Torsion (a 180° rotation of the gut so that the anus and mantle cavity lie anterior) is a functional homology of all gastropods, although it is secondarily reduced in opisthobranchs and pulmonates. Anatomical complexity has also become secondarily simplified, including the radula, the circulatory system, and digestive anatomy. External fertilization and pelagic larvae are also considered ancestral traits, with internal fertilization, direct development and encapsulated eggs being derived traits. In contrast, respiratory systems, neuro-secretory structures, and life histories have increased in complexity through evolutionary time. A detailed introduction to gastropod biology can be found in Fretter and Graham (1962), and in volumes on the general biology of molluscs edited by Wilbur (1983) or the biology of pulmonates edited by Fretter and Peake (1975, 1978).

II. ANATOMY AND PHYSIOLOGY

A. External and Internal Morphology

1. Shell

The structure of the shell is important in systematics. Shells can have a simple conical shape (Fig. 2A), as in the limpets, family Ancyliidae, with new shell material secreted at the margin. Second, the shell can be planospiral (with the whorls all in one plane), as in the pulmonate family Planorbidae (Fig. 2B). Whorls may be elevated into a "spire," as in the pulmonate families Physidae and Lymnaeidae, and in various prosobranch families (Fig. 2 C, D). Russell-Hunter (1983) discusses how new shell material is secreted by the mantle for each of these three basic shapes. If shells are placed with the spire facing away from the observer and the aperture (opening from which the foot extends) upward, shells with the aperture on the left are sinistral (e.g., the physids), whereas those on the right are dextral (e.g., the lymnaeids and prosobranchs). Spiral shells have a central supporting member, the columella, similar to the center support of a spiral staircase. The columella adds to the strength of the shell, and provides an attachment point for the soft parts via the columellar muscle.

A spiral shell (Fig. 2D) is convenient for illustrating terminology used in systematics. The pointed end of the shell above the aperture is the apex. Shell length in spiral shells is measured from the apex to the lower tip of the aperture, while the greatest diameter is used in planospiral shells. The spire is separated into a number

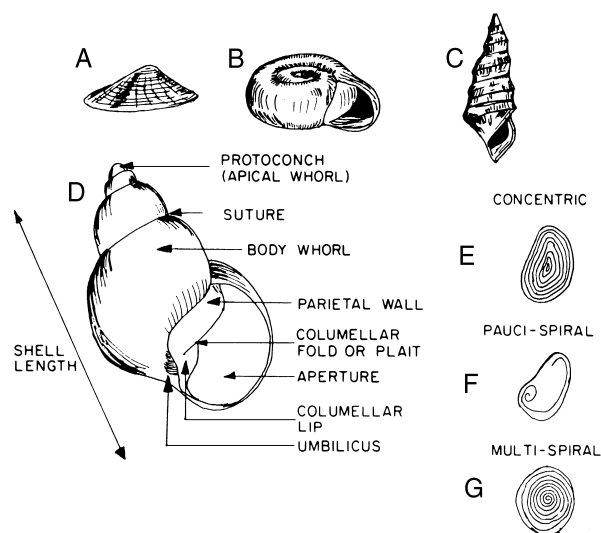


FIGURE 2 Basic anatomy of the shell, including shell architecture (A, conical; B, planospiral; C and D, spiral, with major shell features indicated in D) and three types of opercula (E, concentric, F, paucispiral, and G multispiral).

of whorls by sutures (Fig. 2). The most apical whorl is the nuclear whorl or protoconch, the initial shell of the newly hatched snail or "spat." The final and biggest whorl (representing the most recent shell growth) is the body whorl, ending in the aperture. Whorls may be rounded and sutures deep and well defined (as in a typical lymnaeid shell, Fig. 2D), or they may be flattened and sutures shallow, as in the prosobranch family Pleuroceridae (Fig. 2C). Spiral shells thus have a variety of shapes. If the whorls are flat, the shell is termed cone-shaped, while moderately inflated whorls produce a "subglobose" shell, and shells that are almost circular are globose; there is a continuum between these three shapes. Shell thickness varies from thin and fragile (as in many pulmonates) to thick and resistant to crushing (as in the prosobranchs).

Part of the aperture is often reflected over the body whorl at the columella (Fig. 2D) to form an inner lip. If there is a channel between the inner lip and the body whorl, the shell is umbilicate or perforate (the opening of the channel is called the umbilicus and leads up and inward into the columella). Imperforate shells lack an umbilicus. While freshwater shells are not as ornate as their marine relatives (Vermeij and Covich, 1978), shells may have spines, ridges running along the margins of the whorls (called carina), colored bands, or small malleations (hammerings) on the surface. Ridges at right angles to the whorls are called costae, while smaller ridges running spirally along the whorls are lirae. The operculum is useful in classifying prosobranchs. If the growth lines lie completely within each other, the operculum is concentric; whereas, lines arranged in a spiral are termed multispiral or paucispiral (see examples in Fig. 2 E–G). Further discussion on shell sculpture is given in Fretter and Graham (1962) and Burch (1989).

The shell is composed of an outer periostracum of organic (mostly protein) composition which may limit shell abrasion or dissolution of shell calcium carbonate by acid waters. Beneath the periostracum is a thick layer of crystalline calcium carbonate with some protein material as a matrix for the calcium crystals (Russell-Hunter, 1978). Calcium carbonate is either absorbed directly from water or is sequestered from food (McMahon, 1983). Snails in calcium-poor waters (<5 mg/L, Lodge *et al.*, 1987) expend energy to absorb calcium against a gradient, and many species are therefore limited to calcium-rich habitats.

2. Soft Anatomy

The soft parts are separated into: (1) head, (2) foot, (3) visceral mass, and (4) the mantle (Fig. 3). Aquatic pulmonates and prosobranchs possess eyes at the base of their tentacles, unlike terrestrial pulmonates

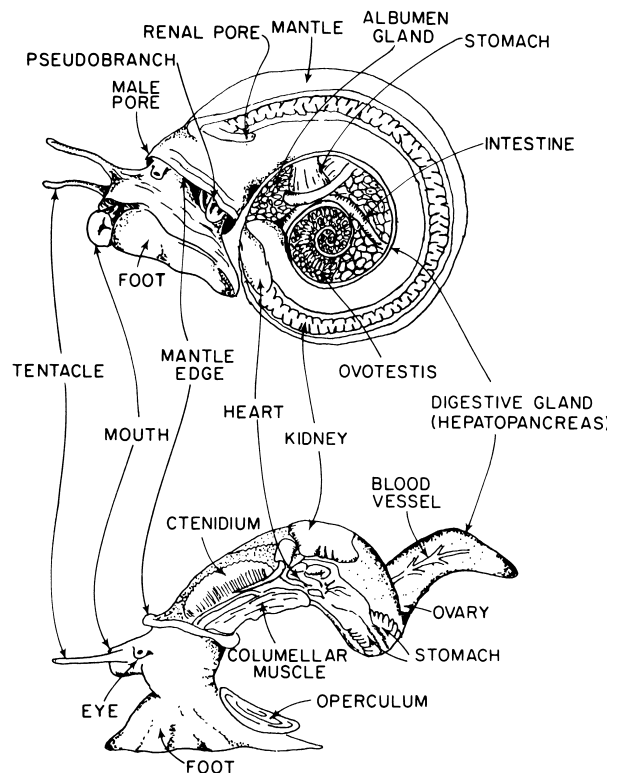


FIGURE 3 Basic internal anatomy (with shell removed) of a planorbid pulmonate (above, after Burch, 1989), and a pleurocerid prosobranch (below, after Pechenik, 1985).

whose eyes are at the tips of the tentacles. The muscular foot is provided with both cilia and secretory epithelium to secrete mucus for locomotion, as well as pedal muscles which produce waves of contraction to push the animal forward. The visceral hump includes most of the organs of digestion and reproduction. The mantle covers the visceral mass, and underlays the shell, which it secretes. The anterior mantle, over the head, possesses a mantle cavity, where the gill or ctenidium is located in prosobranchs. Gastropods have ganglia innervating each of these areas. Further information on internal anatomy can be found in Fretter and Graham (1962), Barnes (1987), Pechenik (1985), or Hyman (1967).

B. Organ System Function

1. Reproductive System

Prosobranchs are usually dioecious, and males use the enlarged right tentacle as a copulatory organ (in the viviparids), or possess a specialized penis or verge (in the hydrobiids, pomatiopsids, and valvatids) or have no copulatory organ (thiarids and pleurocerids). The penis is usually located behind the male's right tentacle. Many pleurocerids lay clutches of a few eggs, whereas

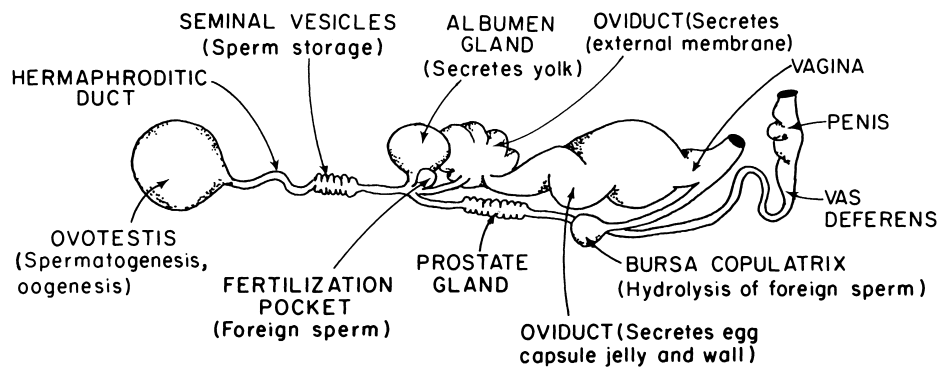


FIGURE 4 Anatomy of the reproductive system of the monoecious pulmonate *Physella* (after Duncan, 1975). Sperm are produced in the ovotestis, stored in the seminal vesicle, exit via vas deferens, and are inserted into the vagina of a second individual via the introvertible penis; or sperm may fertilize the same individual's eggs in the hermaphroditic duct. Most foreign sperm are hydrolyzed in *Physella* in the bursa copulatrix, but some do fertilize eggs in the fertilization pocket. The albumen gland secretes yolk around the egg, and the oviduct wall secretes both the egg membrane and the jelly and external wall of the egg case.

viviparids produce eggs which hatch and develop in a fold of the anterior mantle (the pallial oviduct), and are born free-living. Some viviparids in the genus *Campeloma*, especially more northern populations, are parthenogenetic (Van Cleave and Altringer, 1937; Vail, 1978; Johnson, 1992).

Pulmonates, in contrast, are all monoecious. The basic components of the pulmonate reproductive system are shown in Figure 4. Sperm and eggs are produced in the ovotestis and exit via a common hermaphroditic duct in all pulmonates except ancyliids, which have two openings and are thus obligate cross-fertilizers. The albumen gland adds protein and nutrients to the egg. Eggs are either fertilized in the hermaphroditic duct by the same individual's sperm, or by sperm from another individual near the junction of the hermaphroditic duct and the oviduct. The external egg membranes are then secreted in the oviduct. Eggs are laid in gelatinous egg cases and attached to plants, submerged wood, other snails or rocks. Males have an introvertible penis, and fertilization is internal. Duncan (1975) gives a more detailed discussion of egg and sperm formation, copulation and fertilization, and egg capsule deposition.

Although pulmonates are simultaneous hermaphrodites, most species out-cross when possible. Pulmonates that "self" usually mature at later ages and have lower fecundity. For example, *Physella heterostropha* suffers a reduction of 65% in fecundity when not allowed to out-cross (Wethington and Dillon, 1993). Snails act as males or females based on the amount of stored sperm that they possess (Wethington and Dillon, 1996). Similarly, the African snail *Bulinus globosus* suffers a 50% reduction in fecundity, and an

18% reduction in hatching rate, under obligate self-fertilization, indicating a significant genetic load of recessive lethal genes (Jarne *et al.*, 1991). In other physids (Eileen Jokinen, personal communication), the male system is larger in juveniles than in adults, and protandry (a form of sequential hermaphroditism where individuals switch sex from male to female as they age and increase in size) may occur.

With the costs to fitness indicated in the preceding paragraph, one might wonder why hermaphroditism occurs in pulmonates. Most pulmonates are slow-moving and go through seasonal "bottlenecks" (precipitous declines in density). The chances of finding a mate in such situations are small, providing a selective advantage for monoecy. Pulmonates are dispersed passively as spat trapped in mud on birds feet (Boag, 1986 and references therein), and solitary, monoecious immigrants have an obvious advantage. The cost of inbreeding depression is evidently less than not being able to reproduce at all. Parthenogenesis (being able to reproduce without males) may have a similar adaptive value for prosobranch snails that are isolated in small headwater streams (Vail, 1978).

2. Digestive System

Food is brought into the mouth by rasping movements of the radula, a filelike structure (Fig. 5) resting on a cartilage (the odontophore) to which muscles which extend and retract the radula are attached. When the radula is extended, it contacts the substratum, and algal particles are scraped off when retractors pull the radula back into the mouth. The radula may also pulverize food particles by grinding them against the roof of the mouth. A long esophagus leads to the

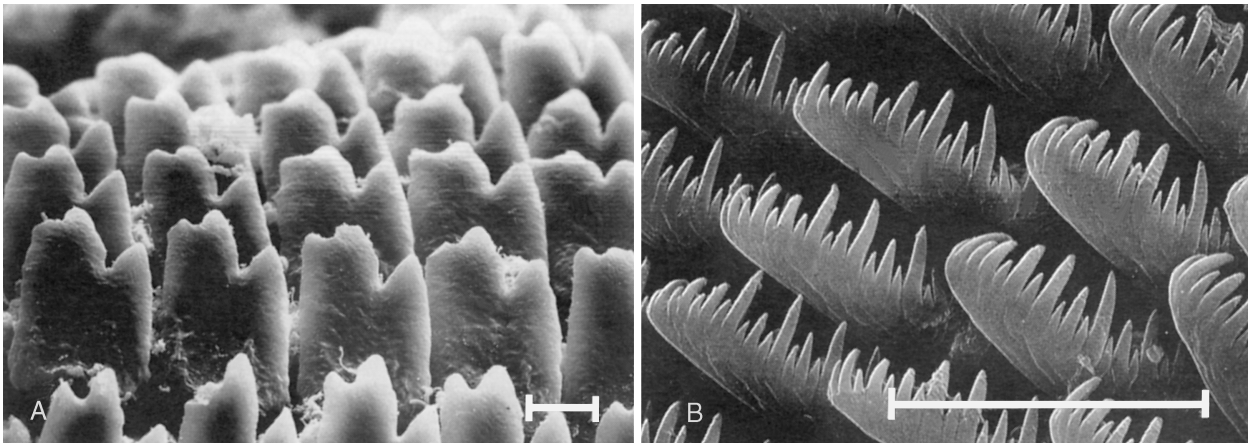


FIGURE 5 Scanning electron microscope photographs of radular teeth of (A) the lymnaeid, *Pseudosuccinea columella* and (B) the physid, *Physella vernalis* (from Kesler *et al.*, 1986). Note the lymnaeid has fairly large teeth with few cusps. These teeth, along with large, cropping jaws in the buccal mass, a grinding gizzard equipped with sand, and high cellulase levels allow it to specialize on filamentous green algae (Kesler *et al.*, 1986). *Physella* has many, small teeth with long cusps, arranged in chevron-shaped rows, useful for piercing detritus and attached bacteria.

stomach, located in the visceral mass. Some gastropods possess a specialized crop where sand grains further abrade food particles. Digestive enzymes are produced by the digestive gland, the hepatopancreas. Considerable digestion also occurs intracellularly in the hepatopancreas. Snails are one of the few animal groups to possess and possibly synthesize cellulases (Kesler, 1983; Kesler *et al.*, 1986), that degrade the algal cell walls.

3. Respiratory and Circulatory Systems

The respiratory system differs radically between prosobranchs and pulmonates. Freshwater prosobranchs have a single ctenidium or gill (Aldridge, 1983). The ctenidium, usually in the mantle cavity, has leaflike triangular plates richly supplied with blood vessels. Oxygen poor blood passes across the plates in the opposite direction to oxygen-rich water currents (generated by ctenidial cilia). This countercurrent mechanism assures diffusion of oxygen from water into the blood. Pulmonates lost their gill during their intermediate terrestrial phase, and have a vascularized pocket in the mantle used as a lung (hence their name). The opening of the lung is the pneumostome. Pulmonates either rely on surface breathing or have a limited capacity for oxygen transfer across their epithelial tissues (McMahon, 1983). Some physids and lymnaeids fill the mantle pocket with water and use it as a derived gill (Russell-Hunter, 1978). Ancyliids and planorbids have re-adapted further to aquatic conditions by using a conical extension of epithelium as a gill, and planorbids also have a respiratory pigment, hemoglobin, which increases the efficiency of oxygen transport (McMahon, 1983).

4. The Excretory System

Gastropods have a permeable epidermis and are subject to osmotic inflow of water from their hypo-osmotic surroundings. Thus, they must pump out excess water in their urine. The gastropod coelom is little more than a small cavity (pericardium) surrounding the heart. The coelomic fluid is largely a filtrate of the blood, containing waste molecules, such as ammonia, that are filtered across the wall of the heart. Additional wastes are actively secreted into the coelom by the walls of the pericardium. The coelomic fluid then enters a metanephridial tubule (the coelomoduct) where selective resorption of salts and further secretion of wastes occurs. The urine is then discharged into the mantle cavity. Freshwater gastropods excrete nitrogen both as ammonia and as urea. Ammonia is adaptive in aquatic environments because, although it is toxic, it is extremely soluble and readily diffuses away. Pulmonates often produce urea which is better in terrestrial situations, or during hibernation or estivation, because it is relatively nontoxic and can be stored in the blood until able to be excreted (McMahon, 1983). Further discussion of excretion can be found in Martin (1983) for gastropods in general and in Machin (1975) for pulmonates.

C. Environmental Physiology

Pulmonates usually face wider extremes of temperature variation than do most prosobranchs (McMahon, 1983). Most temperate pulmonates, for example, can withstand temperatures near 0°C for several months, whereas tropical pulmonates can withstand

temperatures near 40°C for extended periods. This is undoubtedly adaptive because of the seasonal and diurnal variation in temperature in many pond habitats. Pulmonates better regulate changes in metabolic rate with changing temperatures than do prosobranchs. For example, Q_{10} values for 18 pulmonate species were less (averaging 2.2) than in 13 prosobranch species (averaging 2.8) (McMahon, 1983). As the average temperature increases, snails grow faster and reproduce at an earlier age, with more generations per year. For example, the subtropical pulmonate *Physella cubensis* grows slowly and will not mature at 10°C (Thomas and McClintock, 1990), but hatching times and ages at maturity decrease, and growth rates increase as laboratory temperatures are increased to 30°C.

Increasing water temperature is also the cue for onset of reproduction in many temperate pulmonates. The ability of pulmonates to reproduce in cold water allows adults to breed early in the spring and juveniles to grow rapidly to adult size before the end of the summer. Pulmonates can secrete a mucus covering over the aperture, called an epiphragm, to retard moisture loss during dry periods (Boss, 1974; Jokinen, 1978).

In terms of adaptation to hypoxia, pulmonates: (1) tolerate greater variation in dissolved oxygen than do prosobranchs (possibly because prosobranchs rarely experience hypoxia in the littoral zones of lakes or the fast flowing rivers they are common in); and (2) also regulate oxygen consumption at varying levels of dissolved oxygen better than prosobranchs, which are "oxy-conformers" (Brown *et al.*, 1998). Pulmonates apparently withstand lower oxygen tensions by either

surface breathing or reliance on anaerobic metabolism (McMahon, 1983).

