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MOLLUSCA: BIVALVIA

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I. INTRODUCTION

North American (NA) freshwater bivalve molluscs (class Bivalvia) fall in the subclasses Paleoheterodonta (Superfamily Unionoidea) and Heterodonta (Superfamilies Corbiculoidea and Dreissenoidea). They have enlarged gills with elongated, ciliated filaments for suspension feeding on plankton, algae, bacteria, and microdetritus. The mantle tissue underlying and secreting the shell forms a pair of lateral, dorsally connected lobes. Mantle and shell are both single entities. During development, the right and left mantle lobes extend ventrally from the dorsal visceral mass to enfold the body. Each lobe secrets a calcareous shell valve which remains connected by a mid-dorsal isthmus (Allen, 1985). Like all molluscs, the shell valves consist of outer proteinaceous and inner crystalline calcium carbonate elements (Wilbur and Saleuddin, 1983). The lateral mantle lobes secrete shell material marked by a high proportion of crystalline calcium carbonate making them thick, strong and inflexible, while the mantle isthmus secretes primarily protein, forming a dorsal elastic hinge ligament uniting the calcareous valves (Fig. 1). The hinge ligament is external in all freshwater bivalves. Its elasticity opens the valves while the anterior and posterior shell adductor muscles (Fig. 2) run between the valves and close them in opposition to the hinge ligament which opens them on adductor muscle relaxation.

The mantle lobes and shell completely enclose the bivalve body, resulting in cephalic sensory structures becoming vestigial or lost. Instead, external sensory structures are concentrated on the mantle margins where they are exposed to the external environment when the valves open. Compared to other molluscs, the bivalve body is laterally compressed and dorso-ventrally expanded, adapting them for burrowing in sediments, enclosure by shell valves and mantle protecting their soft tissues from abrasion and preventing fine sediments from entering the mantle cavity where they could interfere with gill suspension feeding. These adaptations along with a highly protrusile, muscular, spadelike foot used for burrowing, have made bivalves the most successful infaunal suspension feeders in marine and freshwater habitats.

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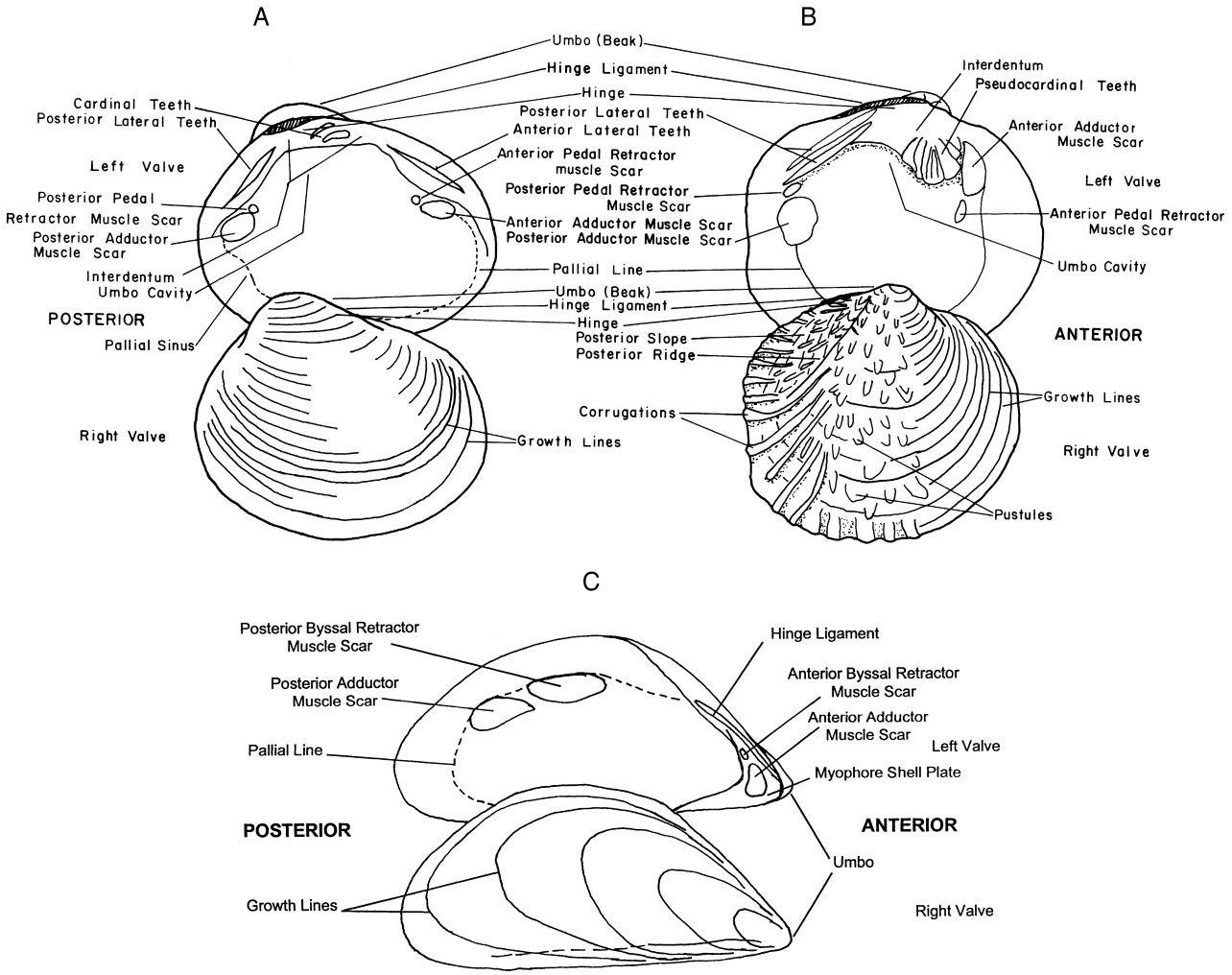

FIGURE 1 General morphological features of the shells of (A) corbiculoidean, (B) unionoidean, and (C) dreissenoidean freshwater bivalves.

The NA bivalve fauna is the most diverse in the world, consisting of approximately 308 extent native and seven introduced taxa (Turgeon *et al.*, 1998). The majority of species fall in the superfamily Unionoidea with 278 native NA and 13 recognized subspecies in 49 genera in the family, Unionidae and five species in two genera in the family, Margaritiferidae. Many species in this group have unique morphological adaptations and highly endemic, often endangered populations (Neves *et al.*, 1997). In the superfamily, Corbiculoidea, the family Sphaeriidae, has 36 native and four introduced NA species. While falling into only four genera, the Sphaeriidae are more cosmopolitan than unionoideans (note "unionoideans" as used here refers to all species within the superfamily, Unionoidea while "unionid" used later in the chapter refers only to those unionoidean species in the family, Unionidae), several genera and species having pandemic distributions. *Corbicula fluminea* falls within the Corbiculacea (family Corbiculidae). This species invaded NA freshwaters in the early 1900s and now extends throughout the coastal and southern United States and Mexico, becoming the dominant benthic species in many habitats (McMahon, 1983a,1999). More recently, two dreissenid species, *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel) have invaded North America. *D. polymorpha* was discovered in Lake St. Clair and Lake Erie in 1988 after introduction in 1986. It now extends throughout the Great Lakes, St. Lawrence River, and the Mississippi River and most of its major tributaries (Mackie and Schloesser, 1996). *D. bugensis* was first found in the Erie-Barge Canal and eastern Lake Erie, NY, in 1991 and has since spread through Lakes Erie and Ontario and the St. Lawrence River (Mills *et al.*, 1996). Both species are likely to have been simultaneously introduced as planktonic veliger larvae released with ballast water from ships entering the Great Lakes from ports on the Bug and

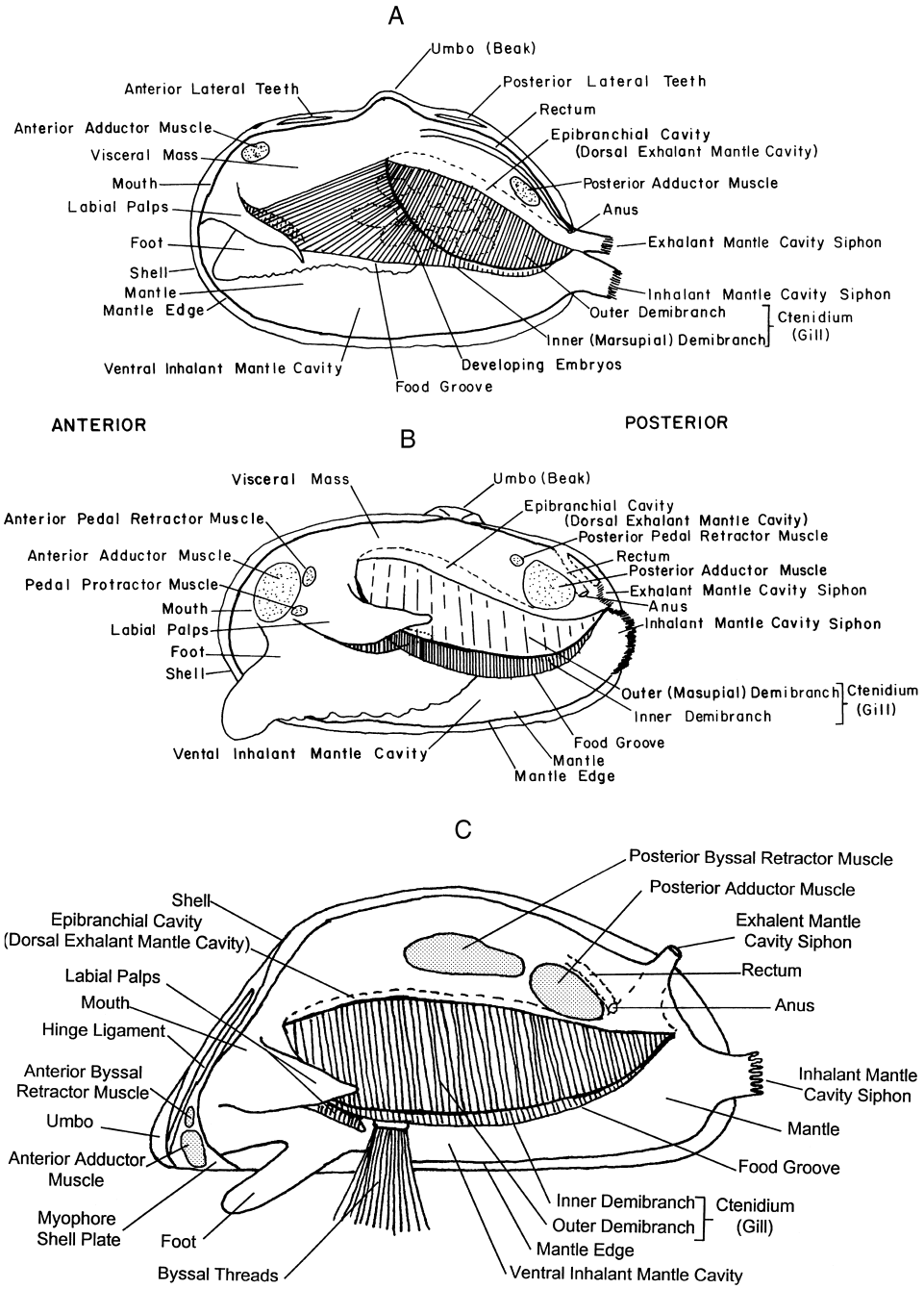

FIGURE 2 General external anatomy of the soft tissues of (A) corbiculoidean, (B) unionoidean, and (C) dreissenoidean freshwater bivalves.

Dnieper rivers in the Black Sea, Ukraine (Marsden *et al.,* 1996, Mills *et al.,* 1996).

II. ANATOMY AND PHYSIOLOGY

NA freshwater bivalves fall into three superfamilies: Unionoidea, Corbiculoidea, and Dreissenoidea. External shell morphology among these groups vary (Fig. 1), but their soft tissue morphologies are relatively similar and, thus, will be discussed in general terms below.

A. External Morphology

1. Shell

Bivalve shells consist of calcium carbonate ($CaCO_3$) crystals embedded in a proteinaceous matrix, both secreted by underlying mantle tissue. In most

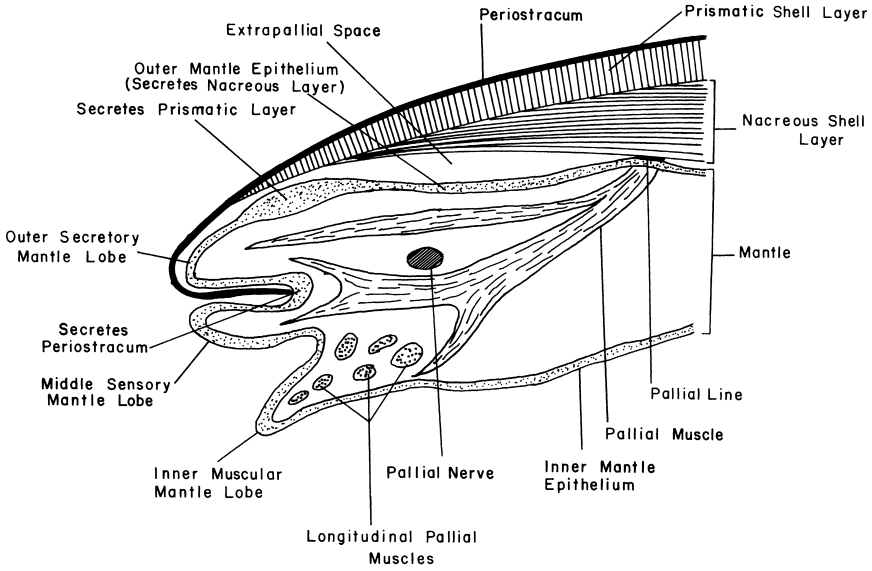

FIGURE 3 A crosssection through the mantle and shell edges of a typical freshwater unionoidean bivalve displaying the anatomic features of the shell, mantle, and mantle edge. Sphaeriids have a complexed cross-lamellar shell structure and lack nacre, but their mantle edge has a similar structure.

bivalves, the shell consists of three parts: an outer proteinaceous periostracum secreted from the periostracal groove in the mantle edge, and underlying, calcareous prismatic and nacre layers in which $CaCO_3$ crystals are embedded within an organic matrix (Fig. 3). The periostracum is initially secreted free of the other layers, but soon fuses with the underlying prismatic layer secreted by a portion of the mantle edge just external to the periostracal groove (Fig. 3). The prismatic layer consists of a single layer of elongated $CaCO_3$ crystals oriented 90° to the horizontal shell plane (Fig. 3). The periostracum edge seals the extrapallial space between mantle and shell, allowing $CaCO_3$ concentrations in that space to reach saturation levels required for crystal deposition (Saleuddin and Petit, 1983). The tanned protein of the periostracum is impermeable to water, preventing shell $CaCO_3$ dissolution. Layers of conchiolin (i.e., tanned protein) occurring within unionoidean shells, are suggested to retard shell dissolution in calcium poor freshwaters and are not found in the Corbiculoidea or Dreissenoidea (Kat, 1985). The nacreous layer is continuously secreted by underlying mantle epithelium. It consists of consecutive layers of small $CaCO_3$ crystals deposited parallel to the shell plane embedded in an organic matrix of chitinlike mucopolysaccharide and protein (Machado *et al.*, 1994) (Fig. 3). Microstructure and texture patterns of $CaCO_3$ crystals differ among major molluscan classes and interspecifically within groups (Hedegaard and Wenk, 1998). Continual secretion of the nacreous layer thickens and strengthens the shell, thus accounting for most of its mass.

Calcium (Ca^{2+}) and bicarbonate (HCO_3^-) necessary for shell $CaCO_3$ crystal deposition are transported from the external medium across the body epithelium into the hemolymph (blood). HCO_3^- ions are also generated from metabolically released CO_2 reacting with hemolymph water ($CO_2 + H_2O \rightleftarrows H^+ + HCO_3^-$). These ions are actively transported across the mantle into the extrapallial fluid for $CaCO_3$ deposition into the shell matrix (Wilbur and Saleuddin, 1983).

$CaCO_3$ crystal formation requires release of protons (H^+) ($Ca^{2+} + HCO_3^- \rightleftarrows CaCO_3 + H^+$) which must be removed from the extrapallial fluid in order to maintain the high pH required for $CaCO_3$ deposition (extrapallial fluid pH 7.4–8.3). It is proposed that H^+ combines with HCO_3^- to form H_2CO_3, followed by dissociation into CO_2 and H_2O which diffuse from the extrapallial fluid into the hemolymph. The enzyme, carbonic anhydrase, which catalyzes this reaction, is present in mantle tissue (Wilbur and Saleuddin, 1983). Extrapallial fluid pH is higher in freshwater than marine bivalves, favoring shell $CaCO_3$ deposition at the lower Ca^{2+} concentrations of the dilute hemolymph of freshwater species (Wilbur and Saleuddin, 1983).

$CaCO_3$ and shell matrix precipitate from the extrapallial fluid. Ca^{2+} and HCO_3^- are actively concentrated in the extrapallial fluid, thus favoring $CaCO_3$ deposition (Wilbur and Saleuddin, 1983). The organic shell matrix separates individual calcareous crystals

and binds them with the crystal layers into a unified structure. It also has crystal-nucleating sites (possibly composed of Ca^{2+}-binding polypeptides) on which $CaCO_3$ crystals initially form. $CaCO_3$ crystals grow on these sites to produce a new layer of nacre (Wilbur and Saleuddin, 1983).

A minimum of one ATP appears to be required for deposition of two Ca^{2+}ions, with additional ATP required for active HCO_3^- transport (Wilbur and Saleuddin, 1983). Thus, fast-growing bivalves or those with massive shells must devote increased proportions of maintenance energy to shell mineral deposition. Deposition of shell organic matrix and periostracum also requires metabolic energy in the form of four ATP for every peptide bond. Although rarely more than 10% of shell dry mass, the shell organic matrix can account for 30–50% of the total dry organic matter (i.e., shell + tissue organic matter), requiring up to one-third of the total energy allocated to organic growth (Wilbur and Saleuddin, 1983). Fast-growing, thin-shelled species may devote proportionately less assimilated energy to shell production than slower growing, thick-shelled species, allowing greater energy allocation to tissue growth and reproduction, thereby increasing fitness. However, a thinner, more fragile shell increases probability of predation, lethal desiccation or damage and/or dislodgment from the substrate, reducing fitness. Shell sculpture and shape appear highly correlated with habitat among unionoideans. Species adapted to soft substrates in low-flow habitats have thinner shells, with smaller hinge teeth and greater lateral compression preventing sinking into the substrate while those adapted to faster flowing habitats with harder substrates have, thicker, more inflated, more sculptured shells which anchor them more firmly in the substrate, preventing dislodgment during high water flow (Watters, 1994a). Similarly, concentric sulcations on the shells of *Corbicula fluminea* increase anchoring capacity in their lotic habitats (McMahon, 1999). Therefore, the ratio of energy allocation to shell versus tissue growth appears to be an adaptive strategy, energetic trade-offs between these two processes being evolved under species-specific niche selection pressures (see Section III.B).

Shell external morphology varies among species. Externally, shells may have concentric or radial corrugations of varying sizes and densities, ridges, pigmented rays or blotches in the periostracum. These features, along with shape of the posterior shell ridge and overall shell shape are major taxonomic characters for distinguishing species (see Section V). Another major external shell feature is the umbo or beak, an anteriorly curving, dorsally projecting structure on each valve, which is the oldest portion of the shell (Fig. 1).

Major internal shell features include the hinge and projecting hinge teeth, which interlock to hold the valves in exact juxtaposition, forming the fulcrum on which they open and close, and various mussel scars. These can also be major taxonomic characters (see Section V). In corbiculids, massive conical cardinal teeth form just below the umbos (one in the right and two in the left valve), anterior and posterior of which lie lateral teeth, usually in the form of elongate lamellae (Fig. 1A). In contrast, unionoideans have no true cardinal teeth. Instead, massive, raised, pseudocardinal teeth develop near the umbonal end of the anterior lateral teeth, serving a function similar to cardinal teeth. Elongated, lamellar, posterior lateral teeth extend posteriorly from the umbos (Fig. 1A). Among the unionoideans, hinge teeth are vestigial or lost in the tribe Anodontini. The superfamily, Dreissenoidea, is characterized by a mussel-type shell without teeth in which the anterior end is greatly reduced and posterior end expanded. Thus, the umbos lie at the anterior end making the shell decidedly, anteriorly pointed (Fig. 1C). The nacre of freshwater bivalve shells may have species-specific colors. Internal-shell muscle scars mark the insertion points of anterior and posterior adductor muscles, anterior and posterior pedal (foot) retractor muscles, pedal protractor muscles and pallial line muscles which attach the mantle margin to the shell (Figs. 2 and 3). Posteriorly, the pallial line may be indented marking the pallial sinus into which inhalant and exhalant siphons are withdrawn during valve closure. The extent of the pallial sinus is directly correlated with size and length of the siphons.

2. Locomotory Structures and Burrowing

With the exception of epibenthic dreissenoids which attach to hard substrates with proteinaceous byssal threads, the vast majority of NA freshwater bivalves burrow in sediments. Some species lie on a hard substrate, using the foot to wedge into crevices or under rocks. All species locomote with a muscular, motile, anterio-ventrally directed, protrusile foot (Fig. 2).

Bivalve burrowing has been detailed by Trueman (1983) and described for the unionidean, *Anodonta cygnea* (Wu, 1987). The burrowing cycle begins with relaxation of the adductor muscles, allowing shell valves to open against the substratum by hinge ligament expansion, thus anchoring the shell in place. Contraction of transverse and circular muscles around pedal hemolymph sinuses (i.e., open blood spaces) causes the foot to narrow and lengthen, forcing it anteriorly into the substrate. Once extended, its distal tip is anchored either by expansion with hemolymph or lateral curving into the substrate. Shell adductor muscles then contract, rapidly closing the valves, releasing their hold on the

substrate. Rapid valve closure expels a jet of water from the mantle cavity, anteriorly through the pedal gape, loosening compacted sediments at the anterior shell margin. Thereafter, alternating contraction of anterior and posterior pedal retractor muscles simultaneously rock the anterior shell margin dorsoventrally and pull it forward into the loosened sediments against the anchored foot tip. Once a new position is achieved, shell adductor muscles relax, re-anchoring the open valves in the substrate, reinitiating the burrowing cycle. NA freshwater bivalves have relatively short siphons (the mantle edges are not fused to form true siphons in unionoideans and siphons are highly reduced or absent in some species of *Pisidium*), thus, they generally are found either just beneath the sediment surface or with the posterior shell margins just above it. Living near the sediment surface can lead to dislodgment, thus a number of riverine unionoidean taxa have shell and pedal morphologies adapted for rapid reburial (Watters, 1994a).

Many juvenile freshwater bivalves crawl considerable distances over the substrate before settlement, holding the shell valves upright on an extended, dorsoventrally flattened foot. Such surface locomotion also occurs among adult sphaeriids (Wu and Trueman, 1984) and in juvenile *C. fluminea* (observed by the author). Crawling involves extension of the foot, anchoring its tip with mucus and/or a muscular attachment sucker, followed by pedal retractor muscle contraction which pulls the body forward. Pedal surface locomotion is reduced or lost in most adult unionoideans, but is retained to varying degrees in adult sphaeriids, *C. fluminea* and dreissenids. Adult dreissenids may spontaneously release from the byssus and crawl long distances before re-attachment. Single byssal threads are produced during crawling to prevent dislodgment. Pedal locomotion is particularly common in juvenile and immature dreissenids and allows their escape from locally poor conditions or highly dense mussel clumps (Clarke and McMahon, 1996a).

B. Organ-System Function

1. Circulation

Bivalves have an 'open' circulatory system in which hemolymph is not always enclosed in vessels. Rather, circulatory fluid is carried by vessels from the heart to various parts of the body where it passes into open, spongy hemocoels (i.e., blood sinuses). In the hemocoels, it bathes tissues directly, percolating through them before returning to the heart via the gills. Circulatory fluid in open systems is called "hemolymph." Bivalves have large hemolymph volumes, accounting for 49–55% of total body water (Jones, 1983). The bivalve heart ventricle uniquely surrounds the rectum and pumps oxygenated hemolymph from the gills and mantle via the kidney through anterior and posterior vessels (Jones, 1983, Narain and Singh, 1990) (Fig. 4) which subdivide into smaller vessels to various parts of the body, including pallial arteries to the mantle and visceral arteries to the visceral mass and foot. These secondary arteries further subdivide into many tiny vessels that open into the hemocoels where cellular exchange of nutrients, gases, and wastes occurs. Thereafter, deoxygenated hemolymph is carried from the body tissues and organs to the mantle and gills to be reoxygenated and, thence, to the heart. Evolution of an open circulatory system in molluscs, including bivalves, is associated with coelom reduction. The heart ventricle is surrounded by a coelomic remnant, the "pericardial cavity," enclosed by the pericardial epithelium or "pericardium." Other coelomic remnants include spaces comprising the kidneys ('coelomoducts') and gonads (Jones, 1983).

Like most bivalves, the hemolymph of all freshwater species has no specialized respiratory pigments for O_2 transport (Bonaventura and Bonaventura, 1983). Instead, O_2 is transported dissolved directly in the hemolymph fluid which has an O_2-carrying capacity essentially equivalent to water. The very low metabolic demands and extensive gas exchange surfaces (mantle and gills) of bivalves allow maintenance of a primarily aerobic metabolism in spite of a reduced hemolymph O_2-carrying capacity. As proteinaceous respiratory pigments are the primary blood pH buffer in most animals, bivalve blood acid–base balance is dependent on other mechanisms (see Section II.C.3).

2. Gills and Gas Exchange

In lamellibranch bivalves, including all NA freshwater species, the gills are expanded beyond the requirements for gas exchange as they are also used for suspension (filter) feeding (Fig. 2), the main mode of food acquisition for the majority of species (see Section III.C.2). The left and right gills, or ctenidia, consist of an axis which extends anterolaterally along the visceral mass. Many long, thin, inner and outer filaments extend laterally from the axis. In all NA freshwater bivalves, filaments are fused together (an evolutionarily advanced condition) and penetrated by a series of pores or ostia (i.e., eulamellibranch condition). From the axis, the filaments first extend ventrally (descending filament limbs) and then reflect dorsally (ascending filament limbs) to attach distally to the dorsal mantle wall (outer filaments) or the dorsal side of the visceral mass (inner filaments), forming two V-shaped, porous curtains called the outer and inner "demibranchs" (Fig. 5).