Approximately 45% of freshwater gastropods are restricted to waters with calcium concentrations greater than 25 mg/L, and 95% to levels greater than 3 mg/L. Although it may not take much energy to absorb calcium from water, assuming adequate water hardness, it may be energetically costly to secrete calcium into the shell against an electrochemical gradient. For example, in the northeastern United States (Jokinen, 1987), *Aplexa elongata*, *Helisoma (Planorbella) trivolvis*, and all lymnaeids except *Fossaria* are limited to calcium-rich waters. McMahon (1983) and Lodge *et al.* (1987) discuss the degree of calcium regulation, and the relationship of external calcium level to shell thickness and growth. Shell accretion may lag behind rapid tissue growth in eutrophic habitats, producing thinner shelled individuals (McMahon, 1983).

III. ECOLOGY AND EVOLUTION

A. Diversity and Distribution

Although widespread in Asia, pleurocerids reach their greatest abundance in the rivers and streams of the southeastern United States (Table I). Most are fairly large snails that are quite common in rocky riffles or shoals in both headwaters and large rivers. However, many species have been lost to stream alteration by impoundments, and present-day diversity has decreased dramatically (see Section III.E). Females possess an egg laying sinus on the right side of the foot (Dazo, 1965).

TABLE I The Diversity of Freshwater Snail Families in North America^a

Subclass	Family	Number of genera	Number of species	Area of greatest diversity ^b
Prosobranchia	Ampullaridae	2	4	SE
	Bithyniidae ^c	1	1	NE
	Hydrobiidae	28	152	U
	Micromelaniidae	1	1	SE
	Neritinae	1	1	SE
	Pleuroceridae	7	156	SE
	Pomatiopsidae	1	6	SE, W
	Thiaridae ^c	2	3	S
	Valvatidae	1	11	U
	Viviparidae	5	29	E
Pulmonata	Acroloxidae	1	1	W, NE
	Ancylidae	4	13	U
	Lymnaeidae	9	58	N
	Physidae	4	43	U
	Planorbidae	11	47	U

^a Data compiled from Burch (1989) and Neves *et al.* (1998).

^b N, North; E, East; W, West; S, South and U, ubiquitous.

^c Introduced.

Shell anatomy is used to classify genera, although many species show considerable variation in shell characters. The shells of pleurocerids are solid and the aperture may bear a canal anteriorly. The operculum is corneous and paucispiral.

Viviparids are worldwide in distribution, and these large snails are fairly diverse (Table I) throughout the eastern states and Canadian provinces. *Campeloma*, *Lioplax*, and *Tulotoma* are endemic to North America. Although the first two genera are widespread, *Tulotoma* was once considered extinct and has only recently been rediscovered in the Coosa River in Alabama, where this filter feeding, brooding snail is common under rocks in shallow water shoals in large tributaries (Hershler *et al.*, 1990). *Viviparus* is quite common in rivers and lakes throughout eastern North America. Another large viviparid *Cipangopaludina chinensis* was introduced to the United States in the 1890's and has now spread throughout the United States, especially in hard-water lakes with sandy or muddy substrates (Jokinen, 1982).

Ampullarids are a tropical, mostly amphibious family with a mantle cavity provided both with a gill and a lung. The two genera present in Florida, *Pomacea* and *Marisa*, are quite large snails (50–60 mm). *Marisa* has also been introduced to rivers in central Texas.

The Neritinae are a marine, tropical group. A few species have invaded estuarine and freshwater habitats, for example *Neritina reclinata* in Florida, Georgia, Alabama, and Mississippi. The paucispiral, calcareous operculum has a pair of projections which lock the operculum against the teeth on the aperture, providing a stronger defense.

Of the 20 species of valvatids in the northern hemisphere, 11 are found in North America (Table I), mostly in lakes in northern states. Valvatids are egg-laying hermaphrodites, with a single, featherlike gill carried on the left side, and a pallial tentacle carried on the right side of the shell as the animal crawls. Valvatids have small (approximately 5 mm diameter) dextral shells, with a corneous, slightly concave and thin, multispiral operculum. The spire is only slightly elevated, and the shells are sometimes carinated.

Hydrobiids are extremely diverse and exist in freshwater, brackish, and marine habitats. They are small but have a thick shell which protects them from fish predation, and they dominate the gastropod assemblages of many northern lakes (Brown, 1997). There are 103 genera worldwide (Burch, 1989), and they are diverse in North America (Table I). In fact, hydrobiids may be the most diverse group of freshwater snails, as 58 new species in the genus *Pyrgulopsis* were recently described from small springs in the southwestern

United States (Hershler, 1998). Although these populations often reach high densities, many species are endemic to only a few springs, increasing chances of extinction. The genus *Fluminicola*, which is common in rivers in the northwestern United States, is also quite diverse (Hershler and Frest, 1996). The hydrobiids have small, dextral shells with a paucispiral operculum. Because of the similarity of their shells, the structure of the verge (penis) is used in classification.

The six North American pomatiopsids are similar in general anatomy to the hydrobiids. Pomatiopsids are, however, amphibious and are often found inhabiting stream banks several meters above the water's surface, while hydrobiids are truly aquatic (Burch, 1989). Pomatiopsid systematics are discussed by Davis (1979).

Thiarid females are parthenogenetic, brooding eggs in a pouch in the neck region, which opens on the right side. The similar-shelled pleurocerids, discussed above, are on the contrary dioecious and oviparous.

Ancylids have a worldwide distribution, and all possess a simple cone-shaped shell. In North America, they have reached moderate diversity (Table I). Ancylids have sinistral shells, with the apex inclined slightly to the right, and the gill (pseudobranch) and many of the internal organs opening on the left side of the body. Their streamlined shape allows them to colonize fast-flowing streams, where they are common on rocks or macrophytes, although some species are also common in lentic environments.

The family Acroloxidae occurs mainly in Eurasian lakes and ponds. Only one species of *Acroloxus* occurs in the United States, in Colorado and southeastern Canada. Since the apex in *Acroloxus* is tipped to the left, the aperture is considered to be dextral, unlike the ancylid limpets.

Lymnaeids are worldwide in distribution, and are the most diverse pulmonate group in the northern United States and Canada (Table I). Lymnaeids have broad triangular tentacles, and lay long, sausage-shaped egg masses. Lymnaeids have fairly uncomplicated, large teeth on their radula (Fig. 5), which are useful for cropping long strands of filamentous algae (Kesler *et al.*, 1986). One group of lymnaeids, found along the Pacific coast of North America, has limpet-shaped shells, but they are larger than ancylids.

Physids also have a worldwide distribution and are ubiquitous in North America (Table I); few aquatic environments lack physids, because of their ease of introduction. Their shells are small, sinistral, with raised spires. Their tentacles and foot are slender and they have fingerlike mantle extensions (except for the genus *Aplexa*) and lay soft, crescent-shaped egg masses. Their radular teeth are smaller and more complicated in shape than in the lymnaeids (Fig. 5), and they are

better at harvesting more tightly attached periphyton species like diatoms, or in feeding on detritus (Kesler *et al.*, 1986). Their rate of crawling is much more rapid than most gastropods, and this along with their early age at maturity and high fecundity explains why they are so wide-spread (Brown *et al.*, 1998).

Planorbids are widespread and fairly diverse snails (Table I), and range in size from minute (1 mm) to quite large (30 mm) in North America. They possess hemoglobin as a respiratory pigment, sometimes giving the tissue a red hue. Their egg cases are flat and circular, with harder membranes than those of the lymnaeids or physids. Planorbids are considered closely related to the ancylids (McMahon, 1983).

B. Reproduction and Life History

Freshwater snails are extremely interesting because of the variety of observed life-history patterns. For example, freshwater pulmonates are oviparous (egg-laying) hermaphrodites, and are usually annual and semelparous (i.e., they reproduce once and die). On the other hand, almost all prosobranchs are dioecious and are often iteroparous, with perennial life cycles. Prosobranchs can be oviparous or ovoviviparous (Russell-Hunter, 1978; Calow, 1978, 1983; Brown, 1983). Annual species have essentially a 1 year life cycle, whereas perennials often live and reproduce for 5 years or more.

Russell-Hunter (1978) and Calow (1978) have classified life histories for freshwater gastropods (Fig. 6). At one end are annual adults that reproduce in the spring

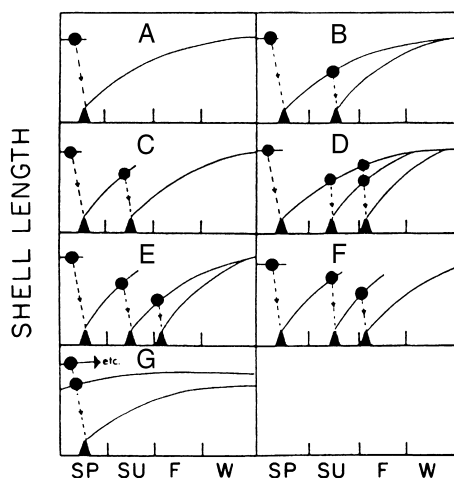


FIGURE 6 The variety of life cycles in freshwater snails. Curves represent the growth of individual cohorts (in millimeters of shell length), circles represent size at maturity while triangles represent appearance of egg cases in samples. Panel A represents annual semelparity, and B–F represent increasing numbers of cohorts per year, while panel G represents perennial iteroparity (from Calow, 1978). SP, spring; S, summer; F, fall and W, winter.

and die (e.g., there is complete replacement of generations). Most pulmonates belong to this group, including species from the genera *Lymnaea*, *Physella*, and *Aplexa* (the original studies are listed in Calow, 1978). In the second category (Fig. 6B), reproduction occurs in both spring and late summer with both cohorts surviving the winter, or (Fig. 6C) where there again is complete replacement of generations. In Figure 6D–F, there are three reproductive intervals, with varying degrees of replacement of generations. These would predominantly be populations in subtropical or tropical environments. Finally, there are populations that can truly be considered perennial and iteroparous (Fig. 6G); most are prosobranchs. For example, the pleurocerid genus *Elimia* has life cycles lasting from 6 to 11 years in Alabama streams, with several cohorts overlapping at any one time (Richardson *et al.*, 1988; Hury *et al.*, 1994). Adults reproduce in the spring and summer and are more common in areas of low current velocity, while juveniles are common in the fall in high flow areas (Hury *et al.*, 1994; Johnson and Brown, 1997).

Jokinen (1985) also found Russell-Hunter and Calow's life-cycle categories useful in describing life-cycle patterns in twelve species of gastropods inhabiting a small Connecticut lake. Four species, *Ammicola limosa*, *Helisoma anceps*, *Helisoma (Planorbella) companulatum* and *Laevapex fuscus*, had simple, annual patterns. Four species had at least two breeding seasons a year, with varying replacement of cohorts, including *Pseudosuccinea collumella*, *Planorbula armigera*, *Promenetus exacuous*, and *Gyraulus deflectus*. Three species, *Fossaria modicella*, *Gyraulus circumstriatus*, and *Physella ancillaria*, had continuous breeding throughout the field season. The prosobranch *Campeloma decisum* was the only species with a perennial reproductive pattern. Jokinen (1985) suggested that divergence in life history patterns between taxonomically similar species lessened competition, by allowing some species to specialize on detritus (common in the spring), and others periphyton (common in the summer).

Marine snails have enormous fecundity, but individual eggs are extremely small. Most marine snails are prosobranchs, and freshwater prosobranchs (their descendants) probably have relatively small eggs as a result. In fact, viviparids and thiarids may have evolved ovoviviparity (and in some cases the production of larger embryos) to cope with the much more unpredictable conditions in freshwaters (Calow, 1978, 1983). Similarly, the loss of the planktonic veliger, and shortening of the developmental period in oviparous freshwater snails has been attributed to the more variable physicochemical conditions (Calow, 1978).

Reproductive effort (percent of energy devoted to reproduction) is lower in iteroparous freshwater snails

than in semelparous ones (Browne and Russell-Hunter, 1978). For example, pulmonate families are semelparous with relatively high reproductive output (Brown, 1983). Pulmonates also reproduce at smaller sizes and earlier ages, produce more eggs, have larger clutch sizes, greater shell growth rates, shorter life cycles and smaller final shell sizes than viviparid prosobranchs.

The reduced fecundity but increased parental care found in viviparids (vs semelparous pulmonates) increases offspring survival. Life tables for *Viviparus georgianus* (Jokinen *et al.*, 1982) and for the pulmonate *Lymnaea elodes* (Brown *et al.*, 1988) indicate that survival to maturity is indeed much less than 1% in all of the pulmonate populations, but over 40% in the ovoviviparous prosobranch. Prosobranchs are also sexually dimorphic in life-history patterns. Female viviparids live longer (males usually survive for only one reproductive season) and reach larger sizes (Van Cleave and Lederer, 1932; Browne, 1978; Jokinen, 1982; Jokinen *et al.*, 1982. Pace and Szuch, 1985; Brown *et al.*, 1989).

Numerous studies have implicated periphyton productivity (Eisenberg, 1966, 1970; Burky, 1971; Hunter, 1975; Browne, 1978; Aldridge, 1982; Brown, 1985) in determining voltinism patterns, growth rates, fecundity, and gastropod secondary production (see review in Russell-Hunter, 1983). Other important factors include water hardness and temperature. For example, populations of *Elimia* in limestone-substrate streams in Alabama have greater annual production than populations in relatively impermeable slate or sandstone-substrate streams (Huyrn *et al.*, 1995), both because of the higher alkalinity and greater buffering of low temperatures in the winter by ground water. Similarly, populations of *Lymnaea stagnalis* in Canada often take several seasons to complete their life cycle (Boag and Pearlstone, 1979) while populations are annual in the warmer waters of Iowa (Brown, 1979).

Lymnaea peregra in wave-swept habitats in English lakes have *r*-selected life-history traits (e.g., early reproduction and high reproductive output) in comparison to populations in less-harsh habitats (Calow, 1981). However, other studies of life history variation in molluscs do not agree as well with the predictions of *r*- and *K*-theory (see discussion in Burky, 1983). Transplant studies, where individuals from separate populations are reared in a common environment, have usually indicated that environmental effects on life histories are much more important than genetic differences between populations. For example, populations of *Lymnaea elodes* reared in more productive ponds lay nine times as many eggs, have an annual versus a biennial reproductive cycle, and reach larger individual sizes (Brown, 1985).

Although genetic polymorphism has been studied using gel electrophoresis in terrestrial pulmonates and freshwater prosobranchs more than in aquatic pulmonates, freshwater snails still appear to have levels of genetic polymorphism intermediate to terrestrial and marine species (Brown and Richardson, 1988). Terrestrial snails inhabit patchily-distributed microclimates which increase chances for low population densities and self fertilization, resulting in little genetic polymorphism within populations. Freshwater snails decline to low densities because of seasonal bottlenecks and thus may also self. Marine environments are less seasonal, and many marine snails have planktonic larvae, facilitating gene flow and increasing polymorphism.

C. Ecological Interactions

1. Habitat and Food Selection, Effects on Producers

Slow moving, silty habitats are occupied by pulmonates or detritivorous prosobranchs such as viviparids, whereas fast current areas are dominated by limpets or prosobranch grazers like pleurocerids (Harman, 1972). There is also evidence for habitat selection on the species level. *Campeloma decisum* is positively rheotactic (moves upstream) and aggregates at any barrier (e.g., logs, riffle zones, etc., Bovbjerg, 1952). *Physella integra* and *Lymnaea emarginata* prefer cobble substrates with attached periphyton, while *Helisoma anceps* and *Campeloma rufum* prefer sand (Clampitt, 1973; Brown and Lodge, 1993). Most gastropods in northern Wisconsin lakes, however, prefer periphyton covered cobble over sand or macrophytes (Brown and Lodge, 1993). Cobble, since it offers greater surface area and is present year-round, develops a richer periphyton coating. Substrate selection may even occur on a finer level: gastropods from an English pond prefer periphyton from the macrophytes the snails were found on in the field (Lodge, 1986). Snails often move among habitats as well. Migrations occur to deeper water in the fall in lakes and back to the littoral zone in the spring (Cheatum, 1934; Clampitt, 1974; Boag, 1981). Pond pulmonates on the other hand burrow into the substrate with declining temperatures (Boerger, 1975).

Freshwater gastropods are herbivores or detritivores, but occasionally ingest carrion (Bovbjerg, 1968) or small invertebrates associated with periphyton (Cuker, 1983). Periphyton is easier to scrape, and contains higher concentrations of nitrogen and other limiting nutrients than macrophyte tissue (Russell-Hunter, 1978; Aldridge, 1983). For example, carbon to nitrogen (e.g., carbohydrate to protein) ratios are below 10.1:1, while macrophytes have ratios of 24.1:1 (McMahon *et al.*, 1974). Algal and diatom remains therefore dominate in the guts of snails (Calow, 1970;

TABLE II Feeding Preferences of Freshwater Snails

Feeding type	Family	References
Algivores (scrapers)	Ancylidae	Calow (1973a, b, 1975)
	Lymnaeidae	Bovbjerg (1968, 1975), Brown (1982), Calow (1970), Cuker (1983), Hunter (1980), Kairesalo and Koskimies (1987), Kesler <i>et al.</i> (1986), Lodge, (1986)
	Neritinae	Jacoby (1985)
	Pleuroceridae	Aldridge (1982, 1983), Dazo (1965), Goodrich, (1945)
Detritivores or bacterial feeders	Viviparidae	Duch (1976), Jokinen <i>et al.</i> , (1982)
	Physidae	Brown (1982), Kesler <i>et al.</i> , (1986), Townsend (1975)
	Planorbidae	Calow (1973b, 1974a, b)
Filter feeders	Viviparidae	Chamberlain (1958), Pace and Szuch, (1985), Reavell (1980)
	Bithyniidae	Tashiro (1982), Tashiro and Colman (1982), Brendelberger and Jurgens, (1993)
	Viviparidae	Brown <i>et al.</i> (1989)

1973a, 1975; Calow and Calow, 1975; Reavell, 1980; Kesler *et al.*, 1986; Lodge, 1986; Madsen, 1992). However, gastropods at high densities can exhaust periphyton and then consume macrophytes, suppressing macrophyte species richness (Sheldon, 1987).

Feeding preferences for the freshwater gastropod families are summarized in Table II. Lymnaeids are "microherbivores", scraping algae and diatoms from rocks or macrophytes, but grow more rapidly when animal tissue is in their diet (Bovbjerg, 1968). For example, although *Pseudosuccinea columella* (a lymnaeid) is an omnivore, it still consumes more algae than the sympatric *Physa vernalis* (Kesler *et al.*, 1986). The lymnaeid also possesses higher levels of cellulases, as well as a radula and jaws well adapted for cropping algae (Fig. 5), and a gizzard filled with sand that can macerate food. The physid, a detritivore, lacks these adaptations.

Both the limpet family Ancylidae and the prosobranch family Pleuroceridae are also considered to graze on periphyton (Table II). *Ancylus fluviatilis* selectively grazes diatoms, but the limpet has little effect on periphyton communities, due either to adaptations of algal and diatom species to grazing or to relatively low limpet abundances (Calow, 1973a, b). Aldridge (1983) concluded that pleurocerid grazers feed on periphyton rather than macrophyte tissue again because of higher levels of nitrogen.

The prosobranch *Bithynia tentaculata* both grazes on periphyton and uses its ctenidium to capture phytoplankton that is consolidated into a mucous string which loops from the mantle cavity to the mouth (Brendelberger and Jurgens, 1993). Indeed, filter feeding may be more efficient than scraping as increasing levels of phytoplankton shade out periphyton, explaining why this species has become so abundant in nutrient rich, eutrophic lakes in New York (Tashiro, 1982; Tashiro and Colman, 1982).

Viviparus georgianus is a micro-algivore (Duch, 1976; Jokinen *et al.*, 1982) or a detritivore (Pace and

Szuch, 1985). Most viviparids, however, are probably detritivores or utilize bacteria associated with detritus (Table II). As macrophytes decompose, nitrogen levels increase, again increasing their value as food resources. For example, *Viviparus* reaches extremely high densities (from 151 to 608 individuals m²) in wooded streams in Michigan (Pace and Szuch, 1985) and detritus-rich bayous in Louisiana (up to 1,700 individuals m², Brown *et al.*, 1989).

Both physids (Kesler *et al.*, 1986) and planorbids (Calow, 1973b, 1974a) prefer detritus (Table II). For example, although widely-spread species like *Physella gyrina* and *Helisoma trivolvis* did not prefer detritus over periphyton in laboratory experiments, another physid, *Aplexa elongata*, which is much more common in wooded ponds with a rich detritus food base, preferred detritus (Brown, 1982).

Originally, snail algivores were considered indiscriminant grazers, taking all components of the periphyton (Hunter, 1980; Hunter and Russell-Hunter, 1983). However, limpets and planorbids are selective (Calow, 1973a, b), and *Lymnaea peregra* grazes selectively on filamentous green algae (Lodge, 1985). *Planorbis vortex* ingests diatoms in greater quantities than found in the periphyton, but is still predominantly a detritivore.

Gastropods have the ability to locate macrophytes through distant chemoreception (Croll, 1983). For example, *Lymnaea peregra* is positively attracted to *Ceratophyllum demersum* because of dissolved organic materials excreted by the macrophyte (Bronmark, 1985b). Similarly, *Potamopyrgus jenkinsi* orients toward both plant and animal extracts (Haynes and Taylor, 1984), while *Biomphalaria glabrata* either orients toward or away from specific macrophytes (Bousefield, 1979).

Almost all experimental manipulations have indicated snail grazers can decrease periphyton standing crops (Table III, see also review in Bronmark, 1989). For example, *Physella* at high densities reduces algal

TABLE III The Effects of Experimental Manipulations of Gastropods on Periphyton Biomass, Production and Assemblage Structure

Group	Genus	Decreased algal biomass?	Increased algal production?	Favored adnate species?	Studies
Prosobranchs	<i>Elimia</i> or <i>Juga</i> (N = 11)	73%	17%	100%	Mulholland <i>et al.</i> (1983), Steinman <i>et al.</i> (1987), Lamberti <i>et al.</i> (1987), Marks and Lowe (1989), McCormick and Stevenson (1989), Hill and Harvey (1990), Mulholland <i>et al.</i> (1991), Tuchman and Stevenson (1991), Hill <i>et al.</i> (1992), Rosemond <i>et al.</i> (1993)
	<i>Theodoxus</i> (N = 1)	Y	NO	Y	Jacoby (1985)
	<i>Ammicola</i> (N = 1)	Y	N.M.	Y	Kesler (1981)
Pulmonates	<i>Physella</i> (N = 3)	100%	N.M.	100%	Doremus and Harman (1977), Lowe and Hunter (1988), Swamikannu and Hoagland (1989)
	<i>Promenetus</i> (N = 1)	NO	NO	NO	Doremus and Harman (1977)
	<i>Lymnaea</i> , <i>Physella</i> , <i>Helisoma</i>	Y	Y	Y	Hunter (1980)

Percentages refer to the number of studies noting an affect. For single studies: Y, effect; NO, no effect, N.M., not measured.

biomass by 97%, and richness by 66% (Lowe and Hunter, 1988). In some cases, snails also increase algal production, perhaps by decreasing total biomass and lowering algal competition for light or nutrients, removing senescent cells, or increasing rates of nutrient cycling. Pulmonate gastropods can also alter the quality (e.g., nitrogen-to-carbon ratios and chlorophyll a levels) of periphyton (Hunter, 1980), as can prosobranchs in streams (Steinman *et al.*, 1987). Although low levels of grazing may stimulate production, higher snail densities decrease both biomass and production (McCormick and Stevenson, 1989; Swamikannu and Hoagland, 1989). Grazing may not, however, have as much of an impact on shaded streams, where light may be the primary limiting factor (Hill and Harvey, 1990). Even in unshaded streams there may be little overall effect of grazers, because the loss of the algal over-story to grazing is compensated for by the competitive release and increased growth of adnate algae (Hill and Harvey, 1990).

Snail grazers selectively remove larger filamentous green algae, and leave smaller, adnate species behind (Table III). Under slight gastropod grazing pressure, periphyton assemblages are dominated by filamentous green algae, but more intensely grazed assemblages are dominated by more tightly adhering or toxic species such as cyanobacteria. Snail grazers may, in fact, indirectly facilitate macrophytes, if periphyton coverings shade and limit macrophyte growth, and snails prefer periphyton. For example, the growth of *Ceratophyllum demersum* increased when gastropod grazers were present (Bronmark, 1985b), although increased growth also occurred when plants were exposed only to snail-

conditioned water, indicating increased nutrient recycling was a cause (Underwood, 1991). Similarly, when sunfish depress snail abundances and increase periphyton abundance in fish enclosures, they may indirectly depress macrophytes (Martin *et al.*, 1992). The molluscivorous tench (a fish) can have similar cascading effects on European gastropods, periphyton, and macrophytes (Fig. 7). Thus, interactions between gastropod predators, snails, periphyton, and macrophytes may be very complex in natural systems.

2. Factors Regulating Population Size

One of the first demonstrations of population regulation under field conditions was with *Lymnaea elodes* (Eisenberg, 1966, 1970). When the density of adult snails in pens in a small pond was increased, adult fecundity declined, as did juvenile survival. With addition of a high quality resource, spinach, an increase in the number of eggs per mass occurred. Evidently, the availability of micronutrients in periphyton was the crucial variable (Eisenberg, 1970). Brown (1985) provided additional evidence by transferring juvenile *Lymnaea elodes* among a series of ponds differing in periphyton productivity. There was an exponential increase in juvenile growth rates with increasing pond productivity, and snails in the most productive pond laid nine times as many eggs as snails in the two less productive ponds. A number of field studies also provide indirect evidence for the importance of resource abundance: populations in more eutrophic habitats have more generations a year, more rapid shell growth, and lay more eggs (Burky, 1971; Hunter, 1975; McMahan, 1975; Eversole, 1978). Highly eutrophic sites may however

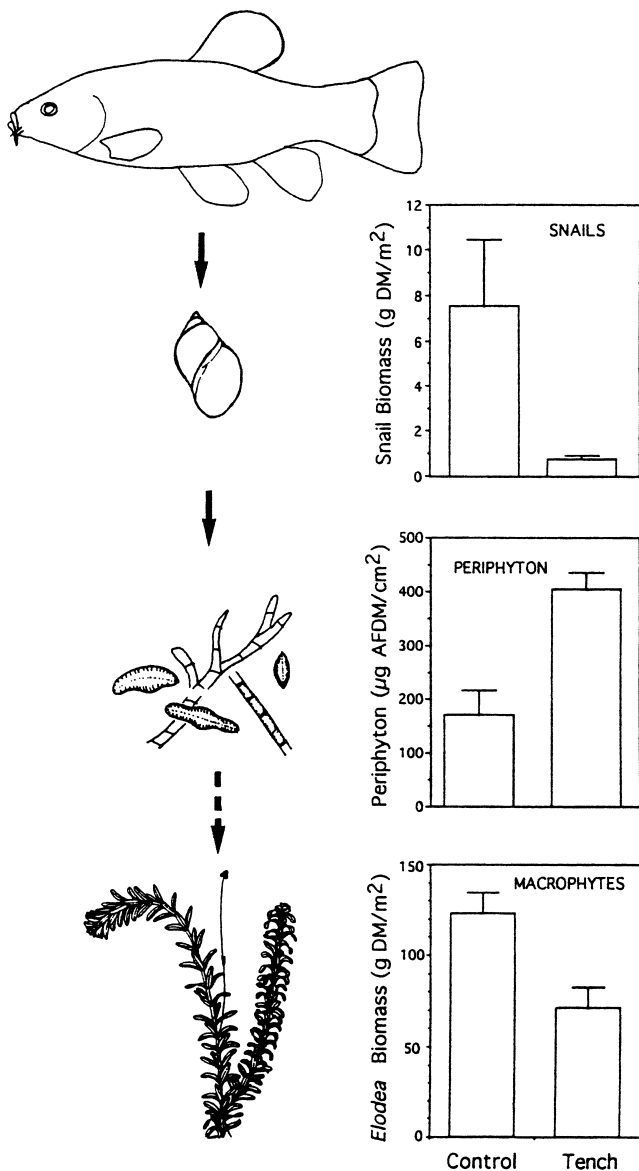


FIGURE 7 Cascading (also called top-down) effects of a molluscivorous fish (the tench) on gastropods, periphyton and macrophytes, based on a field manipulation (from Bronmark and Vermaat, 1998). Note how snail numbers are depressed by fish predation (top), and reduced gastropod grazing results in periphyton increases, and macrophytes are shaded by increasing periphyton cover, and decrease.

be detrimental to gastropods. For example, gastropod diversity declined over a fifty year period as Lake Oneida, New York, became increasingly eutrophic (Harman and Forney, 1970). In lotic systems, manipulation of periphyton resources and the abundances of pleurocerid grazers have indicated both that food resources can control snail density and size distributions, and that the snails can, in turn, control their food resources (Hill *et al.*, 1992; Rosemond *et al.*, 1993).

Although less studied than the role of periphyton, the parasitic larvae of trematode worms may also impact snail population dynamics and evolution (Holmes, 1983). The adult worm produces eggs that are expelled in the feces of the final host (a vertebrate) and hatch into an infectious larval stage called a miracidium. Depending on the parasite group, the miracidium either penetrates the epithelium of the snail or is consumed as an egg and hatches within the snail. Once inside the snail host, miracidia asexually produce several stages (redia and sporocysts) which eventually produce thousands of cercaria that infect the final host or another intermediate host. Infections either accelerate or decelerate snail growth (Brown, 1978; Anderson and May, 1979; Holmes, 1983, see discussion in Minchella *et al.*, 1985). Immediately after infection or exposure, snail egg production rates increase dramatically (Minchella and Loverde, 1981), evidently reducing the eventual costs to snail fitness. As parasites consume the ovotestis and hepatopancreas, however, both growth and egg production of "patent" snails (those infections in the final stage where cercaria are emerging from snails) drop below that of uninfected snails (Minchella *et al.*, 1985).

The role of trematodes in controlling snail populations is unclear, as prevalence (percentage of population infected) varies considerably (Brown, 1978; Holmes, 1983). For example, prevalence in *Lymnaea elodes* in Indiana ponds varied from as low as 4% to as high as 49% (Brown *et al.*, 1988). Prevalences were higher in less productive ponds, evidently because food limitation caused longer snail life cycles that increased chances for snails to be located by miracidia. Life-table models predicted that the number of offspring produced per adult in the next generation declined by 14 to 21% in parasitized populations of *L. elodes*.

Assemblages of trematode larval species within a snail host can themselves be considered communities, with relative abundances and types of biotic interactions dependent on the snail species, the type of final host, and the microhabitat the snail occupies. For example, multispecies infections are common and interspecific competition rare in *Physella gyrina*, evidently because it is quite mobile and reproduces continually throughout the field season, traits which increase chance of infection (Snyder and Esch, 1993). *Helisoma anceps* is more sedentary and has a simple annual life-history pattern; its parasitic trematode community is characterized by fewer multiple infections and a competitive dominance hierarchy among parasites. Regarding microhabitats, trematode larvae that infect snails when eggs are consumed (and that have frogs as final hosts) are more common in snails collected from shallow habitats in ponds (Sapp and Esch, 1994); in contrast, while larvae that infect snails as miracidia (and

TABLE IV Comparison of Average Standing Stocks, Productivity, and Turn-over Times for Populations of Pulmonate and Prosobranch Snails Reported in Russell-Hunter and Buckley (1983)

Subclass	Mean biomass ^a + s.e.	Mean production ^b + s.e.	Mean turnover time ^c + s.e.
Pulmonata	0.98 ± 0.50 (6)	5.71 ± 2.44 (10)	98.0 ± 9.46 (10)
Prosobranchia	4.64 ± 1.80 (4)	3.56 ± 0.51 (5)	385.3 ± 33.5 (4)

(N) Number of species averaged.

^a g C/m².

^b mg C/m² per day.

^c days.

have waterfowl as final hosts) occur in all microhabitats, but only when the final hosts are common.

Trematode parasites and their snail hosts are also extremely interesting from a co-evolutionary viewpoint (Holmes, 1983; Minchella *et al.*, 1985). Because invertebrates cannot easily acquire resistance to parasites, frequency-dependent selection may operate to ensure the fitness of any genotype less vulnerable to a particular trematode (Holmes, 1983). Parasites may also cause a shift in investment of resources from costly reproduction to growth and maintenance and, thus, even increase survivorship of infected snails (see also Baudoin, 1975; Minchella *et al.*, 1985). Because trematode larvae evolve surface antigens that mimic those of the snail host, application of one evolutionary model, called the "red queen" hypothesis, suggests that gastropods are constantly evolving new antigen phenotypes merely to stay ahead of their trematode parasites. For example, the New Zealand prosobranch *Potamopyrgus* has both sexual morphs (able to produce genetically more variable offspring through recombination) and parthenogenetic morphs. The frequency of sexual reproduction is positively correlated with trematode prevalence, as one would expect if sexual morphs have an advantage (Lively, 1987). Sexual morphs are also more common in shallow water, where waterfowl (the final hosts) occur (Lively and Jokela, 1995). Infected snails are also more likely to forage during the day than uninfected snails or gravid females, suggesting parasites may modify snail behavior so they are more likely to be consumed by waterfowl, to complete the life cycle (Levri and Lively, 1996). Experimental studies in New Zealand have suggested trematode populations are locally adapted to better infect their own host populations than snails from different lakes (Lively, 1989). Gene flow has not swamped such local adaptation, even though rates of gene flow are greater among parasite populations than among their snail hosts (Dybdhal and Lively, 1996). However, sexual reproduction may not be favored in all snail-trematode systems. In *Campeloma*, certain trematode metacercaria actually

feed on sperm, and parthenogenetic morphs thus have an advantage (Johnson, 1992).

3. Production Ecology

Average standing crop biomass, productivity, and turnover times (these terms are explained in the glossary) differ between prosobranchs and pulmonates (Table IV, summarized from Russell-Hunter and Buckley, 1983). Standing crops are greater on the average for prosobranchs than for pulmonates, although prosobranch populations studied to date have not included genera with smaller individuals, such as *Ammicola* and *Valvata*.

Even if pulmonates have lower standing stocks, their rapid growth and short life cycles still result in higher average production rates and shorter turnover times (Table IV). For example, two pleurocerid grazers in an Alabama stream, *Elimia cahawbensis* and *E. clara*, have considerable biomasses of 2–5 g ash-free dry mass (=AFDM) per square meter, but slow growth rates and long life cycles result in relatively low rates of secondary production (0.5–1.5 g AFDM/m²). The combination of high biomass and low production results in a low production to biomass ratio of 0.3 (Richardson *et al.*, 1988). Prosobranch detritivores may, however, have higher production rates. *Viviparus subpurpureus* and *Campeloma decisum*, with high densities and short life cycles in Louisiana bayous, have high standing crop biomasses (10–20 g AFDM/m²) and production rates (20–40 g AFDM/m² per year) among the highest known for freshwater molluscs (Richardson and Brown, 1989).

4. Ecological Determinants of Distribution

Water hardness and pH are often considered major factors determining the distributions of freshwater snails (Boycott, 1936; Macan, 1950; Russell-Hunter, 1978; Okland, 1983; Pip, 1986). For example, in the acid-rain affected lakes of the Adirondack mountains of New York, Jokinen (1991) found that snail diversity declined with declining pH and increasing altitude.

However, in lake districts with adequate calcium (above about 5 mg/L CaCO₃), or in the normal (nonacidified) range of pH, relationships between physico-chemical parameters and gastropod diversity are less clear (Lodge *et al.*, 1987; Jokinen, 1987). For example, species in New York lakes overlap broadly in the ranges of physico-chemical variables in which they occur (Harman and Berg, 1971). Physico-chemical parameters, therefore, set the limits for gastropod distributions, but are not as important in explaining the relative abundance patterns and densities of gastropods in most hard-water, circum-neutral lakes.

On a biogeographic scale, a factor determining gastropod distributions is dispersal ability. Studies have indicated diversity increases with the area of lakes and ponds (Lassen, 1975; Browne, 1981; Bronmark, 1985a; Jokinen, 1987). Since immigration rates generally increase and extinction rates decrease with increasing habitat size, larger habitats, all else being equal, usually support more species (MacArthur and Wilson, 1967). Jokinen (1987), following the ideas of Diamond (1975), found that snail species were not distributed randomly with increasing snail diversity. Five snails were "high-S" species (e.g., those that occurred only at the most diverse sites) including *Valvata tricarinata*, *Gyraulus deflectus*, *Laevapex fuscus*, and two species of *Lyogyrus*. Most gastropods were widely distributed across sites ("C-D" tramps in Diamond's terminology). The species with the greatest dispersal ability (called "super tramps" by Diamond) were found only at low diversity sites; these included the lymnaeid *Pseudosuccinea collumella* and the limpet *Ferrissia fragilis*.

After dispersal, successful colonization depends on the presence of suitable substrates. For example, a significant relationship exists between the number of gastropod species and the number of substrates in lakes and streams in New York, USA (Harman, 1972). In fact, substrate preferences determined in the laboratory are good predictors of the types of ponds where the snails are common (e.g., algivores in open ponds, detritivores in wooded ponds; Brown, 1982). Gastropod diversity is also positively related to macrophyte biomass, probably because macrophytes increase surface area for periphyton colonization (Brown and Lodge, 1993).

Disturbance may also determine the assemblage of snails. In temporary ponds, diversity is lowered by frequent drying; and in habitats that go hypoxic, diebacks of macrophyte and gastropod populations will also occur (Lodge and Kelly, 1985; Lodge *et al.*, 1987). Disturbance may also limit some species from areas such as wave-swept shores, littoral zones of reservoirs, etc. Similarly, in streams, current velocity may affect distribution and growth. Adult *Elimia* avoid high-flow areas, perhaps because increased flow makes movement

more difficult and lowers grazing rates or increases metabolic rate, thus lowering adult size (Johnson and Brown, 1997). Juveniles, because they are smaller and can exploit the boundary layer, are actually more common in fast-flowing areas.

In large lakes, biotic interactions such as interspecific competition or predation, are important in determining gastropod diversity and abundance (Lodge *et al.*, 1987). In regards to competition, some evidence suggests it is rare in freshwater snails. For example, pulmonate pond snails in the midwestern USA overlap little on food and habitat dimensions of the niche, although some species do compete (Brown, 1982). Other studies also indicate differences in resource utilization. For example, the European ancyloid *Ancylus fluviatilis* prefers diatoms and is found on the top of cobble where periphyton is abundant; whereas the co-occurring planorbid *Planorbis contortus* is a detritivore and occurs more often under stones, where detritus accumulates (Calow, 1973a, b, 1974a, b). Similarly, *Pseudosuccinea columella* and *Physa vernalis* possess differences in their gut and radulae allowing coexistence in New England ponds (Kesler *et al.*, 1986). Furthermore, niche partitioning may also be facilitated by differences among snails in enzymatic activity (Calow and Calow, 1975; Brendelberger, 1997) or radular morphology (Barnese *et al.*, 1990).

However, there is some indirect evidence for competition. First, there are often fewer coexisting congeners in field samples than would be expected, based on mathematical simulations (Dillon, 1981, 1987). Second, competition has been inferred from changes in relative abundance of gastropod species through time, that is, by apparent competitive exclusion (Harman, 1968). Third, niche overlap can, in fact, be higher in more diverse snail assemblages found in large lakes. For example, the abundances of gastropod species are often positively associated with high-diversity macrophyte beds in lakes, and experiments show most species have similar preferences for macrophytes (Brown, 1997). Finally, pulmonates are common in ponds or in vegetated areas of lakes, while prosobranchs are rare in ponds and common in lakes and rivers. One explanation could be competitive exclusion of pulmonates from lakes by prosobranchs, or exclusion of prosobranchs from ponds by the same mechanism. However, additional explanations include greater vulnerability of prosobranchs to hypoxic conditions in ponds, poorer dispersal abilities of prosobranchs, or the fact that thin-shelled pulmonates are more vulnerable to shell-crushing fish common in lakes or rivers (Brown *et al.*, 1998).