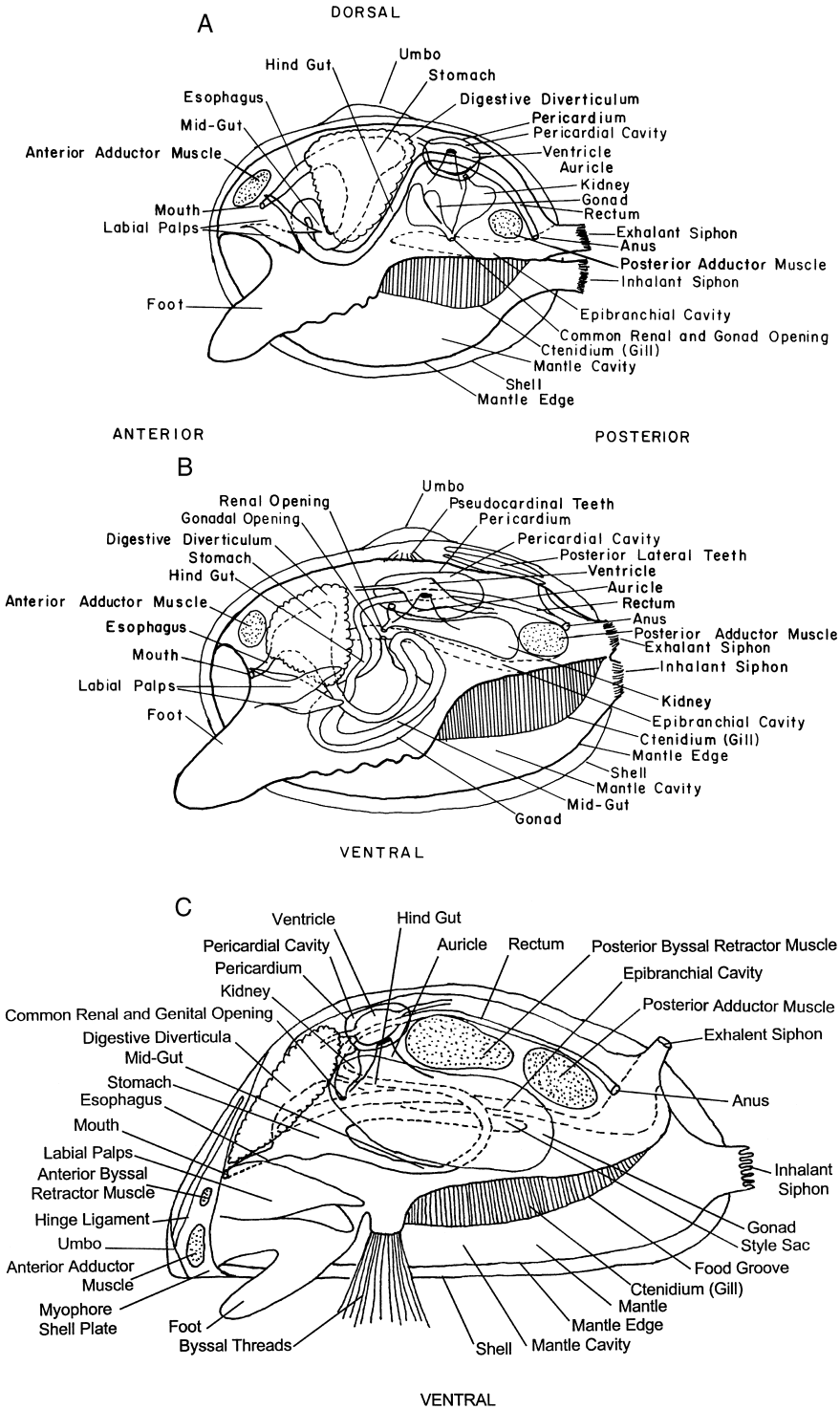

FIGURE 4 General internal anatomy, organs, and organ systems of the soft tissues of (A) corbiculoidean, (B) unionoidean, and (C) dreissenoidean freshwater bivalves.

The demibranchs completely separate the mantle cavity into ventral inhalant and dorsal exhalant portions. The descending and ascending filament limbs are held closely adjacent by tissue bridges called "interlamellar junctions" and enclose an area called a "water tube" or interlamellar space (Fig. 5).

Feeding and respiratory currents are sustained by 'lateral cilia' on the adjacent external filament surfaces

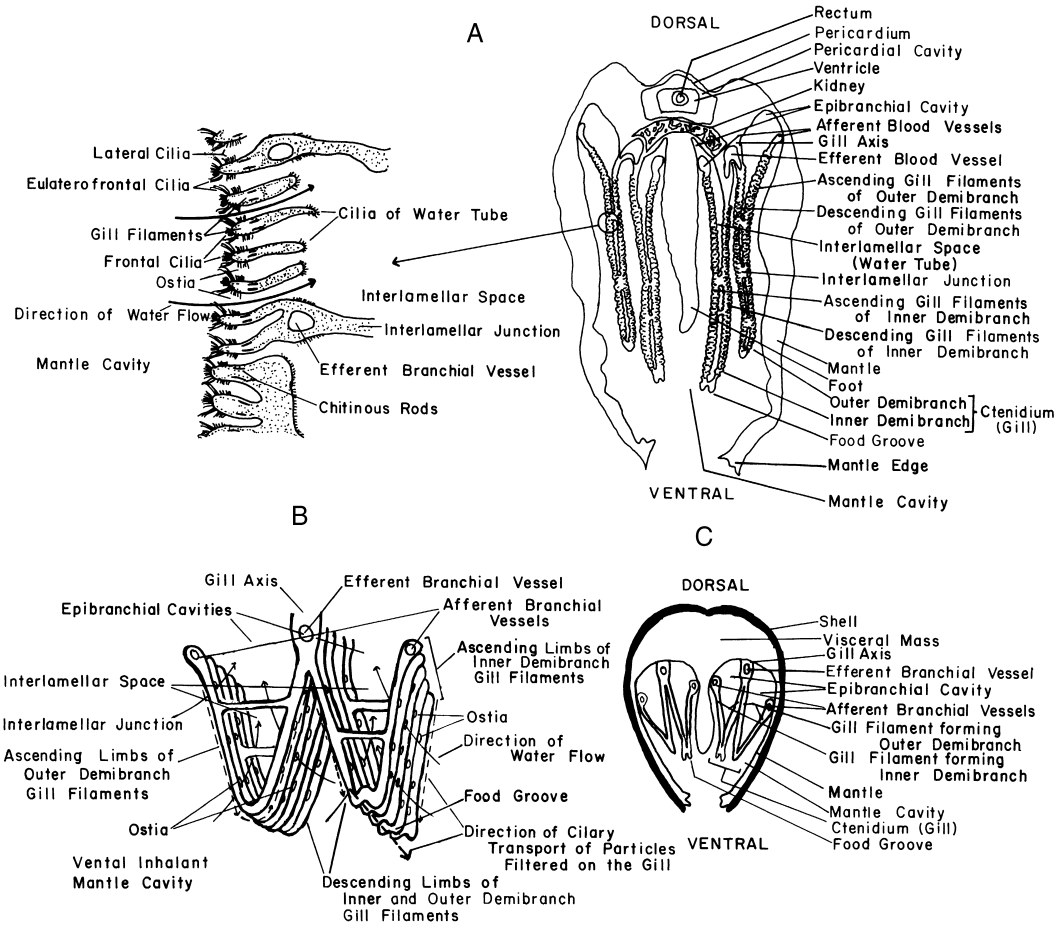

FIGURE 5 The structural features of the gills (ctenidia) of freshwater bivalves. (A) Cross section through the central visceral mass, ctenidia, and mantle of a typical freshwater unionoidean, with high magnification view showing details of filaments, ostia, and ciliation. (B) Diagrammatic representation of the respiratory and feeding currents across the ctenidium. (C) Diagrammatic cross-sectional representation of lammellibranch bivalve ctenidia.

(Fig. 5). They drive water entering the inhalant mantle cavity via the inhalant siphon or siphonal notch through the ostia between filaments into the water tubes. Water passes dorsally up the water tubes into the dorsal 'exhalant mantle cavity,' called the "suprabranchial cavity" or "epibranchial cavity," formed above the ctenidial curtain where it flows posteriorly, exiting via the exhalant siphon or siphonal notch (Figs. 2 and 5).

While the lateral cilia drive water across the gill, rate of water flow is partially controlled by size of the ostia. In unionoideans, two muscle bands control ostial pore size. Antero-posterior oriented muscle bands are attached to vertically oriented chitinous filament supporting rods which alternate with rows of ostia. Horizontal muscle contraction pulls adjacent supporting rods together to reduce ostial pore diameter, slowing water flow. A second set of muscle bands run dorsoventrally between rows of ostia and, when contracted, increase ostial diameter, increasing flow rate. Ostial diameter of unionoidean gills increased 2–3 times with external application of the neurotransmitter, serotonin, and external serotonin and dopamine application increased lateral cilia activity, suggesting that gill water flow is ultimately under nervous system control (Gardiner *et al.,* 1991). Similar muscular control of ostial diameter occurs in *Dreissena polymorpha* where contraction of horizontally oriented muscle bands and spincterlike ostial muscles reduce ostial diameter, slowing water flow. External application of serotonin relaxes these muscles increasing ostial diameter and gill water flow (Medler and Silverman, 1997).

3. Excretion and Osmoregulation

Freshwater bivalves, like all freshwater animals, have hemolymph and tissue osmotic concentrations

greater than the very dilute freshwater medium, resulting in constant ion loss and water gain. Osmoregulatory problems are compounded by the extensive gill and mantle surfaces of bivalves over which ion and water fluxes occur (Dietz, 1985). To reduce these fluxes, freshwater bivalves have evolved the lowest hemolymph and cell osmotic concentrations of any metazoan, being 20–50% of that found in most other freshwater species (Dietz, 1985). In spite of their reduced osmotic concentration, the extensive epithelial surfaces of bivalves still cause water and ion fluxes to be greater than those recorded in other freshwater species, leading to urine clearance rates of 20–50 ml/k per hour (Dietz, 1985).

In unionoideans, Na^+ is taken up in exchange for outward transport of the metabolic waste cations, H^+ and NH_4^+, and, perhaps, Ca^{2+}. Chloride (Cl^-) ion uptake is in exchange for metabolically produced HCO_3^- or OH^-. Active Ca^{2+} uptake also occurs (Burton, 1983). In freshwater snails, the major source of Ca^{2+} is ingested food (McMahon, 1983b), while the relative roles of food and transport in the Ca^{2+} balance of freshwater bivalves are unknown. Sodium ion (Na^+) uptake does not require presence of Cl^- which is indicative of separate transport systems for these ions (Burton, 1983); however, freshwater dreissenids appear to co-transport Na^+ and Cl^- (Horohov *et al.,* 1992). While active transport is the major route by which unionoideans gain ions, exchange diffusion (i.e., transport of an ion linked with diffusion of a second ion species down its concentration gradient) accounts for 67% of Na^+ uptake in *C. fluminea*. *C. fluminea* and *D. polymorpha* have higher ion-transport rates than unionoideans and sphaeriids, reflecting their geologically recent penetration of freshwaters (Dietz, 1985, Horohov *et al.,* 1992, Wilcox and Dietz, 1995). *C. fluminea* has a hemolymph solute concentration that is higher (Dietz, 1985) and *D. polymorpha,* that is lower than most other freshwater bivalves (Dietz *et al.,* 1996a). The low hemolymph ion-concentration of *D. polymorpha* occurs in spite of its high rates of active ion uptake, indicating that it is much more ion-permeable than other freshwater bivalves, perhaps due to its recent evolutionary invasion of freshwaters (Dietz *et al.,* 1994, 1995, 1996a, b). In contrast, epithelial ion permeability in *C. fluminea* is low (Zheng and Dietz, 1998a) and active ion uptake rate high (Zheng and Dietz, 1998b), allowing maintenance of higher hemolymph ion concentrations and tolerance greater ambient osmolarity variation than other freshwater bivalves (Zheng and Dietz, 1998b). Interestingly, exchange diffusion may account for up to 90% of Cl^- turnover in unionoideans in pond water, but when salt-depleted, active transport dominates Cl^-uptake (Dietz, 1985). Na^+ and Cl^- uptake can occur over the body epithelia in unionoideans, but the majority occurs over the gills (Dietz, 1985), with the epithelial cells of water canals connecting gill ostia to water tubes being a major site for active ion and osmotic regulation (Kays *et al.,* 1990). Active ion uptake and hemolymph-ion concentrations in unionoideans and, by inference, other freshwater bivalves, may be regulated by neurotransmitter substances released by gill neurons (Dietz *et al.,* 1992).

Excess water is eliminated via coelomoducts or kidneys. The heart auricle walls initially ultrafilter the blood. Hydrostatic pressure generated by auricle contraction forces blood fluid, ions and small organic molecules through the auricle walls into the pericardial cavity surrounding the heart. Filtration occurs through podocyte cells of the pericardial gland lining the inner auricular surface and, perhaps, through the efferent branchial vein running from the longitudinal kidney vein to the auricles (Martin, 1983) (Fig. 6). Only larger hemolymph protein, lipid and carbohydrate molecules cannot pass the pericardial gland filter. The filtrate exits the pericardial cavity via left and right "renopericardial openings" in the pericardial wall to enter the "reopericardial canals" leading to the left and right kidneys. Larger organic waste molecules are actively transported into the filtrate by the kidney. In the Unionoidea, the rectal wall is extremely thin where surrounded by the ventricle, suggesting that larger organic waste molecules may be transported through it directly into the rectum in this region (Narain and Singh, 1990). Competed excretory fluid passes via "nephridiopores" into the epibranchial cavity to be carried on exhalant water flow out the exhalant siphon (Figs. 2 and 4A) (Martin, 1983).

While little studied in freshwater bivalves, the kidney is the presumed site of major active ion resorption from the filtrate into the hemolymph. Dietz and Byrne (1999) have demonstrated reabsorption of filtrate sulfate ion (SO_4^{-2}) in the kidney of *D. polymorpha*. As kidney walls appear relatively impermeable to water, active filtrate-ion resorption leads to formation of a dilute excretory fluid facilitating excess water excretion with filtrate osmolarity being 50% that of hemolymph in the unionid, *Anodonta cygnea* (Martin, 1983). Filtrate-ion reabsorption is less energetically expensive than active-ion uptake from the freshwater medium because ion-concentration gradients between coelomoduct fluid and hemolymph are far less than those between hemolymph and freshwater.

Due to rapid water influx, an elevated excretory fluid production is required in freshwater bivalves to maintain osmotic balance, being approximately 0.03 mL/g wet tissue per day in *A. cygnea* (Martin, 1983). In *D. polymorpha* excretory fluid production was 2–3 mL/g dry

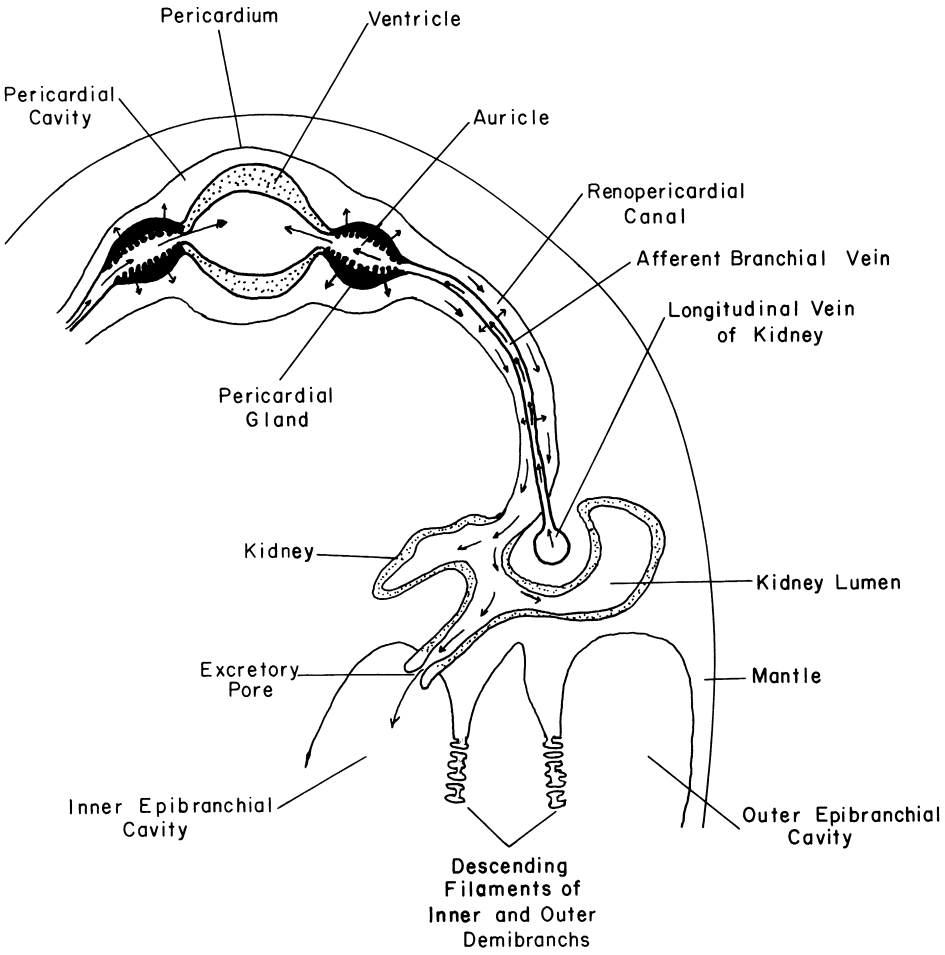

FIGURE 6 Cross-sectional representation of the anatomic features of the excretory system of a typical freshwater bivalve. Arrows indicate pathways for the excretion of excess water in the hemolymph through the excretory system to be eliminated at the excretory pore (redrawn from Martin, 1983).

tissue per day (Dietz and Byrne, 1999) which, when converted to a wet tissue weight value of 0.1–0.15 mL/g dry tissue weight per day (based on dry tissue weight being 0.05 wet tissue weight) is 3.3–5.0 times greater than that of *A. cygnea* (Martin, 1983), reflecting the high epithelial osmotic permeability of *D. polymorpha* compared to other freshwater bivalves (Dietz *et al.,* 1996a, b). In spite of renal ion absorption, the excretory fluid of freshwater bivalves has a considerably higher ion concentration than freshwater, making excretion a major avenue of ion loss. Ions lost by excretion and epithelial diffusion are recovered by active transport from the medium across epithelial surfaces, particularly that of the gills (Dietz, 1985, also see Section II.C.6).

The main nitrogenous waste product of freshwater bivalves is ammonia (NH_3) diffused across external epithelia as dissolved NH_3 or ammonium ion (NH_4^+). NH_4^+ can also be actively transported to the external medium. In marine bivalves, 65–72% of nitrogen excretion is as ammonia/ammonium ion and 13–28% as urea (Florkin and Bricteux-Gregoire, 1972), values likely to be similar in freshwater species. Some freshwater unionoideans appear to be able to detoxify ammonia/ammonium ions by conversion to urea and, perhaps, amino acids and proteins (Mani *et al.,* 1993).

4. Digestion and Assimilation

Freshwater bivalves are suspension (filter) feeders, filtering algae, bacteria and suspended microdetrital particles from water flowing through the gill. Filtered material is transported by gill ciliary tracks to the "labial palps" where it is sorted on corrugated ciliated surfaces into food and nonfood particles before food particles are carried by cilia to the mouth. Some freshwater species may also utilize the foot to feed on sediment organic detrital particles (Reid *et al.,* 1992). Filter and pedal detritus feeding are described in Section III.C.2, while this section is devoted to food digestion and assimilation.

The bivalve mouth is a simple opening flanked laterally by left and right pairs of labial palps, whose ciliary tracks deliver filtered food from the gills to the mouth as a constant stream of fine particles. After ingestion, food particles pass through a short, ciliated esophagus where mucus secretion and ciliary action bind them into a mucus string before entering the stomach. The stomach, lying in the anterio-dorsal portion of the visceral mass (Fig. 4), is a complex structure with ciliated sorting surfaces and openings to a number of digestive organs and structures. On its ventral floor, posterior to the opening of the midgut, is an elongated, evaginated, blind-ending tube, the "style sac." The distal end of the style sac secretes the "crystalline style," a long mucopolysaccharide rod that projects from the style sac into the stomach. Style-sac cells secrete digestive enzymes into the style matrix and have cilia which slowly rotate the style. Stomach and style pH ranges from 6.0–6.9, acidity depending on phase of digestion (Morton, 1983).

The rotating style tip projects against a chitinous plate or "gastric shield" on the dorsal roof of the stomach. The gastric shield is penetrated by microvilli from underlying epithelial cells, believed to release digestive enzymes onto the shield surface (Morton, 1983). Style rotation mixes stomach contents and winds the esophageal mucus food string on to the style tip where slow release of its embedded enzymes begins extracellular digestion. Abrasion of the style tip against the gastric shield, triturates food particles and allows their further digestion by enzymes released from the eroding style matrix and from digestive epithelial cells underlying the shield.

After initial trituration and digestion at the gastric shield, food particles released into the stomach may have several fates. Particles are size-sorted. A ciliated ridge, the "typhlosole," running the length of the midgut returns large particles to the stomach for further digestion and trituration and eventually selects and passes indigestible particles to the hindgut/rectum for egestion. Ciliated surfaces on the posterior "sorting caecum" of the stomach direct sufficiently small food particles into tubules of the "digestive diverticulum" for final intracellular digestion (Fig. 4). The diverticula have the lowest fluid pH of the gut (Morton, 1983). Larger food particles falling on the caecum are recycled into the stomach for further trituration and enzymatic digestion, thus particles may pass over its ciliated sorting surfaces several times before acceptance for intracellular digestion or rejection into the rectum to form feces.

Digestive cells lining the lumina of the tiny, blind-ending, terminal tubules of the digestive diverticula take up fine food particles by endocytosis into food vacuoles for final digestion and assimilation. After completion of intracellular digestion/assimilation, the apical portions of the digestive cells, which contain food vacuoles with undigested wastes and digestive enzymes, are shed into the tubule lumina as "fragmentation spherules" which are returned to the stomach on ciliated rejection pathways. Breakdown of fragmentation spherules in the stomach releases their food vacuole contents, hypothesized to be a major source of stomach acidity and extracellular digestive enzymes (Morton, 1983).

Rejected indigestible matter passes through the short hindgut into the rectum for egestion from the anus, opening into the epibranchial cavity on the posterior face of the posterior shell adductor muscle just upstream from the exhalant siphon or opening, allowing feces expulsion on the exhalant current. Undigested particles are consolidated into discrete, dense, fecal pellets by mucus secreted by the hindgut/rectum, preventing their uptake on the inhalant current.

The cerebropleural and visceral ganglia release neurohormones which influence glycogenesis (Joosse and Geraerts, 1983). The vertebrate glycogenic hormones, insulin and adrenalin, have similar effects on unionoideans. Insulin injected into the Indian unionid, *Lamellidens corrianus,* resulted in declining hemolymph glucose concentration and increase in pedal and digestive diverticular glycogen stores, while adrenaline injection induced glycogen store breakdown and increased hemolymph sugar concentration (Jadhav and Lomte, 1982b). Elevated hemolymph glucose concentrations stimulates gut epithelial cells to produce an insulin-like substance in the unionoideans, *Unio pictorum* and *A. cygnea,* which stimulated activity of glucose synthetase, increasing uptake of hemolymph glucose into glycogen stores (Joose and Geraerts, 1983). Cerebropleural ganglionic neurosecretory hormones regulate pedal and digestive diverticular accumulation and release of protein and nonprotein stores in *L. corrianus* (Jadhav and Lomte, 1983).

5. Reproductive Structures

The paired gonads of freshwater bivalves lie close to the digestive diverticula. Among unionoideans, their paired condition is difficult to discern. Unionoidean gonads envelop the lower portions of the intestinal tract and sometimes extend into the proximal portions of the foot (Fig. 4B), while those of sphaeriids, *C. fluminea,* and freshwater dreissenids lie more dorsally in the visceral mass, extending on either side of the stomach, intestine and digestive diverticula (Fig. 4A, and C; Mackie, 1984; Claudi and Mackie, 1993). A short gonoduct leading from each gonad opens into the epibranchial cavity allowing gamete release on exhalant

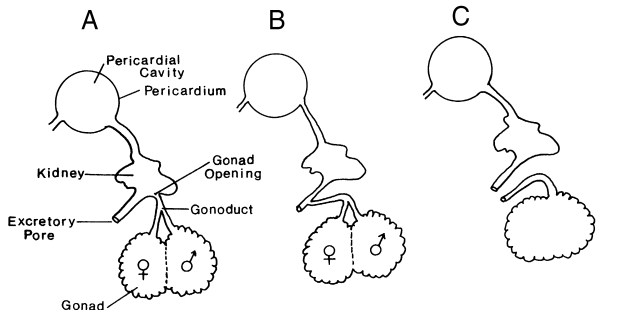

FIGURE 7 Schematic representations of typical reproductive systems of bivalves. (A) The primitive condition in some marine bivalve species: male or female gametes are released from the gonoduct opening into the kidney and passed externally through the excretory pore (shown here is a primitive marine hermaphroditic bivalve; the anatomy is essentially similar in gonochoristic species). (B) Hermaphroditic freshwater corbiculoidean bivalves (*Corbicula fluminea* and sphaeriids): male and female gametes are passed through the gonoducts into the kidney duct close to the excretory pore from which gametes are shed. (C) Gonochoristic freshwater unionoideans: gametes pass to the outside through a gonoduct and gonopore totally separate from the kidney duct and excretory pore. (After Mackie, 1984.)

currents (Fig. 4). Among unionoideans, which are generally gonochoristic except for a few hermaphroditic species of Anodontinae and Ambleminae (Hoeh *et al.*, 1995), the tracts and openings of the renal and reproductive systems are entirely separate, an advanced condition (Fig. 7C). In sphaeriids and *C. fluminea,* which are hermaphroditic, the gonads have distinct regions in which either male or female acini produce sperm or eggs. In these latter groups and the gonochoristic freshwater dreissenids, ducts carrying eggs or sperm unite into a single gonoduct carrying gametes from each gonad into the distal end of the kidney—allowing gamete discharge into the epibranchial cavity via the nephridial canal and nephridiopore (Fig. 7A)—or directly into the nephridial canal, discharging through a common pore on a papilla in the epibranchial cavity (Fig. 7B; Mackie, 1984; Kraemer *et al.*, 1986).

Almost all NA freshwater bivalves are ovoviviparous, brooding developing embryos in specialized gill marsupia. Only the dreisssenids release sperm and eggs externally, leading to development of free swimming larvae (Nichols, 1996). In brooding species, interlamellar spaces are modified to form gill marsupia (brood chambers). Fully formed juveniles are released from the marsupia via the exhalant siphon in sphaeriids and *C. fluminea*. In unionoideans, bivalved "glochidia larvae" are released from either the exhalant siphon, specialized gill pores, or ruptures in the ventral margin of the marsupial gills. Unionoidean glochidia parasitize fish hosts before metamorphosing into free—living juveniles. Interlamellar spaces of the outer demibranch form marsupia in unionoideans except in the subfamily, Ambleminae, which form marsupia in both demibranchs (Burch, 1975b). In contrast, marsupia form in the inner demibranchs of sphaeriids and *C. fluminea*. Among species of the unionid genus, *Lampsilis,* marsupia develop only in the posterior portions of the outer demibranch from which glochidia are released through small pores directly into the inhalant siphon (for further details, see Section III.B.1).

In *C. fluminea,* interlamellar marsupial brooding spaces have no specialized structures. In sphaeriids, embryos are enclosed in specialized brood chambers evaginated from gill filaments into the interlamellar space. Among anodontid unionids, the marsupial interlamellar space is divided by septa into separate chambers associated with each filament. Each space is further subdivided by lateral septa into a central marsupium and inner and outer water tubes transport water from the gill ostia to the epibranchial cavity, an advanced structure not found in other unionoidean groups. In the primitive unionoidean families, Margartiferidae and Ambleminae, the entire outer demibranch forms the marsupium, while among the more advanced tribes, Pleurobemini and Lampsilini, the marsupia are limited to specific portion of the outer demibranch (Mackie, 1984).