Indeed, Lodge *et al.* (1987) argue that predators determine the composition of gastropod assemblages in lakes. Indirect evidence includes the fact that gastropods

have a number of anti-predator adaptations. These include thick shells to protect against shell-crushing predators (Vermeij and Covich, 1978; Stein *et al.*, 1984; Brown and DeVries, 1985; Saffran and Barton, 1993; Brown, 1998), as well as escape behaviors such as shaking the shell or crawling above the water to protect against shell-invading invertebrate predators (Townsend and McCarthy, 1980; Bronmark and Malmqvist, 1986; Brown and Strouse, 1988; Alexander and Covich, 1991 a, b; Covich *et al.*, 1994). Molluscivores are common in lakes and rivers. For example, the pumpkinseed sunfish, *Lepomis gibbosus*, and the redear or shell-cracker sunfish, *Lepomis microlophus*, specialize on gastropod prey and have pharyngeal teeth adapted to crush shells. Crayfish will select snails instead of grazing on macrophytes if given a choice (Covich, 1977), using their mandibles to chip shells back from the aperture and selecting species with thinner shells (Saffran and Barton, 1993; Brown, 1998).

Although Osenberg (1989) argued that lentic snail assemblages are limited by food resources, most experimental evidence supports a strong role for predators in determining snail diversity and abundance (Table V). For example, the central mud minnow can significantly lower the density of relatively thin-shelled snails in permanent ponds. When fish densities were manipulated in pens, the number of eggs and juveniles of *Lymnaea*

elodes was significantly less in the presence of fish. The small, gape-limited fish feed on eggs and juveniles and may restrict *Lymnaea elodes* from permanent habitats such as large marshes or lakes. Pumpkinseed sunfish also strongly prefer large, weak-shelled gastropod species in laboratory experiments, and thin-shelled species also decline dramatically in pumpkinseed enclosures in lakes (see references in Table V). Thus, most thin-shelled pulmonates should occur in lakes only in macrophyte beds, where they have a refuge from visual predators; and sandy areas should be dominated by thicker shelled pulmonates like *Helisoma* or by prosobranchs. Indeed, gastropod distributions among habitats within Indiana and Wisconsin lakes do follow these patterns (Lodge *et al.*, 1987; Brown and Lodge, 1993; Lodge *et al.*, 1998). In fact, fish predators may indirectly benefit poorer gastropod competitors by preferentially removing dominant species. Lake trout, for example, preferentially consume larger lymnaeids, releasing valvatids from competition in arctic lakes (Hershey, 1990; Merrick *et al.*, 1991). However, experimental manipulations suggest such indirect effects do not extend through four trophic levels. Piscivores (top predators feeding on fish) in Swedish lakes cannot depress predators of snails to the extent that interactions cascade down the food web to facilitate snails which negatively impact periphyton (Bronmark and Weisner, 1996).

TABLE V Summary of Experimental Field Manipulations Testing the Role of Snail Predators in Controlling Their Prey

Study	Prey	Predator	Conclusions
Brown and Devries 1985	<i>Lymnaea elodes</i>	mud minnows	decreased abundance of eggs and juveniles of thin-shelled <i>L. elodes</i>
Sheldon 1987	assemblage	sunfish	removal of fish increased snails which decreased macrophytes through herbivory
Kesler and Munns 1989	assemblage	belastomatid bugs	decreased snail abundances in New England pond
Osenberg 1989	assemblage	littoral sunfish	fish controlled only rare, large snail spp., competition between snails considered more important
Hershey (1990), Merrick <i>et al.</i> (1991)	assemblage	lake trout	trout removed better competitor (<i>L. elodes</i>), which favored poorer competitor, <i>Valvata</i>
Martin <i>et al.</i> 1992	assemblage	<i>L. microlophus</i> <i>L. macrochiras</i>	fish decreased snails 10-fold, increased periphyton biomass 2-fold, decreased algal cell size, decreased macrophytes.
Bronmark <i>et al.</i> 1992	assemblage	pumpkinseed (<i>L. gibbosus</i>)	fish decreased snails, increased periphyton, favored adnate algae
Bronmark 1994	assemblage	Tench	fish decreased snails, increased periphyton, decreased macrophytes
Lodge <i>et al.</i> 1994	assemblage	<i>O. rusticus</i>	crayfish decreased snails and macrophytes, had no effect on periphyton
Daldorph and Thomas 1995	assemblage	sticklebacks	fish decreased thin-shelled snail spp., increased periphyton
Bronmark and Weisner 1996	assemblage	piscivores & molluscivores	molluscivores did decrease snails, but piscivores did not control molluscivores and increase snails indirectly

Assemblage refers to a natural community of gastropods.

Invertebrate, shell-invading predators may also limit snail populations or cause shifts in gastropod relative abundances. Although some leeches, such as *Nepheleopsis obscura*, have fairly low feeding rates (Brown and Strouse, 1988), crayfish can consume up to or over a hundred snails per night. The crayfish *Orconectes rusticus* significantly reduced snail abundances in enclosure experiments in Wisconsin lakes (Table V), and an interlake survey indicated that snail abundances were negatively correlated with crayfish catches. Crayfish also affect gastropod habitat selection: even though cobble habitat is preferred by many snails (see earlier discussion), it also provides refugia from fish predators for crayfish. Crayfish predation overrides the effects of rich food resources (Weber and Lodge, 1990).

Crayfish are also quite selective molluscivores. They prefer thinner-shelled gastropods (Saffran and Barton, 1993; Brown, 1998), and often prefer juvenile snails which have shorter handling times and higher profitability unless these more vulnerable prey are protected by macrophytes (Nystrom and Perez, 1998). Crayfish predators also shift size distributions of *Physella virgata* upwards in Oklahoma streams. This may be due both to size-selective predation and to the diversion of energy of the snail from reproduction to growth in order to reach a size-based refuge from predation (Crowl, 1990; Crowl and Covich, 1990). Interestingly, only snails in vulnerable size classes respond by crawling out of the water after predation by crayfish has occurred on conspecifics (Alexander and Covich, 1991b). Other invertebrate predators may also be important. For example, belostomatid bugs can eat as many as five snails per bug per day in the laboratory (Kesler and Munns, 1989).

Fish predators may alter snail foraging behavior as well. In experiments, *Physella* selects refugia in the presence of sunfish predators, only leaving when sufficiently starved (Turner, 1997). This behavioral interaction may provide an additional explanation for why periphyton biomass increases when fish predators are present. For example, use of open habitats by snails decreases with increasing predation risk from sunfish (Fig. 8), with the result that periphyton biomass also increases (Turner, 1997). Interestingly, such indirect facilitation of periphyton does not occur upon experimental addition of crayfish to enclosures, probably because crayfish are also omnivorous and graze on periphyton (Lodge *et al.*, 1994).

5. Suggestions for Further Work

Studies of the production ecology of smaller prosobranchs, as well as snail populations in other areas besides the northeastern United States are still needed. Questions still exist on subjects such as:

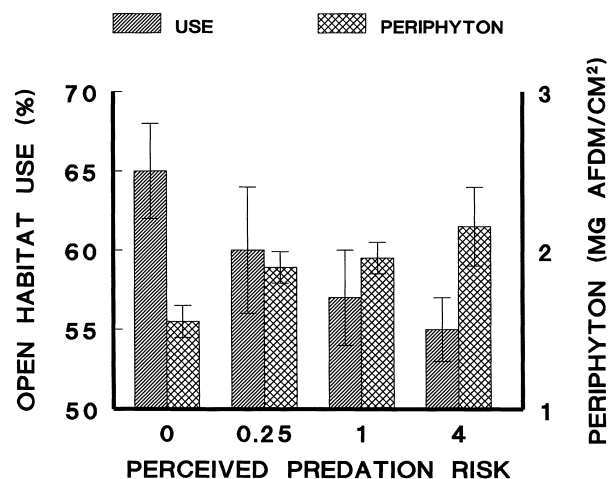


FIGURE 8 Indirect effect of mortality from fish predation on snail grazing rates. As more crushed snails were added to experimental pools (predation risk perceived by snails, x-axis), snails used refuges more, resulting in reduced use of open areas (left y-axis). Note how periphyton biomass (ashfree dry mass or AFDM, right y-axis) increased in open area as a result of reduced snail grazing (after Turner, 1997).

1. How pulmonates are physiologically adapted to relatively ephemeral or hypoxic aquatic habitats, including studies of differences in metabolic pathways and nitrogen excretion (McMahon, 1983).
2. The relative roles of the physiological and ecological constraints to shell versus tissue growth, given the remarkable intraspecific variation in shell structure and composition in freshwater gastropods.
3. Physiological bases of feeding preferences (such as relative cellulase activities, etc.).
4. Micro-preferences (e.g., preferences for certain algae or diatom species), for example, whether detritivores are consuming leaves or more nutritious bacteria or fungi.
5. The nutritional quality or toxicity of different food types and their role in preferences by gastropods.

Further research on abiotic and biotic factors influencing snail assemblages is also necessary. Abiotic factors such as pond drying, anoxia, floods, or macrophyte die-offs could explain much about gastropod population dynamics or species composition. Further work is also necessary to determine whether the allopatric distributions of pulmonates and prosobranchs are due to competition (see discussion in Brown *et al.*, 1998). Further work is needed as well on the relative role of invertebrate predators like leeches, belostomatid bugs, and scyomyzid fly larvae (Eckblad, 1973) in structuring snail assemblages.

D. Evolutionary Relationships

Marine prosobranchs are ancestral to freshwater prosobranchs and terrestrial and freshwater pulmonates. Freshwater prosobranchs adapted to the dilute osmotic conditions of estuaries and then rivers, and most modern families are widespread because their adaptive radiations predated continental breakups and drift. Davis (1979, 1982) and Clarke (1981) pointed out that prosobranch dispersal is limited in most cases to slow movement of adults along streams and rivers. Such populations are more likely to become isolated, promoting chances of speciation and adaptive radiation. Examples include the dramatic adaptive radiation of hydrobiids (Davis, 1982) and pleurocerids in lotic habitats (Burch, 1989; Lydeard *et al.*, 1997).

In contrast, pulmonates, due to their greater rates of passive dispersal as spat on birds and insects, have more widespread distributions. For example, they are widespread in the northern and northeastern states, as well as in Canada (Harman and Berg, 1971; Clarke, 1981). Immigration rates to ponds average 0.8 and can be as high as 9 species per year (Lassen, 1975; Davis, 1982). Pulmonates also predominate in shallow, more ephemeral habitats less than 100 km² in area and with durations less than 10³ years. Populations probably do not exist long enough in such habitats for speciation to occur, explaining why pulmonates are less speciose than prosobranchs (Russell-Hunter, 1983; Clarke, 1981; Davis, 1982).

Pulmonates apparently evolved from intertidal prosobranchs that relied less and less on aquatic respiration (Morton, 1955; McMahan, 1983). Modern estuarine pulmonates like *Melampus* may resemble these ancestral species. The intermediate, terrestrial pulmonates lost the ctenidium, and gave rise both to modern terrestrial pulmonates (order Stylommatophora) and the aquatic pulmonates (order Basommatophora). Figure 9 illustrates a hypothetical phylogeny of aquatic pulmonates based on progressive re-adaptation to aquatic habitats (see discussion in McMahan, 1983). Lymnaeids are in some cases still amphibious (e.g., occurring in temporary wetlands), while physids are intermediate in their adaptation to aquatic habitats (some species come to the surface to breathe, while others have filled the lung with water and can be found in deeper lakes). Ancylids and planorbids have secondarily acquired more aquatic specializations such as the evolution of secondary gills, and in the planorbids, hemoglobin.

Several phylogenetic trees for freshwater snails have been published recently, using both classical morphological and recently developed molecular methods. Jung (1992) used the more traditional characters of shell and

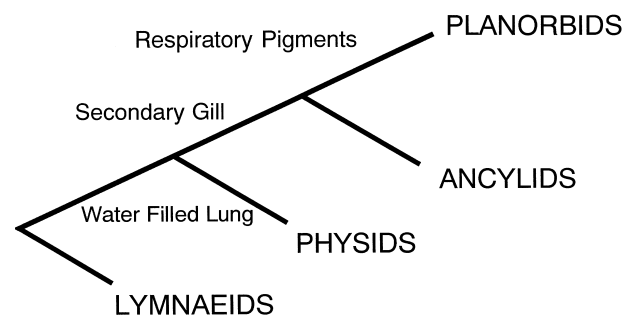


FIGURE 9 Hypothetical phylogeny for freshwater pulmonates assuming increased adaptation through time to secondarily-invaded aquatic habitats. The argument is that air-breathing lymnaeids are limited to shallow water, while physids, which in some cases can fill their lung with water and use it as a gill, are found in deeper water, and ancylids and planorbids are the most specialized for an aquatic life style, with secondarily derived epithelial gills and in the planorbids, hemoglobin.

soft anatomy to propose a cladogram (Fig. 10) for certain species of planorbids, using 65 characters. He pointed out that systematic studies should not rely on preserved specimens, since fixation alters soft anatomy. In his phylogeny, *Biomphalaria* is considered more ancestral, and *Planorbella trivolvis* and *Helisoma anceps* the most derived species.

Remigio and Blair (1997) published a phylogeny for certain lymnaeid species, using populations from both North America and Europe (Fig. 11). They considered molecular methods, such as sequencing ribosomal DNA in mitochondria, superior techniques in comparison to other characters such as shell morphology, which often converge among genera. For example, based on molecular information, they considered karyotypes with 18 chromosomes to be ancestral, and 16 chromosomes to be a derived character, unlike

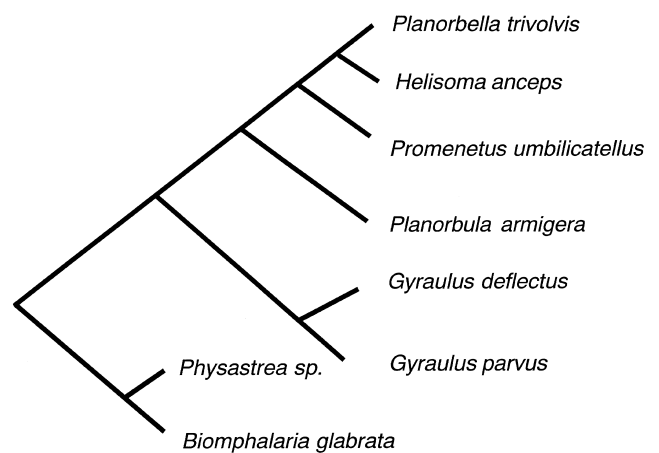


FIGURE 10 Simplified cladogram for several planorbid species studied by Jung (1992), based on shell and soft anatomy.

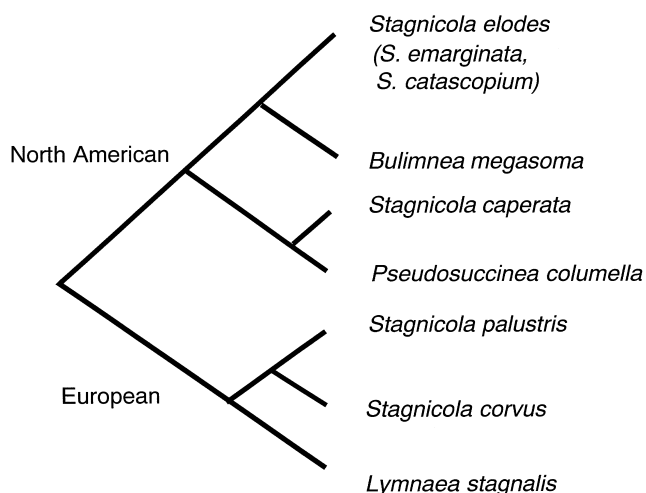


FIGURE 11 Cladogram for a subgroup of the lymnaeid species found in both North America and Europe, based on molecular data. Simplified from Remigio and Blair (1997).

earlier studies. European and North American stagnicolids (*S. elodes* and *S. palustris*) were not considered each other's closest relatives, contrary to interpretations based on morphology. *Stagnicola catascopium*, *S. emarginata*, and *S. elodes*, based on genetic divergence, could actually be conspecific taxa. On the other hand, two populations of *Lymnaea stagnalis* (one in Germany and the other in Italy) were genetically quite divergent, indicating isolation by the geographic barrier of the Alps. The authors propose that lymnaeids evolved in the late Jurassic to early Cretaceous on the common continent Laurasia, and were separated into distinct Palearctic and Nearctic groups at the start of the Cenozoic (65 million years ago) when ancestral species still had 18 chromosomes. The genus *Stagnicola* was probably extant at that time, explaining why North American and European species are so divergent.

Lydeard *et al.* (1997) used mitochondrial rDNA sequences to study the evolutionary relationships of representative prosobranch snails in the Mobile River Basin in the southeastern United States (Fig. 12). This basin may have once had the most diverse gastropod fauna in the world, with 118 species and nine families. Pleurocerids make up almost two thirds of the surviving fauna. Because of impoundments, the genus *Gyrotoma*, once found in shallow riffles in the Coosa River, has gone extinct, along with 14 species of *Elimia*, and 11 species of *Leptoxis*. Lydeard's phylogeny considers 14 prosobranch species (with *Melanopsis* as an out group) and suggests *Elimia* and *Pleurocera* are monophyletic genera, but that *Leptoxis* is paraphyletic. The remaining *Elimia* species in the Mobile Basin are genetically fairly similar, while the remaining three species of

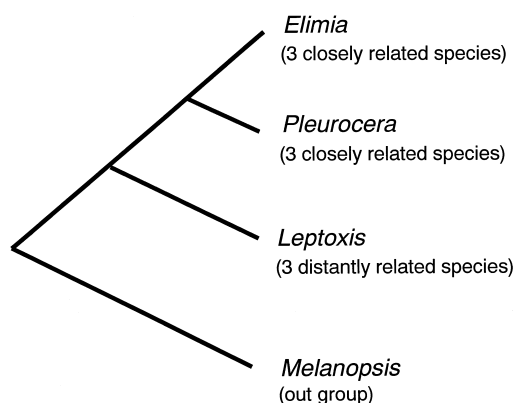


FIGURE 12 Cladogram for a subgroup of species in several prosobranch genera in the Mobile River Basin, based on molecular data. The greater divergence of leptoxid species suggests a polyphyletic origin for this genus. Simplified from Lydeard *et al.* (1997).

Leptoxis are quite divergent in their mitochondrial 16S rDNA sequence.

Further studies of genetic relationships among pleurocerids found in the Mobile River Basin suggest that earlier species descriptions, relying solely on shell morphology, have overestimated the true diversity of the system. For example, Lydeard *et al.* (1998), again looking at 16S rDNA sequences, considered *Elimia hydei* basal to all other elimiads, and *Elimia crenatella*, *E. showalteri*, *E. fascians*, and *E. caelatura* to be true species. The low genetic divergence within another clade led them to question the status of six species: *Elimia carinocostata*, *E. gerhardtii*, *E. haysiana*, *E. alabamiensis*, *E. olivula*, and *E. cylindracea*. Dillon and Lydeard (1998) used allozyme polymorphism to study relationships among Mobile Basin leptoxids. They argued that *Leptoxis praerosa* and *L. picta* were deserving of species status, but that *L. taeniata* and *L. ampla* should be subsumed within *L. picta*. On the other hand, Dillon and Ahlstedt (1997) used allozyme variation to show that *Athernia anthonyi* and *Leptoxis praerosa* were different species, although adult shell morphology is similar.

Several caveats about the evolution of freshwater snails should be kept in mind (Davis, 1982). First, phylogenetic analyses, and therefore biogeographic studies, are often limited by the poor systematic information available on many groups, as well as the poor fossil record (only shells are preserved, which often show convergence). Second, a number of factors can explain current distributions, as illustrated for hydrobiids and pomatiopsids by Davis (1982): (1) phylogenetic events such as centers of origin and adaptive radiation; (2) past history events such as continental drift and geological alteration of stream and river flow; (3) dispersal powers, and (4) ecological factors (see earlier discussion).

E. Conservation Biology of Freshwater Snails

Freshwater snails, especially prosobranch species in the southeastern United States, are facing rates of extinction similar to the more widely known case of North American unionid bivalves (Lydeard and Mayden, 1995; Neves *et al.*, 1998; Jenkinson and Todd, 1998). Freshwater snails account for 60% of all North American molluscan species, and 61% of these snails are in the Southeast. Historically, there were 118 species of snails in the Mobile River Basin, 96 species in the Tennessee River, and 36 species each in the Cumberland and Apalachicola River basins. Thirty-eight of the 118 species in the Mobile River Basin are known to be extinct. The decline in diversity in the Mobile River Basin varies from 33 to 84% in different drainages.

Nine species of gastropods are currently listed as federally endangered (Bogan, 1999), although over 200 species from 11 families are candidates (69% of which are in the Southeast). In the southeastern states alone, two viviparids, 50 hydrobiids, 83 pleurocerids, nine pulmonates, three ancyliids and six planorbid species are considered at risk (Neves *et al.* 1998). Many of the same factors that have imperiled unionid bivalves are responsible: impoundments which inundate shallow riffles and decrease oxygen and alter water temperature, increased turbidity from agricultural activities, improper sewage treatment, and other pollution sources, to name but a few. Organic enrichment, pesticides and pathogens endanger about a quarter of the impaired river-miles in North American rivers, while excess nutrients and siltation occur, respectively, in 37 and 45% of the impacted river-miles (Neves *et al.*, 1998). At the current time there is little governmental interest in managing imperiled snail populations, although the large, knobbed-shell species, *Io fluviatilis*, has been successfully reintroduced to one river in its original range.

IV. COLLECTING AND CULTURING FRESHWATER GASTROPODS

A number of sampling techniques exist (reviewed in Russell-Hunter and Buckley, 1983), although some are not quantitative. The least quantitative technique, but one that often gives large numbers of individuals and a good idea of species composition, is sweep netting with a net of 1-mm mesh (Brown, 1979, 1997).

In soft sediments or sand, quantitative samples can be collected with an Ekman grab or a corer. When sampling macrophytes, the sampler must collect both plants with attached snails and the substrate with any bottom-dwelling species. Examples of such samplers are described in Gerking (1957), Savino and Stein (1982) and

Lodge *et al.* (1994). In coarse sand, Ponar dredges are the best alternative. In cobble, little recourse to direct counts of given areas by visual search is available. One can estimate densities by individually covering the rocks with aluminum foil, and then estimating the area from weight-to-area regressions for the foil.

The best sorting technique for gastropods is hand-sorting. Large adults can be removed visually, while samples are washed through a graded series of sieves (the smallest having a mesh of approximately 0.5 mm) to remove mud but retain smaller snails. Samples are then carefully backwashed from the sieves into shallow water on flat white trays, the vegetation teased apart, and the whole tray examined in a systematic fashion to remove small gastropods and egg cases.

Temperate gastropods will grow well at 15–20°C, while subtropical species grow better at 20–25°C. Any hard substrate with a dense periphyton covering can be added for food, although artificial foods such as lettuce, cereal, or spinach are sometimes used. Provide food only as needed to avoid fouling containers. Detritivores should be fed leaf litter colonized with bacteria and fungi (i.e., held for at least 2 weeks in a pond or stream).

Avoid crowding of snails, as growth and reproduction are sensitive to density. An approximate rule is one snail per liter. Water should be re-circulated through a gravel or charcoal filter, or at least be changed weekly. Conspecifics should be paired so that mating can occur. Culturing of “weedy” species like physids is best done at low temperatures to retard egg production, and constant removal of egg cases is necessary to prevent population “explosions”. Adequate lighting (with a 12L:12D cycle) is necessary to promote periphyton growth in aquaria (gro-lites® work well).

V. IDENTIFICATION OF THE FRESHWATER GASTROPODS OF NORTH AMERICA

The following key is modified from Burch's (1989) key for North American freshwater snails. Taxa are keyed down to genera in all families except the diverse hydrobiids. Readers interested in keying specimens down to the species level should consult Burch (1989) or keys addressing regional snail faunas (Harman and Berg, 1971; Jokinen, 1983; Thompson, 1984; Jokinen, 1992).

After collecting specimens, first relax them with tricaine methane sulfonate, menthol crystals, polypropylene phenoxylol, or sodium nembutol and then preserve them in 70% ethyl alcohol. Preserved specimens are better than dried shells, as possession of an operculum will be one of the determinations necessary.

Collect a number of different-sized specimens, because closely related genera sometime differ only in adult shell size. Sizes reported in the key, following Burch (1989), are small shells less than 10 mm, medium between 11 and 29, and large greater than 30 mm in length. Size bars in keys are in millimeters. Refer to the glossary for shell sculpture terminology like costae, lirae, etc. In some cases, soft tissue characters are used in the key (for example the structure of the verge, or penis, located behind the male's right tentacle, is important in hydrobiids). The shells of preserved individuals can be carefully crushed and removed, after living snails are relaxed with any of the chemicals mentioned above. Examine the verge under a dissecting microscope.

If examination of the radula is necessary, dissect out the buccal mass (a muscular mass behind the mouth that surrounds the radula) from a relaxed specimen and place it in a 10% potassium hydroxide solution to digest the tissue. After several hours, remove any remaining tissue and rinse the radula in 70% alcohol, stain it and mount it on a slide for examination under a compound microscope. However, digestion with strong bases may damage the radula. An alternative technique (Holznagel, 1998) is more involved, but also provides a method to extract DNA

for phylogenetic work, and can be used with frozen or alcohol-fixed specimens (but not those preserved in formalin). First prepare stock solutions of NET buffer and Proteinase-K. For the former, add 1 mL pH 8.0 Tris buffer, 2 mL 0.5 M EDTA (ethylene diamine tetra-acetic acid), 1 mL 5M NaCl, and 20 mL of 10% SDS (sodium dodecyl sulfate) solution to 76 mL of de-ionized water. For the latter, add 20 mg Proteinase-K to 1 mL de-ionized water and store at -20°C until use. Next remove the body from the shell. This is fairly easy in recently thawed or relaxed specimens, but for nonrelaxed specimens the shell may have to be gently cracked and removed from the body. Dissect away the head, and rinse with water. Place the tissue in a 1.5 mL microcentrifuge tube with 500 μL of NET buffer and 10 μL of Proteinase-K. Cap the tube and place it on a 37°C mixing table for 3 h (for fixed specimens) or 4 days (for dried specimens). The buffer and enzyme may need daily replacement. Observe the radula under a dissecting scope to determine if tissue digestion is complete, and rinse it with de-ionized water several times. The supernatant can be used for extraction of DNA with phenol/chloroform techniques (see Sambrook *et al.*, 1989). Store the radula in 25% ethanol until ready for mounting on a microscope slide.

A. Taxonomic Key to Families and Selected Genera of Freshwater Gastropods

1a.	Shell an uncoiled cone (limpet, or cap shaped) (Fig. 2).....	2
1b.	Shell coiled.....	8
2a(1a).	Apex nearly central; adult up to 12 mm; Pacific drainage. . . Family Lymnaeidae.....	3
2b.	Apex to the right or left of the median line; adult 7 mm or less; dextral or sinistral	4
3a(2a).	Apex central (Fig. 13A).....	<i>Lanx</i>
3b.	Apex anterior; Columbia river (Fig. 13B).....	<i>Fishera</i>
4a(2b).	Shell dextral (apex tips to left when viewed with aperture facing up); Rocky Mountain lakes, northeastern Ontario and north-central Quebec (Fig. 13C)	Family Acroloxidae..... <i>Acroloxus</i>
4b.	Shell sinistral (apex tips to right when viewed with aperture facing up); throughout North America	Family Ancyliidae.....5
5a(4b).	Shell elevated, apex in midline, tinged with pink or red inside and out, radially striate, with a notch-shaped depression in unworn specimens; apertural lip broad and flat. In southeastern rivers (Fig. 13D)	<i>Rhodacmea</i>
5b.	Shell height variable; apex in midline or to right, the same color as the rest of the shell, finely radially striate or smooth; widely distributed in lotic or lentic habitats	6
6a(5b).	Apex with fine radial striae, eroded in older specimens; aperture width variable, open or with a horizontal shelf in the posterior; one lobed, flat pseudobranch; widely distributed in lotic and lentic habitats (Fig. 13E)	<i>Ferrissia</i>
6b.	Shell more depressed; apex without radial striae; aperture ovate to subcircular, always open; two-lobed pseudobranch, the lower elaborately folded; in eastern states and south in lentic habitats.....	7
7a(6b).	Apex tipped to right, tentacles colorless; In canals in southern Florida and Texas (Fig. 13F).....	<i>Hebetancyllus</i>
7b.	Apex in midline; Tentacles with a black core; East of the Mississippi in lentic habitats, occasionally in south-central streams (Fig. 13G).....	<i>Laevapex</i>

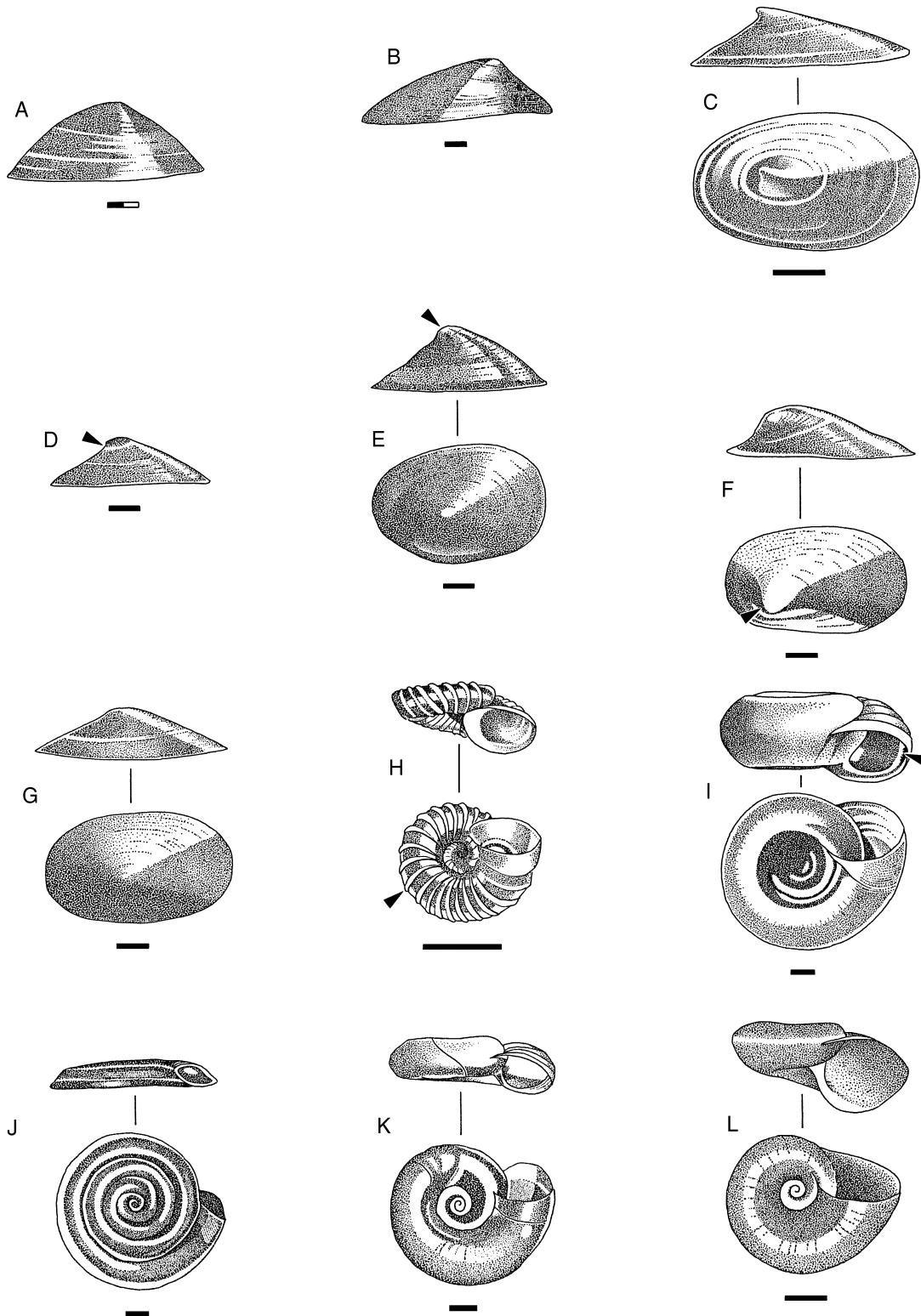


FIGURE 13 Representative limpets and planorbids. (A) The lymnaeid limpet *Lanx patelloides* (note large size, west coast distribution); (B) lymnaeid limpet *Fisherola nutalli*; (C) *Acoloxus*; (D) Ancyloid limpet *Rhodacmea rhodacme* (= *hinkezi*) (note notched depression and southeastern distribution); (E) ancyloid limpet *Ferrissia rivularis* (note elevated shell, some species possess posterior "shelf" in shell); (F) ancyloid 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) *Armiger crista* (note costae); (I) *Planorbula armigera* (= *jenksii*) (note teeth in aperture); (J) *Drepanotrema kermatoides*; (K) *Gyraulus deflectus*; and (L) *Menetus dilatatus* (A–L after Burch, 1982).

8a(1b).	Shell planospiral (Fig. 2); blood (hemolymph) nearly always red (contains hemoglobin); pseudobranch (false gill) near pneumostome or anus; mantle margin simpleFamily Planorbidae	9
8b.	Shell with raised spire.....	20
9a(8a).	Adult less than 8 mm in diameter.....	10
9b.	Adult more than 10 mm in diameter	16
10a(9a).	Shell with transverse raised ridges (costae). Canada and northern United States. (Fig. 13H).....	<i>Armiger</i>
10b.	Shell without costae	11
11a(10b).	Adults 2 mm or less in diameter; Coosa River, Alabama	<i>Neoplanorbis</i>
11b.	Adults more than 2 mm in diameter	12
12a(11b).	Aperture or body whorl with internal "teeth" or lamellae set back one quarter whorl from aperture (Fig. 13I).....	<i>Planorbula</i>
12b.	Aperture or body whorl without teeth.....	13
13a(12b).	Shell extremely flat, multiwhorled, or with numerous, low, close-set spiral ridges (lirae). Florida, Texas and southern Arizona (Fig. 13J)	<i>Drepanotrema</i>
13b.	Shell not extremely flat or multi whorled, lacking lirae	14
14a(13b).	Body whorl height equal from one side to the other (Fig. 13K).....	<i>Gyraulus</i>
14b.	Body whorl rapidly increases in height toward aperture.....	15
15a(14b)	Body whorl rounded (Fig. 13L).....	<i>Menetus</i>
15b.	Body whorl with angular edge (carina) (Fig. 14a)	<i>Promenetus</i>
16a(9b).	Adult greater than 30 mm; operculum present; penis to right of mantle; gelatinous eggs; In Florida, and introduced to rivers in central Texas.....Family Pilidae	(Ampullaridae) (Fig. 18a)..... <i>Marisa</i>
16b.	Adults less than 30 mm, operculum absent	17
17a(16b).	Shell thin, fragile, body whorl relatively depressed; Florida, Texas, Arizona (Fig. 14B).....	<i>Biomphalaria</i>
17b.	Shell thicker, solid; body whorl often high.....	18
18a(17b).	Body whorl extremely large; Western in distribution (Fig. 14C).....	<i>Vorticifex</i>
18b.	Body whorl not extremely large	19
19a(18b).	Shell spire (left side) with deep conical depression, with strong carina (Fig. 14D).....	<i>Helisoma</i>
19b.	Shell spire (left side) with shallow depression, whorls rounded on at least one side, without carina; aperture lip sometimes flared (Fig. 14E,F)	<i>Planorbella</i>
20a(8b).	Shell sinistral (aperture to left when shell viewed with spire pointing away from observer); mantle margin may be digitate or lobed.....Family Physidae.....	21
20b.	Shell dextral (aperture to right)	24
21a(20a)	Mantle edge with fingerlike projections.....	22
21b.	Mantle edge without projections, but may be serrated	23
22a(21a).	Projections on both sides of mantle.....	<i>Physa</i>
22b.	Projections on parietal side of mantle (Fig. 14G–I)	<i>Physella</i>
23a(21b).	Serrations extend beyond apertural lip, partly overlap shell; Texas (Fig. 14J)	<i>Stenophysa</i>
23b.	Shell elongate, surface black and glossy, sutures smooth, in wooded ponds in Canada and northern United States (Fig. 14K)	<i>Aplexa</i>
24a(20b).	Aperture with teeth on the parietal inner margin; operculum present and calcareous, paucispiral (Fig. 2); adult length about 20 mm; gill featherlike. Florida and southern Georgia	Family Neritinae
24b.	Shell without teeth on parietal wall, operculum present or absent.....	25

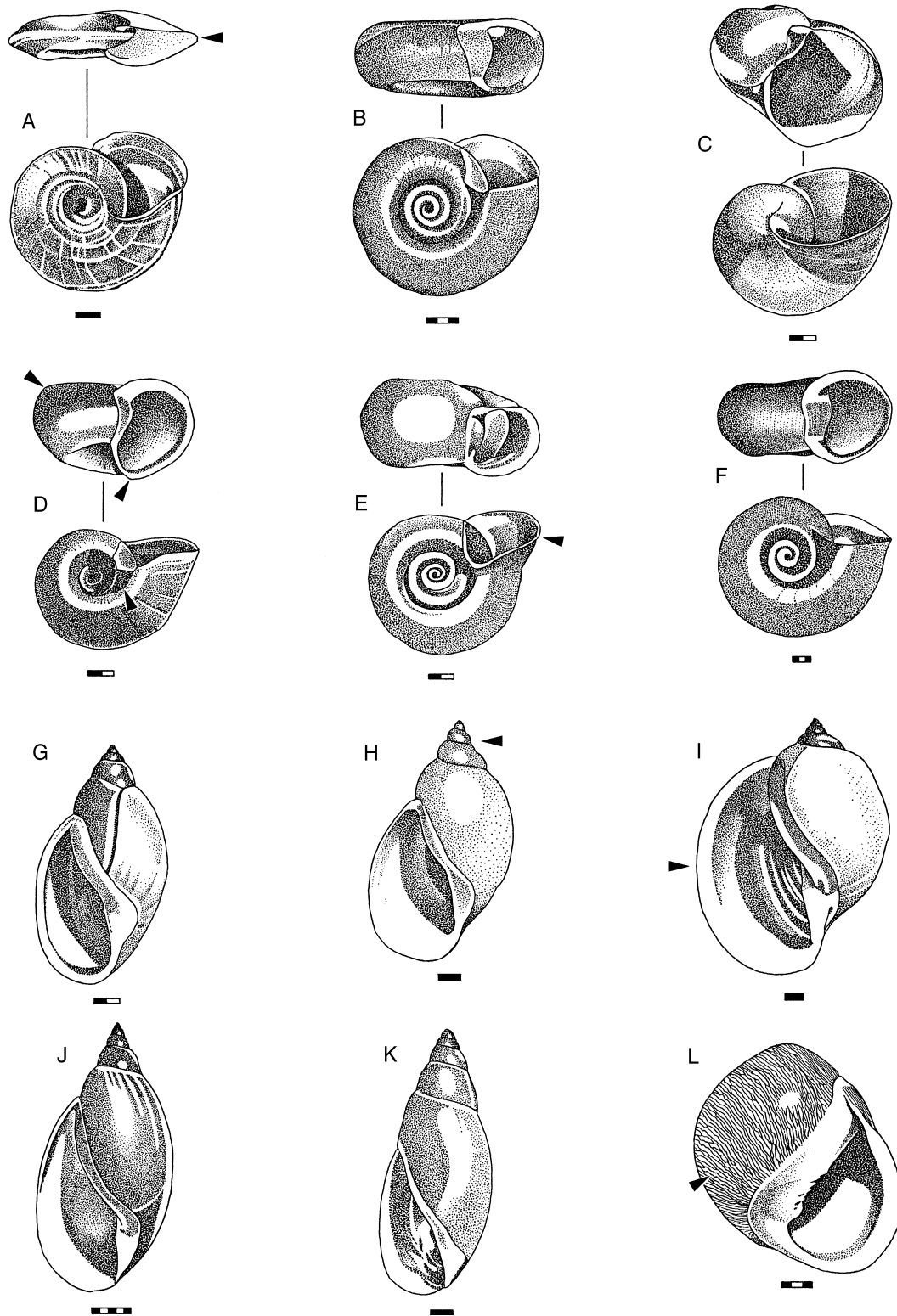


FIGURE 14 Representative planorbids, physids, and neritids. (A) *Promenetus exacuus* (note flaired body whorl and carina); (B) *Biomphalaria glabrata*; (C) *Vorticifex* (= *Parapholyx*) *effusa*; (D) *Helisoma anceps* (note strong growth lines and carina); (E) *Planorbella* (= *Helisoma*) *companulata* (sometimes called *companulatum*, note flaired lip of aperture); (F) *Planorbella* (= *Helisoma*) *trivolvis* (this species reaches 20 mm in diameter and is extremely common); (G) *Physella* (= *Physa*) *gyrina* (very similar and possibly subspecies are *P. anatina* and *P. virgata* of the midwest and south, the only physid to reach 20 mm shell length); (H) *Physella* (= *Physa*) *integra* (note the more elevated spire than *P. gyrina*, rarely reaches 10 mm shell length); (I) *Physella* (= *Petrophysa*) *zionis* (note the large aperture); (J) *Stenophya*; (K) *Aplexa elongata* (note the spindle shape and lustrous almost-black shell); and (L) *Neritina reclinata* (note markings on shell and teeth on parietal wall). [A–I after Burch, 1982.]