Some unionoidean species display sexual dimorphism, generally rare in other freshwater bivalves. In sexually dimorphic species, glochidial incubation distends the female outer marsupial demibranch (Mackie, 1984). Thus, posterior portions of the valves of female lampsilines are inflated compared to males, accommodating the expanded posterior marsupia. Less obvious general inflation of the female shell occurs in the anodontids (Mackie, 1984).

Monoecious unionoideans (some species Anodontinae and Ambleminae) and all sphaeriids are generally simultaneous hermaphrodites, concurrently producing mature eggs and sperm. *C. fluminea* has an unusual pattern of producing only eggs early after maturity (shell length $\approx$6 mm) followed later by sperm production, thereafter, remaining simultaneously hermaphroditic throughout life (Kraemer and Galloway, 1986).

Bivalves lack copulatory organs. Except for dreissenids which release both sperm and eggs externally (Nichols, 1996), freshwater bivalves release only sperm externally which is transported on inhalant currents of other individuals to unfertilized eggs in the gill marsupia. Among corbiculids, self-fertilization appears common in sphaeriids, occurring near the conjunction of male and female gonoducts (Mackie, 1984), while, in *C. fluminea,* embryos frequently occur in the lumina of gametogenic follicles and gonoducts, indicative of self fertilization within the gonad (Kraemer *et al.,* 1986). Self-fertilization makes hermaphroditic species highly invasive (see Section III.B).

Temperature appears to be the main reproductive stimulus in most freshwater bivalves. Gametogenesis and fertilization are initiated above and maintained within critical ambient water temperature thresholds. Other environmental factors which may influence reproduction include: neurosecretory hormones, density dependent factors, diurnal rhythms, food availability and parasites. Evidence for neurosecretory and density controls has been demonstrated in sphaeriids (Mackie, 1984). Zebra mussels spawn in response to the neurosecretory hormone, serotonin, and presence of algal extracts (Ram *et al.,* 1996). Evidence of increasing activity and metabolic rate during dark hours in unionoideans (McCorkle *et al.,* 1979; Englund and Heino, 1994a), *C. fluminea* (McCorkle-Shiley, 1982) and *D. polymorpha* (Borcherding, 1992) suggests that spawning activity and gamete/glochidial/juvenile release rates may also display diurnal rhythmicity.

Sperm of freshwater bivalves may have ellipsoid or conical nuclei and acrosomes of variable complexity (Mackie, 1984). Unionoidean sperm have rounded or short cylindrical heads considered a primitive condition (Rocha and Azevedo, 1990; Lynn, 1994) while that of *Dreissena* and *Corbicula* have elongate heads (Kraemer *et al.,* 1986; Ram *et al.,* 1996). The sperm of *C. fluminea* is uniquely biflagellate (Kraemer *et al.,* 1986). Sperm with elongate heads may be adapted for swimming in gonadal and oviductal fluids more viscous than water and are associated with internal fertilization in gonadal ducts rather in marsupia (Mackie, 1984). However, the elongate-headed sperm of *D. polymorpha* is an exception to this rule, because it externally fertilizes the egg. *D. polymorpha* has sperm with a straight head and an oval, bulbous acrosome while *D. bugensis* sperm has a curved head with a conically shaped acrosome (Denson and Wang 1994). There appears to be specific site for sperm recognition and entry on the vegetal pole of unionoidean eggs (*Truncilla truncata*) where the vitelline coat forms a corrugated surface surrounding a truncated cone (Focarelli *et al.,* 1990).

The eggs of freshwater bivalves are round and have greater yolk volumes than marine species with planktonic larvae. Only freshwater dreissenids have relatively small eggs (40–70 μm) associated with their external fertilization and small, free-swimming veliger larva, which grows considerably in the plankton before settlement and metamorphoses to a juvenile (219–365 μm) (Nichols, 1996). The larger, yolky eggs of all other species contain nourishment supporting development to a more advanced juvenile/glochidium stage. The Sphaeriidae, the smallest adult freshwater bivalves, produce the largest eggs, resulting in very small brood sizes ranging from 6–24 per adult in the genus *Sphaerium,* 1–135 per adult in the genus *Musculium,* and 3.3–6.7 per adult in the genus *Pisidium* (Burky, 1983). Adult *Musculium partumeium,* only 4.0 mm in shell length (SL), release juveniles of 1.4 mm SL (Hornbach *et al.,* 1980; Way *et al.,* 1980). In contrast, unionoideans and *C. fluminea* have smaller eggs and release smaller glochidia/juveniles (generally $<$0.3 mm SL) and have much larger brood sizes (10^3–10^6 per adult) (Burky, 1983; McMahon, 1999). The small eggs of zebra mussels allow them to have massive fecundities of $>10^6$ per adult female (Nichols, 1996) required for successful external fertilization and planktonic larval development. Evolutionary implications of bivalve fecundities are discussed in Section III.B.

The bivalve egg is surrounded by a vitelline membrane that is relatively thin in sphaeriids and thicker in unionoideans and *C. fluminea* (Mackie, 1984). In unionoideans, it remains intact throughout most of embryonic development. It disintegrates during early development in sphaeriids (Heard, 1977), allowing developing embryos to absorb nutrients from brood sacs without embryos and/or from nutrient cells lining the interlamellar spaces of marsupial gills. In dreissenids, the vitelline membrane is lost early to release the free-swimming trochophore larvae which metamorphoses into a planktonic veliger (Nichols, 1996). The vitelline membrane is also lost early to release a free-swimming trochophore retained through development of a juvenile clam in the marsupial gills of *C. fluminea* (Kraemer and Galloway, 1986).

6. Nervous System and Sense Organs

The bivalve head, entirely enclosed within the mantle and shell valves, is not in direct contact with the external environment. Thus, cephalic structures including sense organs have been lost, the head having only a mouth and associated labial palps (Fig. 2). Loss of cephalic sense organs has lead to bivalve nervous system being far less centralized than other advanced molluscan species. A pair of cerebropleural ganglia lateral to the esophagus near the mouth, are interconnected by dorsal, superesophageal commissures (Fig. 8). From these extend two pairs of nerve chords. Paired dorsal nerve chords extend posteriorly through the visceral mass to a pair of visceral ganglia on the anterio-ventral surface of the posterior shell adductor muscle while paired cerebro-pedal nerve chords innervate a pair of pedal ganglia in the foot (Ruppert and Barnes, 1994).

The pedal and cerebropedal ganglia exert motor control over the pedal and anterior shell adductor muscles, while motor control of the siphons and posterior shell adductor muscle is affected by the visceral ganglia. Coordination of pedal and valve movements

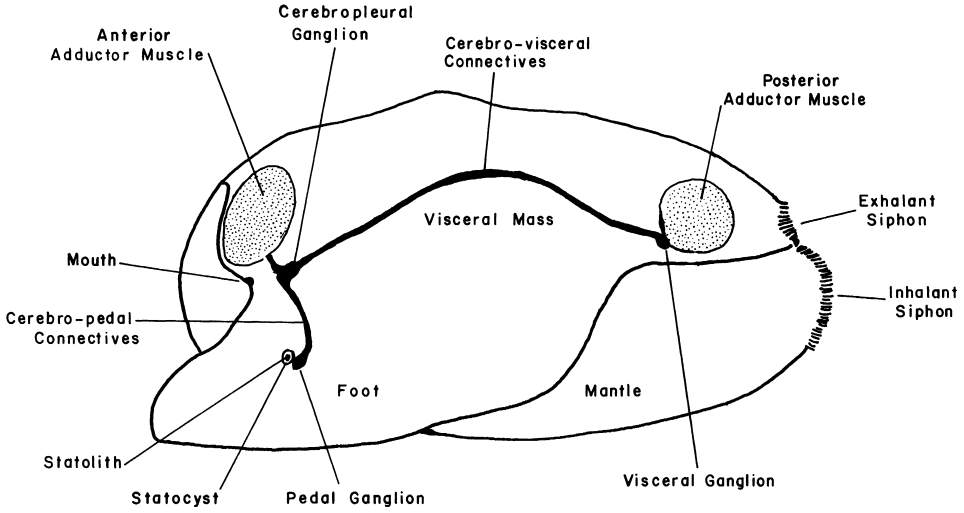

FIGURE 8 The anatomic features of the central nervous system of a typical unionoidean freshwater bivalve (central nervous system anatomy is essentially similar in freshwater corbiculoidean and dreissenoidean bivalves).

during burrowing and locomotion (see Section II.A.2) resides in the cerebropedal ganglia.

Sense organs are concentrated on the mantle edge and in siphonal tissues most directly exposed to the external environment. Mantle edge sense organs are most concentrated on the middle sensory mantle lobe (Fig. 3). Photoreceptor cells detect changes in light intensity associated with shadow reflexes, phototaxis and diurnal rhythms; while tentacles and stiffened, immobile stereocilia are associated with tactile mechanoreceptor organs perceiving direct contact displacement (touch) or vibrations. On the siphon margins, such tactile receptors prevent drawing of large particles into the mantle cavity. When these mechanoreceptors are impinged by large particles, the siphons are closed by sphincter muscles and/or rapidly withdraw to prevent particle entry. Stronger mechanical stimuli to the siphons cause the valves to be rapidly adducted, forcing water from the siphons, ejecting any impinging material. Under intense mantle or siphon stimulation, siphons are withdrawn and the valves tightly closed, a common predator defense behavior in all bivalve species.

A pair of statocysts lying near or within the pedal ganglia are enervated by commissures from the cerebropedal ganglion (Fig. 8). Statocysts are greatly reduced in sessile marine species (i.e., cemented oysters), suggesting their importance to locomotion and burrowing in free-living freshwater species. They are lined with ciliary mechanoreceptors responding to pressure exerted by a calcareous statolith or series of smaller, granular statoconia held within the statocyst vesicle (Kraemer, 1978). As gravity sensing organs, statocysts detect body orientation and, thus function in geotactic and positioning responses during burrowing and pedal locomotory behavior.

Bivalves have a pair of organs called osphradia on the dorsal wall of epibranchial cavity, underlying the visceral ganglion in unionoideans and *C. fluminea* (Kraemer, 1981). Because they are profusely enervated, and neuronally connected to the visceral ganglion, shell adductor muscles and kidney, they have been considered sense organs, but their sensory function(s) are debated. In gastropods, where osphradia are located on the incurrent side of the ctenidium, they have been considered to be mechanoreceptors, sensing suspended particles in inhalant water flow, or chemoreceptors. However, in bivalves, the epibranchial (exhalant) mantle cavity position of osphradia where they receive only filtered water and their lack of extensive neuronal gill connections appear to preclude either a mechano- or chemoreceptor function. Rather, bivalve osphradia are hypothesized to be light sensing organs that control seasonal activities such as spawning, or which provide sensory input to kidney function, and/or diurnal patterns of shell valve adduction (Kraemer, 1981).

C. Environmental and Comparative Physiology

1. Seasonal Cycles

Freshwater bivalves display seasonal physiological responses associated with temperature and reproductive cycles. Metabolic rates vary seasonally in freshwater bivalves (for reviews see Burky, 1983; Hornbach, 1985; McMahon, 1996, 1999) with rates being generally greatest in summer and least in winter due to

TABLE I Seasonal Variation in the Oxygen Consumption Rates ($\dot{V}_{O_2}$) of Selected Species of Freshwater Bivalves

Species and source	*mg dry tissue weight*	*Maximum* $\dot{V}_{O_2}$ *μl* O_2*/h*	*Minimum* $\dot{V}_{O_2}$ *μl* O_2*/h*	*Ratio min:max* $\dot{V}_{O_2}$	$Q_{10(Acc.)}$[a]	*Seasonal temperature range* (°C)
Sphaerium striatinum	25 mg	31.5	1.40	22.5:1	4.7	2–22
Hornbach *et al.* (1983)	7 mg	15.8	0.78	20.3:1	4.5	2–22
	2 mg	8.7	0.24	33.6:1	5.8	2–22
Pisidium compressum	3 mg	0.71	0.04	17.5:1	—	—
Way and Wissing (1984)	0.9 mg	0.27	0.03	9.0:1	—	—
	0.05 mg	0.13	0.02	6.5:1	—	—
Pisidium variabile	3 mg	1.13	0.22	5.14:1	—	—
Way and Wissing (1984)	0.9 mg	0.42	0.10	4.20:1	—	—
	0.05 mg	0.15	0.02	7.5:1	—	—
Pisidium walkeri	1.3 mg	1.11	0.85	1.3:1	1.1	1–26
Burky and Burky (1976)	0.02 mg	0.017	0.0074	2.3:1	1.4	1–26
Corbicula fluminea	348 mg	430.6	34.4	12.5:1	3.2	7–29
Williams (1985)	204 mg	308.2	31.5	9.8:1	2.8	7–29
	60 mg	143.3	25.8	5.6:1	2.2	7–29
Dreissena polymorpha Quigley *et al.* (1992)	—	7.2	2.1	3.6:1	2.3	6–21
Pyganodon grandis	10 g	4690	400	11.7:1	2.7	6–31
Huebner (1982)	5 g	2690	250	10.8:1	2.6	6–31
Lampsilis radiata	5 g	2090	170	12.3:1	2.8	6–31
Huebner (1982)	2 g	810	80	10.1:1	2.6	6–31

[a] $Q_{10(Acc.)}$ is the respiratory Q_{10} value computed from a change in the $\dot{V}_{O_2}$ value recorded for individuals field acclimated to their respective seasonal maximum and minimum temperatures.

temperature effects (Burky, 1983; Hornbach, 1985). Annual variation in metabolic rate can be extensive (Table I). Maximal summer O_2 consumption rates ($\dot{V}_{O_2}$) may be 20–33 times minimal winter rates over a seasonal range of 2–22°C in *Sphaerium stratinum* (Hornbach *et al.*, 1983) or as little as 1.3 times minimal winter rates in *Pisidium walkeri* (1–26°C) (Burky and Burky, 1976) (Table I).

Immediate temperature increases induce a corresponding metabolic rate increase in ectothermic animals such as bivalves. Acute, temperature-induced variations in metabolic rate or $\dot{V}_{O_2}$ (or in any rate function) are represented by Q_{10} values, the factor by which a rate function changes with a 10°C temperature increase, computed over any temperature range as:

$$Q_{10} = \left(\frac{\text{Rate}_2}{\text{Rate}_1}\right)^{10/[T_2 - T_1]}$$

where Rate_1 is the rate at lower temperature, Rate_2 the rate at higher temperature, T_1 the lower temperature (°C), and T_2 the higher temperature (°C). Q_{10} for metabolic rate in the majority of ectotherms is 2–3, essentially that of chemical reactions. Thus, Q_{10} values outside this range indicate active metabolic regulation, values <1.5 suggesting active metabolic suppression and, >3.5, active metabolic stimulation with temperature change. Freshwater bivalve Q_{10} values are highly variable within and among species, ranging from 0.2 to 14.8 among 20 species of sphaeriids (Hornbach, 1985) and from 1.2 to 3.72 among three species of sphaeriids (Alimov, 1975). Q_{10} ranged from 1.5 to 4.1 for *D. polymorpha* over 10–30°C depending on prior acclimation temperature and temperature range of determination (Alimov, 1975; McMahon, 1996). For 10°C acclimated individuals of *C. fluminea*, respiratory Q_{10} was 2.1 over 5–30°C (McMahon, 1979a). Among unionoideans, in *Lampsilis siliquoidea*, Q_{10} ranged from 1.88 to 4.98 and in *Pyganodon grandis*, from 1.27 to 10.35 (Huebner, 1982). While numerous environmental and physiological factors may affect the Q_{10} values of freshwater bivalves, no general patterns emerge. Rather, metabolic response to temperature appears to have evolved under species-specific microhabitat selection pressures (Hornbach, 1985).

Temperature effects could lead to massive seasonal metabolic fluctuations; rates being suboptimal during colder months and supraoptimal during warmer months. Thus, many ectothermic species display metabolic temperature acclimation, involving compensatory adjustment of metabolic rate to a new temperature regime over periods of a few days to several weeks. Typically, metabolic rates are adjusted upward upon acclimation to colder temperatures and downward upon acclimation to warmer temperatures which

dampens metabolic fluctuation with seasonal temperature change, allowing year-round maintenance of near optimal metabolic rates. For most species, such "typical" seasonal metabolic acclimation is partial, with metabolic rates not returning to an absolute optimal level in a new temperature regime. The degree of metabolic temperature compensation can be detected by comparing Q_{10} values of $\dot{V}_{O_2}$ in instantaneous response to acute temperature change with those measured after acclimation [Acclimation Q_{10} or $Q_{10(Acc.)}$]. If $Q_{10(Acc.)}$ approximates 1.0, metabolic temperature compensation is nearly perfect with $\dot{V}_{O_2}$ regulated near an optimal level throughout the year. If $Q_{10(Acc.)}$ is less than 2.0 or considerably less than acute Q_{10}, acclimation is partial, with the metabolic rate approaching, but not reaching, the optimal level. If $Q_{10(Acc.)}$ is 2–3 or equivalent to the acute Q_{10}, the species is incapable of temperature acclimation. If $Q_{10(Acc.)}$ is greater than 3.0 or acute Q_{10}, inverse (reverse) acclimation is displayed in which acclimation to a colder temperature further depresses metabolic rate, and further stimulates it on acclimation to a warmer temperature.

Three of the above acclimation patterns occur in freshwater bivalves: (1) no capacity for acclimation (i.e., $Q_{10(Acc.)}$ equivalent to acute Q_{10}) is displayed by the unionids *P. grandis* and *L. radiata* (Huebner, 1982) and *D. polymorpha* (Quigley *et al.,* 1992; McMahon, 1996); (2) partial acclimation, by *Pisidium walkeri* where $Q_{10(Acc.)}$ is considerably less than acute Q_{10} (Burky and Burky, 1976); and (3) reverse acclimation (i.e., $Q_{10(Acc.)}$ is greater than acute Q_{10}) displayed by *Sphaerium striatinum* (Hornbach *et al.,* 1983) and *C. fluminea* (Williams and McMahon, unpublished data) (Table I). The adaptive advantage of reverse acclimation has been questioned because it results in massive seasonal swings in metabolic rates, but among freshwater bivalves it may reduce utilization of energy stores during nonfeeding, overwintering periods (Burky, 1983).

$\dot{V}_{O_2}$ is also related to individual size or biomass in all animals as follows:

$$\dot{V}_{O_2} = aM^b$$

where M is the individual biomass, and a and b are constants. It can be rewritten as a linear regression in which $\dot{V}_{O_2}$ and M are transformed into logarithmic values:

$$\text{Log}_{10}\ \dot{V}_{O_2} = a + b(\text{Log}_{10}\ M)$$

where a and b are the Y-intercept (i.e., $\dot{V}_{O_2}$ at $\text{Log}_{10}\ M = 0$ or $M = 1$) and slope (i.e., increase in $\text{Log}_{10}\ \dot{V}_{O_2}$ per unit increase in $\text{Log}_{10}\ M$), respectively. Thus, a measures the relative magnitude of $\dot{V}_{O_2}$ and b, the rate of increase in $\dot{V}_{O_2}$ with increasing biomass. If $b = 1$, $\dot{V}_{O_2}$ increases in direct proportion to M. If b is >1, $\dot{V}_{O_2}$ increases at a proportionately greater rate than M, and if b is <1, $\dot{V}_{O_2}$ increases at a proportionately slower rate than M. Thus, b values <1 indicate that weight-specific $\dot{V}_{O_2}$ (i.e., $\dot{V}_{O_2}$ per unit body mass) decreases with increasing body mass while $b > 1$ indicates that it increases with increasing mass. Conventional wisdom suggests that b values range from 0.5 to 0.8 such that weight specific $\dot{V}_{O_2}$ decreases with increasing body mass. While generally true for vertebrates, it is less characteristic of invertebrates, and particularly of molluscs, including freshwater bivalves. Among 14 species of sphaeriids, b ranged from 0.12 to 1.45 (Hornbach, 1985). Limited data suggest that unionoideans have more typical b values, being 0.9 for *L. radiata,* and 0.77 for *P. grandis* (Huebner, 1982), with a b value range of 0.71–0.75 being reported for a number of unionoideans (Alimov, 1975). A b value of 0.63 is reported for *D. polymorpha* (Alimov, 1975). For *C. fluminea, b* ranged from 1.64–1.66 depending on season, temperature and individual condition (Williams and McMahon, unpublished data). Alimov (1975) estimated an average b of 0.73 for this species. The b value changes with season in some species (Hornbach *et al.,* 1983; Way and Wissing, 1984), but remains constant in others (Burky and Burky, 1976; Huebner, 1982) and can also vary with reproductive condition, reported to increase in some brooding adult sphaeriids (Way and Wissing, 1982) but not in others (Burky, 1983; Hornbach, 1985). Metabolic rate may also vary with physiologic state, increasing in starved individuals of *C. fluminea* (Williams and McMahon, unpublished data) and declining in *Musculium partumieum* during estivation or habitat drying (Way *et al.,* 1981).

Comparison of a values among species of *Pisidium* indicated that weight-specific $\dot{V}_{O_2}$ in this group (mean $a = 0.399$) is about 1/3 that of species of *Musculium* (mean $a = 1.605$) or *Sphaerium* (mean $a = 1.439$) (Hornbach, 1985). Reduced metabolic rate in pisidiids may reflect their reduced relative gill surface areas (Hornbach, 1985) and hypoxic interstitial suspension feeding habitats (Lopez and Holopainen, 1987), reduced metabolic demand of profundal pisidiids perhaps accounting for their high tolerance of hypoxia (Burky, 1983; Holopainen, 1987).

Annually, a in *C. fluminea* varied from −0.12 to 1.43 (mean = 0.72) (Williams and McMahon, unpublished data) while overall a for *D. polymorpha* was 0.140 (Alimov, 1975). The annual range in a for *P. grandis* was −0.13 to −1.098 (mean = −0.563) and, for *L. radiata*, −0.403 to −1.331 (mean = −0.800) (Huebner, 1982) while Alimov (1975) reported a to range from 0.016 to 0.096 for a number of unionoideans. The elevated a of *C. fluminea* and *D. polymorpha* relative to unionideans and sphaeriids (range = 0.399–1.605) indicates that both species have higher $\dot{V}_{O_2}$ and metabolic rates than other freshwater bivalves. In contrast, the low a values among unionideans reflect their relatively low metabolic rates compared to other freshwater bivalve groups.

In bivalves, shell production and tissue growth account for a large proportion of metabolic demand, requiring greater than 20% of total metabolic expenditure in young marine blue mussels, *Mytilus edulis* (Hawkins *et al.,* 1989). Thus, unionoideans with the slowest growth rates among freshwater bivalves (see section III.B.2) also have the lowest metabolic rates, while the fast-growing *C. fluminea* and *D. polymorpha* have the highest metabolic rates (McMahon, 1996, 1999).

In some sphaeriids, $\dot{V}_{O_2}$ is influenced by growth and reproductive cycles: maximal metabolic rates occurring during periods of peak adult and brooded juvenile growth (Burky and Burky 1976; Hornbach *et al.,* 1983; Way *et al.,* 1981; Way and Wissing, 1984), perhaps as a result of the elevated metabolic demands associated with tissue growth (Hawkins *et al.,* 1989), elevated $\dot{V}_{O_2}$ of brooded developmental stages, and the energetic costs of providing maternal metabolites to brooded juveniles (Mackie, 1984). In contrast, metabolic rates in *C. fluminea* (Williams and McMahon, unpublished data) and unionoideans (Huebner, 1982) were unaffected by embryo brooding, perhaps because these species do not provide maternal nourishment to brooded embryos.

Filtration rates also vary seasonally and with abiotic conditions in sphaeriids. In *S. striatinum* (Hornbach *et al.,* 1984b) and *M. partumeium* (Burky *et al.,* 1985a), filtration rates decreased with increased particle concentration and decreased temperature. Maximal filtration rates occurred during warmer summer months and peaked during reproduction. In *M. partumeium,* filtration rate and $\dot{V}_{O_2}$ declined in aestivating individuals prior to summer habitat drying (Way *et al.,* 1981; Burky, 1983). Filtration rate is directly correlated with temperature in *D. polymorpha,* being maximal in summer (MacIsaac, 1996) while it appears to be relatively temperature independent in field-acclimated specimens of *C. fluminea* (Long and McMahon, unpublished data).

Freshwater bivalves also display distinct seasonal cycles in tissue biochemical content, primarily related to reproductive cycle. Protein, glycogen and lipid contents are maximal during gonad development and gametogenesis in the freshwater unionid, *Lamellidens corrianus,* and are minimal during glochidial release (Fig. 9A); a pattern repeated in protein and lipid contents of individual tissues (Fig. 9B–D) (Jadhav and Lomte, 1982a). Similarly, overwintering, nonreproductive individuals of *C. fluminea* had twice the biomass and greater nonproteinaceous energy stores than

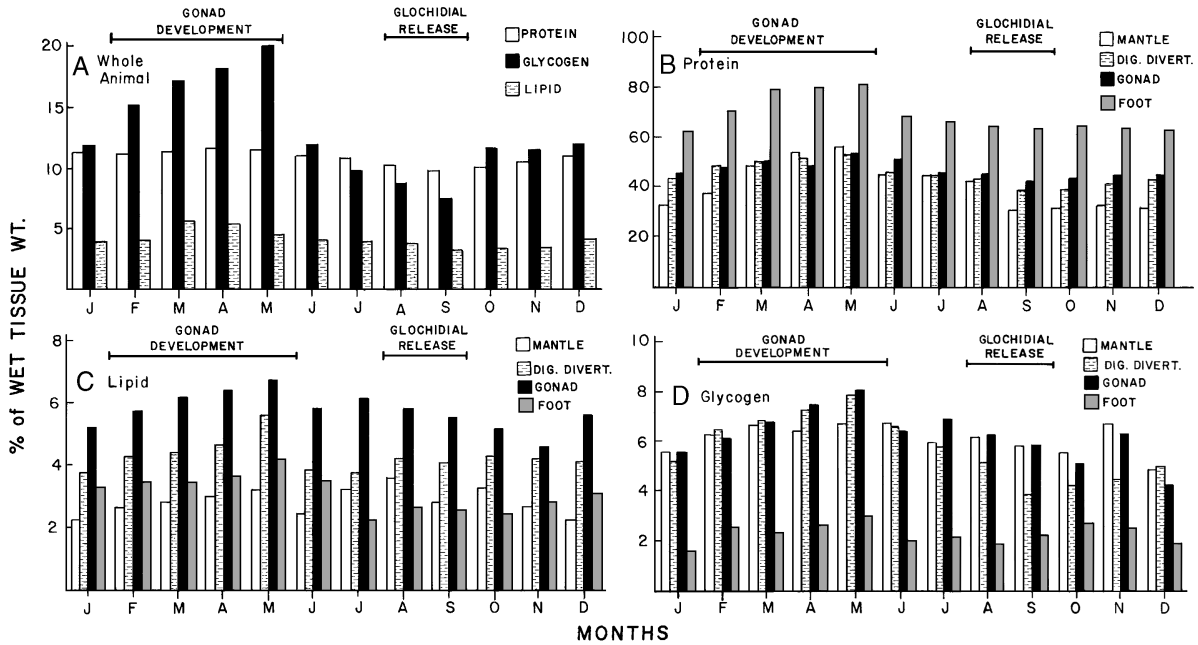

FIGURE 9 Seasonal variation in the protein, lipid, and glycogen contents of the wholebody and various tissues of the freshwater unionoidean mussel, *Lamellidens corrianus*, relative to the reproductive cycle. All organic contents are expressed as percentages of wet tissue weight. (A) Annual vartiation in whole-body contents of proteins (open histgrams), glycogen (solid histograms), and lipid (cross-hatched histograms). Remaining figures represent levels of protein (B), lipid (C) or glycogen (D) in the mantle (open histograms), digestive diverticulum (cross-hatched histograms), gonad (solid histograms), and foot (stippled histograms). Horizontal bars at the top of each figure represent reproductive cycles, indicating periods during which either gonads develop or glochidia are released. Gonad development is associated with increases in organic content, and glochidial release, with decreases in organic content of the whole body and various tissues. (From the data of Jadhav and Lomte, 1982a.)

summer reproductive individuals (Williams and McMahon, 1989). Thus, reproductive effort appears to require massive mobilization of organic energy stores from somatic tissues to support gonad development and gametogenesis in freshwater bivalves.

In the sphaeriids, *Sphaerium corneum* and *Pisidium amnicum,* increase in tissue glycogen content after fall reproduction was associated with a two-to-three-fold increase in anoxia tolerance of winter- over summer-conditioned individuals, the low glycogen contents of summer-conditioned individuals apparently reducing their capacity for anaerobic metabolism. Thus, fall accumulation of glycogen stores not only supported spring gametogenesis, but also provided anaerobic substrate for survival of winter anoxia induced by ice cover (Holopainen, 1987).

2. Diurnal Cycles

Freshwater bivalves display diurnal cycles of metabolic activity. Active Na^+ uptake peaked during dark hours in *C. fluminea* (McCorkle and Shiley, 1982) and the unionid, *Toxolasma texasiensis* (Graves and Dietz, 1980). This rhythmicity was lost in constant light, suggesting that ion uptake rates were driven by exogenous changes in light intensity. Such diurnal ion transport rhythms appear closely linked to activity rhythms. In the unioniodeans, *Ligumia subrostrata,* (McCorkle *et al.,* 1979), and European *Anodonta anatina* and *Unio tumidus* (Englund and Heino, 1994a) valve gaping activity peaks during dark periods. Rhythmic gaping in *L. subrostrata* was lost in constant light, suggesting this behavior is also driven by exogenous variation in light intensity (McCorkle *et al.,* 1979). Similarly, diurnal O_2 consumption rate rhythms in *L. subrostrata* appeared driven by light intensity, declining with increase in, and increasing with decrease in light intensity, however, it also had an endogenous component, persisting for 14 days in constant light (McCorkle *et al.,* 1979). Thus, at least some freshwater bivalves may have diurnal activity rhythms, being most active during dark hours. Such activity rhythms may reflect diurnal feeding and vertical migration cycles, individuals feeding at the sediment surface at night and retreating below it during daylight to avoid visual fish and bird predators. Interestingly, diurnal valve movements do not occur in *D. polymorpha* (Walz, 1978a, b), whose byssal attachment prevents burrowing; however, others have reported diurnal valve movement in this species (Borcherding, 1992).

3. Other Factors Affecting Metabolic Rates

Bivalve $\dot{V}_{O_2}$ can be suppressed by pollutants such as heavy metals, ammonia, and cyanide, which degrade metabolic functioning (Lomte and Jadhav, 1982a) leading to extirpation (Starrett, 1971; Williams *et al.,* 1992) or reduced growth rates (Grapentine, 1992). Increased levels of suspended solids impaired $\dot{V}_{O_2}$ and induced starvation in three unionoidean species, indicating interference with gill respiratory and filter-feeding currents (Aldridge *et al.,* 1987). It also suppresses $\dot{V}_{O_2}$ (Alexander *et al.,* 1994) and filtration rate in *D. polymorpha* (Lei *et al.,* 1996). Similary, high particle concentrations depress filtration rates in *C. fluminea* (Way *et al.,* 1990a). Bivalve metabolic rates may also be density dependent. $\dot{V}_{O_2}$ declined with increased density in the unionid, *Elliptio complanata*. $\dot{V}_{O_2}$ was three times greater in singly held individuals relative to groups of seven or more, suggesting release of a pheromone suppressing metabolic rates of nearby individuals (Paterson, 1983).

Unionoideans and sphaeriids display varying degrees of respiratory regulation when subjected to progressive hypoxia (Burky, 1983). Both *D. polymorpha* (McMahon, 1996) and *C. fluminea* (McMahon, 1979a) are highly O_2 dependent, their $\dot{V}_{O_2}$ declining proportionately with declining partial pressure of O_2 (P_{O_2}). Such species are generally relatively intolerant of prolonged hypoxia and restricted to well-oxygenated habitats. In contrast, other freshwater bivalve species are oxygen independent and regulate $\dot{V}_{O_2}$ at relatively constant levels with progressive hypoxia until a critical $\dot{V}_{O_2}$ is reached below which $\dot{V}_{O_2}$ declines proportionately with further decline in P_{O_2}. Such species can inhabit waters periodically subjected to prolonged hypoxia. Thus, the sphaeriids, *Sphaerium simile* and *Pisidium casertanum,* from hypoxic profundal habitats are relatively O_2 independent (Burky, 1983) while the shallow temporary pond species, *Musculium partumeium,* is relatively poor O_2 regulator (Hornbach, 1991). The Austrailian riverine unionoidean, *Alathyria jacksoni,* rarely experiencing hypoxia, is a relatively poor O_2 regulator while a periodically hypoxic, Australian, pond species, *Velesunio ambiguus,* was a strong oxygen regulator (Sheldon and Walker, 1989). Similarly, the lentic unionioidean, *A. cygnea* regulated $\dot{V}_{O_2}$ at a P_{O_2} as low as 14.3 Torr (0.9% of full air O_2 staturation), maintaining near constant hemolymph O_2 concentrations during progressive hypoxia by increasing gill ventilation (Massabuau *et al.,* 1991) while maintaining a near-constant heart rate (Michaelidis and Anthanasiadou, 1994). The unioniodeans, *Elliptio complanata* and *Pyganodon grandis,* from a small, Canadian, euthrophic lake, were extreme O_2 regulators, maintaining near constant $\dot{V}_{O_2}$ down to 1 mg O_2/L (P_{O_2} $\approx$18 Torr, 11.3% of full air O_2 saturation) (Fig. 10) (Lewis, 1984). Their capacity for extreme $\dot{V}_{O_2}$ regulation is adaptive, as winter ice cover made the lake severely hypoxic and overwintering individuals burrow deeply into hypoxic sediments (Lewis, 1984). In contrast, the

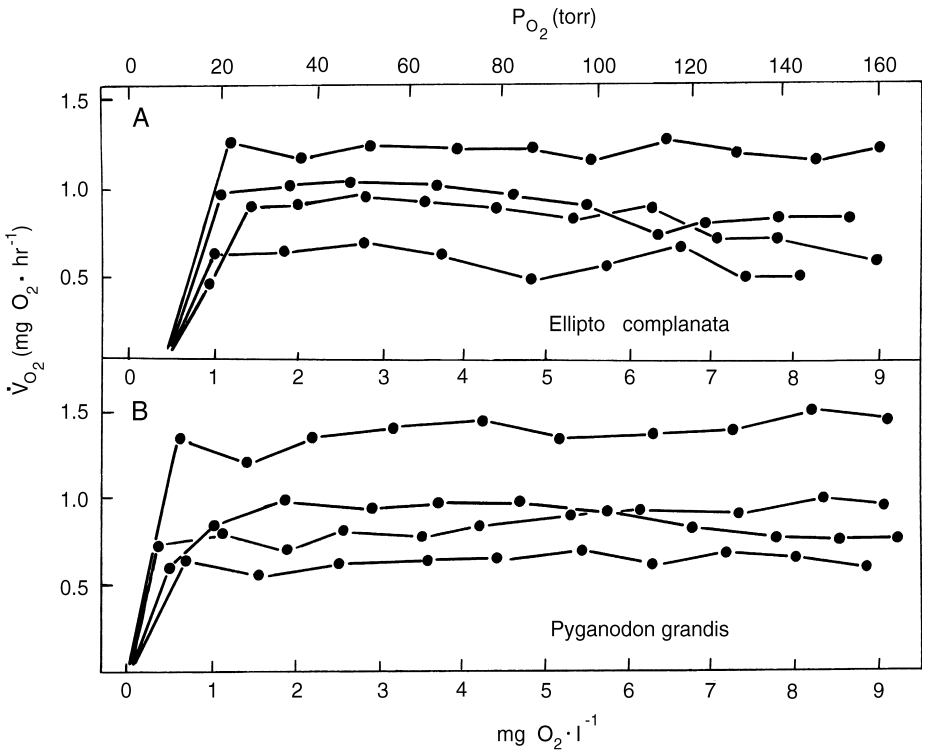

FIGURE 10 Respiratory responses of the freshwater unionoidean mussels, *Elliptio complanata* and *Pyganodon grandis* to ambient O_2 concentrations declining from near full-air saturation (8–9 mg O_2/l, lower horizontal axis, P_{O_2} = 140–160 torr or mg Hg, upper horizontal axis) to the concentration at which O_2 uptake ceases. Respiratory responses of four individuals of (A) *E. complanata*, and (B) four individuals of *P. grandis*. Both species maintained normal O_2 uptake rates at a P_{O_2} as low as 15–20 torr (9–13 percent of full-air O_2 saturation) suggesting elevated capacity for O_2 regulation of oxygen uptake. (Redrawn from Lewis, 1984.)

$\dot{V}_{O_2}$ of tropical and semitropical species not experiencing winter hypoxia tends to be more O_2 dependent (McMahon, 1979a; Das and Venkatachari, 1984), the $\dot{V}_{O_2}$ of the subtropical species, *C. fluminea,* declining to very low levels with just a 30% decline in P_{O_2} below full air O_2 saturation levels (McMahon, 1979a).

Some freshwater bivalves are very tolerant of extreme hypoxia or even anoxia allowing survival in hypoxic conditions below the thermocline of stratified lakes or above reducing substrates (Butts and Sparks, 1982; Belanger, 1991). Profundal sphaeriid species tolerate extreme hypoxia and anoxia throughout summer lake stratification (Holopainen and Jonasson, 1983), surviving 4.5 to >200 days of anoxia, depending on season and temperature (Holopainen, 1987). The unionoidean *A. cygnea* survived 22 days of anoxia (Zs.-Nagy *et al.,* 1982). In contrast, other freshwater bivalves are highly intolerant of hypoxia/anoxia, including *D. polymorpha* and *C. fluminea,* restricting them to well-oxygenated waters (Effler and Siegfried, 1994; Johnson and McMahon, 1998; Matthews and McMahon, 1999). Byssal thread production was inhibited in *D. polymorpha* below a P_{O_2} of 40 Torr (25% of full air O_2 saturation) (Clarke and McMahon, 1996b).

Individual size also affects tolerance of anoxia/hypoxia. Juveniles of the unionoidean, *Elliptio complanata,* are less hypoxia-tolerant than adults (Sparks and Strayer, 1998). In contrast, anoxia and hypoxia tolerance decreases with increased size in *C. fluminea* and *D. polymorpha* (Johnson and McMahon, 1998, Matthews and McMahon, 1999). The general trend for decreased juvenile hypoxia tolerance among freshwater bivalves may restrict some species to well-oxygenated habitats even though the adults may be hypoxia-tolerant (Sparks and Strayer, 1998).

Under anoxia, bivalves rely on anaerobic metabolic pathways which are not those of glycolysis; but, instead, involve simultaneous catabolism of glycogen and aspartate or other amino acids to yield the end products, alanine and succinate. Succinate can be further degraded into volatile fatty acids such as proprionate or acetate (Zs.-Nagy *et al.,* 1982; de Zwaan, 1983; van den Thillart and de Vries, 1985). Anoxic for 6 days, *A. cygnea* maintained 52–94% of aerobic ATP levels,

higher than could occur by typical glycolytic pathways, due to its anaerobic oxidation of succinate (Zs.-Nagy *et al.,* 1982). These alternative anaerobic pathways are more efficient than glycolysis (2 mol of ATP preduced per mole of glucose catabolized), producing 4.71–6.43 mol of ATP per mole of glucose catabolized (de Zwaan, 1983). Indeed, typical glycolytic pathway enzyme activities are reduced in *A. cygnea* during hypoxia (Michaelidis and Athanasiadou, 1994) which favors metabolite catabolism by alternative pathways and allows greater tolerance of hypoxia/anoxia than less efficient glycolysis. Further, the higher ATP yields of the alternative pathways allow excretion of anaerobic endproducts, rather than retention of acidic lactate to deleterious levels as occurs in species dependent on glycolysis (de Zwaan, 1983).

During anerobiosis, buildup of acidic end products in bivalve tissues and hemolymph can cause considerable tissue and hemolymph acidosis (i.e., decrease in pH). Without respiratory pigments, freshwater bivalve hemolymph has little inherent buffering capacity, thus bivalves mobilize shell calcium carbonate into the hemolymph through the mantle epithelium (Machado *et al.,* 1990) to buffer acidosis (Heming *et al.,* 1988; Byrne and McMahon, 1994; Burnett, 1997). Thus, when anaerobic, pallial fluid pH of the unionoidean *Margaritifera margaritifera* remained highly constant, but its Ca^{2+} concentration increased (Heming *et al.,* 1988). Similarly, blood Ca^{2+} levels rose eightfold in *L. subrostrata* (Dietz, 1974) and nearly fivefold in *C. fluminea* (Byrne *et al.,* 1991a) under anoxia induced by emersion in a pure N_2 atmosphere. A three-fold increase in hemolymph Ca^{2+} concentration occurred in *Pyganodon grandis* made anoxic by 6 days air emersion (Byrne and McMahon, 1991).

The gills of unionoideans (Steffens *et al.*1985) harbor extensive extracellular calcium phosphate concretions that could buffer hemolymph pH. However, their mass increases during prolonged hypoxia and is inversely related to hemolymph pH and directly to blood Ca^{2+} concentration, suggesting that Ca^{2+} released from the shell during hypoxia is sequestered in gill concretions to prevent its loss by excretion or diffusion. On return to normoxia, release and redeposition in the shell of concretion Ca^{2+} is likely to be much less energetically demanding than replacement of lost shell Ca^{2+} from the dilute freshwater medium (Silverman *et al.,* 1983). The enzyme, carbonic anhydrase, is bound to these concretions, facilitating exchange of concretion Ca^{2+} (uptake or release) with the hemolymph (Istin and Girard, 1970a, b).

4. Desiccation Resistance

Body water content in freshwater bivalves can vary greatly seasonally and during drought periods. Thus, many species have evolved adaptations allowing tolerance of prolonged emersion and desiccation stress (Cáceres, 1997). Freshwater bivalves may be emersed for weeks or months during seasonal or unpredictable droughts (Byrne and McMahon, 1994). Lack of mobility leaves individuals stranded in air as water levels recede, while others occur in habitats that dry completely. Unlike other freshwater invertebrates (Cáceres, 1997), bivalves have no obvious structures for maintenance of aerial gas exchange when emerged, However, they have behavioral and physiological adaptations that maintain aerobic metabolism while minimizing water loss rates (Byrne and McMahon, 1994).

Survival of emersion in freshwater bivalves is correlated with capacity to control water loss. Among freshwater species, *C. fluminea* and *D. polymorpha* are highly emersion intolerant, tolerating only 8–36 days (McMahon, 1979b) or 3–27 days emersion (McMahon *et al.,* 1993), respectively, depending on temperature and relative humidity. *Dreissena bugensis* is even less emersion tolerant than *D. polymorpha* (Ussary and McMahon, 1994; Ricciardi *et al.,*1995). In these species and unionoideans, death occurs in most cases at a critical threshold of water loss regardless of temperature or relative humidity; thus, rate of water loss dictates emersion tolerance times (McMahon, 1979b; McMahon *et al.,* 1994; Byrne and McMahon, 1994; Ricciardi *et al.,* 1995). In contrast, sphaeriids inhabiting temporary ponds survive emersion for several months during summer drying (Burky, 1983). In some species, juveniles and adults survive emersion (Collins, 1967; McKee and Mackie, 1980), while in others, only juveniles survive (McKee and Mackie, 1980; Way *et al.,* 1981). Sphaeriids burrow into sediments prior to emersion (Burky, 1983) as do some unionoideans (Cáceres, 1997).

$\dot{V}_{O_2}$ declines in both emersed, aestivating *M. partumeium* (Way *et al.,* 1981) and emersed individuals of *C. fluminea* (McMahon and Williams, 1984; Byrne *et al.,* 1990). Reduction in metabolic demand in emersed individuals allows long-term maintenance on limited energy reserves.

Freshwater bivalves have a number of mechanisms for maintaining gas exchange while emersed. *Sphaerium occidentale* is emersed for several months in its ephemeral pond habitats. In air, its $\dot{V}_{O_2}$ is 20% that of aquatic rates. Gas exchange occurs across specialized pyramidal cells extending through shell punctae which allows continuous valve closure, minimizing water loss (Collins, 1967). In *C. fluminea,* aerial $\dot{V}_{O_2}$ is 21% that of aquatic rates (McMahon and Williams, 1984). Emersed specimens periodically gape and expose mantle tissue margins cemented together with mucus (Byrne *et al.,* 1988) during which high rates of aerial $\dot{V}_{O_2}$ are sustained while no O_2 uptake occurs during valve closure (McMahon and Williams, 1984).

Bursts of metabolic heat production occur during mantle edge exposure, associated with aerial oxygen consumption and apparent repayment of an O_2 debt accumulated during intervening anaerobic periods of valve closure (Byrne *et al.,* 1990). Thus, periodic mantle margin exposure allows maintenance of aerial gas exchange while greatly reducing the tissue surface area exposed and duration of exposure, greatly reducing water loss rates (Byrne and McMahon, 1994). Frequency and duration of mantle edge exposure is reduced in *C. fluminea* with increased temperature, decreased relative humidity and increasing duration of emersion, suggesting that increased desiccation pressure leads to a greater reliance on anaerobic metabolism to slow evaporative water loss (Byrne *et al.,* 1988).

Emersed unionoideans periodically expose their mantle edges (Byrne and McMahon, 1994). Emersed specimens of *Ligumia subrostata* periodically expose mantle edges and maintain aerial $\dot{V}_{O_2}$ at 21–23% of aquatic rate (Dietz, 1974). Periodic mantle edge exposure also occurs in emersed specimens of *M. margaritifera* (Heming *et al.,* 1988), *Pyganodon grandis* (Byrne and McMahon, 1991), *Pyganodon grandis, Toxolasma parvus* and *Uniomersus tetralasmus* (Byrne and McMahon, 1994). *P. grandis* has a thin shell whose margins do not completely seal when closed and a high frequency of mantle edge exposure when emersed (>25–90% of emersion time), resulting in rapid water loss and poor emersion tolerance (2–32 days). It avoids desiccation by rapid down-shore migration during reductions in habitat water levels (Byrne and McMahon, 1994). More emersion-tolerant species like *T. parvus* and *U. tetralasmus* have thicker, tightly sealing shells and their frequency and duration of mantle edge exposure is reduced with increasing duration of emersion and decreasing relative humidity, conserving water as desiccation pressure increases. *T. parvus* continuously closes the valves in latter stages of emersion, allowing it to survive emersion up to 145 days (Byrne and McMahon, 1994). *U. tetralasmus* is found in small, variable-level, lentic habitats and is highly emersion tolerant. In air, it occludes the siphons with viscous mucus, preventing direct atmospheric exposure of inner mantle tissues. Its frequency and duration of mantle edge exposure is quite low compared to other species and it ceases mantle edge exposure in the latter stages of emersion, making water loss rates lower than recorded for other freshwater bivalves and allowing it to survive emersion for up to 578 days (Byrne and McMahon, 1994).

In air, unionoideans and *C. fluminea* utilize shell Ca^{2+} to buffer accumulating HCO_3^- (Byrne and McMahon, 1994) manifested by accumulation of Ca^{2+} and HCO_3^- in mantle cavity fluids of emersed *M. margaritifera* (Hemming *et al.,* 1998) and hemolymph of emersed *C. fluminea* (Byrne *et al.,* 1991a) and *P. grandis* (Byrne and McMahon, 1991). Mantle edge exposure allows release of CO_2 generated by metabolic and shell-buffering processes in both *C. fluminea* (Byrne *et al.,* 1991a) and unionoideans (Byrne and McMahon, 1991).

In emersed *C. fluminea* there is little evidence of O_2 debt payment after re-immersion, suggesting that this and other freshwater bivalves may remain primarily aerobic while emersed (Byrne *et al.,* 1990).

The Unionoidea include the most emersion-tolerant NA freshwater bivalve species (for a review, see Byrne and McMahon, 1994). Their capacity to tolerate prolonged emersion and/or migrate vertically with changing water levels (White, 1979) may partially account for their dominance in larger NA river drainages subject to extensive seasonal water-level fluctuations. Unionoidean growth, reproduction and other life-history phenomena may be partially driven by seasonal water-level variation. Thus, anthropomorphic impoundment/regulation of flow rates and levels within these drainages could be contributing to the present decline of their unionoidean populations and species diversity (Williams *et al.,* 1992).

The mode of nitrogen excretion or detoxification during emersion is unresolved for freshwater bivalves. Ammonium ion, NH_4^+, is the major nitrogenous excretory product of aquatic molluscs (Bishop *et al.,* 1983). Due to its toxicity, NH_4^+ is generally not accumulated in emersed molluscs even though its high solubility precludes release as ammonia gas (NH_3). When emersed, aquatic snails detoxify NH_4^+ by conversion to urea or uric acid, to be excreted on re-immersion. However, most bivalves cannot convert NH_4^+ to urea or uric acid (Bishop *et al.,* 1984). Without the capacity to detoxifiy NH_4^+, how do freshwater bivalves tolerate emersion? *Corbicula fluminea,* unlike intertidal bivalves (Bishop *et al.,* 1983), does not catabolize amino acids during emersion, precluding NH_4^+ formation (Byrne *et al.* 1991b). Similarly, the unionideans, *Lamellidens corrianus* and *L. marginalis,* depend almost exclusively on carbohydrate metabolism while emersed (Lomte and Jadhav, 1982c; Sahib *et al.,* 1983). Interestingly, some unionoideans may be capable of converting ammonia to urea or other protective metabolites (Summathi and Chetty, 1990; Mani *et al.,* 1993) which may partially account for their extensive emersion tolerance.

Tolerance of emersion may also be associated with physiological and biochemical alterations in emersed individuals. Thus, individuals of *Sphaerium occidentale* and *Musculium securis* from an emersed population were more emersion tolerant than individuals from an immersed, active population (McKee and Mackie, 1980), suggesting that gradual emersion may induce emersion resistant biochemical and physiological

alterations such as a shift to carbohydrate dominated catabolism and reduced metabolic demand. Such biochemical and physiological compensation may be mediated by neurosecretory hormones (Lomte and Jadhav, 1981a).

There have been almost no studies of freeze tolerance in freshwater bivalves even though many species occupy shallow, temperate habitats in which winter water-level reduction could emerse individuals in subfreezing air. Marine intertidal mytilid mussels tolerate exposure to subfreezing conditions by allowing freezing of hemolymph and interstitial fluids while preventing cell freezing, an adaptation manifested by their lack of hemolymph supercooling during freezing (Aarset, 1982). In contrast, *D. polymorpha* is intolerant of emersion below −3°C (Clarke *et al.,* 1993) and displays hemolymph supercooling (Paulkstis *et al.,* 1996). Poor freeze tolerance in *D. polymorpha* may reflect its tendency to settle at depths of >1 m, preventing winter emersion (Clarke *et al.,* 1993). Freeze sensitivity/tolerance in other freshwater bivalves (particularly shallow water species) is ripe for further study.

5. Gill Calcium Phosphate Concretions in Unionoideans

Dense calcium phosphate [$Ca_3(PO_4)_2$] concretions occur in unionoidean tissues. Mantel concretions may provide Ca^{2+} for shell deposition (Davis *et al.,* 1982; Jones and Davis, 1982; Istin and Girard, 1970a). The mantle contains high concentrations of the enzyme, carbonic anhydrase which may be bound to the concretions (Istin and Girard, 1970b). This enzyme catalyzes the reaction of CO_2 and H_2O to form bicarbonate ion (HCO_3^-), suggesting that it facilitates mobilization of concretion Ca^{2+}.

Dense extracellular calcium phosphate concretions (diameter = 1–3 μm) also occur in unionoidean gills (Silverman *et al.,* 1983, 1988; Steffens *et al.,* 1985). They develop from amorphous material initially concentrated in membrane bound vesicles in gill connective tissue cells (Silverman *et al.,* 1989). Concretions account for up to 60% of gill dry weight in some species (Silverman *et al.,* 1985). They are most dense along parallel nerve tracts oriented at 90° to the gill filaments (Silverman *et al.,* 1983; Steffens *et al.,* 1985). They are 25% protein by dry weight. One of the proteins is similar to vertebrate, calcium-binding calmodulin. This protein is most abundant in protein granules of concretion-forming cells prior to concretion mineral deposition, suggesting that it acts as site for calcium phosphate deposition (Silverman *et al.,* 1988).

Besides storing shell Ca^{2+} released to the hemolymph to buffer respiratory acidosis (see Section II.C.3), gill concretions provide a ready source of maternal Ca for shell deposition in brooded glochidia (Silverman *et al.,* 1985, 1987). Thus, gill concretion mass in brooding individuals of *L. subrostrata* and *P. grandis* was only 47 and 70% that of nonbrooding individuals, respectively (Silverman *et al.,* 1985). ^{45}Ca tracer studies indicate that 90% of glochidial shell Ca was of maternal origin in *P. grandis,* the most likely source being gill concretions, with nonmineralized Ca accounting for only 8% of glochidial Ca in *L. subrostrata* (Silverman *et al.,* 1987).

6. Water and Salt Balance

In hypo osmotic freshwater, bivalves lose ions and gain water from their hyperosmotic tissues and hemolymph. Excess body water is excreted as a fluid hypo-osmotic to tissues and hemolymph via the kidneys while ions lost in excretion and over surface epithelia are actively recovered over the gills and epithelial tissues as described in Section II.B.3 (reviewed by Deaton and Greenberg, 1991). Relatively salinity tolerant *C. fluminea* survives exposure to a salinity of 10–14 ppt (Morton and Tong, 1985), above which it remains isosmotic to the medium (Gainey and Greenberg, 1977). Unionoideans and *D. polymorpha* have lower hemolymph osmolarities than *C. fluminea* (Dietz *et al.,* 1996a) and generally lose capacity for osmotic and volume regulation above 3–4 ppt (Hiscock, 1953; Wilcox and Dietz, 1998). *C. fluminea* regulates fluid volume by actively increasing hemolymph free amino acid concentration in hyperosmotic media (Gainey and Greenberg, 1977; Matsushima *et al.,* 1982), preventing water loss by active equilibration of hemolymph and medium osmolarity. Such volume regulation does not occur in other freshwater bivalves because their low tissue osmolarities limit the free amino acid pool (Yamada and Matsushima, 1992; Dietz *et al.,* 1996a,b, 1998). Volume regulation may have been lost in unionoideans and *D. polymorpha,* because they are not exposed to hyperosmotic conditions in freshwater. Instead, both groups retain only limited cell volume regulation through regulation of intracellular inorganic ion concentrations (Dietz *et al.,* 1996a, b, 1998). The elevated osmotic concentration and free amino acid pool volume regulation of *C. fluminea* reflects its recent evolution from an estuarine ancestor (Dietz, 1985) in which such adaptations are common (Deaton and Greenberg, 1991).