25a. Spire short, operculum multispiral; shell sometimes carinate; external, featherlike gill visible when foot is extended (Fig. 15A, B)
Family Valvatidae *Valvata*

25b. Spire longer26

26a. Without operculum; shell relatively fragile and easily crushed; respiration by pouch in mantle cavity.....Family Lymnaeidae 27

26b. Shell stronger; operculum and gills present.....Subclass Prosobranchia33

27(26a). With large, globose body whorl and extremely large aperture (Fig. 15C).....*Radix*

27b. Body whorl more narrow28

28a(27b). Shell very narrow and elongate; southern Ontario; north-central United States to Vermont (Fig. 15D)*Acella haldemani*

28b. Shell not especially narrow29

29a(28b) Shell tear-shaped, transparent and fragile, with large, oval aperture and body whorl, small spire; amphibious. Eastern North America (Fig. 15E).....*Pseudosuccinea*

29b. Shell not extremely thin or fragile30

30a(29b) Adults more than 35 mm in length.....31

30b. Adults less than 35 mm in length32

31a(30a). Shell with narrow, pointed spire, moderately fragile; in marshes or streams in north-central and eastern United States, Canada (Fig. 15F).....*Lymnaea stagnalis*

31b. Shell globose, thick, with relatively wide spire. Great Lakes and St. Lawrence River drainages (Fig. 15G).....*Bulinna megasoma*

32a(30b). Adult shell more than 13 mm, with microscopic spiral striations or malleations; columella with a well-developed twist or plait. Widely distributed in ponds and marshes in northern states or in alpine regions of western states (Fig. 15H)*Stagnicola*

32b. Adult shell less than 13 mm, spiral sculpture usually absent; columella without a twist or plait; (Fig. 15I).....*Fossaria*

33a(26b). Operculum multispiral or paucispiral (Fig. 2), outer margins not concentric34

33b. Operculum concentric (center may be paucispiral)47

34a(33a). Adult less than 7 mm; males possess verge (penis) behind right tentacle35

34b. Adults more than 15 mm in length, males lack verge.....40

35a(34a). Spire high, head-foot region divided on each side by longitudinal groove; eyes in prominent swellings on the outer bases of the tentacles; amphibious or terrestrial; crawls with steplike movement; (Fig. 16A)Family Pomatiopsidae.....*Pomatiopsis*

35b. Shell length variable; head-foot region not divided; eyes at same location but not on prominent swellings; totally aquatic.....
Family Hydrobiidae36

36a(35b). Verge simple, no accessory lobes (Fig. 17A).....Subfamily Lithoglyphinae
.....*Lepyrium, Cochliopina, Fluminicola, Antrobia, Clappia, Somatogyrus*

36b. Verge with accessory lobes (Fig. 17 B-E).....37

37a(36b). Verge with two arms (mitten shaped, Fig. 17B, C).....38

37b. Verge with three or more divisions (Fig. 17D, E)39

38a. Verges with one small and one large lobe with glandular areasSubfamily Nymphophilinae (Fig 17B)
.....*Orygocerus, Birgella, Striobia, Marstonia, Rhapinema, Notogilla, Spilochlamys, Cincinnatia, Pyrgulopsis, Fontelicella, Naticola*

38b. Verges with branches of approximately similar diameter
Subfamily Amnicolinae (Fig. 17C)*Ammicola, Lyrogysus, Hauffenia, Horatia*

39a. Verges with three accessory lobes branching off main lobe (Fig. 17D).....Subfamily Hydrobiinae
.....*Probythinella, Hoyia, Tryonia, Pyrgophorus, Littoridinops, Aphaostracon, Hyalopyrgus*

39b. Verge ending in three similar-sized lobes (Fig. 17E).....Subfamily Fontigentinae*Fontigens*

40a(34b). Mantle edge papillate; parthenogenetic (males absent); females brood young in a pouch posterior to head; Introduced from Florida to TexasFamily Thiaridae41

40b. Mantle edge smooth; dioecious (males present), females oviparous, with egg-laying sinus on the right side of the foot.....
Family Pleuroceridae42

41a(40a). Rounded whorls with spiral grooves and transverse raised lines (costae) (Fig. 16B)Introduced in Florida to Arizona
.....*Melanoides*

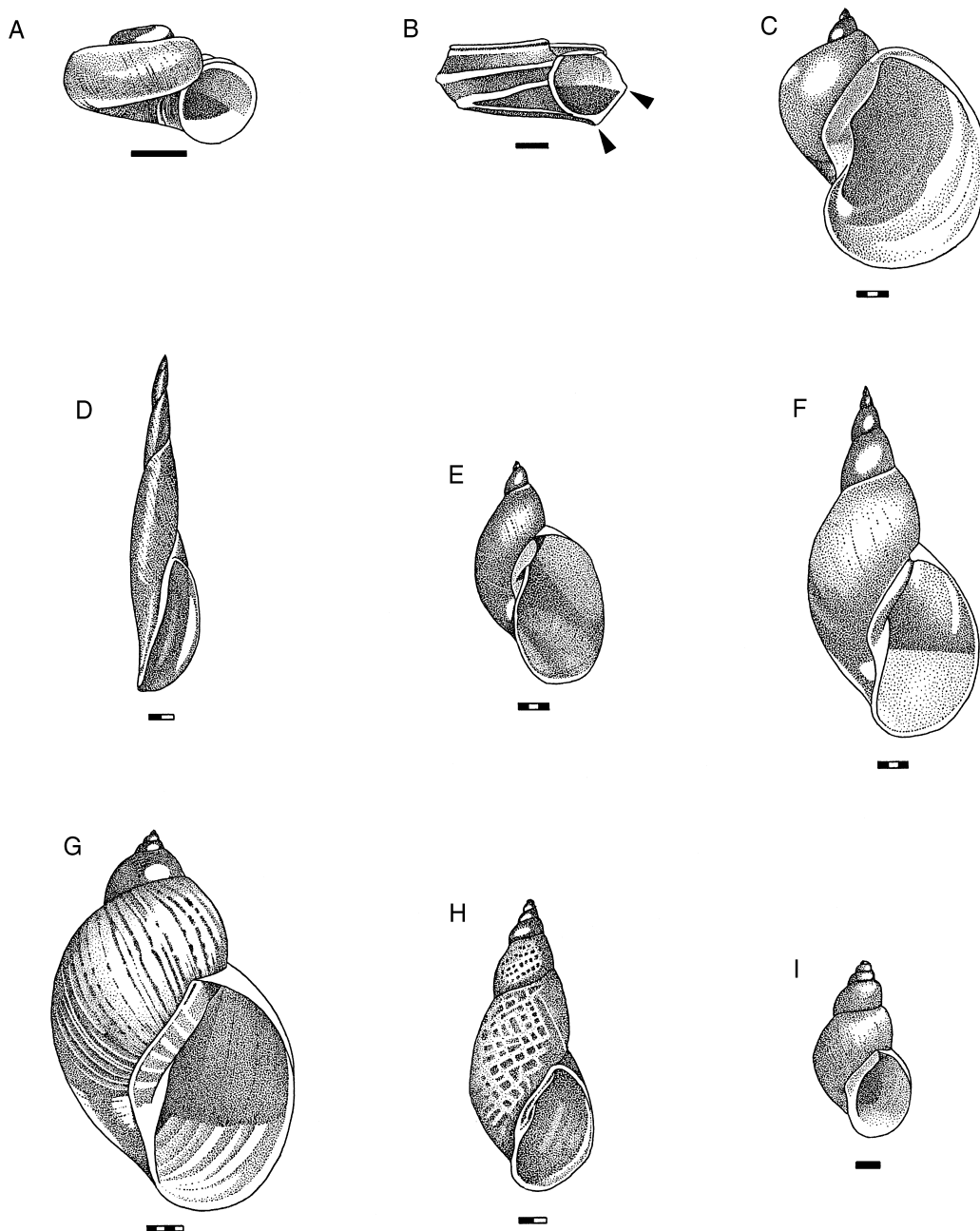


FIGURE 15 Representative valvatids and lymnaeids. (A) *Valvata sincera*; (B) *Valvata tricarinata* (note carina); (C) *Radix* (= *Lymnaea*) *auricularia* (note expanded body whorl); (D) *Acella haldemani* (note extremely narrow shell); (E) *Pseudosuccinea columella* (note thin, transparent shell and amphibious habit); (F) *Lymnaea stagnalis* (note large and fragile shell); (G) *Bulimnea megasoma* (note thick, large shell); (H) *Stagnicola* (= *Lymnaea*) *elodes* (note that malleations sometimes present, and this species is common only in ponds and marshes, rarely lakes); and (I) *Fossaria* (= *Lymnaea*) *humilis* (note small size and amphibious habit). [Figures A–I after Burch, 1982.]

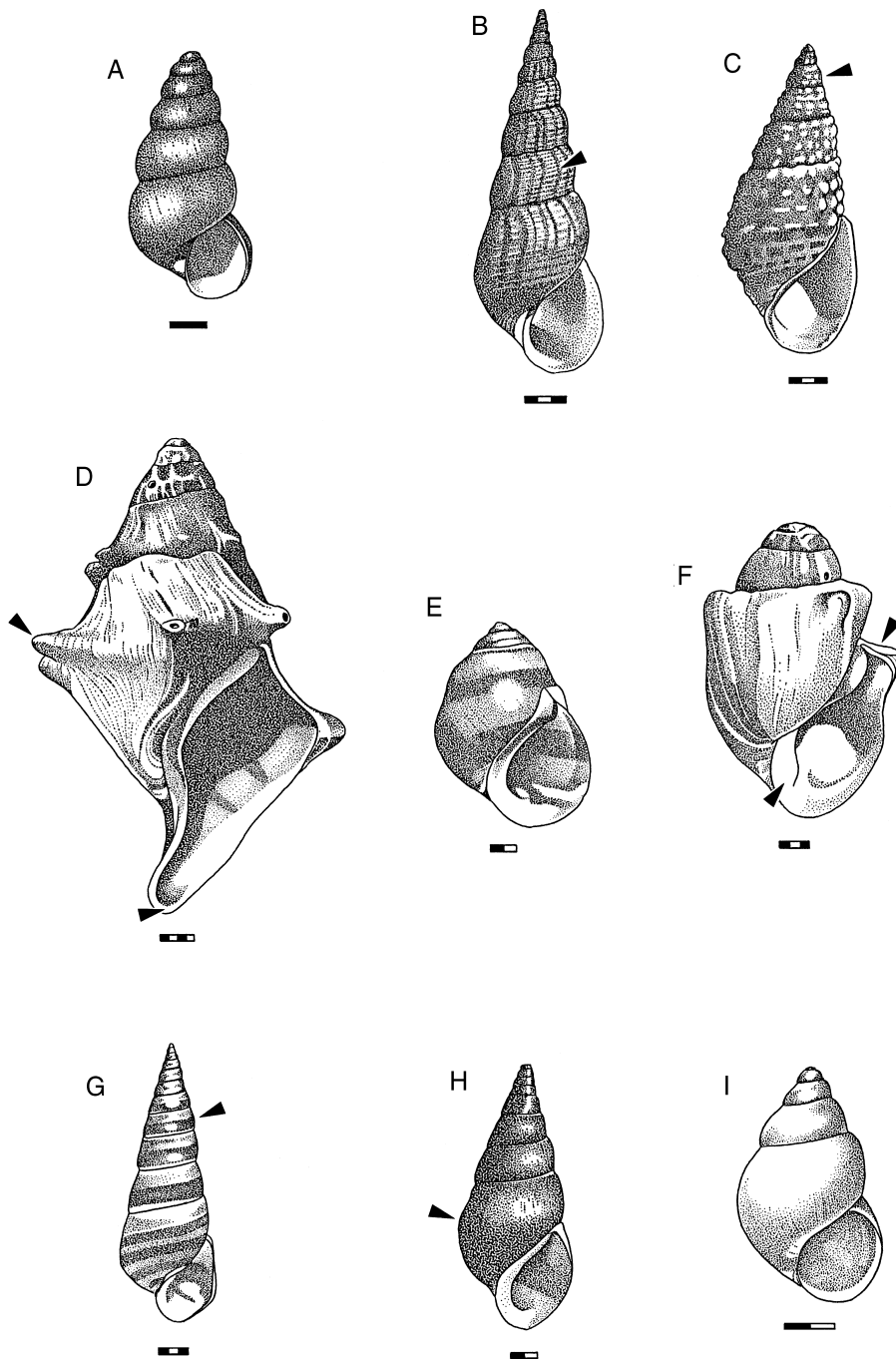


FIGURE 16 Representative potamiopsids, pleurocerids and bithyniids. (A) *Pomatiopsis lapidaria*; (B) *Melanoides tuberculata* (note costae and lirae); (C) *Thiara granifera* (note tubercles and flattened whorls near apex); (D) *Io fluviatilis* (length of spines variable); (E) *Leptoxis praerosa*; (F) *Lithasia geniculata* (note thickened anterior aperture lip and shoulders on whorls); (G) *Pleurocera acuta* (note acute angle on anterior aperture and relatively flat whorls); (H) *Elimia* (= *Goniobasis*, = *Oxytrema*) *livescens* (note more rounded whorls, although there is tremendous variation in shell sculpture in this genus); and (I) *Bithynia tentaculata*. [A–I after Burch, 1982.]

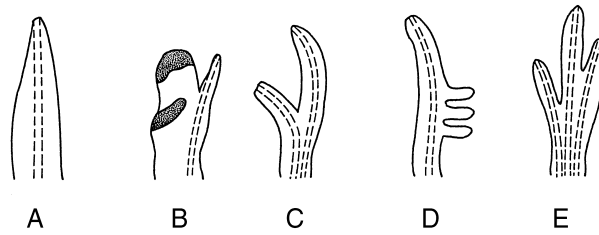


FIGURE 17 Structure of the verge (penis) in various subfamilies of hydrobiids. (A) Simple, single axis verge of subfamily Lithoglyphinae; (B) glandular crests on verge of subfamily Nymphophilinae; (C) two-ducted verge of subfamily Amnicolinae; (D) verge with accessory lobes in subfamily Hydrobiinae; and (E) three-ducted verge of subfamily Fontigentinae [A–E after Burch, 1982].

- 41b. Whorls flat near spire; spiral rows of nodules on shell (Fig. 16C)Introduced to Florida and Texas*Thiara*
- 42a(40b). Large, often with elongated spines and a long, anterior canal on aperture (Fig. 16D); rivers in eastern Tennessee and western Virginia*Io*
- 42b. Shell size and sculpture quite variable; aperture sometimes ends with a short canal43
- 43a(42b). Shell medium-to-small, a subglobose, or globose cone (Fig. 16E); lateral radular teeth with broad, bluntly rounded median cusps;*Leptoxis*
- 43b. Shell usually a narrow cone; lateral radular teeth with narrow, triangular median cusps.....44
- 44a(43b). Shell length medium, either cone-shaped or sub-globose, often with spines or nodules; inside margin of the aperture thickened, aperture meets body whorl nearly at right angle (Fig. 16F).....*Lithasia*
- 44b. Shell length and sculpture variable, base of aperture either rounded or with a short canal; inner margin of the aperture without thickening45
- 45a. Anterior (basal tip of) aperture usually pointed; whorls flat-sided.....Mississippi, Great Lakes and Hudson River drainages (Fig. 16G)*Pleurocera*
- 45b. Anterior aperture and whorls more rounded46
- 46a(45b). In river drainages east of the Mississippi River (Fig. 16H)*Elimia*
- 46b. In river drainages west of the Mississippi*Juga*
- 47a(33b). Adults less than 15 mm; operculum calcareous; from Wisconsin to Pennsylvania and New York (Fig. 16I).....Family Bithyniidae
Bithynia tentaculatum
- 47b. Adults more than 20 mm (some up to 50 or 60 mm); operculum corneous48
- 48a(47b). Globose, length up to 60 mm; penis on right side of mantle; calcareous eggs. FloridaFamily Pilidae (Ampullariidae) (Fig. 18B)
.....*Pomacea*
- 48b. Subglobose, right tentacle thicker in males, used as a penis; females ovoviviparous.....Throughout the United States and Canada
Family Viviparidae49
- 49a(48b). Adults over 35 and up to 50 mm; shell relatively thin, whorls not shouldered (Fig. 18C); introduced throughout United States.....
.....*Cipangopaludina*
- 49b. Shell thick and less than 35 mm50
- 50a(49b). Shell sometimes with one or two spiral rows of nodules; outer margin of aperture concave (when observed from the side); inside (columellar) margin of operculum folded inward; Alabama rivers (Fig. 18D).....*Tulotoma*
- 50b. Shell without nodules; aperture not as above51
- 51a(50b). Operculum with spiral center and concentric edge; whorls with a median angle or low ridge (Fig. 18E).....*Lioplax*
- 51b. Operculum entirely concentric; whorls without angles or ridges52
- 51a(51b). Shell often with colored bands or hirsute in juveniles; aperture nearly circular (Fig. 18F).....*Viviparus*
- 51b. Colored bands absent; aperture longer than wide, forms shoulder at junction with body whorl (Fig. 18G).....*Campeloma*