Both unionoideans and *C. fluminea* respond to maintenance in very dilute media by increasing active Na^+ uptake rate to maintain hemolymph ion concentration (Dietz, 1985). The activity of (Na^+ and K^+)-activated ATPase, an enzyme required for active Na^+/K^+ transport, increased in mantle and kidney tissues of salt-depleted *C. fluminea,* suggesting activation of Na^+ transport. This response did not occur in the salt-depleted

Lampsilis straminca claibornesis, suggesting that active ion uptake regulation has been lost in unionoideans with a longer freshwater fossil history than *C. fluminea* (Deaton, 1982). In *C. fluminea* Cl^- is the major blood ion, maintained by elevated active epithelial Cl^- uptake. In contrast, in the unionoidean, *Toxolasma texasiensis,* Cl^- and HCO_3^- are equivalent hemolymph anionic components. Because HCO_3^- can be readily mobilized by respiratory and metabolic processes, unionoideans may depend to a greater extent on active Na^+ relative to Cl^- uptake to maintain hemolymph osmotic balance (Byrne and Dietz, 1997). The anionic hemolymph component of *D. polymorpha,* like that of *C. fluminea,* is dominated by Cl^-, but this species actively absorbs equal levels of Na^+ and Cl^- to maintain ionic stasis, suggesting co-transport of these ions (Horohov *et al.,* 1992). Retention of Cl^- as the main hemolymph anion in *C. fluminea* and *D. polymorpha* reflects their recent evolution from estuarine ancestors (Deaton and Greenberg, 1991; Byrne and Dietz, 1997; Horohov *et al.,* 1992), while the greater dependence of *C. fluminea* on Cl^- uptake for ionic regulation and its increased hemolymph osmotic concentration (Dietz *et al.,* 1994) suggests that it entered freshwater more recently than *D. polymorpha.* Interestingly, although *D. polymorpha* can hyperosmotically regulate hemolymph ion concentrations in dilute freshwaters, it is less tolerant of elevated medium ion concentrations than other bivalves restricting its penetration of estuarine habitats (Horohov *et al.,* 1992; Dietz *et al.,* 1994, 1998; Wilcox and Dietz, 1998).

In the Asian unionoidean, *Anodonta woodiana,* mantle cavity water osmolarity at 34 mosmol/L was 76% that of the hemolymph (45 mosmol/L) with pallial fluid Na^+, K^+, and Cl^- concentrations being 71, 76 and 72% those of the hemolymph, respectively. Maintenance of elevated mantle water ion concentrations suggests that it acts as an osmotic buffer, reducing the gradient for, and, thus, the rate of diffusive ion loss to the dilute freshwater medium (Matsushima and Kado, 1982). However, loss of a hyperosmotic mantle fluid to the external medium through the exhalant siphon could also be a major route for ion loss.

In unionoideans and *C. fluminea,* the enzyme, carbonic anhydrase (CA), which catalyzes formation of carbonic acid (H_2CO_3) from water and carbon dioxide, occurs in gill and mantle tissues (Henery and Saintsing, 1983). H_2CO_3 degrades into H^+ and CO_3^- (bicarbonate ion) which are counter ions for active Na^+ and Cl^- uptake (Horohov *et al.,* 1992; Dietz *et al.,* 1994; Byrne and Dietz, 1997). Gill and mantle CA activity increases when freshwater bivalves are held in extremely dilute media while CA inhibition by actazolamide results in reduced Na^+ and Cl^- uptake rates, strong evidence of the role of CA in ion regulation (Henery and Saintsing, 1983).

Freshwater bivalve hemolymph osmotic concentrations are the lowest recorded for multicellular invertebrates (Dietz, 1985; Deaton and Greenberg, 1991). Among unionoideans, hemolymph osmolarity for the European species, *Anodonta cygnea,* was 40–50 mosmol/L or 4–5% that of seawater. *D. polymorpha* has the lowest hemolymph concentration of all freshwater bivalves (30–36 mosmol/L or 3.0–3.6% that of seawater) (Dietz *et al.,* 1994), while *C. fluminea* has the highest value at 65 mosmol/L (6.5% that of seawater) (Zheng and Dietz, 1998a). That for other freshwater invertebrates ranges from 100 to 400 mosmol/L or 10–40% that of seawater (Burky, 1983). Low hemolymph osmotic concentrations in freshwater bivalves reduce the gradient for transepithelial osmosis and ion diffusion across their extensive mantle and gill epithelial surfaces to that which can be balanced by water excretion and active ion uptake at energetically feasible levels (Burton, 1983). Hydrostatic pressure generated by heart beat in *A. cygena* allows filtration of enough hemolymph plasma into the pericardial space to account for urine production and is twice that of the marine clam, *Mya arenaria,* suggesting that freshwater bivalves can excrete water at higher rates than less hypoosmotically stressed estuarine species (Jones and Peggs, 1983). Exposure of *Pyganodon* sp. to a very dilute medium induced formation of extensive extracellular membrane spaces in the deep infoldings of kidney epithelial cells, perhaps increasing surface area for active ion uptake from excretory fluids producing a more dilute urine and/or allowing increased excretion of excess water (Khan *et al.,* 1986).

Increasing osmotic gradients for water uptake from marine through estuarine into freshwater habitats required that the external epithelia of bivalves became increasing impermeable to water with their evolutionary transition through these environments. Thus, increased epithelial osmo-resistance characterizes all freshwater bivalves (Deaton and Greenberg, 1991; Dietz, 1985; Dietz *et al.,* 1994; Byrne and Dietz, 1997; Zheng and Dietz, 1998a). Among freshwater bivalves, *C. fluminea* is least osmotically permeable (Zheng and Dietz, 1998a) and *D. polymorpha* most permeable (Dietz *et al.,* 1995), while unionoideans are of intermediate permeability (Dietz *et al.,* 1996a, b; Zheng and Dietz, 1998a). The "osmotically tight" epithelium of *C. fluminea* allows it to maintain higher hemolymph osmolarity than other freshwater bivalves while producing normal excretory fluid volumes (Zheng and Dietz, 1998a). In contrast, "osmotically leaky" epithelium in *D. polymorpha* results in very elevated excretory fluid production (Dietz *et al.,* 1995), requiring extremely high rates of epithelial ion uptake to replace ions lost in voluminous excretory fluids (Dietz and Byrne, 1997). Thus, the main

osmoregulatory adaptations of *C. fluminea* and *D. polymorpha* are quite different, the former being reduced epithelial permeability, and that of the latter, increased water excretion and active epithelial ion uptake.

Hormones regulate osmotic control in freshwater bivalves. Cyclic AMP (cAMP) stimulates active Na^+ uptake by unionoideans, while prostglandins inhibit it. In contrast, prostglandin inhibitors stimulate N^+ uptake (Dietz *et al.,* 1982; Graves and Dietz, 1982; Saintsing and Dietz, 1983). Serotonin stimulates tissue accumulation of cAMP, increasing active Na^+ uptake. Thus, an antogonistic relationship between serotonin and prostaglandins modulates adenylate cyclase-catalyzed cAMP stimulation of active Na^+ uptake. Not surprisingly, high concentrations of serotonin occur in unionoidean gill nerve tracts (Dietz, 1985; Dietz *et al.,* 1992). Gill concentrations of the neurotransmitters, dopamine and norepinephrine, greatly declined in unionoideans salt-depleted in extremely dilute mediums, while serotonin was regulated at near-normal levels, suggesting that serotonin regulates Na^+ uptake for ionic balance. The circadian rhythms of Na^+ uptake in freshwater clams (Graves and Dietz, 1980; McCorkle-Shiley, 1982) may be mediated by an antagonistic serotonin/prostaglandin hormonal system (Dietz, 1985).

When cerebropleural or visceral ganglia were ablated, individuals of the Indian unionoidean, *Lamellidens corrianus,* rapidly lost osmoregulatory capacity which was restored by injection of ganglia extracts, indicating that ganglion neurosectory hormones are involved in water balance (Lomte and Jadhav, 1981b). The affinity of the pedal ganglion of *A. cygena* for monoamines controlling ion/water balance is temperature dependent indicative of a seasonal component to osmoregulation (Hiripi *et al.,* 1982).

III. ECOLOGY AND EVOLUTION

A. Diversity and Distribution

North American freshwater bivalves distributions, particularly for unionoideans, have been well described. Species distribution maps for unionoideans and sphaeriids exist for Canada (Clarke, 1973), the United States (LaRocque, 1967a) and for the whole of North American (Burch, 1975a, b; Parmalee and Bogan, 1998). LaRocque (1967b) describes living and Pleistocene fossil assemblages at specific NA localities. There is also a massive literature, too numerous to cite here, describing species occurrences or species assemblages in various NA drainage systems.

Native (non-introduced) NA sphaeriid species have broad distributions, often extending from the Atlantic to Pacific coasts. Introduced to NA from southeast Asia in early 1900s (McMahon, 1999), *Corbicula fluminea* (i.e., light-colored shell morph of *Corbicula*) has a similarily widespread NA distribution, inhabiting drainages on the west coast of the United States, the southern tier of states, and throughout states east of the Mississippi River, with the exception of the most northern states, and into northern Mexico (McMahon, 1999) (Fig. 11). A second, unidentified species of *Corbicula* (i.e., the dark-colored shell morph) is restricted to isolated, spring-fed drainages in southcentral Texas and southern California and Arizona (Fig. 11) (Britton and Morton, 1986). In contrast, NA unionoidean species generally have more restricted distributions. Few species range on both sides of the continental divide and a large number are limited to single drainage systems (Burch, 1975b; LaRocque, 1967a).

1. Dispersal

Widespread NA distributions of sphaeriids and *Corbicula* relative to unionoideans reflect fundamental differences in their dispersal capacities. Unionoideans depend primarily on host fish glochidial transport for dispersal (Kat, 1984), their ranges reflecting those of their host fish species (Haag and Warren, 1998). While host fish glochidial transport increases probability of dispersal into favorable habitats, as host fish and adult unionoidean habitat preferences generally coincide (Kat, 1984), it limits the extent of dispersal, leading to highly endemic species. For example, electrophoretic studies of peripheral Nova Scotian populations of unionoideans suggest that they invade new habitats mostly by host fish dispersal (Kat and Davis, 1984), barriers to host fish dispersal being barriers to unionid dispersal. Thus, distributions of modern and fossil NA interior basin unionoidean assemblages are limited to areas below major waterfall barriers to fish host upstream migration in the Lake Champlain drainage system of New York, Vermont, and Quebec (Smith, 1985a) and re-establishment of *Anodonta implicata* populations in the upper Connecticut River drainage closely followed restoration of its anadromous glochidial clupeid fish host populations, by construction of fishways past numerous impoundments preventing upstream fish host dispersal (Smith, 1985b). Vaughn and Taylor (2000) have found that >50% of the variation in unionoidean assemblages is associated with regional distribution and abundances of fishes, indicating that fish community structure is a determinant of mussel community structure.

Sphaeriids and *C. fluminea* have evolved dispersal mechanisms that make them more invasive than unionoideans, accounting for their more cosmopolitan distributions. Juvenile sphaeriids disperse between

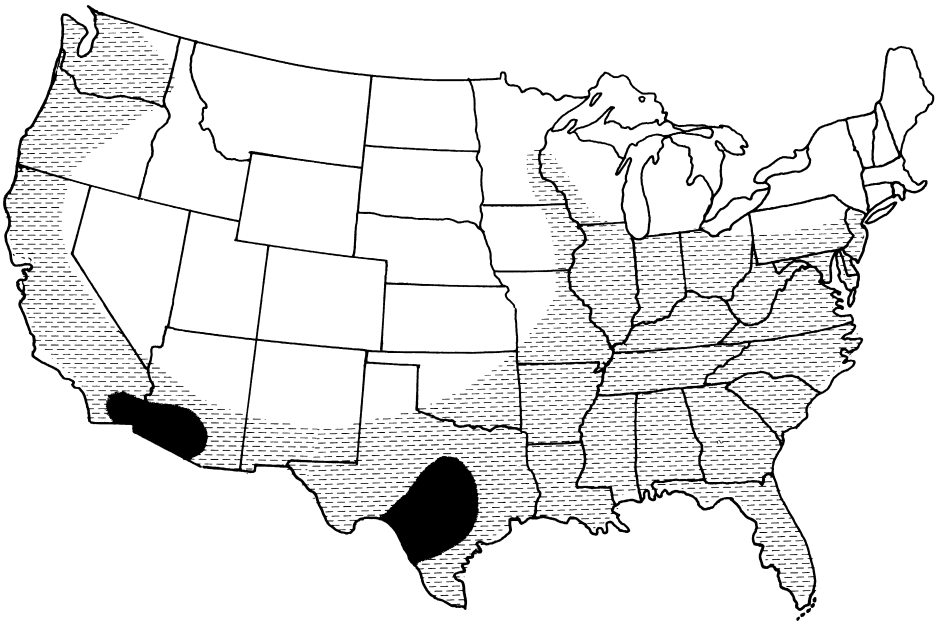

FIGURE 11 Distribution of *Corbicula* in the United States. Hatched area is the distribution of the light-colored morph of *Corbicula, Corbicula fluminea*. The solid areas are the distribution of the dark-colored morph of *Corbicula*, yet to be assigned a species designation.

drainage systems by clamping shell valves onto limbs of aquatic insects, feathers of water fowl (Burky, 1983), or even limbs of salamanders (Davis and Gilhen, 1982) first noted by Darwin (1882). Some sphaeriids survive ingestion and regurgitation by ducks, which commonly feed on them, allowing long-distance dispersal (Burky, 1983). The rapid spread of *C. fluminea* through NA drainage systems (McMahon, 1999), while partly anthropomorphically mediated, also resulted from its natural dispersal capacities. The long juvenile mucilaginous byssal thread or filamentous algae on which juveniles settle becomes entangled in the feet or feathers of shore birds or water fowl, making them transport vectors (McMahon, 1999). Its natural dispersal capacity has allowed it to spread into areas of northern Mexico where human-mediated transport is highly unlikely (Hillis and Mayden, 1985), and into southern Britain during interglacial periods (McMahon, 1999). *Dreissena polymorpha,* byssally attaches to floating wood or boat and barge hulls, facilitating long distance transport (Mackie and Schloesser, 1996), and to macrophytic vegetation that can be transported across drainages by nesting shore birds and water fowl.

Juveniles of *C. fluminea* can be passively transported long distances downstream suspended in water currents (McMahon, 1999). Water currents also disperse the planktonic veliger of *D. polymorpha* (Mackie and Schloesser, 1996). Adult *C. fluminea* can be carried downstream over substratum by water currents (Williams and McMahon, 1986), a process facilitated by production of a mucus dragline from the exhalant siphon (Prezant and Charlermwat, 1984). Passive hydraulic dispersal of juvenile and adult *C. fluminea* not only accounts for its extraordinary ability to invade downstream portions of drainages after introduction (1999), but also leads to its impingement and fouling of industrial, agricultural, and municipal raw-water systems (1999). Similarly, current-mediated transport of free-swimming veliger and passively suspended juvenile *D. polymorpha,* and of adults attached to floating substrates or carried as clumps of individuals over the bottom accounts for its dispersal in European drainage systems after escape from the Caspian Sea (Mackie and Schloesser, 1996). This species rapidly spread downstream throughout the Great Lakes and St. Lawrence River from its original upstream introduction into Lake St. Clair in 1985–1986 (Mackie and Schloesser, 1996). It has also been carried throughout most of the Mississippi River and adjoining tributaries both by downstream hydrological transport and upstream by attachment to the hulls of commercial barges (Mackie and Schloesser, 1996) (Fig. 12). Zebra mussels invaded the lower Great Lakes, St. Lawrence River and Erie-Barge Canal by 1990, later invading portions of the upper Great Lakes, the Hudson River, and the Finger Lakes. *D. polymorpha* entered the Mississippi Drainage from Lake Michigan through the Illinois River and spread

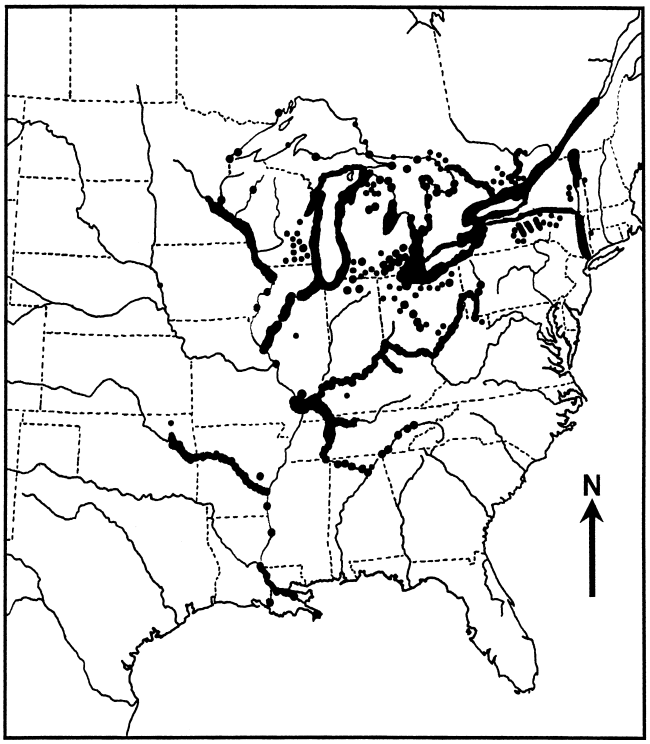

FIGURE 12 Distribution of the zebra mussel, *Dreissena polymorpha*, in North America as of Spring, 2000.

downstream to the Mississippi Delta and upstream to La Crosse, Wisconsin. It had invaded all major tributaries of the Mississippi River by 1998 with the exception of the Missouri River, where the first specimens were reported upstream of its confluence with the Platte River in 1999. As of early 2000, *D. polymorpha* occupied drainages in 21 eastern and midwestern U.S. states and in the Canadian provinces of Ontario and Quebec, including 62 confirmed populations in small, isolated inland lakes (Fig. 12). *Dreissena bugensis,* the second dreissenid species occupying NA inland waters is sympatric with *D. polymorpha* in Lakes Huron, Erie, and Ontario and the western end of the Erie-Barge Canal (New York Sea Grant, 1999).

Capacity for downstream transport and byssal attachment has made *D. polymorpha* a major NA biofouling pest species, recapitulating its history in Europe (Claudi and Mackie, 1993). Juvenile sphaerids are also passively, hydrologically transported downstream (McKillop and Harrison, 1982) which may be an important dispersal mode for many species in this family. In contrast, hydrological transport is extremely rare in unionoideans (Imlay, 1982).

As both sphaeriids and *C. fluminea* are self-fertilizing hermaphrodites (see Section II.B.5), a single individual can found a new population. In contrast, *D. polymorpha, D. bugensis* and the majority of unionoideans are gonochoristic, requiring simultaneous introduction of males and females to found a new population, thus reducing their capacity as invaders.

2. Anthropomorphic Impacts

The diversity of native NA unionoid bivalves is represented by two of the six recognized families of the Unionoidea: Margaritiferidae with two genera and five species; and Unionidae with 49 genera, 278 species, 13 subspecies (Turgeon *et al.,* 1998; Johnson, 1998; Williams and Fradkin, 1999). North American unionoidean diversity represents 51 of the approximately 165 unionoidean genera, and between one-fourth and one-third of the world's unionoidean species diversity (Bogan, 1993; Bogan and Woodward, 1992). Neves *et al.* (1997) documented that 261 of these taxa or 91% of NA unionoidean diversity occurs in the southeastern United States where it is focused in the Mobile Bay, Tennessee and Cumberland River basins. Alabama, with parts of the Mobile Bay and Tennessee River basins, has the greatest unionoidean diversity with 175 taxa followed by Tennessee with 129 taxa.

This great diversity of unionoidean bivalves began to be impacted as it began to be described, with European expansion across North America. It was noticed quite early on that the unionoidean fauna was declining (Higgins, 1858). By the turn of the 20th century, people were observing that the unionoidean fauna of entire regions was being decimated or had disappeared. Rhoads (1899) described extirpation of mussels from the Monongahela River at Pittsburgh due to damming and pollution. Ortmann (1909) noted the loss of the freshwater mussels, crayfish and fish fauna from the upper Ohio River Basin in western Pennsylvania due to acid run-off from coal mines and the complete destruction of the Pigeon River unionoidean fauna in east Tennessee by pollution (Ortmann, 1918). Van der Schalie (1938) warned that the Tennessee Valley Authority's construction of dams on the Tennessee River could lead to long-term negative impacts on, and the eventual destruction of, its freshwater fauna.

Extinction of NA freshwater bivalve species was not reported until Stansbery (1970, 1971) listed 11 presumed extinct taxa. Turgeon *et al.,* (1988) listed 13 taxa, Williams *et al.,* (1993) listed 12% of the unionoid taxa as extinct, and most recently Turgeon *et al.,* (1998) listed 35 taxa as presumed extinct (Table II). As of 1997, 77 NA unionid taxa were endangered, 43 threatened and 73 of special concern with only 70 species listed as currently stable and additional species being added to federal and state lists yearly (Williams *et al.,* 1993; Neves *et al.,* 1997). Massive historical losses of unionoideans have been revealed by comparison of

TABLE II Extinct Freshwater Unionoidean Bivalves

Species	*Common name*	*States of occurrence*
Alasmidonta mccordi Athearn, 1964	Coosa elktoe	AL
Alasmidonta robusta Clarke, 1981	Carolina elktoe	NC, SC
Alasmidonta wrightiana (Walker, 1901)	Ochlockonee arcmussel	FL
Elliptio nigella (Lea, 1852)	Winged spike	AL, GA
Epioblasma arcaeformis (Lea, 1831)	Sugarspoon	AL, KY, TN
Epioblasma biemarginata (Lea, 1857)	Angled riffleshell	AL, KY, TN
Epioblasma flexuosa (Rafinesque, 1820)	Leafshell	AL, IL, IN, KY, OH,TN
Epioblasma florentina florentina (Lea, 1857)	Yellow blossom	AL, KY, TN
Epioblasma haysiana (Lea, 1834)	Acornshell	AL, KY, TN, VA
Epioblasma lenior (Lea, 1842)	Narrow catspaw	AL, TN
Epioblasma lewisii (Walker, 1910)	Forkshell	AL, KY, TN
Epioblasma obliquata obliquata (Rafinesque, 1820)	Catspaw	AL, IL, IN, KY, OH, TN
Epioblasma personata (Say, 1829)	Round combshell	IL, IN, KY, OH
Epioblasma propinqua (Lea, 1857)	Tennessee riffleshell	AL, IL, IN, KY, OH,TN
Epioblasma sampsonii (Lea, 1861)	Wabash riffleshell	IL, IN, KY
Epioblasma stewardsonii (Lea, 1852)	Cumberland leafshell	AL, KY, TN
Epioblasma torulosa gubernaculum (Reeve, 1865)	Green blossom	TN, VA
Epioblasma torulosa torulosa (Rafinesque, 1820)	Tubercled blossom	AL, IL, IN, KY, OH,TN, WV
Epioblasma turgidula (Lea, 1858)	Turgid blossom	AL, AR, TN
Lampsilis binominata Simpson, 1900	Lined pocketbook	AL, GA
Medionidus mcglameriae van der Schalie, 1939	Tombigbee moccasinshell	AL
Pleurobema altum (Conrad, 1854)	Highnut	AL, GA
Pleurobema avellanum Simpson, 1900	Hazel pigtoe	AL
Pleurobema bournianum (Lea, 1840)	Scioto pigtoe	OH
Pleurobema chattanoogaense (Lea, 1858)	Painted clubshell	AL, GA, TN
Pleurobema flavidulum (Lea, 1861)	Yellow pigtoe	AL
Pleurobema hagleri (Frierson, 1900)	Brown pigtoe	AL
Pleurobema hanleyianum (Lea, 1852)	Georgia pigtoe	AL, GA, TN
Pleurobema johannis (Lea, 1859)	Alabama pigtoe	AL
Pleurobema murrayense (Lea, 1868)	Coosa pigtoe	AL, GA, TN
Pleurobema nucleopsis (Conrad, 1849)	Longnut	AL, GA
Pleurobema rubellum (Conrad, 1834)	Warrior pigtoe	AL, GA, TN
Pleurobema troschelianum (Lea, 1852)	Alabama clubshell	AL, GA, TN
Pleurobema verum (Lea, 1861)	True pigtoe	AL
Quadrula tuberosa (Lea, 1840)	Rough rockshell	TN, VA

(From Williams *et al.,* 1998b.)

present species assemblages with those of earlier surveys or with recent fossil assemblages (Neves and Zale, 1982; Parmalee and Klippel, 1982, 1984; Parmalee *et al.,* 1982; Ahlstedt, 1983; Havlik, 1983; Stern, 1983; Hoeh and Trdan, 1984; Miller *et al.,* 1984; Hartfield and Rummel, 1985; Taylor, 1985; Mackie and Topping, 1988; Nalepa and Gauvin, 1988; Starnes and Bogan, 1988; Baily and Green, 1989; Bogan, 1990; Anderson *et al.,* 1991; Counts *et al.,* 1991; Hornbach *et al.,* 1992; Parmalee and Hughes, 1993; Hoke, 1994; Blalock and Sickel, 1996). Extirpations of sphaeriid faunae are far less common, but have occurred (Paloumpnis and Starrett, 1960; Mills *et al.,* 1966). Unionoidean assemblages in Indian middens near the upper Ohio River yielded at least 32 species, while a 1921 survey yielded only 25 of the midden species, and a 1979 survey, only 13 of the midden species in the same area, indicative of massive species extirpation (Taylor and Spurlock, 1982). Similar historical loss of Indian midden species has occurred in the Tennessee River Drainage (Parmalee, 1988). Further evidence of environmental change in the upper Ohio River includes recent establishment of 15 unionid species previously unreported on Indian middens or earlier surveys (Taylor and Spurlock, 1982).

Such historical data clearly indicate the toll that anthropomorphic activities are taking on the NA unionoidean fauna (Neves, 1993; Neves *et al.,* 1997). The United States Fish and Wildlife Service began listing unionoideans as threatened and endangered after passage of the Endangered Species Act of 1973. By 1998, 56 taxa were listed as endangered (Turgeon *et al.,* 1998), with about 70% of NA unionoideans at some level of imperilment (Williams *et al.,* 1993). Bogan (1998) reviewed the causes for decline of NA freshwater bivalve diversity and attributed it, and species extinctions, to habitat destruction (loss of both

unionoidean and host fish habitat), pollution including acid mine runoff, pesticides, heavy metals, commercial exploitation and introduced species. Bogan (1997) summarized this:

> "The central cause of this decline and decimation of the freshwater molluscan fauna is the modification and destruction of their aquatic habitat, with sedimentation as a leading major factor. Sources of sedimentation include poor agricultural and timbering practices. Damming of major rivers has also had a dramatic impact on this fauna with the loss of unionid obligate host fish due to changes in local water quality and loss of habitat. In-stream gravel mining, dredging, and canalization have further eliminated stable aquatic habitat. Acidic mine drainage and various point and non-point pollution sources also continue to decimate local aquatic mollusk populations."