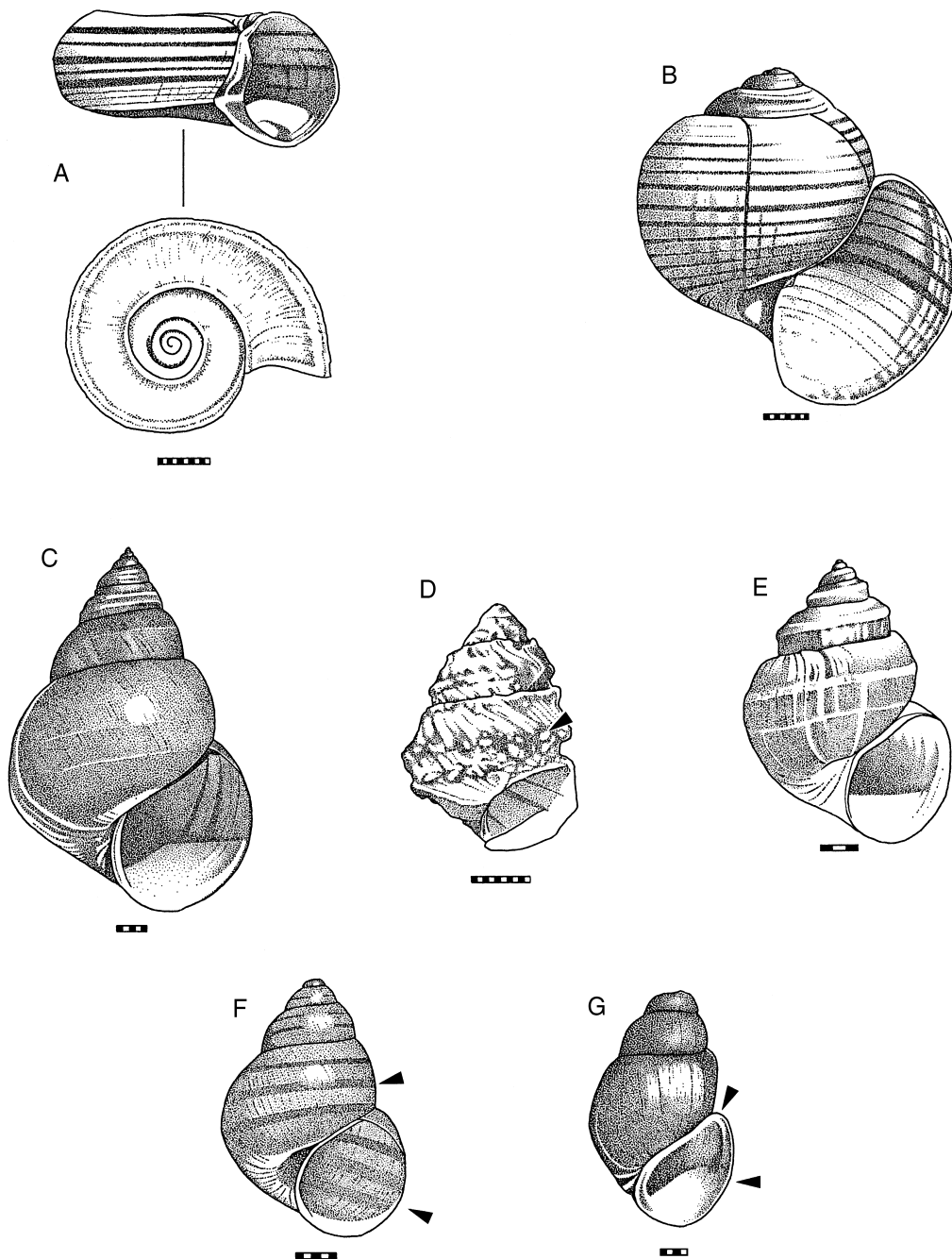


FIGURE 18 Representative ampullarids and viviparids. (A) *Marisa cornuarietis* (note large, planospiral shell, occurs in southern Florida and introduced to rivers in central Texas); (B) *Pomacea paludosa* (large, 'Apple' snail common in southern Florida); (C) *Cipangopaludina japonica* (a large, introduced, but now common species in North America); (D) *Tulotoma magnifica* (in some southeastern rivers, note tubercles which may be absent in some morphs or species); (E) *Lioplax subcarinata*; (F) *Viviparus georgianus* (common, note circular operculum, and bands which may disappear in adults); (G) *Campeloma decisum* (some times referred to as *decisa*; note operculum is longer than it is wide, and shouldered junction of aperture and body whorl). [Figures A–G after Burch, 1982.]

ACKNOWLEDGMENTS

I would like to thank Dr. Jeffery Tamplin for the considerable effort involved in drafting the excellent figures for the key, and Mr. Sean Keenan for his invaluable help in preparing the chapter.

LITERATURE CITED

- Aldridge, D. W. 1982. Reproductive tactics in relation to life cycle bioenergetics in three natural populations of the freshwater snail, *Leptoxis carinata*. *Ecology* 63:196–208.
- Aldridge, D. W. 1983. Physiological ecology of freshwater prosobranchs, *in*, Russell-Hunter, W. D. Ed., *The Mollusca*, Vol. 6, pp. 329–358, Academic Press, Orlando, FL.
- Alexander, J. E., Jr., Covich, A. P. 1991a. Predator avoidance by the freshwater snail *Physella virgata* in response to the crayfish *Procambarus simulans*. *Oecologia* 87:435–442.
- Alexander, J. E., Jr., Covich, A. P. 1991b. Predation risk and avoidance behavior by two freshwater snails. *Biological Bulletin* 180:387–393.
- Anderson, R. M., May, R. M. 1979. Prevalence of schistosome infections within molluscan populations: observed patterns and theoretical predictions. *Parasitology* 79:63–94.
- Bandel, K. 1997. Higher classification and pattern of evolution of the gastropoda. *Cour. Forsch. Inst. Senckenberg* 201:57–81.
- Barnes, R. D. 1987. *Invertebrate Zoology*, 5th ed., Saunders, Philadelphia, PA.
- Barnese, L. E., Lowe, R. L., Hunter, R. D. 1990. Comparative grazing efficiency of pulmonate and prosobranch snails. *Journal of the North American Benthological Society* 9:35–44.
- Baudoin, M. 1975. Host castration as a parasite strategy. *Evolution* 29:335–352.
- Bieler, R. 1992. Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics* 23:311–338.
- Boag, D. A. 1981. Differential depth distribution among freshwater pulmonate snails subjected to cold temperatures. *Canadian Journal of Zoology* 9:733–737.
- Boag, D. A. 1986. Dispersal in pond snails: potential role of water-fowl. *Canadian Journal of Zoology* 64:904–909.
- Boag, D. A., Pearlstone, P. S. M. 1979. On the life cycle of *Lymnaea stagnalis* (Pulmonate:Gastropoda) in southwestern Alberta. *Canadian Journal of Zoology* 52:353–362.
- Boerger, H. 1975. Movement and burrowing of *Helisoma trivolvis* (Say) (Gastropoda: Planorbidae) in a small pond. *Canadian Journal of Zoology* 53:456–464.
- Bogan, A.E. 1999. North American freshwater gastropod diversity and conservation. *in*: *The First Symposium of the Freshwater Mollusk Conservation Society*. 17–19, March, 1999 Chattanooga, TN (Abstract).
- Boss, K. J. 1974. Oblomovism in the Mollusca. *Transactions of the American Microscopical Society* 93:460–481.
- Bousefield, J. D. 1979. Plant extracts and chemically triggered positive rheotaxis in *Biomphalaria grabrata* (Say), snail intermediate host of *Schistosoma mansoni*. *Journal of Applied Ecology* 16:681–690.
- Bovbjerg, R. V. 1952. Ecological aspects of dispersal of the snail *Campeloma decisum*. *Ecology* 33:169–176.
- Bovbjerg, R. V. 1968. Responses to food in lymnaeid snails. *Physiological Zoology* 41:412–423.
- Boycott, A. E. 1936. The habitats of freshwater Mollusca in Britain. *Journal of Animal Ecology* 5:116–186.
- Brendelberger, H. 1997. Determination of digestive enzyme kinetics: a new method to define trophic niches in freshwater snails. *Oecologia* 109:34–40.
- Brendelberger, H., Jurgens, S. 1993. Suspension feeding in *Bithynia tentaculata* (Prosobranchia: Bithyniidae) as affected by body size, food and temperature. *Oecologia* 94:36–42.
- Bronmark, C. 1985a. Freshwater snail diversity: effects of pond area, habitat heterogeneity and isolation. *Oecologia* 67:127–131.
- Bronmark, C. 1985b. Interactions between macrophytes, epiphytes, and herbivores: an experimental approach. *Oikos* 45:26–30.
- Bronmark, C. 1989. Interactions between epiphytes, macrophytes and freshwater snails: a review. *Journal of Molluscan Studies* 55:299–311.
- Bronmark, C. 1994. Effects of tench and perch on interactions in a freshwater benthic food chain. *Ecology* 75:1818–1824.
- Bronmark, C., Malmqvist, B. 1986. Interactions between the leech *Glossiphonia complanata* and its gastropod prey. *Oecologia* 69:268–276.
- Bronmark, C., Klosiewski, S. P., Stein, R. A. 1992. Indirect effects of predation in a freshwater, benthic food chain. *Ecology* 73:1662–1674.
- Bronmark, C., Weisner, S.E.B. 1996. Decoupling of cascading trophic interactions in a freshwater, benthic food chain. *Oecologia* 108:534–541.
- Bronmark, C., Vermaat, J. E. 1998. Chapter 3. Complex-fish-snail-epiphyton interactions and their effects on submerged freshwater macrophytes *in*, Jepperson, E., Sondergaard, M., Cristofferson, K. Eds., *The structuring role of submerged macrophytes in lakes*, Springer, New York, pp. 47–68.
- Brown, D. S. 1978. Pulmonate molluscs as intermediate hosts for digenetic trematodes, *in*, Fretter, V., Peake, J. Eds. *Pulmonates*, Vol. 2A, Systematics, evolution, and ecology. Academic Press, New York, pp. 287–333.
- Brown, K. M. 1979. The adaptive demography of four freshwater pulmonate snails. *Evolution* 33:417–432.
- Brown, K. M. 1982. Resource overlap and competition in pond snails: an experimental analysis. *Ecology* 63:412–422.
- Brown, K. M. 1983. Do life history tactics exist at the intraspecific level? Data from freshwater snails. *American Naturalist* 121:871–879.
- Brown, K. M. 1985. Intraspecific life history variation in a pond snail: The roles of population divergence and phenotypic plasticity. *Evolution* 39:387–395.
- Brown, K.M. 1997. Temporal and spatial patterns of abundance in the gastropod assemblage of a macrophyte bed. *American Malacological Bulletin* 14:27–33.
- Brown, K. M. 1998. The role of shell strength in the foraging of crayfish for gastropod prey. *Freshwater Biology* 40:255–260.
- Brown, K. M., DeVries, D. R. 1985. Predation and the distribution and abundance of a pulmonate pond snail. *Oecologia* 66:93–99.
- Brown, K. M., Richardson, T. D. 1988. Genetic polymorphism in gastropods: a comparison of methods and habitat scales. *American Malacological Bulletin* 6:9–17.
- Brown, K. M., Strouse, B. H. 1988. Relative vulnerability of six freshwater gastropods to the leech *Nepheleopsis obscura* (Verrill). *Freshwater Biology* 19:157–166.
- Brown, K. M., Leathers, B. K., Minchella, D. J. 1988. Trematode prevalence and the population dynamics of freshwater pond snails. *American Midland Naturalist* 120:289–301.
- Brown, K. M., Varza, D. E., Richardson, T. D. 1989. Life cycles and population dynamics of two subtropical viviparid snails (Prosobranchia: Viviparidae). *Journal of the North American Benthological Society* 8:222–228.

- Brown, K.M., Lodge, D.M. 1993. The importance of specifying null models: are invertebrates really more abundant in vegetated habitats? *Limnology and Oceanography* 38: 217–275.
- Brown, K. M., Alexander, J. E., Thorp, J. H. 1998. Differences in the ecology and distribution of lotic pulmonate and prosobranch gastropods. *American Malacological Bulletin* 14:91–101.
- Browne, R. A. 1978. Growth, mortality, fecundity, and productivity of four lake populations of the prosobranch snail, *Viviparus georgianus*. *Ecology* 59: 742–750.
- Browne, R. A. 1981. Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. *Journal of Biogeography* 8: 75–83.
- Browne, R. A., Russell-Hunter, W. D. 1978. Reproductive effort in molluscs. *Oecologia* 27:23–27.
- Burch, J. B. 1989. North American Freshwater Snails. Malacological Publications, Hamburg, MI, 365 pp.
- Burky, A. J. 1971. Biomass turnover, respiration, and interpopulation variation in the stream limpet *Ferrissia rivularis*. *Ecological Monographs* 41: 235–251.
- Burky, A. J. 1983. Physiological ecology of freshwater bivalves, in: Russell-Hunter, W. D., Ed., *The Mollusca*, Vol. 6, Ecology, pp. 281–327, Academic Press, Orlando, FL.
- Calow, P. 1970. Studies on the natural diet of *Lymnaea peregra obtusa* (Kobelt) and its possible ecological implications. *Proceedings of the Malacological Society of London* 39:203–215.
- Calow, P. 1973a. Field observations and laboratory experiments on the general food requirements of two species of freshwater snail, *Planorbis contortus* Linn. and *Ancylus fluviatilis*. *Proceedings of the Malacological Society of London* 40:483–489.
- Calow, P. 1973b. The food of *Ancylus fluviatilis* (Mull.), a littoral, stone-dwelling herbivore. *Oecologia* 13:113–133.
- Calow, P. 1974a. Evidence for bacterial feeding in *Planorbis contortus* Linn. (Gastropoda: Pulmonata) *Proceedings of the Malacological Society of London* 41:145–156.
- Calow, P. 1974b. Some observations on the dispersion patterns of two species populations of littoral, stone-dwelling gastropods (Pulmonata). *Freshwater Biology* 4:557–576.
- Calow, P. 1975. The respiratory strategies of two species of freshwater gastropods (*Ancylus fluviatilis* Mull. and *Planorbis contortus* Linn.) in relation to temperature, oxygen concentration, body size, and season. *Physiological Zoology* 48:114–129.
- Calow, P. 1978. The evolution of life-cycle strategies in fresh-water gastropods. *Malacologia* 17:351–364.
- Calow, P. 1981. Adaptational aspects of growth and reproduction in *Lymnaea peregra* from exposed and sheltered aquatic habitats. *Malacologia* 21:5–13.
- Calow, P. 1983. Life-cycle patterns and evolution, in: Russell-Hunter, W. D. Ed., *The Mollusca*, Vol. 6, Ecology, pp. 649–680. Academic Press, Orlando, FL.
- Calow, P., Calow, L. J. 1975. Cellulase activity and niche separation in freshwater gastropods. *Nature* 255:478–480.
- Chamberlain, N. A. 1958. Life history studies of *Campeloma decisum*. *Nautilus* 72: 22–29.
- Cheatum, E. P. 1934. Limnological investigations on respiration, annual migratory cycle, and other related phenomena in freshwater pulmonate snails. *Transactions of the American-Microscopical Society* 53:348–407.
- Clampitt, P. T. 1973. Substratum as a factor in the distribution of pulmonate snails in Douglas Lake, Michigan. *Malacologia* 12: 379–399.
- Clampitt, P. T. 1974. Seasonal migratory cycle and related movements of the fresh-water pulmonate snail, *Physa integra*. *American Midland Naturalist* 92:275–300.
- Clarke, P. H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, Ottawa, Canada.
- Covich, A. P. 1977. How do crayfish respond to plants and Mollusca as alternate food resources? *Freshwater Crayfish* 3:165–169.
- Covich, A.P., Cowl, T.A., Alexander, J.E., Jr., Vaughn, C.C. 1994. Predator-avoidance responses in freshwater decapod-gastropod interactions mediated by chemical stimuli. *Journal of the North American Benthological Society* 13:283–290.
- Cox, L.R. 1960. Gastropoda. General characteristics of Gastropoda, in: *Treatise on Invertebrate Paleontology, Part I. Mollusca* 1, Moore, R.C. Ed., pp. 84–169, Lawrence: Univ. of Kansas.
- Croll, R. P. 1983. Chemoreception. *Biological Reviews* 58:293–319.
- Crowl, T. A. 1990. Life-history strategies of a freshwater snail in response to stream permanence and predation: balancing conflicting demands. *Oecologia* 84:238–243.
- Crowl, T. A., Covich, A. P. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* 247:949–951.
- Cuker, B. E. 1983. Competition and coexistence among the grazing snail *Lymnaea*, Chironomidae, and microcrustacea in an arctic epilithic lacustrine community. *Ecology* 64:10–15.
- Daldorph, P. W. G., Thomas, J. D. 1995. Factors influencing the stability of nutrient-enriched freshwater macrophyte communities: the role of sticklebacks *Pungitius pungitius* and freshwater snails. *Freshwater Biology* 33:271–289.
- Davis, G. M. 1979. The origin and evolution of the Pomatiopsidae, with emphasis on the Mekong River hydrobiid gastropods. *Monographs of the Academy of Natural Sciences, Philadelphia*, Number 20.
- Davis, G. M. 1982. Historical and ecological factors in the evolution, adaptive radiation, and biogeography of freshwater molluscs. *American Zoologist* 22:375–395.
- Dazo, B. Z. 1965. The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens*. *Malacologia* 2:1–80.
- Diamond, J. M. 1975. Assembly of species communities, in: Cody, M., Diamond, J. M. Eds., *Ecology and Evolution of Communities*. pp. 342–344.
- Dillon, R. T. 1981. Patterns in the morphology and distribution of gastropods in Oneida Lake, New York, detected using computer-generated null hypotheses. *American Naturalist* 118:83–101.
- Dillon, R. T. 1987. A new Monte Carlo method for assessing taxonomic similarity within faunal samples: reanalysis of the gastropod community of Oneida Lake, New York. *American Malacological Bulletin* 5:101–104.
- Dillon, R.T., Jr., Ahlstedt, S.A. 1997. Verification of the specific status of the endangered Anthony's river snail, *Athearnia anthonyi*, using allozyme electrophoresis. *Nautilus* 110:97–101.
- Dillon, R.T., Jr., Lydeard, C. 1998. Divergence among Mobile Basin populations of the pleurocerid snail genus, *Leptoxis*, estimated by allozyme electrophoresis. *Malacologia* 39:113–121.
- Doremus, C. M., Harman, W. N. 1977. The effects of grazing by physid and planorbisid freshwater snails on periphyton. *Nautilus* 91:92–96.
- Duch, T. M. 1976. Aspects of the feeding habits of *Viviparus georgianus*. *Nautilus* 90:7–10.
- Duncan, C. J. 1975. Reproduction, in: Fretter and Peake, Eds., *Pulmonates*, Vol. 1, Functional anatomy and physiology. Academic Press, Orlando, FL, pp. 309–366.
- Dybdahl, M. F., Lively, C. M. 1996. The geography of coevolution: comparative population structures for a snail and its trematode parasite. *Evolution* 50:2264–2275.
- Eckblad, J. W. 1973. Experimental predation studies of malacophagous larvae of *Sepedon fuscipennis* (Diptera: Sciomyzidae) and aquatic snails. *Experimental Parasitology* 33:331–342.
- Eisenberg, R. M. 1966. The regulation of density in a natural population of the pond snail, *Lymnaea elodes*. *Ecology* 47:889–906.
- Eisenberg, R. M. 1970. The role of food in the regulation of the pond snail, *Lymnaea elodes*. *Ecology* 51:680–684.

- Eversole, A. G. 1978. Life cycles, growth and population bioenergetics in the snail *Helisoma trivolvis* (Say). *Journal of Molluscan Studies* 44:209–222.
- Fretter, V., Graham, A. 1962. British prosobranch molluscs. Ray Society, London.
- Fretter, V., Peake, J. 1975. Pulmonates, Vol. 1, Functional anatomy and physiology. Academic Press, Orlando, FL.
- Fretter, V., Peake, J. 1978. Pulmonates, Vol. 2A, Systematics, Evolution, and Ecology. Academic Press, Orlando, FL.
- Gerking, S. D. 1957. A method of sampling the littoral macrofauna and its application. *Ecology* 38:219–225.
- Goodrich, B. 1945. *Goniobasis livescens* of Michigan. Miscellaneous Publications of the Museum of Zoology of the University of Michigan 64:1–26.
- Harman, W. N. 1968. Replacement of pleurocerids by *Bithynia* in polluted waters of central New York. *Nautilus* 81:77–83.
- Harman, W. N. 1972. Benthic substrates: their effect on fresh-water mollusca. *Ecology* 53:271–277.
- Harman, W. N., Forney, J. L. 1970. Fifty years of change in the molluscan fauna of Oneida Lake, New York. *Limnology and Oceanography* 15:454–460.
- Harman, W. N., Berg, C. O. 1971. The freshwater snails of central New York. *Search (Agriculture)* 1:1–68.
- Haynes, A., Taylor, B. J. R. 1984. Food finding and food preference in *Potamopyrgus jenkensi* (E. A. Smith) (Gastropoda: Prosobranchia) *Archives fur Hydrobiologie* 100:479–491.
- Hershey, A. E. 1990. Snail populations in arctic lakes: competition mediated by predation? *Oecologia* 82:26–32.
- Hershler, R. 1998. A systematic review of the hydrobiid snails (Gastropoda:Rissooidea) of the Great Basin, Western United States. Part I. Genus *Pyrgulopsis*. *Veliger* 41:1–132.
- Hershler, R., Frest, T.J. 1996. A review of the North American freshwater snail genus *Fluminicola* (Hydrobiidae). *Smithsonian Contributions to Zoology*. 583:1–41.
- Hershler, R., Pierson, J.M., Krotzer, R.S. 1990. Rediscovery of *Tulotoma magnifica* (Conrad) (Gastropoda:Viviparidae). *Proceedings of the Biological Society of Washington* 103:815–824.
- Hill, W. R., Harvey, B. C. 1990. Periphyton responses to higher trophic levels and light in a shaded stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2307–2314.
- Hill, W. R., Boston, H. L., Steinman, A. D. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. *Canadian Journal of Fisheries and Aquatic Sciences* 49:504–512.
- Holmes, J. C. 1983. Evolutionary relationships between parasitic helminths and their hosts. *in: Futuyma, D. J., Slatkin, M. Eds., Coevolution*, pp. 161–185. Sinauer, Sunderland, MA.
- Holznagel, W.E. 1998. Research note: a non-destructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material. *American Malacological Bulletin* 14:181–183.
- Hunter, R. D. 1975. Growth, fecundity, and bioenergetics in three populations of *Lymnaea palustris* in upstate New York. *Ecology* 56:50–63.
- Hunter, R. D. 1980. Effects of grazing on the quantity and quality of freshwater aufwuchs. *Hydrobiologia* 69:251–259.
- Hunter, R. D., Russell-Hunter, W. D. 1983. Bioenergetic and community changes in intertidal aufwuchs grazed by *Littorina littorea*. *Ecology* 64:761–769.
- Hury, A. D., Koebel, J. W., Benke, A. C. 1994. Life history and longevity of the pleurocerid snail *Elimia*: a comparative study of eight populations. *Journal of the North American Benthological Society* 13:540–556.
- Hury, A. D., Benke, A. C., Ward, G. M. 1995. Direct and indirect effects of geology on the distribution, biomass, and production of the freshwater snail *Elimia*. *Journal of the North American Benthological Society* 14:519–534.
- Hyman, L. H. 1967. The invertebrates, Vol. VI, Mollusca I. McGraw-Hill, New York.
- Jacoby, J. M. 1985. Grazing effects on periphyton by *Theodoxus fluviatilis* (Gastropoda) in a lowland stream. *Journal of Freshwater Biology*. 3:265–274.
- Jarne, P., Finet, L., Delay, B., Thaler, L. 1991. Self-fertilization versus cross-fertilization in the hemaphroditic freshwater snail *Bulinus globosus*. *Evolution* 45:1136–1146.
- Jenkinson, J. J., Todd, R. M. 1998. Management of native molluscan resources, *in: Benz, G. W., Collins, D. E. Eds., Aquatic fauna in peril: the southeastern perspective*. Southeast Aquatic Research Institute, Special Publication 1.
- Johnson, S. G. 1992. Parasite-induced parthenogenesis in a freshwater snail: stable, persistent patterns of parasitism. *Oecologia* 89:533–541.
- Johnson, P. D., Brown, K. M., 1997. The role of current and light in explaining the habitat distribution of the lotic snail *Elimia semicarinata*. *Journal of the North American Benthological Society*. 15:344–369.
- Jokinen, E. H. 1978. The aestivation pattern of a population of *Lymnaea elodes*. *American Midland Naturalist* 100:43–53.
- Jokinen, E. H. 1982. *Cipangopaludina chinensis* (Gastropods:Viviparidae) in North America, review and update. *Nautilus* 96:89–95.
- Jokinen, E. H. 1983. The freshwater snails of Connecticut. State Geological and Natural History Survey of Connecticut, Department of Environmental Protection, Publication 109.
- Jokinen, E. H. 1985. Comparative life history patterns within a littoral zone snail community. *Verh. Internat. Verein. Limnol.* 22:3292–3299.
- Jokinen, E. H. 1987. Structure of freshwater snail communities: species–area relationships and incidence categories. *American Malacological Bulletin* 5:9–19.
- Jokinen, E. H. 1991. The malacofauna of the acid and non-acid lakes and rivers of the Adirondack mountains and surrounding lowlands, New York state, U.S.A. *Verh. Internat. Verein. Limnol.* 24:2940–2946.
- Jokinen, E. H. 1992. The freshwater snails (Mollusca: Gastropoda) of New York state. *New York State Museum Bulletin* 482, 112 pp.
- Jokinen, E. H., Guerette, J., Kortmann, R. W. 1982. The natural history of an ovoviviparous snail, *Viviparus georgianus* (Lea), in a soft-water eutrophic lake. *Freshwater Invertebrate Biology* 1:2–17.
- Jung, Y. 1992. Phylogenetic relationships of some planorbid genera (Gastropoda: Lymnophila). *Malacological Review* 25:73–102.
- Kairesalo, T., Koskimies, I. 1987. Grazing by oligochaetes and snails on epiphytes. *Freshwater Biology* 17:317–324.
- Kesler, D. H. 1981. Periphyton grazing by *Ammicola limosa*: an enclosure-exclosure experiment. *Journal of Freshwater Ecology* 1:51–59.
- Kesler, D. H. 1983. Cellulase activity in gastropods: should it be used in niche separation? *Freshwater Invertebrate Biology* 2:173–179.
- Kesler, D. H., Jokinen, E. H., Munns, W. R., Jr. 1986. Trophic preferences and feeding morphology of two pulmonate snail species from a small New England pond, U.S.A. *Canadian Journal of Zoology* 64:2570–2575.
- Kesler, D. H., Munns, W. R., Jr. 1989. Predation by *Belostoma flumineum* (Hemiptera): an important cause of mortality in freshwater snails. *Journal of the North American Benthological Society* 8:342–350.
- Kosuge, S. 1966. The family Triphoridae and its systematic position. *Malacologia* 4:297–324.
- Lamberti, G. A., Ashkenas, L. R., Gregory, S. V., 1987. Effects of three herbivores on periphyton communities in laboratory streams. *Journal of North American Benthological Society* 6:92–104.

- Lassen, H. H. 1975. The diversity of freshwater snails in view of the equilibrium theory of island biogeography. *Oecologia* 19:1–8.
- Levri, E. P., Lively, C. M. 1996. The effects of size, reproductive condition and parasitism on foraging behavior in a freshwater snail, *Potamopyrgus antipodarum*. *Animal Behavior* 51:891–901.
- Lively, C. M. 1987. Evidence from a New Zealand snail for the maintenance of sex by parasitism. *Nature* 328:519–521.
- Lively, C. M. 1989. Adaptation by a parasitic trematode to local populations of its host. *Evolution* 43:1663–1671.
- Lively, C. M., Jokela, J. 1995. Spatial variation in infection by digenetic trematodes in a population of freshwater snails (*Potamopyrgus antipodarum*). *Oecologia* 103:509–517.
- Lodge, D. M. 1985. Macrophyte–gastropod associations: observations and experiments on macrophyte choice by gastropods. *Freshwater Biology* 15:695–708.
- Lodge, D. M. 1986. Selective grazing on periphyton: a determinant of freshwater gastropod microdistributions. *Freshwater Biology* 16:831–841.
- Lodge, D. M., Kelly, P. 1985. Habitat disturbance and the stability of freshwater gastropod populations. *Oecologia* 68:111–117.
- Lodge, D. M., Brown, K. M., Klosiewski, S. P., Stein, R. A., Covich, A. P., Leathers, B. K., Bronmark, C. 1987. Distribution of freshwater snails: spatial scale and the relative importance of physicochemical and biotic factors. *American Malacological Bulletin* 5:73–84.
- Lodge, D. M., Kershner, M. W., Aloï, J. E., Covich, A. P. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75:1265–1281.
- Lodge, D. M., Stein, R. A., Brown, K. M., Covich, A. P., Bronmark, C., Garvey, J. E., Klosiewski, S. P. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Australian Journal of Ecology* 23:53–67.
- Lowe, R. L., Hunter, R. D. 1988. Effects of grazing by *Physa integra* on periphyton community structure. *Journal of the North American Benthological Society* 7:29–36.
- Lydeard, C., Mayden, R. L. 1995. A diverse and endangered aquatic ecosystem of the Southeast United States. *Conservation Biology* 9:800–805.
- Lydeard, C., Holznagel, W. E., Garner, J., Hartfield, P., Pierson, M. 1997. A molecular phylogeny of Mobile River drainage basin pleurocerid snails (Caenogastropoda: Cerithioidea). *Molecular Phylogenetics and Evolution* 7:117–128.
- Lydeard, C., Yoder, J.H., Holznagel, W.E., Thompson, F.G., Hartfield, P. 1998. Phylogenetic utility of the 5'-half of mitochondrial 16S rDNA gene sequences for inferring relationships of *Elimia* (Cerithioidea:Pleuroceridae). *Malacologia* 39:183–193.
- Macan, T. T. 1950. Ecology of freshwater Mollusca in the English Lake District. *Journal of Animal Ecology* 19:124–146.
- MacArthur, R. H., Wilson, E. O., 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ, USA.
- Machin, J. 1975. Water relationships, *in*: Fretter, V., Peake, J. Eds., *Pulmonates*, Vol. 1, Functional anatomy and physiology, pp. 105–164. Academic Press, Orlando, FL.
- Madsen, H. 1992. Food selection by freshwater snails in the Gezira irrigation canals, Sudan. *Hydrobiologia* 228:203–217.
- Marks, J. C., Lowe, R. L. 1989. The independent and interactive effects of snail grazing and nutrient enrichment on structuring periphyton communities. *Hydrobiologia* 185:9–17.
- Martin, A. W. 1983. Excretion., *in*: Wilbur, K. M. Ed., *The molluscs*, Vol. 5, Physiology, pp. 353–407. Academic Press, Orlando, FL.
- Martin, T. H., Crowder, L. B., Dumas, C. F., Burkholder, J. M. 1992. Indirect effects of fish on macrophytes in Bayes Mountain Lake: Evidence for a littoral trophic cascade. *Oecologia* 89:476–481.
- McCormick, P. V., Stevenson, R. J. 1989. Effects of snail grazing on benthic algal community structure in different nutrient environments. *Journal of the North American Benthological Society* 8:162–172.
- McMahon, R. F. 1975. Growth, reproduction, and bioenergetic variation in three natural populations of a freshwater limpet *Laevapex fuscus*. *Proceedings of the Malacological Society of London* 41:331–352.
- McMahon, R. F. 1983. Physiological ecology of freshwater pulmonates, *in*: Russell-Hunter, W. D. Ed. *The mollusca*, Vol. 6, Ecology, pp. 359–430, Academic Press, Orlando, FL.
- McMahon, R. F., Hunter, R. D., Russell-Hunter, W. D. 1974. Variation in aufwuchs at six freshwater habitats in terms of carbon biomass and of carbon: nitrogen ratio. *Hydrobiologia* 45:391–404.
- Merrick, G. W., Hershey, A. E., McDonald, M. E. 1991. Lake trout (*Salvelinus namaycush*) control of snail density and size distribution in an arctic lake. *Canadian Journal of Fisheries and Aquatic Sciences*. 48:498–502.
- Minchella, D. J., Loverde, P. T. 1981. A cost of increased early reproductive effort in the snail *Biomphalaria glabrata*. *American Naturalist* 118:876–881.
- Minchella, D. J., Leathers, B. K., Brown, K. M., McNair, J. K. 1985. Host and parasite counter-adaptations: An example from a freshwater snail. *American Naturalist* 126:843–854.
- Morton, J. E. 1955. The evolution of the Ellobiidae with a discussion on the origin of the pulmonata. *Proceedings of the Zoological Society of London* 125:127–168.
- Mulholland, P. J., Newbold, J. D., Elwood, J. W., Horn, C. L. 1983. The effect of grazing intensity on phosphorus spiralling in autotrophic streams. *Oecologia* 58:358–366.
- Mulholland, P. J., Steinman, A. D., Palumbo, A. V., Elwood, J. W., Kirschtel, D. B. 1991. Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. *Ecology* 72:966–982.
- Neves, R. J., Bogan, A. E., Williams, J. D., Ahlstedt, S. A., Hartfield, P. W. 1998. Status of aquatic mollusks in the southeastern United States: A downward spiral of diversity, *in*: Benz, G.W., Collins, D. E. Eds. *Aquatic fauna in peril: The southeastern perspective*. Southeast Aquatic Research Institute, Special Publication 1.
- Nystrom, P., Perez, J. R. 1998. Crayfish predation and the common pond snail (*Lymnaea stagnalis*): the effect of habitat complexity and snail size on foraging efficiency. *Hydrobiologia* 368:201–208.
- Okland, J. 1983. Factors regulating the distribution of freshwater snails (Gastropoda) in Norway. *Malacologia* 24:277–288.
- Osenberg, C. W. 1989. Resource limitation, competition and the influence of life history in a freshwater snail community. *Oecologia* 79:512–519.
- Pace, G. L., Szuch, E. J. 1985. An exceptional stream population of the banded apple snail, *Viviparus georgianus*, in Michigan. *Nautilus* 99:48–53.
- Pechenik, J. A. 1985. *Biology of the invertebrates*. Prindle, Weber & Schmidt, Boston.
- Pip, E. 1986. The ecology of freshwater gastropods in the central Canadian region. *Nautilus* 100:56–66.
- Ponder, W.F., Lindberg, D.R. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of Linnaean Society* 119:83–265.
- Reavell, P. E. 1980. A study of the diets of some British freshwater gastropods. *Journal of Conchology* 30:253–271.
- Remigio, E. A., Blair, D. 1997. Molecular systematics of the freshwater snail family Lymnaeidae (Pulmonata: Basommatophora) utilizing mitochondrial ribosomal DNA sequences. *Journal of Molluscan Studies* 63:173–185.
- Richardson, T. D., Scheiring, J. F., Brown, K. M. 1988. Secondary production of two lotic snails (Pleuroceridae: *Elimia*). *Journal of the North American Benthological Society* 7: 234–245.

- Richardson, T. D., Brown, K. M. 1989. Secondary production of two subtropical viviparid prosobranchs. *Journal of the North American Benthological Society* 8:229–236.
- Rosemond, A. D., Mulholland, P. J., Elwood, J. W. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74:1264–1280.
- Russell-Hunter, W. D. 1978. Ecology of freshwater pulmonates, *in*: Fretter, V., Peake, J., Eds., *The pulmonates*, Vol. 2A, Systematics, evolution and ecology, pp. 335–383, Academic Press, Orlando, FL.
- Russell-Hunter, W. D. 1983. Ecology of freshwater pulmonates, *in*: Russell-Hunter, W. D. Ed., *The Mollusca*, Vol. 6, Ecology. pp. 335–383, Academic Press, Orlando, FL.
- Russell-Hunter, W. D., Buckley, D. E. 1983. Actuarial bioenergetics of nonmarine molluscan productivity. *in*: Russell-Hunter, W. D., Ed., *The Mollusca*, Vol. 6, Ecology. pp. 463–503, Academic Press, Orlando, FL.
- Saffran, K. A., Barton, D. R. 1993. Trophic ecology of *Orconectes propinquus* (Girard) in Georgian Bay (Ontario, Canada). *Freshwater Crayfish* 9:350–358.
- Sambrook, J., Fritsch, E.F., Maniatis, T. 1989. *Molecular cloning, a laboratory manual*, 2nd ed., Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, (3 vols).
- Sapp, K. H., Esch, G. W. 1994. The effects of spatial and temporal heterogeneity as structuring forces for parasite communities in *Helisoma anceps* and *Physa gyrina*. *American Midland Naturalist* 132:91–103.
- Savino, J. F., Stein, R. A. 1982. Predator-prey interaction between large-mouth bass and bluegills as influenced by simulated submerged vegetation. *Transactions of the American Fisheries Society* 111:255–266.
- Sheldon, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology* 68:1920–1931.
- Snyder, S. C., Esch, G. W. 1993. Trematode community structure in the pulmonate snail *Physa gyrina*. *Journal of Parasitology* 79:205–215.
- Stein, R. A., Goodman, C. G., Marschall, E. A. 1984. Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* 65:702–715.
- Steinman, A. D., McIntire, C. D., Lowry, R. R. 1987. Effects of herbivore type and density on chemical composition of algal assemblages in laboratory streams. *Journal of North American Benthological Society* 6:189–197.
- Swamikannu, X., Hoagland, K. D. 1989. Effects of snail grazing on the diversity and structure of a periphyton community in an eutrophic pond. *Canadian Journal of Fisheries & Aquatic Sciences* 46:1698–1704.
- Tashiro, J. S. 1982. Grazing in *Bithynia tentaculata*: age specific bioenergetic patterns in reproductive partitioning of ingested carbon and nitrogen. *American Midland Naturalist* 107: 133–150.
- Tashiro, J. S., Colman, S. D. 1982. Filter feeding in the freshwater prosobranch snail *Bithynia tentaculata*: bioenergetic partitioning of ingested carbon and nitrogen. *American Midland Naturalist* 107:114–132.
- Thomas, D. L., McClintock, J. B. 1990. Embryogenesis and the effects of temperature on embryonic development, juvenile growth rates, and the onset of oviposition in the freshwater pulmonate gastropod *Physella cubensis*. *Invertebrate Reproduction and Development* 17:65–71.
- Thompson, F. G. 1984. *The freshwater snails of Florida: A manual for identification*. Univ. of Florida Press, Gainesville, FL.
- Townsend, C. R. 1975. Strategic aspects of time allocation in the ecology of a freshwater pulmonate snail. *Oecologia* 19:105–115.
- Townsend, C. R., McCarthy, T. K. 1980. On the defense strategy of *Physa fontinalis* (L.), a freshwater pulmonate snail. *Oecologia* 46:75–79.
- Tuchman, N. C., Stevenson, P. J. 1991. Effects of selective grazing by snails on benthic algal succession. *Journal of North American Benthological Society* 10:430–443.
- Turner, A. M. 1997. Contrasting short-term and long-term effects of predation risk on consumer-habitat use and resources. *Behavioral Ecology* 8:120–125.
- Underwood, G. J. C. 1991. Growth enhancement of the macrophyte *Ceratophyllum demersum* by the presence of the snail *Planorbis planorbis*: the effects of grazing and chemical conditioning. *Freshwater Biology* 26:325–334.
- Vail, V. A. 1978. Seasonal reproductive patterns in three viviparid gastropods. *Malacologia* 17:73–97.
- Van Cleave, H. J., Altringer, D. A. 1937. Studies on the life cycle of *Campeloma rufum*, a freshwater snail. *American Naturalist* 71:167–184.
- Van Cleave, H. J., Lederer, L. G. 1932. Studies on the life cycle of the snail, *Viviparus contectoides*. *Journal of Morphology* 53: 499–522.
- Vermeij, G. J., Covich, A. P. 1978. Co-evolution of freshwater gastropods and their predators. *American Naturalist* 112: 833–843.
- Weber, L. M., Lodge, D. M. 1990. Periphytic food and predatory crayfish: relative roles in determining snail distribution. *Oecologia* 82:33–39.
- Wethington, A. R., Dillon, R. T. Jr. 1993. Selfing, outcrossing, and mixed mating in the freshwater snail *Physa heterostropha*: lifetime fitness and inbreeding depression. *Invertebrate Biology* 116: 192–199.
- Wethington, A. R., Dillon, R. T., Jr. 1996. Gender choice and gender conflict in a non-reciprocally mating simultaneous hermaphrodite, the freshwater snail, *Physa*. *Animal Behavior* 51: 1107–1118.
- Wilbur, K. M. 1983. *The Mollusca*, Vol. 1–6. Academic Press, Orlando, FL.