Evidence of negative anthropomorphic impacts on unionoidean populations is extensive. The freshwater pearling industry can extirpate entire populations (Laycock, 1983), overfishing for pearls being a major factor in the decline of the pearl mussel, *Margaritifera magaritifera* in Great Britain (Young and Williams, 1983a). Commercial unionid shell fisheries that provide seed pearls for the marine cultured pearl industry negatively impact NA populations (Williams *et al.,* 1993). Impoundments of rivers slow flow and allow accumulation of silt, leading to mussel fauna reductions (Duncan and Thiel, 1983; Parmalee and Klippel, 1984; Stern, 1983; Starnes and Bogan, 1988; Blay, 1990; Williams *et al.,* 1992; Houp, 1993; Parmalee and Hughes, 1993). Impoundments also eliminate glochidial fish hosts (Mathiak, 1979) or prevent fish host dispersal of glochidia. Release of cold, hypolimnetic water from impoundments negatively impacts downstream unionoidean populations (Ahlstedt, 1983; Clarke, 1983; Vaughn and Taylor, 1999). Controlled water releases from impoundments lead to major flow-rate oscillations, either scouring the bottom of suitable mussel substrates during high flows or causing lethal aerial exposure during low flows (Miller *et al.,* 1984; Vaughn and Taylor, 1999). Channelization of drainage systems for navigation or flood control is detrimental to unionoideans. Increased flow velocity and propeller wash elevate suspended solids, which interfere with mussel filter feeding and O_2 consumption (Aldridge *et al.,* 1987; Payne and Miller, 1987). It reduces availability of stabilized sediments, sand bars, and low-flow areas, all preferred unionoidean habitats (Payne and Miller, 1989; Strayer and Ralley, 1993; Strayer, 1999a).

Pollution adversely affects bivalves. Unionoidean faunas can be negatively impacted or extirpated by industrial pollution (Zeto *et al.,* 1987; Wade *et al.,* 1993), urban wastewater effluents (sewage, silt, pesticides) and resultant eutrophication and hypoxia (Gunning and Suttkus, 1985; St. John, 1982; Neves and Zale, 1982; Arter, 1989; Strayer, 1993), silt and acid discharges from mines (Taylor, 1985; Warren *et al.,* 1984; Anderson *et al.,* 1991) siltation from bank erosion due to deforestation, destruction of riparian zones, and poor agricultural practice (Hartfield, 1993; Williams *et al.,* 1993) or disturbance and silt from river-bed gravel mining (Brown and Curole, 1997). Advent of modern sewage treatment on the Pearl River, Louisiana, allowed re-establishment of five previously absent unionid species (Gunning and Suttkus, 1985).

Nonindigenous species (i.e., "biological pollution") present a new threat to NA unionoidean taxa. The nonindigenous zebra mussel, *D. polymorpha,* byssally attaches in great numbers to the exposed, posterior, siphonal shell regions of unionoideans, leading to their slow starvation as the zebra mussels strip suspended food particles from their inhalant current. Thus, zebra mussel infestations have extirpated a number of unionoidean species populations from the lower Great Lakes (Schloesser *et al.,* 1996).

3. Physical Factors

Physical factors influence bivalve distributions. While environmental requirements are species specific, a number of generalities appear warranted. Sediment type clearly affects distribution patterns. Unionoideans are generally most successful in areas where flow is moderate with a stable substrate of coarse sand or sand–gravel mixtures, and are generally absent from substrates with heavy silt loads and very low water flow (Strayer and Ralley, 1993; Strayer, 1999a). In the Wisconsin and St. Croix rivers, only 7 of 28 unionid species occurred in sand–mud sediments, the majority preferring sand–gravel mixtures. Only three species, *Pyganodon grandis, Lampsilis teres,* and *L. siliquoidea,* preferred sand–mud substrates (Stern, 1983). Some unionoidean species select preferred sediment types (Baily, 1989). In rivers subjected to periodic high flows, unionoideans oriented with siphons facing upstream to a greater extent than those in stable flow rivers, a position which presents the narrowest profile to the current, reducing chances of flow-induced dislodgment (Di Maio and Corkum, 1997). The relatively specific substrate and flow requirements of many unionoidean species may account for their patchy and clumped distributions (Strayer, 1999a). Courser sediments allowing free exchange of interstitial and surface waters may be a requirement for early survival of recently excysted juvenile unionoideans with low pH, hypoxia, and ammonia accumulation in interstitial water being correlated with juvenile mortality in sediments where free water exchange is reduced (Buddensiek *et al.,* 1993). Thus, sediment limitations for juvenile development may result in patchy or clumped adult unionoidean distributions. In contrast, *C. fluminea* is able to colonize

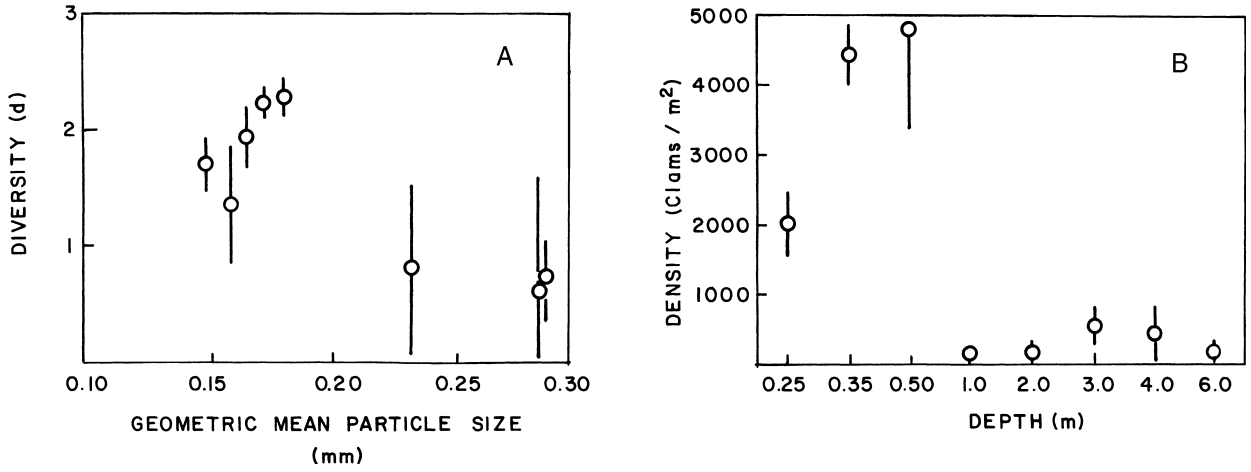

FIGURE 13 Sediment relationships in sphaeriid clam communities from sites along a depth transect in Britannia Bay, Ottawa River, Canada. (A) Mean sphaeriid density (Shannon–Weaver *d*) values for various sphaeriid communities in relation to mean sediment geometric particle size. (B) Mean sphaeriid density values at various depths. Vertical bars about points are 95 percent confidence limits. Note increase in diversity with decrease in mean sediment particle size and maximization of density at depths less than one meter. (Redrawn from data of Kilgour and Mackie, 1988.)

habitats ranging from bare rock through gravel/sand to silt (McMahon, 1999), which has allowed it to invade a wide variety of NA drainage systems. Its optimal habitat is oxygenated sand or gravel–sand (Belanger *et al.,* 1985).

In contrast to unionoideans, species diversity in *Pisidium* increases with decreasing particle size (Fig. 13A), becoming maximal at a mean particle diameter of 0.18 mm (Kilgour and Mackie, 1988). In southeastern Lake Michigan, *Pisidium* density and diversity were maximal in very fine sand–clay and silt–clay sediments, while peak *Sphaerium* diversity occurred at somewhat larger particle sizes (Zbeda and White, 1985). Thus, there are differences in substrate preferences among sphaeriids, perhaps associated with sediment organic detritus feeding mechanisms in *Pisidium* (see Section III.C.2).

Apparent differences in substrate preferences may be associated with species-specific differences in optimal water velocities. Unionoideans are most successful where velocities are low enough to allow sediment stability, but high enough to prevent excessive siltation (Strayer and Ralley, 1993; Strayer, 1999a), making well-oxygenated, coarse sand and sand–gravel beds optimal habitats for riverine species with such habitats being more critical for survival of juvenile unionoideans than adults (Buddensiek *et al.,* 1993). Low or variable velocities allow silt accumulations that make sediments too soft for maintenance of position in adult unionoideans (Lewis and Riebel, 1984; Salmon and Green, 1983) or which interfere with their filter feeding and gas exchange (Aldridge *et al.,* 1987). In contrast, periodic scouring of substrates during high flows removes substrate and unionoideans, and prevents their successful resettlement (Young and Williams, 1983b). Indeed, unionoidean densities decline in areas of high flow (Way *et al.,* 1990b). Sediment type did not affect burrowing in three lotic unionid species (*P. grandis, Elliptio complanata,* and *Lampsilis siliquoidea)* (Lewis and Riebel, 1984), suggesting that it is not involved in substrate preferences, but unionoideans may move to preferred sediments (Baily, 1989). *C. fluminea,* with its relatively heavy, ridged shell and rapid burrowing ability, is better adapted for life in high current velocities and unstable substrates than most unionoideans (McMahon, 1999). In the Tangipahoa River, Mississippi, it colonizes unstable substrates from which unionoideans are excluded (Miller *et al.,* 1986). In contrast to the majority of unionoideans and *C. fluminea,* many sphaeriid species occur in small ponds and the profundal portions of large lakes, where water flow is negligible and the substrate has high silt contents and heavy organic loads (Burky, 1983). Preference of some sphaeriids for low-flow, silty habitats may reflect interstitial sediment detritus feeding, particularly in *Pisidium* (Lopez and Holopainen, 1987) (see Section III.C.2). Byssal attachment allows *D. polymorpha* to inhabit relatively high flow areas compared to other bivalves (pediveliger larvae settle in flows up to 1.5m/sec). It also makes it successful epibenthic species in lentic habitats with a preponderance of hard substrates from which native NA bivalves are generally eliminated (Claudi and Mackie, 1993).

Water depth affects freshwater bivalve distributions. Most unionoideans prefer shallow habitats less than 4–10 m deep (Stone *et al.,* 1982; Salmon and Green, 1983; Machena and Kautsky, 1988; Way *et al.,* 1990b), although some species occur in deeper lotic waters if well oxygenated. *C. fluminea* is also restricted to shallow, near-shore lentic habitats (McMahon, 1999), as are the majority of *Sphaerium* and *Musculium* species (Fig. 13B) (Zbeda and White, 1985; Kilgour and Mackie, 1988). In contrast, some species of *Pisidium* inhabit profundal regions of lakes (Holopainen and Jonasson, 1983; Kilgour and Mackie, 1988). Depth distributions of *D. polymorpha* vary between habitats; however, adults rarely occur above 2 m and dense populations extend to 4–60 m, but are restricted to well-oxygenated waters above the epilimnion. The quagga mussel, *D. bugensis,* extends to greater, oxygenated depths than *D. polymorpha* in the Great Lakes (Mills *et al.,* 1996), but is unlikely to penetrate hypoxic hypolimnetic waters as it is less hypoxia tolerant than *D. polymorpha* (P. D. Johnson and R. F. McMahon, unpublished data). Recently settled juveniles of *D. polymorpha* migrate to deeper water (Mackie and Schloesser, 1996), perhaps avoiding wave-induced agitation (Clarke and McMahon, 1996b) or ice scour.

Limitation of most lentic bivalves to shallow habitats may reflect their poor hypoxia tolerance. In lentic habitats, hypolimnetic waters are often hypoxic. As many species of unionoideans, *Sphaerium* and *Musculium* (Burky, 1983), *Dreissena* (McMahon, 1996) and *C. fluminea* (McMahon, 1999) cannot maintain normal O_2 uptake under severely hypoxic conditions, they are mostly restricted to shallow, well-oxygenated habitats. Juvenile unionids are less hypoxia-tolerant than adults (Dimock and Wright, 1993), preventing colonization of hypoxic habitats. In contrast, many species of *Pisidium* are extreme $\dot{V}_{O_2}$ regulators (Burky, 1983) allowing them to inhabit highly hypoxic hypolimnetic habitats (Jonasson, 1984a, b). However, summer hypoxia retards growth and reproduction in profundal *Pisidium* populations, indicating that hypoxia can deleteriously impact even hypoxia-tolerant species (Halopainen and Jonasson, 1983). Hypoxia-intolerant *C. fluminea* invaded the profundal regions of a small lake only after artificial aeration of its hypoxic hypolimnetic waters (McMahon, 1999). Sewage-induced hypoxia in the Pearl River, Louisiana, extirpated its unionoidean fauna (Gunning and Suttkus, 1985). Even hypoxia-tolerant profundal *Pisidium* communities are extirpated by extreme hypoxia (Jonasson, 1984a).

Ambient pH does not greatly limit the distribution of freshwater bivalves. The majority of species prefer waters of pH above 7.0; species diversity declines in acidic habitats (Okland and Kuiper, 1982). However, unionoideans can grow and reproduce over a pH range of 5.6–8.3, a pH of less than 4.7–5.0 being the absolute lower limit (Fuller, 1974; Okland and Kuiper, 1982; Kat, 1982; Hornbach and Childers, 1987). Low pH may have sublethal effects on unionoideans. It reduces shell thickness (Hinch *et al.,* 1989), tissue cholesterol content (Rao *et al.,* 1987), and hemolymph concentrations of Na^+, K^+, and Cl^- (Pynnönen, 1991; Mäkelä and Oikari, 1992). Unionoidean glochida and juveniles are less low pH tolerant than adults (Huebner and Pynnönen, 1992; Dimock and Wright, 1993), perhaps preventing colonization of mildly acidic waters. In contrast, *Pyganodon grandis* showed no change in hemolymph Na^+, K^+, and Cl^- concentrations after transfer into an acidic lake (pH 5.9) from an alkaline lake (Malley *et al.,* 1988). Some sphaeriids are relatively insensitive to pH or alkalinity. Species richness, growth and reproduction in sphaeriid faunas of six low-alkalinity lakes was similar to those in higher alkalinity lakes (Rooke and Mackie, 1984a, b; Servos *et al.,* 1985). *Musculium partumeium* and *Pisidium casertanum* inhabited acid lakes in New York State (pH $<$6.0) (Jokinen, 1991). Indeed, maximal laboratory growth and reproduction in *Musculium partumeium* occurred at pH 5.0, suggesting adaptation to moderately acidic habitats (Hornbach and Childers, 1987).

Low-pH habitats generally have low calcium concentrations. Low pH leads to shell dissolution and eventual mortality if shell penetration occurs (Kat, 1982). Sphaeriids occur in waters with Ca concentrations as low as 2 mg Ca/L, while the unionid, *Elliptio complanata,* occurs at 2.5 mg Ca/L (Rooke and Mackie, 1984a). Among freshwater bivalves, *D. polymorpha* is the most calciphilous and pH intolerant; adults requiring pH $>$ 6.5 and $>$12 mg Ca/L and veliger larvae requiring pH $>$7.4 and $>$24 mg Ca/L for successful development (McMahon, 1996). Freshwater bivalves actively take up Ca^{2+} at medium concentrations as low as 0.5 mM Ca/L (0.02 mg Ca/L, see Section II.A.1), which is far below their minimal ambient Ca^{2+} concentration of 2–2.5 mg/L. Thus, the minimum ambient calcium concentration appears to be that at which the rate of calcium uptake and deposition to the shell exceeds that of calcium loss from shell dissolution and diffusion, allowing maintenance of shell integrity and growth. As many factors affect shell deposition and dissolution rates (e.g., temperature, pH, and calcium concentration), the minimal Ca concentration and/or pH tolerated by a species may vary between habitats dependent on interacting biotic and abiotic parameters and are often species-specific. Low calcium waters usually have low concentrations of other biologically important ions, making them inhos-

pitable to bivalves even if Ca concentrations are suitable for shell growth.

Temperature influences bivalve distributions; species have specific upper and lower limits for survival and reproduction (Burky, 1983). For example, intolerance of <2°C prevents *C. fluminea* from colonizing drainages in the northcentral United States, which reach 0°C in winter (Fig. 11) (McMahon, 1999), leading to low-temperature winter-population kills on the northern edge of its range (Sickel, 1986). Thus, many northern U.S. *C. fluminea* populations are restricted to areas receiving heated effluents (McMahon, 1999). In contrast, the maximal temperature for development of *D. polymorpha* eggs and larva is 24°C and adults do not tolerate temperatures >30°C, preventing this species from colonizing southern and southwestern U.S. waters which exceed 30°C in summer (McMahon, 1996). Indeed, in the most southern U.S. states, *D. polymorpha* only occurs in the lower Mississippi River which rarely exceeds 30°C (Hernandez *et al.*, 1995).

Water-level variation affects bivalve distributions. Declining water levels during droughts or dry periods expose relatively immotile bivalves for weeks or months to air. Restriction of many bivalve populations to shallow waters makes them susceptible to emersion. Many sphaeriid species and some unionoidean taxa are highly tolerant of air exposure, surviving prolonged seasonal emersion in ephemeral or variable level habitats (Burky, 1983; White, 1979; Byrne and McMahon, 1994). These species display unique emersion adaptations (Byrne and McMahon, 1994 and Section II.C.4).

Freshwater bivalve distribution is also related to stream size or order. Unionoidean species diversity increased with distance downstream in the Sydenhan River, Ontario (Mackie and Topping, 1988). Similarly, stream size proved to be the only useful predictor of unionoidean species richness of six tested factors (i.e., stream size, stream gradient, hydrologic variablity, Ca concentration, physiographic province and presence/absence of tides) in the Susquehanna, Delaware and Hudson River drainages (Strayer, 1993). The number of unionoidean species in Michigan drainage systems increased proportionately with system size; mainly by species additions (Strayer, 1983) (Fig. 14), but species richness could not be completely accounted for by drainage area size (note the high degree of variation in species richness versus drainage area values in Fig. 14), suggesting that other environmental variables affect unionoidean distribution patterns (Strayer, 1993). In the Ohio River drainage, the number of fish species was directly related to drainage area, and the number of unionoidean species directly related to the number fish species, suggesting that

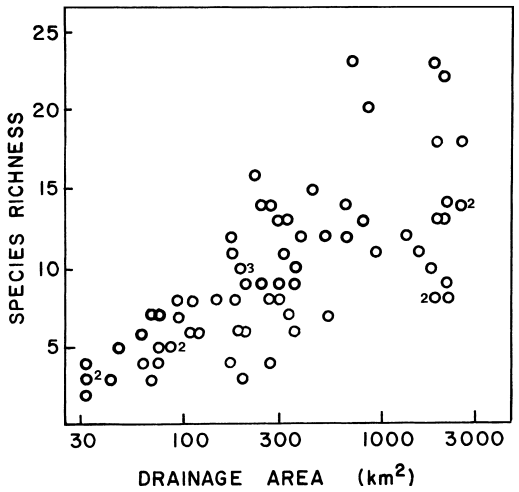

FIGURE 14 Unionoidean mussels species richness (total number of species present at a particular site) as a function of stream size measured by its total drainage area in km^2 in southeastern Michigan, United States. Numbers next to points indicate the number of observations falling on that point. The relationship between drainage area and mussel species richness was statistically significant $r = 0.68$, $P < 0.001$). (Redrawn from Strayer, 1983.)

unionoidean diversity is partially dependent on fish glochidial host species availability (Watters, 1993). Similarly, *Margaritifera hembeli* populations with the highest juvenile recruitment rates occurred in stream reaches with the highest densities of its fish host (Johnson and Brown, 1998). Among other variables affecting species richness are stream hydrology, affected by surface geology and soil porosity. Porous soils retain water, buffering runoff, so that streams draining them have constant flows and rarely dry, allowing them to support greater mussel diversity than streams draining soils of poor water-infiltration capacity that are prone to flooding–drying cycles. In variable-flow streams, emersion or low oxygen in stagnant pools during dry periods, and bottom scouring and high silt loads during floods reduce species richness (Strayer, 1983). Indeed, flow stability, high O_2, reduced flood risk, and low silt loads of larger streams appear to account for their increased bivalve species richness (Fig. 14) (Strayer, 1983, 1993; Way *et al.*, 1990b; Strayer and Ralley, 1993). However, some unionoidean species, such as *Amblema plicata, Pyganodon grandis* and *Fusconaia flava,* are adapted to small, variable flow streams (Strayer, 1983; Di Maio and Corkum, 1995) while other species favor tidally influenced portions of rivers (Strayer, 1993).

The above physical factors may interact to determine distributions of bivalves. The density of the unionoidean, *M. hembeli,* was affected by stream order, hardness, depth, substrate size and compaction, and

flow rate, with highest densities occurring in shallow areas of second-order streams, of hardness >8 mg/L, with higher flow rates, and stable sediments with larger particle sizes (Johnson and Brown, 2000).

B. Reproduction and Life History

North American freshwater bivalves display extraordinary variation in life history and reproductive adaptations. Life-history traits (e.g., those affecting reproduction and survival, including growth, fecundity, life span, age to maturity, and population energetics) have been reviewed for freshwater molluscs (Calow, 1983; Russell-Hunter and Buckley, 1983) and specifically for freshwater bivalves (Burky, 1983; Mackie, 1984; Mackie and Schloesser, 1996; McMahon, 1999). Most research involves the Sphaeriidae, with less information for unionoideans. Sphaeriids are good subjects for life-history studies, because of their greater abundances, ease of collection and laboratory maintenance, relatively simple hermaphroditic life cycles, ovoviviparity, semelparity, release of completely formed miniature adults, and relatively short life spans. In contrast, unionoideans are more difficult subjects because they are gonochoristic, long-lived, interoparous, often rare and difficult to collect, and have life cycles complicated by the parasitic glochidial stage. The life-history traits of *C. fluminea* and *D. polymorpha* have been intensely studied due to their invasive nature and economic importance as fouling organisms (Mackie and Schloesser, 1996; Nichols, 1996; McMahon, 1999).

1. Unionoidea

The life-history characteristics of freshwater unionoideans are clearly different from those of sphaeriids, *C. fluminea* or *D. polymorpha* (Table III). The majority of unionids live in large, stable aquatic habitats which buffer them from periodic catastrophic population reductions, typical of smaller, unstable aquatic environments (see Section III.A). In stable habitats, long-lived adults accumulate in large numbers (Payne and Miller, 1989). A few species inhabit ponds

TABLE III Summary of the Life History Characteristics of North American Freshwater Bivalves, Unionoidea, Sphaeriidae, *Corbicula fluminea, Driessena polymorpha*

Life history trait[a]	*Unionoidea*	*Sphaeriidae*	*Corbicula fluminea*	*Dreissena polymorpha*
Life span (years)	<6–>100 (Species dependent)	<1–>5 (species dependent)	1–4	4–7
Age at maturity (years)	6–12	>0.17–<1.0 (1 year in some species)	025–0.75	0.5–2
Reproductive mode	Gonochoristic (few hermaphroditic species)	Hermaphroditic	Hermaphrodictic self-fertilizing	Gonochoristic
Growth rate	Rapid prior to maturity, slower thereafter	Slow relative to Unionoideans, *C. fluminea* or *D. polymorpha*	Rapid throughout life	Rapid throughout life
Fecundity (young per avg. adult per breeding season)	200,000–17,000,000 per female	3–24 (*Sphaerium*) 2–136 (*Musculium*) 3–7 (*Pisidium*)	35,000	30,000–40,000 per female
Juvenile size at release	Very small, 50–450 μm	Large 600–4150 μm	Very small 250 μm	Extremely small, 40 μm
Relative juvenile survivorship	Extremely low	High	Extremely low	Extremely low
Relative adult survivorship	High	Intermediate	Low 2–41% per year	Intermediate 26–88% per year
Semelparous or iteroparous	Highly iteroparous	Semelparous or Iteroparous (species dependent)	Moderately iteroparous	Moderately iteroparous
Number of reproductive efforts per year	One	1–3 (continuous in some species)	Two (spring and fall)	One (2–8 months long)
Assimilated energy respired (%)	—	21–91 (Avg. = 45%)	11–42	—
Nonrespired energy allocated to growth (%)	85.2–97.5	65–96 (Avg. = 81%)	58–71	96.1
Nonrespired energy allocated to reproduction (%)	2.8–14.8	4–35 (Avg. = 19%)	15	4.9
Turnover time in days (= mean standing crop biomass : biomass per day ratio)	1790–2849	27–1972 (generally <80)	73–91	53–869 (habitat dependent)
Habitat stability	Stable	Intermediately stable	Unstable	Moderately unstable

[a] See text for literature citations to data on which this table was based.

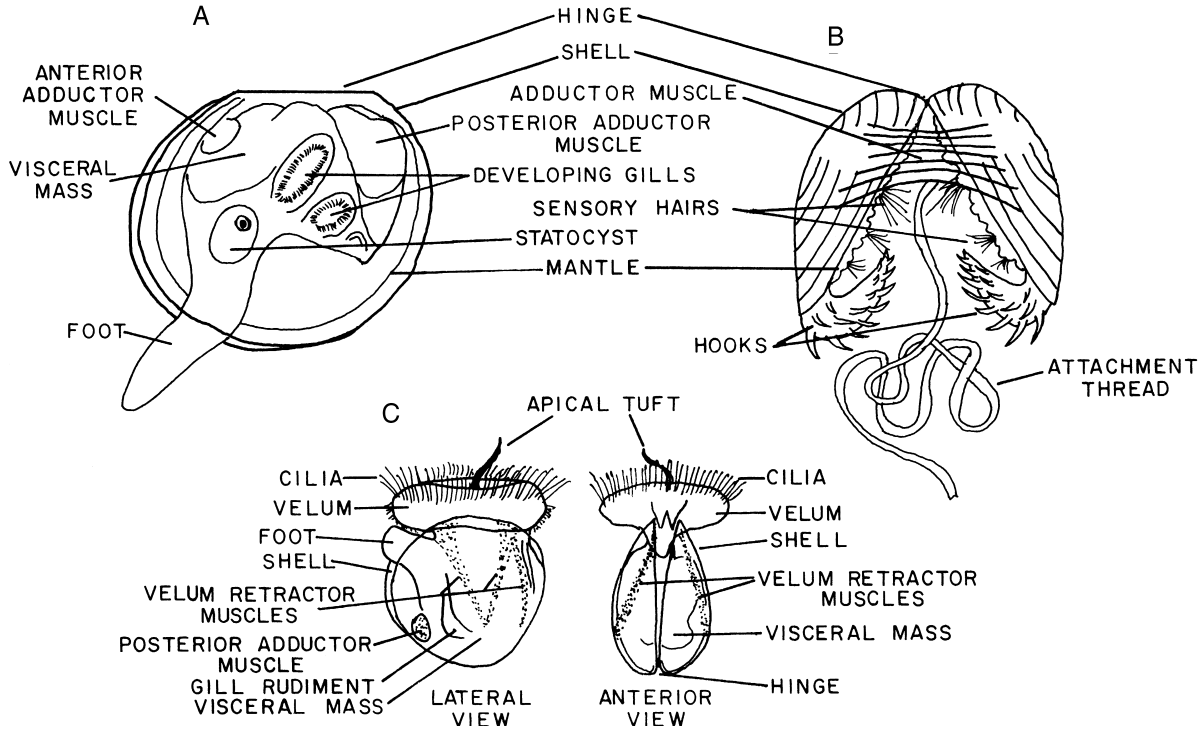

FIGURE 15 Anatomic features of freshwater bivalve larval stages. (A) the D-shaped juvenile of *Corbicula fluminea*, the freshwater Asian clam (shell length = 200 μm). (B) The glochidium larva of unionoideans, which is parasitic on fish. Depicted is the glochidium of *Pyganodon* characterized by the presence of paired spined hooks projecting medially from the ventral edges of the shell valves and an attachment thread; not all unionoidean species have glochidia with these characteristics (50–400 μm in diameter depending on species). (C) Lateral and anterior views of the free-swimming, planktonic veliger stage of *Dreissena polymorpha*, the zebra mussel; the veliger is 40–290 μm in diameter and uses the ciliated velum to swim and feed on phyto- and bacterioplankton. Presence of a foot as shown in this diagram indicates development to the settlement competent pediveliger stage. The juveniles of freshwater sphaeriid species are large and highly developed, having essentially adult features (Fig. 2A) at birth.

(Burch, 1975b), but their life-history traits have not been studied.

An important aspect of the unionoidean life-history traits is their parasitic glochidium larval stage (Fig. 15B). With the exception of *Simpsonaias ambigua,* whose glochidial host is the aquatic salamander, *Necturus maculosus,* all other known NA unionoideans have glochidial fish hosts (Watters, 1994b). The significance of glochidia unionoidean reproduction has been reviewed by Kat (1984) and details of glochidial incubation and development in marsupial brood pouches were described in Section II.B.5. The glochidium has a bivalved shell adducted by a single muscle. Its mantle edge contains sensory hairs. In the genera *Unio, Anodonta, Pygauodon, Megalonaias,* and *Quadrula,* a long threadlike structure projects from the mantle beyond the ventral valve margin which may be involved with detection of and/or attachment to, fish hosts.

There are three general forms of glochidia. In the subfamily Anodontinae, "hooked glochidia" occur, with triangular valves from whose ventral edges project an inward curving hinged hook covered with smaller spines (Fig. 15B). On valve closure, the hooks penetrate the skin, scales, or fins of fish hosts, allowing glochidial attachment and encystment on host external surfaces. The majority of NA unionoideans produce "hookless glochidia" with more rounded valves bearing reinforcing structures and/or small spines or stylets on their ventral margins which generally attach and encyst on fish gills. "Axe-head glochidia" of the genus *Potamilus* have a flared ventral valve margin, and near-rectangular valves which may have hooklike structures on each corner. Their host attachment sites are unknown (Kat, 1984).

Glochidia initially attach to fish by clamping (snapping) the valves onto fins, scales, and/or gill filaments. They are not host-specific in attachment, attaching to any contacted fish (Kat, 1984). In contrast, gravid adult unionids (European *Anodonta anatina*) appear to release glochidia in response to chemicals released by host fish (Jokela and Palokamgas, 1993). Once

released, glochidia display 'snapping' behavior' (i.e., host attachment behavior), the valves being rapidly and repeatedly adducted. In *M. margaritifera,* glochidial valve snapping is stimulated by the presence of mucus, blood, gill tissue, or fins of their brown trout host, but not by water currents or tactile stimulation (Young and Williams, 1984a), suggesting use of chemical cues to detect and attach to host fish.

Glochidia encyst in fish host tissues within 2–36 h of attachment and may or may not grow during encystment, depending on species. Time to juvenile excystment is also species-dependent, ranging from 6 to 160 days, but is reduced at higher temperatures (Zale and Neves, 1982; Kat, 1984). Unsuitable host fish reject glochidia after encystment (Kat, 1984), fish blood serum components dictating host suitability (Neves *et al.,* 1985). Since glochidia nonselectively attach to fish (Kat, 1984; Neves *et al.,* 1985), host suitability appears more dependent on fish immunity than on glochidial host recognition. Indeed, even suitable host fish reject glochidia, rejection rate being host fish species-dependent (Haag *et al.,* 1999). Numbers of *M. margaritifera* glochidia encysted in a brown trout population declined with time (Young and Williams, 1984b), with laboratory studies revealing that only 5–12% of *M. margaritifera* glochidia successfully excyst from infected host fish, indicating host rejection of most encysted individuals (Young and Williams, 1984a).

Unionoideans have adaptations that increase likelihood of glochidia contact with fish hosts. Glochidial release occurs annually, but duration of release is species-dependent with some species having more than one annual release period (Fukuhara and Nagata, 1988; Gordon and Smith, 1990). Cycles of gametogenesis and glochidial release may be controlled by neurosecretory hormones (Nagabhushanam and Lomte, 1981). Tachytictic mussels are short-term breeders, whose glochidial development and release occurs between April and August; shedding of glochidia often corresponding with either migratory periods of anadromous fish hosts, or nesting periods of their host fish. Fish hosts of tachytictic unionoideans often construct nests in areas harboring dense unionoidean populations, where fish host nest construction by fanning away substrates, and fish host fanning of developing embryos provide optimal conditions for glochidial– host contact. Thus, a high proportion of nest-building fish species, such as centrarchids, are glochidial hosts for NA unionoideans (Watters, 1994b). In contrast, bradytictic unionoidean species are long-term breeders, retaining developing glochidia in gill marsupia throughout the year, releasing them in summer (Kat, 1984).

When released from adult mussels, glochidia are generally bound by mucus into discrete packets, which either dissolve, releasing glochidia, or remain intact as discrete "conglutinates" of various species-specific forms and colors. Glochidia with attachment threads (Fig. 15B) are released in tangled mucus threads that dissolve relatively rapidly. Many of these glochidia possess hooks and attach to fish-host external surfaces. Hooked glochidia are larger than other types of glochidia (Bauer, 1994). In some unionoideans, mucilaginous networks of glochidia persist, enhancing host contact by suspending glochidia above the substrate.

Unionids with hookless glochidia that attach to fish gills may release conglutinates that mimic the food items of their fish hosts. They resemble brightly colored oligochaetes, flatworms, or leeches. Some species hold their wormlike conglutinates partially extruded from the exhalant siphon, making them more obvious to fish hosts. Some *Lamsilis* species, such as, *Lampsilis perovalis,* produce a "supercongultinate" that contains all the glochidia in the marsupial gill and resembles a small fish. It is tethered to the female's exhalant siphon by a long, transparent mucus strand (Fig. 16A). In flowing water, it mimics the darting motions of a small fish, eliciting attacks by host fish (Haag *et al.,* 1995). Consumption of such conglutinates releases glochidia within the buccal cavity of the fish followed by transport to gill filament attachment sites on ventilatory currents.

The most unusual unionoidean host food mimicry involves pigmented muscular, posterior mantle edge extensions in female *Lampsilis* and *Villosa*. These "mantle flaps' (Fig. 16B) resemble the small fish or macroinvertebrate prey of their fish hosts (Haag and Warren, 1999). Gravid females extend the posterior shell margins well above the substrate and pulsate the projecting mantle flaps to mimic a small, actively swimming fish or moving macroinvertebrate. When fish strike these mantle lures, glochidia are forcibly released through posterior pores in the marsupial gill (often projected between the mantle flaps, Fig. 16B) assuring glochidial ingestion and contact with the fish host gills (Kat, 1984; Haag and Warren, 1999).

As the glochidia of some unionoideans do not grow while encysted, their parasitic nature has been questioned. However, *in vitro* glochidial culture experiments suggest that they absorb organic molecules from fish tissues and require fish plasma for development and metamorphosis (Isom and Hudson, 1982), indicative of a true host–parasite relationship. Indeed, glochidial infection damages fish hosts, especially juvenile fish (Cunjak and McGladdery, 1991; Panha, 1993).

Like other parasites, glochidia are shed in huge numbers to ensure the maximum host contact and attachment. Unionoidean fecundity ranges from 10,000 to 17,000,000 glochidia per female per breeding season (Parker *et al.,* 1984; Young and Williams, 1984b;

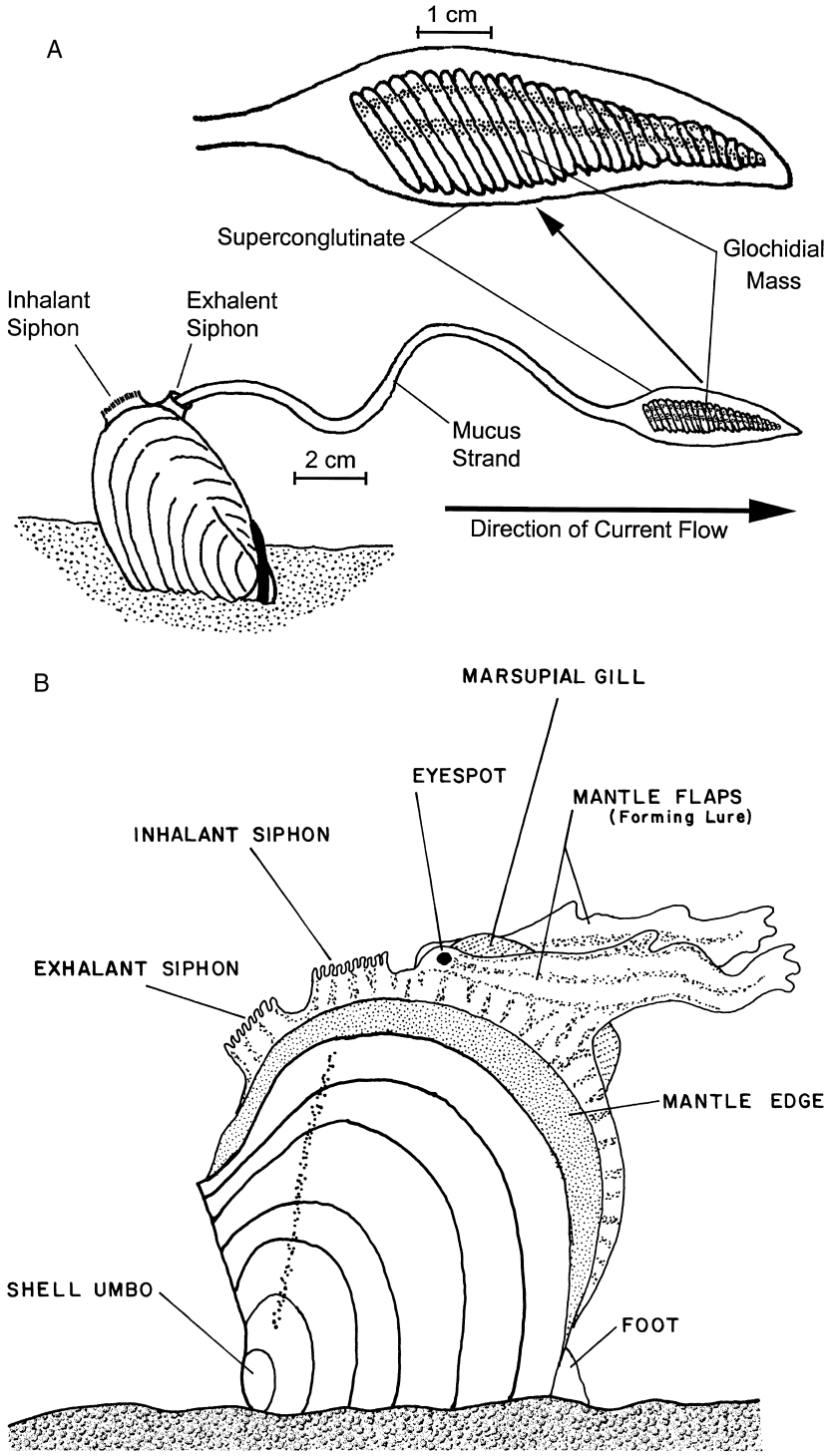

FIGURE 16 Reproductive adaptations in female Lamsilid unionoideans. (A) Superconglutinate tethered on a mucus strand extending from the exhalant siphon of *Lampsilis perovalis*. Glochidia are encapsulated in the flattened terminal lure (detailed in the upper portion of the figure) at the end of the mucus strand which makes darting fishlike movements in water currents, enticing host fish to strike the lure, thus assuring release of glochidia into its buccal cavity for attachment to the fishes' gills. (Redrawn from Haag *et al.*, 1995) (B) The modified, mantle flaps of a female specimen of *Lampsilis ovata*, which mimic the small fish prey (note eye spot and lateral linelike pigmentation) of its predatory host fish species. The posterior portions of the marsupial outer demibranchs are projected from the mantle cavity to lie between the flap lures. When the mantle flap lures are struck by an attacking host fish, glochidia are released through pores in the marsupial gill ensuring their entry into the Figh's buccal cavity and attachment to its gills. Superconglutinates and mantle flap lures are characteristic of the unionoidean genus, *Lampsilis*.

Paterson, 1985; Paterson and Cameron, 1985; Jansen and Hanson, 1991; Bauer, 1994), brood size increasing exponentially with female size (Janson and Hanson, 1991; Bauer, 1994). Probability for glochidial survival to metamorphosis is extremely small. In a natural population of *M. margaritifera,* a species that does not produce glochidial conglutinates, only 0.0004% of released glochidia successfully encysted in fish hosts. Of these, only 5% were not rejected before excystment; and, of those successfully metamorphosing, only 5% established as juveniles in the substrate (Young and Williams, 1984b). Thus, only one in every 100,000,000 shed glochidia became settled juveniles. High glochidial mortality makes the effective fecundity of unionoideans extremely low, which is not unusual for a species adapted to stable habitats. Similarly, only 0.007% of released glochida of *Pyganodon grandis* encysted in their host fish (*Perca flavescens*), however, once encysted, they had relatively high survival, 27% surviving to, and excysting after, two years (Jansen and Hanson, 1991). Based on these data and the fecundity ranges listed in Table III, only 0.002–0.17 of the glochidia produced by a female unionoidean would successfully settle as juveniles in sediment. Therefore, the main advantages of the glochidial stage appear to be a directed dispersal by fish hosts into favorable habitats (Kat, 1984) and utilization of fish-host energy resources to complete development to a juvenile large enough to effectively compete after settlement in adult habitats (Bauer, 1994).

There is a trade-off between glochidial size and number of glochidia released. Species with large glochidia (including toothed glochidia) produce fewer glochidia while species with small glochidia release them in great numbers (Bauer, 1994). Species releasing fewer, larger glochidia, tend to have a greater range of host-fish species and prefer lower flow habitats (Bauer, 1994). Production of many small glochidia occurs in species with limited fish hosts and may increase chances of glochidial–host contact, while having a wide range of host-fish species allows production of fewer, larger glochidia, because chances of glochidium contact with a suitable host are higher. In the highly K-selected, stable habitats of most unionoideans, excysting at a large size makes juvenile mussels more competitive, increasing likelihood of survival to maturity. Thus, small glochidia of unionoideans, such as *Margaritifera,* remain encysted for longer periods (>1000 days), allowing growth to a more competitive size before excystment. In contrast, among species with larger glochidia, the encystment period is much shorter (200–300 days) before attainment of competitive juvenile size. The long encystment periods of small glochidia reduce their chances for successful excystment due to increased chances of host mortality and/or rejection by the host's immune system, selecting for production of greater numbers of glochidia to assure recruitment of enough juveniles to sustain population size (Bauer, 1994).

Glochidial utilization of fish-host energy stores prevents their direct competition with adults for limited food and space resources (Bauer, 1994), as occurs in juvenile *C. fluminea* and *D. polymorpha.* Glochidial parasitism also allows female unionoideans to devote relatively small amounts of nonrespired, assimilated energy to reproduction (2.8–14.5% of total nonrespired, assimilated energy), leaving the majority for somatic tissue growth (Table V) (Negus, 1966; James, 1985; Paterson, 1985). Allocation of a high proportion of energy to tissue growth is characteristic of species adapted to stable habitats (i.e., K-selected species). As unionoideans are often very long-lived (*Margaritifera margaritifera* up to 130–200 years) and highly iteroparous (>6–10 reproductive periods throughout life), allocation of the majority of nonrespired energy to growth increases probability of adult survival to future reproductive efforts. Increased growth rate and reduction of reproductive effort increases competitiveness and lowers probability of predation and/or mortality associated with reproductive effort or dislodgment from the substrate during floods. All these characteristics increase unionoidean fitness in stable habitats (Sibly and Calow, 1986; Bauer, 1994).

In the majority of unionoideans, greatest shell growth occurs in immature individuals during the first 4–6 years of life (Hanson *et al.,* 1988; Payne and Miller, 1989; Harmon and Joy, 1990) (Fig. 17A). Indeed, relative shell growth in young unionids is greater than in sphaeriids or *C. fluminea* and *D. polymorpha* (Table III). Unionoidean shell-growth rate declines exponentially with age, but tissue biomass accumulation rate remains constant or increases with age (Fig. 17A, B; see also Haukioja and Hakala, 1978). Thus, early in life, increases in shell size and biomass occur preferentially over tissue accumulation; whereas after maturity (>6 years), shell growth slows and tissue accumulates at proportionately higher rates. Delayed maturity in unionoideans (6–12 years, Table III) allows allocation of all nonrespired assimilation to growth early in life and, due to an exponential relationship between size and fecundity, leads to reproductive effort being primarily sustained by the oldest, largest individuals (Downing *et al.,* 1993).

Growth rates in unionoideans are affected by abiotic conditions. Shell growth of field-enclosed specimens *P. grandis* declined with depth, being greatest >3 m (Hanson *et al.,* 1988). However, in natural populations, depth did not influence shell growth in *P. grandis* (Hanson *et al.,* 1988) or *A. woodiana* (Kiss and Pekli, 1988), suggesting that vertical migration

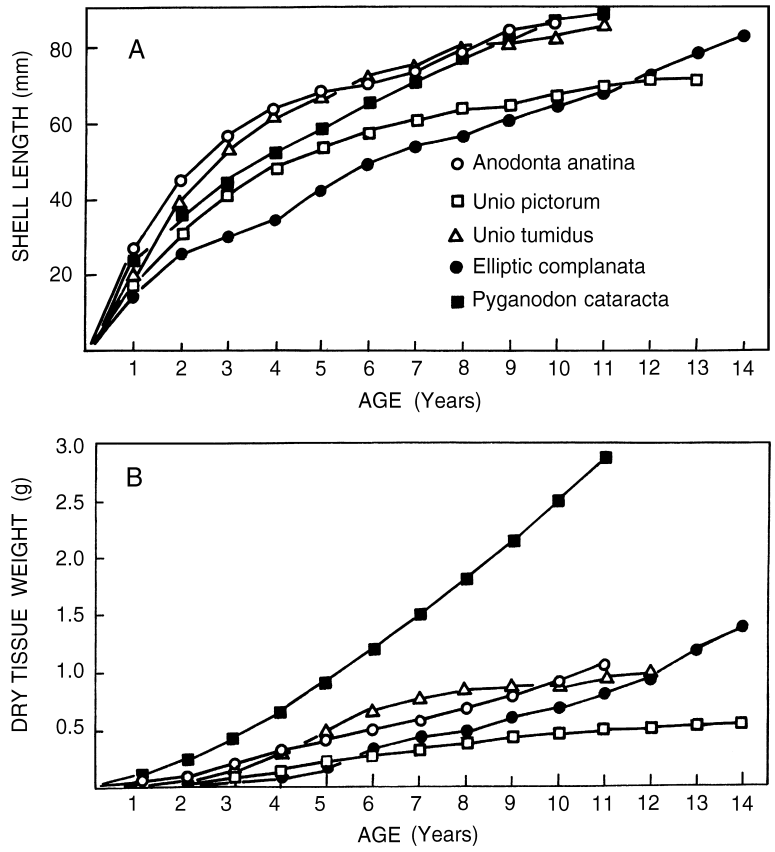

FIGURE 17 The shell and tissue growth of selected species of unionids (*Anodonta anatina*, open circles; *Unio pictorum*, open squares; *Unio tumidus*, open tiangles; *Elliptio complanata*, solid circles; and *Pyganodon cataracta*, solid squares). (A) Mean shell-length increase with increasing age over the entire life span of each species. (B) Mean dry tissue-weight increase with increasing age over the entire life span of each species. Note that increase in shell length declines with age, while dry tissue weight increases either linearly or exponentially with age. (Data from Negus, 1966; Paterson, 1985; and Paterson, and Cameron, 1985.)

may mask depth influences on growth in free-living individuals (Hanson *et al.,* 1988). Unionoidean growth rates also vary seasonally with level of precipitation (Timm and Mutvei, 1993) and can be depressed by pollutants (Harman and Joy, 1990).

Once mature, large adult unionoideans display high age-specific survivorship between annual reproductive efforts, being 81–86% in 5–7 year-old *Anodonta anatina* (Negus, 1966), greater than 80% in mature *M. margaritifera* (12–90 years) (Bauer, 1983), with a lower value of 15.6% in *Pleurobema collina* (Hove and Neves, 1994). High adult survivorship, long life spans, and low juvenile survivorship account for the preponderance of large adult individuals in natural unionoidean populations (Bauer, 1983; James, 1985; Negus, 1966; Paterson, 1985; Paterson and Cameron, 1985; Tevesz *et al.,* 1985; Hansen *et al.,* 1988; Huebner *et al.,* 1990; Woody and Holland-Bartels, 1993; Hove and Neves, 1994; Vaughn and Pyron, 1995). Populations dominated by adults are characteristic of stable, highly competitive habitats (Sibly and Calow, 1986).

The preponderance of large, long-lived adults in unionoidean populations causes them to have high proportions of standing crop biomass relative to biomass production. The relationship between standing crop biomass and biomass production rate can be expressed as turnover time, computed in days as the average standing crop of a population divided by its mean daily productivity rate (Russell-Hunter and Buckley, 1983). Long-lived unionids, with populations dominated by large adults, have extremely long turnover times ranging from 1790–2849 days (computed from data in James, 1985; Negus, 1966; Paterson, 1985; Huebner *et al.,* 1990) compared with sphaeriids (27–1972 days), *C. fluminea* (73–91 days), or *D. polymorpha* (53–869 days) (Table III). Such extended turnover times

characterize long-lived, iteroparous species from stable habitats (Russell-Hunter and Buckley, 1983).

In only one aspect do unionoideans deviate from the life-history traits expected of species inhabiting stable habitats and experiencing extensive competition (i.e., K-selected). That is in the production of large numbers of small young (glochidia). However, as described above, this is an adaptation ensuring sufficiently high probability of glochidial–host fish contact. Thus, species producing conglutinates resembling fish host prey items have greater glochidial–host contact and produce fewer (200,000–400,000 glochidia per female) and larger glochidia (Kat, 1984). In contrast, *M. margaritifera,* which releases very small, dispersed glochidia, has extraordinarily high fecundities (up to 17,000,000 glochidia per female) (Young and Williams, 1984b).

Extended life spans, delayed maturity, low effective fecundities, reduced dispersal, high habitat selectivity, poor juvenile survival and extraordinarily long turnover times make unionoidean populations highly susceptible to human perturbations. Because of their life-history traits (particularly long life spans and low effective fecundities), they do not recover rapidly once decimated by pollution or other human- or naturally-mediated habitat disturbances (see Section III.A). Successful juvenile settlement appears particularly affected by disturbance, with population structures indicating periods when entire annual generations are not recruited (Bauer, 1983; Negus, 1966; Payne and Miller, 1989). Reduction in population densities may reduce fertilization success in unionoideans. Complete failure of fertilization in *Elliptio complanata* occurred at densities <10 mussels/m^2 with densities >40 mussels/m^2 required for 100% of females to be fertilized (Downing *et al.,* 1993). Thus, anthropomorphically influenced reduction of unionoidean population densities to low levels could prevent further recruitment. Such disturbance-induced lack of juvenile recruitment raises the specter of many NA unionoidean populations being composed of dwindling numbers of long-lived adults destined for extirpation as anthropomorphic disturbances prevent reproduction and/or juvenile recruitment in aging adult populations (for an example, see Vaughn and Pyron, 1995).

2. Sphaeriidae

The Sphaeriidae display great intra- and interspecific life history variation (Holopainen and Hanski, 1986; Mackie, 1984; Way, 1988). Like unionoideans, their life-history traits do not fall into suits associated with stable or unstable habitats. Instead, they include the short life spans, early maturity, small adult size, and increased energetic allocation to reproduction associated with adaptation to unstable habitats, and the slow growth rates, low fecundity, and release of large, fully developed young associated with adaptation to stable habitats (Sibly and Calow, 1986) (Table III). Sphaeriids are euryoecic (i.e., have a broad habitat range); some members inhabiting stressful habitats, such as ephemeral ponds, and small, variable flow streams, while others live in stable, profundal lake habitats (Burky, 1983). Here, we generalize the life-history traits of sphaeriids within adaptive and evolutionary frameworks. However, the degree of inter- and intraspecific life-history variation in this group is such that, for each generality, specific exceptions can be cited (Mackie, 1979).

Central to understanding sphaeriid life-history traits is their viviparous reproduction (Mackie, 1978). All species brood embryos in specialized chambers formed from evaginations of the exhalant side of the inner demibranch gill filaments. Maternal nutrient material is supplied to embryos supporting their growth and development to release as fully formed miniature adults (see Section II.B.5). Thus, even though adult sphaeriids are the smallest of all NA freshwater bivalves, they release the largest young (Mackie, 1984). Among 13 sphaeriid species, average birth shell length ranged from 0.6 to 4.15 mm (Burky, 1983; Holopainen and Hanski, 1986; Hornbach and Childers, 1986; Hornbach *et al.,* 1982; Mackie and Flippance, 1983a), much larger than unionoidean glochidia (0.05–0.45 mm, Bauer, 1994), *C. fluminea* juveniles (0.25 mm, McMahon, 1999), or *D. polymorpha* veliger larvae (0.04–0.07 mm, Nichols, 1996) (Table III). Based on shell lengths, newborn sphaeriids have $(3.4–2.1) \times 10^5$ times greater biomass than newborns of other groups. Ratios of maximum adult shell length : birth shell length in sphaeriids range from 2.8:1 to 5.4:1, suggesting that newborn juveniles have biomass 0.6–4.6% of the maximum biomass of adults. There is a significant direct relationship between these two parameters, shown in Figure 18.

Large offspring size reduces sphaeriid fecundity. Average clutch sizes range from 3 to 24 per young per adult for *Sphaerium,* 2 to 136 per young per adult for *Musculium,* and 1.3 to 16 per young per adult for *Pisidium* (Burky, 1983; Holopainen and Hanski, 1986). Even with reduced fecundity, large juvenile biomass requires allocation of large amounts of non-respired energy to reproduction ($\bar{x} = 19\%$, Burky, 1983) compared to unionoideans ($<14.8\%$), *C. fluminea* (15%) or *D. polymorpha* (4.9%) (Table III). As developing juveniles have high metabolic rates (Burky, 1983; Hornbach, 1985; Hornbach *et al.,* 1982) and are supported by adult energy stores (Mackie, 1984), estimates of reproductive costs based on released juvenile biomass may grossly underestimate actual reproductive costs in this group.

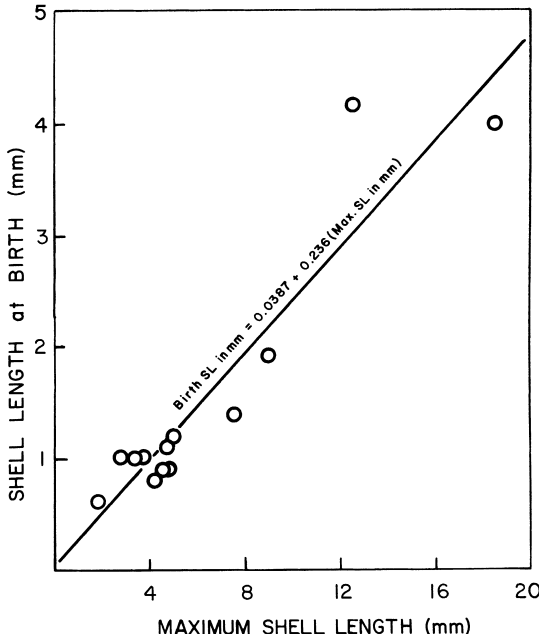

FIGURE 18 The relationship between shell length (SL) of juveniles at birth and maximal SL of adults for 13 species of sphaeriid freshwater clams. Note that juvenile birth length increases linearly with maximal adult size, suggesting that adult size may limit juvenile birth size in sphaeriids. The solid line represents the best fit of a linear regression relating birth size to maximal adult size as follows: Birth SL = 0.0387 + 0.236 mm (maximal adult SL in mm) ($n = 13$, $r = 0.935$, $F = 76.3$, $P < 0.0001$). (Data from Holopainen and Hanski, 1986; Hornbach and Childers, 1986; Hornbach *et al.*, 1982; and Mackie and Flippance, 1983a.)

Life-history hypotheses predict that the low fecundity and large birth size of sphaeriids would maximize fitness in stable habitats. However, the majority of sphaeriids inhabit variable ponds and streams or profundal habitats subject to hypoxia (Burky, 1983; Holopainen and Hanski, 1986). Burky (1983) and Way (1988) have argued that the harsh conditions of such habitats are seasonally predictable, making them, in reality, stable. Thus, sphaeriid species inhabiting them have adaptations that prevent catastrophic population reductions during seasonal episodes of environmental stress (see Section II.C). Thus, sphaeriid populations approach carrying capacity, leading to selection for life-history adaptations associated with the intense intraspecific competition characteristic of life in stable habitats.

Seasonal water-level fluctuation and hypoxia often more severely impact smaller individuals. Thus, production of large, well-developed juveniles by sphaeriids may increase their probability of surviving predictable environmental stress. As such stress can cause high adult mortality (Burky *et al.*, 1985b; Holopainen and Jonasson, 1983; Hornbach *et al.*, 1982; Jonasson 1984b), fitness would also be increased by devoting greater proportions of nonrespired assimilation to any one reproductive effort, as chances of adult survival to the next reproduction are low. Thus, sphaeriids devote relatively higher proportions of energy to reproduction than other freshwater bivalves (Burky, 1983) (Table III). This combination of *r*- selected and K-selected traits, optimizing sphaeriid fitness in habitats with periodic, predictable stress, is a life-history strategy called "bet hedging" (Stearns, 1980).

The early maturation, characteristic of many sphaeriid species (Burky, 1983; Holopainen and Hanski, 1986) (Table III), is due to the advanced development of newborn juveniles, and allows reproduction before onset of seasonal environmental stress. This trait is particulary displayed by sphaeriid species inhabiting ephemeral ponds and streams. They have rapid growth, early maturity, and reduced numbers of reproductive efforts. Thus, *Musculium lacustre, Pisidium clarkeanum,* and *P. annandalei* from temporary drainage furrows in Hong Kong live less than 1 year, and have only one or two life-time reproductive efforts (Morton, 1985, 1986). Similarly, *Musculium lacustre, Pisidium casertanum, P. variable, Sphærium fabule,* and *Musculium securis* had only 1–3 reproductive efforts within life spans of 1 to 2 years (Mackie, 1979) and a lake species, *S. japonicum,* is univoltine and semelparous (Park and Okino, 1994). An ephemeral pond population of *Musculium partumeium* lived 1 year, was semelparous, reproduced just prior to pond-drying, and devoted a large proportion of nonrespired assimilation (18%) to reproduction (Burky *et al.,* 1985b). Ephemeral pond populations of *M. lacustre* were similarly univoltine and semelparous, devoting 19% of nonrespired energy to reproduction (Burky, 1983). A *Sphaerium striatinum* population, subject to flooding, lived 1 year or less and reproduced biannually (Hornbach *et al.,* 1982), devoting 16.1% of nonrespired assimilation to reproduction (Hornbach *et al.,* 1984b). In contrast, when populations of these species occur in more permanent habitats, they become bivoltine, reproducing in both spring and fall. Spring generations are iteroparous, reproducing in the fall and following spring; whereas fall generations are semelparous, reproducing only in the spring (Mackie, 1979; Burky, 1983; Burky *et al.,* 1985b).

Some *Pisidium* species live in the profundal portions of large, more permanent lentic habitats where they tolerate periodic hypoxia after summer formation of the hypolimnion (see Section II.C.3). As these profundal species are tolerant of hypoxia, such environments are more stable than small ponds and streams, although far less productive, reducing food availability (Holopainen and Hanski, 1986). Thus, profundal sphaeriids display life-history strategies differing from those in small ponds and streams

(Burky, 1983; Holopainen and Hanski, 1986). Profundal populations have reduced growth rates, longer life spans of 4 to 5 years, delayed maturation often exceeding 1 year, higher levels of iteroparity, and univoltine reproductive patterns (Holopainen and Hanski, 1986), all life-history traits characteristic of more stable habitats (Sibly and Calow, 1986). Interestingly, shallow-water and profundal populations of the same species of *Pisidium* may display different life-history tactics. Compared to profundal populations, shallow-water populations grow more rapidly, mature earlier, have shorter life spans, and tend toward semelparity (Holopainen and Hanski, 1986), life-history traits associated with unstable habitats. As pisidiids have well-developed dispersal capacities, this variation in life-history tactics among species' populations occupying different habitats in unlikely to result from genetic adaptation. Rather, much of this variation appears to be environmentally induced plasticity and is reflected in the highly variable turnover times reported for sphaeriids (range = 27–1972 days, Table III).

Freshwater bivalve growth rates are highly dependent on ecosystem productivity. Populations from productive habitats have greater assimilation, allowing allocation of greater absolute amounts of nonassimilated energy to growth (Burky, 1983). Shallow, freshwater habitats are usually highly productive, warm, and rarely O_2-limited and, thus, support higher growth rates. Conversely, profundal environments are less productive, cooler, and often O_2-limited, leading to lower growth rates. Since sphaeriids mature at a species-specific size irrespective of growth rate (Burky, 1983; Holopainen and Hanski, 1986), rapid growth leads to early maturity in shallow-water habitats and slow growth to delayed maturity in profundal habitats. Sphaeriids also die at species-specific terminal sizes whether terminal size is attained rapidly or slowly. As growth rate determines the time required to reach terminal size, fast-growing, shallow-water individuals reach terminal sizes more rapidly (often within less than 1 year) allowing participation in only one or two reproductive efforts, while slow-growing, profundal individuals (Holopainen and Hanski, 1986) reach terminal size more slowly, allowing participation in a greater number of reproductive efforts. Similar interpopulation growth rate and reproductive variation has been recorded in several NA sphaeriid species (Mackie, 1979). The fundamentally ecophenotypic nature this variation has been demonstrated for *Pisidium casertanum*. When individuals were reciprocally transferred between two populations with different life-history traits or co-reared in the laboratory, the majority of life-history trait differences proved to be environmentally induced. However, electrophoresis revealed genetic differences between populations and transfer and laboratory corearing demonstrated a small portion of observed variation to be genetically based (Hornbach and Cox, 1987). Extensive ecophenotypic plasticity may account for the euryoecic nature and cosmopolitan distributions of sphaeriids (see Section III.A). Certainly, capacity to adjust growth rates, maturity, reproductive cycles, life cycles, and energetic allocation patterns to compensate for habitat biotic and abiotic variation enables sphaeriids to have relatively wide niches and, thus broad distributions.

3. Corbicula fluminea

The introduced Asian freshwater clam, *Corbicula fluminea,* unlike unionoideans and sphaeriids, has life-history traits adapting it to unstable, unpredictable habitats (McMahon, 1999), making it the most invasive of all NA freshwater bivalves. *C. fluminea* grows rapidly, in part because it has higher filtration and assimilation rates than other bivalves (Foe and Knight, 1986a; Lauritsen, 1986a; Way *et al.,* 1990a). In a natural population, a relatively small proportion of assimilation (29%) was devoted to respiration (Table V), the majority (71%) being allocated to growth and reproduction (Aldridge and McMahon, 1978). Laboratory studies have also showed that 59–78% (Lauritsen, 1986a) or 58–89% of assimilation (Foe and Knight, 1986a) was allocated to tissue production. Thus, *C. fluminea* has among the highest net production efficiencies recorded for any freshwater bivalve, reflected by its low turnover times, ranging from 73 to 91 days (Table III).

The very high proportion of nonrespired assimilation (85–95%) devoted to growth in *C. fluminea* (Aldridge and McMahon, 1978; Long and McMahon, unpublished data), sustains rapid shell growth (shell length = 15–30 mm in the first year of life, 35–50 mm in the terminal third-to-fourth year) (McMahon, 1983a). High growth rates decrease probability of predation, as fish and bird predators feed only on small individuals (Section III.C.3) thus, increasing probability of survival to next reproduction in this moderately iteroparous species. Increase in shell size occurs at the expense of tissue production during summer maximal growth (Long and McMahon, unpublished data), suggesting that larger shells optimize fitness. High growth rates sustain the highest population production rates (10.4–14.6 g organic carbon/m^2 per year, Aldridge and McMahon, 1978) reported for any freshwater bivalve (Burky, 1983), with dense populations producing 1000–4500 g C/m^2 per year (McMahon, 1999).

Newly released juveniles are small (shell length $\approx$250 μm), but completely formed, with a characteristically D-shaped shell, adductor muscles, foot, statocysts,

gills, and digestive system (Kraemer and Galloway, 1986) (Fig. 15A). Juveniles are denser than water and settle and anchor to sediments or hard surfaces with a single mucilaginous byssal thread. However, they are small enough to be suspended in turbulent water currents and hydrologically transported (McMahon, 1999). A relatively low amount of nonrespired assimilation is allocated to reproduction (5–15%; Aldridge and McMahon, 1978; Long and McMahon, unpublished data), equivalent to that of unionids, but less than sphaeriids (19%, Table III). However, the species' elevated assimilation rates allow higher actual allocation to reproduction than in other species.

As the juvenile of *C. fluminea* is small (organic carbon biomass = 0.136 μg), fecundity is large, ranging from 97 to 570 juveniles per adult per day during reproductive efforts, yielding an average annual fecundity of 68,678 juveniles per adult per year (McMahon, 1999). Early juvenile survivorship is extremely low and mortality rates remain high throughout life (74–98% in the first, 59–69% in the second, and 93–97% in the third year) (McMahon, 1999), causing populations to be dominated by juveniles and immatures. High adult mortality and population dominance by immature individuals characterizes species adapted to unstable habitats (Stearns, 1980).

The majority of NA *C. fluminea* populations have two annual reproductive periods (i.e., are bivoltine) (McMahon, 1999). It is hermaphroditic and capable of self-fertilization (Kraemer and Galloway, 1986; Kraemer *et al.,* 1986) such that single individuals can found new populations. Spermiogenesis occurs only during reproductive periods, but gonads contain mature eggs throughout the year (Kraemer and Galloway, 1986).

C. fluminea matures within 3–6 months at a shell length of only 6–10 mm (Kraemer and Galloway, 1986). Thus, juveniles born in spring can grow to maturity and participate in reproduction the following fall (McMahon, 1999) (Table III). Maximum life span is variable between populations and within populations, ranging from 1 to 4 years (McMahon and Williams, 1986a; McMahon, 1999). Early maturity allows this iteroparous species to participate in 2–7 reproductive efforts, depending on life span.

A relatively short life span, early maturity, high fecundity, bivoltine reproduction, high growth rates, small juvenile size, and capacity for downstream dispersal make *C. fluminea* both highly invasive and adapted for life in truly unstable, disturbed lotic habitats subject to unpredictable catastrophic faunal reductions. Its high reproductive potential and growth rates allow it to rapidly attain high densities after invading a new habitat or after catastrophic population declines. Thus, it is successful in NA drainage systems subject to periodic anthropomorphic interference such as channelization, navigational dredging, sand and gravel dredging, commercial and/or recreational boating, and organic and/or chemical pollution, compared to less resilient unionoideans or sphaeriids (McMahon, 1999).

Surprisingly, *C. fluminea* is more susceptible to environmental stresses, such as temperature extremes, hypoxia, emersion, and low pH than most sphaeriids and unionoideans (McMahon, 1999), making it highly susceptible to human disturbance. With only a limited capacity to tolerate unpredictable environmental stress, why is *C. fluminea* so successful in disturbed habitats? The answer lies in its ability to recover from disturbance-induced catastrophic population crashes much more rapidly than either sphaeriids or unionids. *C. fluminea* rapidly re-establishes populations even if disturbance has reduced them to a few widely separated individuals, as all individuals are hermaphrodites capable of self-fertilization and have high fecundities. Downstream dispersal of juveniles from viable upstream populations allows rapid re-establishment of decimated populations, the accelerated growth, high fecundity, and relatively short life spans of this species allowing recovery to normal age–size distributions and densities within 2–4 years (McMahon, 1999). Biannual (bivoltine) reproduction also increases its probability of surviving catastrophic density reductions, as it prevents loss of an entire generation to chance environmental disturbance ("bet hedging," Stearns, 1980). Capacity for rapid recolonization allows *C. fluminea* to sustain populations in substrates subject to periodic flood scouring from which slower growing and late maturing unionoideans are eliminated (Way *et al.,* 1990b, Section III.B.1).

Like sphaeriids, NA *C. fluminea* populations display high interpopulation variation in life-history traits (McMahon, 1999). As there is little or no genetic variation among NA populations (McLeod 1986), this variation must be ecophenotypic. Growth rates increase and time to maturity and life spans decrease in populations from more productive habitats (McMahon, 1999). On the northern border of its NA range, low temperatures reduce growth and reproductive periods, such that populations are univoltine rather than bivoltine. A slow growing *C. fluminea* population was univoltine and semelparous in an oligotrophic Texas lake (McMahon, unpublished data). Even within populations, life-history tactics vary, dependent on year-to-year variations in temperature and primary productivity (McMahon and Williams, 1986a; Williams and McMahon, 1986). As in sphaeriids, ecophenotypic life-history trait variation is adaptive in *C. fluminea,* allowing colonization of a variety of habitats. Thus, this species is highly euryoecic and highly invasive, making it the single most successful and economically

costly aquatic animal introduced to North America (McMahon, 1999).

4. *Dreissena Polymorpha*

The zebra mussel, *Dreissena polymorpha,* is the most recently introduced NA bivalve species (Mackie and Schloesser, 1996). Like C. *fluminea,* its life-history characteristics (McMahon, 1996; Nichols, 1996) make it highly invasive. Unlike other NA bivalves, it releases sperm and eggs making fertilization completely external. Developments leads to a free-swimming planktonic veliger larva (Fig. 15C) which feeds and grows in the plankton for 8–10 days before settlement (Nichols, 1996). The planktonic veliger enhances the zebra mussel dispersal ability. Veligers in the Illinois River traveled at least 306 km downstream before settlement (Stoeckel *et al.,* 1997). Numbers of dispersing veligers can be astounding. Stoeckel *et al.* (1997) estimated that veligers in the Illinois River reached densitiess >250 veligers/L which resulted in veligers passing a fixed point at a rate as 75×10^6 per second. Total annual veliger flux was estimated to be 1.935×10^{14} and 2.131×10^{14} per year in 1994 and 1995, respectively. Adults byssally attached to floating objects are also transported downstream.

Zebra mussels sexually mature in the first or second year of life (first year in most NA populations) have life spans of 3–5 years in Europe and 2–3 years in North America (Mackie and Schloesser, 1996) and, like *C. fluminea,* sustain high growth rates throughout life (Fig. 19). It is iteroparous and univoltine; an individual participating in 3–4 annual reproductive periods within its life span. Reproduction is initiated above 10–12°C, but is maximized above 18°C. Spawning is dependent on abiotic and biotic conditions, producing peaks of veliger density within a reproductive season (McMahon, 1996; Nichols, 1996; Ram *et al.,* 1996; Stoeckel, *et. al.* 1997). The freshly hatched veliger is small (diameter = 40–70 μm), but the pediveliger grows to 180–290 μm just prior to settlement (Nichols, 1996), leading to a 100 to 400-fold biomass increase during the 8–10 day planktonic period.

Maximal *D. polymorpha* adult size ranges from 3.5 to 5 cm depending on growth rate, which, like terminal size, is dependent on habitat primary productivity and temperature. Growth rate of caged mussels in Lake St. Clair, Michigan, initially enclosed at an average shell length (SL) of 4.2 m was 0.095 mm per day over the first 150 days reaching a mean SL of 14.3 mm and, thereafter, slowing down to a mean of 0.015 mm per day for the next 182 days reaching a mean SL of 17.0 mm (Bitterman *et al.,* 1994). Growth rates of young mussels in the lower Mississippi River were temperature-dependent, peaking at 0.06–0.08 mm per day

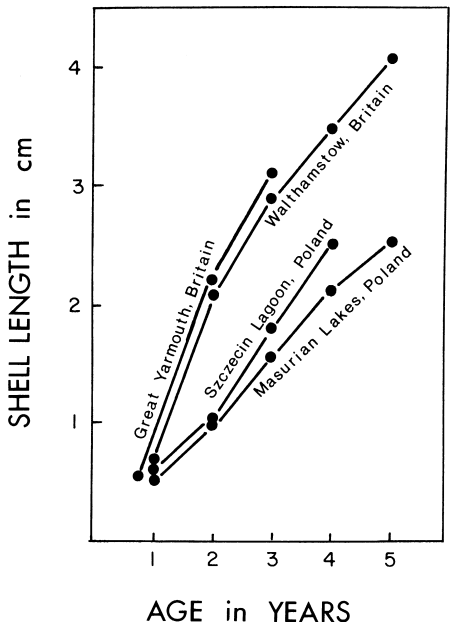

FIGURE 19 Shell-growth rates in European populations of the zebra mussel, *Dreissena polymorpha*. Growth rates for North American populations in Lake Erie are similar to or greater than faster growing British populations depicted in this figure.

at ≈16–17°C and declining at higher temperatures (Allen *et al.,* 1999), a result supporting laboratory studies showing that increasing metabolic demands reduce assimilated energy allocation to growth above 15°C (Walz, 1978a).

Like *C. fluminea, D. polymorpha* allocates a very high percentage (96.1%) of nonrespired assimilation to somatic growth, leaving only 3.9% for reproduction (Mackie *et al.,* 1989; Table III); however, Sprung (1991) reports a 30% postspawning reduction in female body mass, indicating higher reproductive energy allocation in some populations. Allocation of a large proportion of nonrespired assimilation to growth allows individuals to rapidly increase in size, making them more competitive and less subject to predation. Zebra mussel veligers settle on the shells of established individuals, forming thick mats or clusters many shells deep, in which competition for space and food must be intense. Thus, rapid postsettlement juvenile growth is highly adaptive as it allows stable byssal attachment to the substrate and positioning of siphons at the mat surface, where food and O_2 are most available. In spite of the low levels of energy devoted to reproductive effort by *D. polymorpha,* its very small eggs make individual fecundity large, ranging from 30,000 to $>10^6$ eggs per female (Sprung, 1991; Mackie and Schloesser, 1996).

Dreissena polymorpha population densities range from 7000 to 114,000 individuals/m^2 and standing crop biomasses from 0.05–15 kg/m^2 (Claudi and

Mackie, 1993). These high densities and biomasses result from the tendency of juveniles to settle on substrates inhabited by adults forming dense mats or clumps many individuals thick. High individual growth rates and population densities lead to very high productivities, estimated to be 0.05–15 g C/m^2 per year in European populations, and ≈75 g C/m^2 per year in NA Great Lakes populations based on dry tissue mass productivity values in Mackie and Schloesser (1996). The NA productivity value for *D. polymorpha* is still relatively low compared to values of 1000–4500 g C/m^2 per year estimated for dense NA *C. fluminea* populations (McMahon, 1999). Population growth and productivity are highly habitat-dependent in *D. polymorpha,* making turnover times variable, ranging from low values of 53 days (highly productive) to high values of 869 days (low productivity; Table III).

A high growth rate throughout life, elevated fecundity, short life span, and a capacity for adult and larval down-stream dispersal make *Dreissena* (like *Corbicula*) a highly invasive species. However, unlike *C. fluminea, D. polymorpha* populations are restricted to more stable habitats such as larger, permanent lakes and rivers. Its apparent preference for stable habitats is reflected by its endemic range in the Caspian Sea and Ural River (large stable habitats), avoidance of shallow, near-shore lentic- and low-flow lotic habitats, relatively long age to maturity (generally at least 1 year of life), iteroparity, gonochorism, and relatively high adult survivorship (26–88% per year; Mackie and Schloesser, 1996).

Restriction of the original range of *D. polymorpha* to the Caspian Sea and Ural River also suggests a limited dispersal capacity between drainage systems. Its dispersal through Europe occurred only in the nineteenth century (and continues in western Asia today) as interconnenting canal systems transported it between drainages. Dispersal of *D. polymorpha* between drainages is primarily by human vectors, including transport of adults attached to boat/barge hulls, ballast water dumping, and transport of veligers through canal systems interconnecting catchments. Adults are poorly tolerant of emersion (McMahon, 1996), precluding extensive natural overland dispersal unless human-mediated. Thus, dispersal of this species between NA catchments has been primarily by human vectors, with larger, permanent, navigable bodies of water being most susceptible (Mackie and Schloesser, 1996). Without anthropomorphic vectors, dispersal of *D. polymorpha* through NA drainages would almost certainly have proceeded at a much slower pace than recorded for *C. fluminea,* but human activities have already lead to this species being widely distributed in major NA drainages east of the Mississippi River (Ram and McMahon, 1996; New York Sea Grant, 1999).

C. Ecological Interactions

1. Behavioral Ecology

Other than borrowing (see Section II.A.2), information on bivalve behavior is sparse. Reviews of molluscan neurobiology and behavior (Willows, 1985, 1986) have no bivalve references. Lack of information, rather than lack of complex and intriguing behaviors, reflects difficulties in making behavioral observations on predominantly sessile bivalves surrounded by a shell.

There are a number of reproductive behaviors in freshwater bivalves, including those ensuring unionioidean glochidial contact with fish hosts (Section II.B). Adult *C. fluminea* display downstream dispersal behavior during reproductive periods. While juvenile clams (SL <2 mm) are hydrologically transported throughout the year, immatures (SL = 2–7 mm) and adults (SL >7 mm) leave the substrate to be passively hydrologically transported over the sediment surface ("rolling") only prior to reproductive periods (Fig. 20). Dispersing adults have lower dry tissue weights, lower tissue organic carbon-to-nitrogen ratios (Williams and McMahon, 1989), higher levels of ammonia excretion, and reduced molar O_2 consumption-to-N_2 excretion ratios than those remaining in the substrate (Williams and McMahon, 1985), all indicative of poor nutritional condition. Thus, downstream dispersal allows starving individuals to disperse from areas of low food availability and high intraspecific competition into areas more nutritionally favorable for reproductive efforts (Williams and McMahon, 1986, 1989).

Some adult unionoidean bivalves and *C. fluminea* display surface locomotory behavior involving the same movements of foot and valves described in Section II.B.2 for burrowing. Unionoidean surface locomotion is fairly common (Imlay, 1982), leaving tracts in sediments 3–10-m long (Golightly, 1982). The adaptive significance of bivalve surface locomotion is not well understood as it could attract potential predators. However, it may be involved with pedal feeding on organic sediment deposits (see Section III.C.2).

Some species, such as *Pyganodon grandis,* migrate vertically with seasonal changes in water level (White, 1979) to avoid emersion. Other species, such as *Uniomerus tetralasmus, C. fluminea,* and some sphaeriids, remain in position and suffer prolonged emersion (see Section II.C.4). In Texas, fire ants, *Solenopsis invicta,* kill emersed bivalves (McMahon, unpublished), suggesting that this introduced insect may be a new threat to unionoideans and sphaeriids as it expands its range in the southeastern U.S.

Some sphaeriids, *C. fluminea,* and *D. polymorpha* also crawl on hard substrates or macrophytes. *Sphaerium corneum* holds the valves erect and crawls

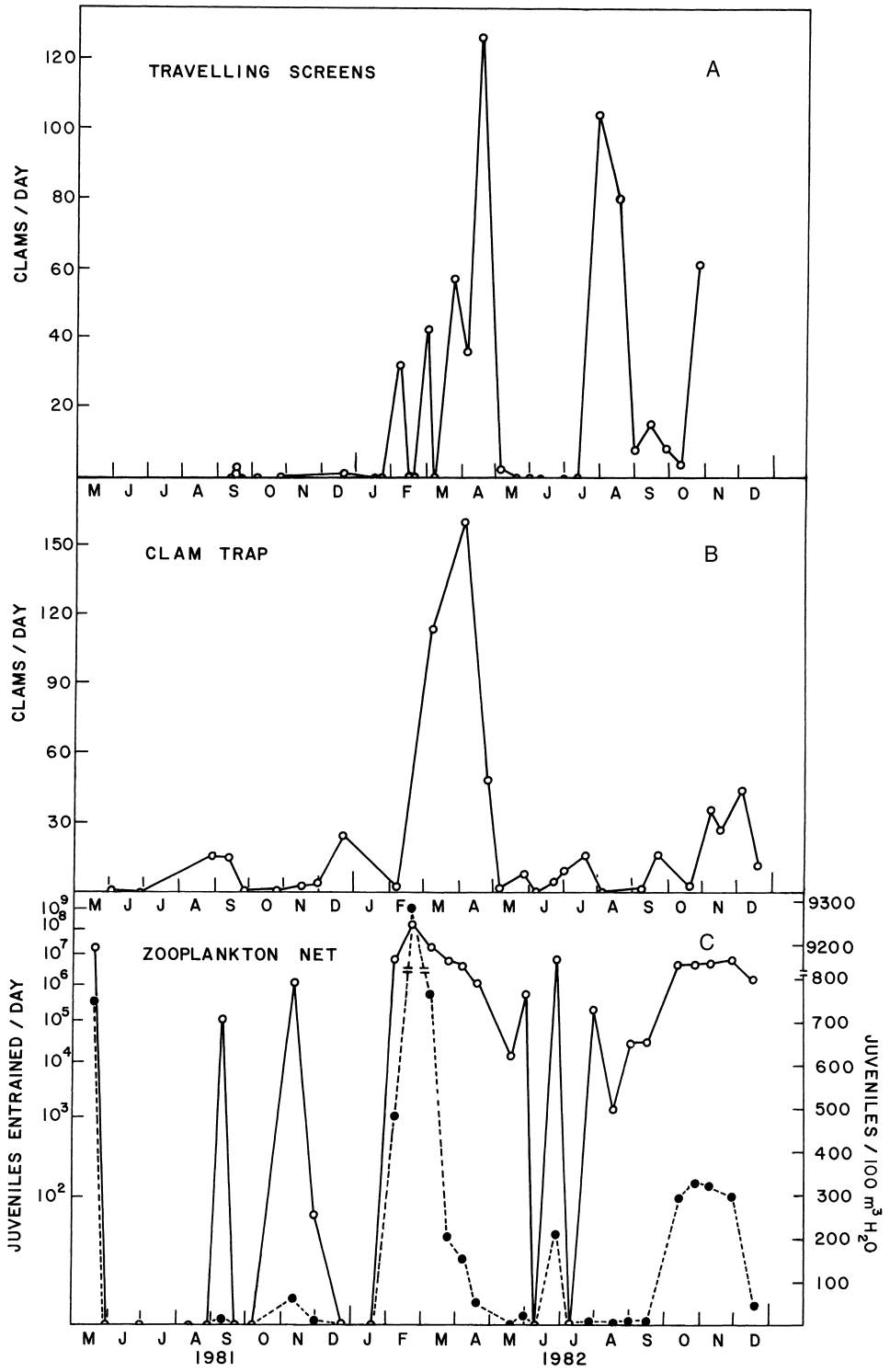

FIGURE 20 Seasonal variation in downstream dispersal behavior by juvenile, subadult and adult *Corbicula fluminea* in the water intake canal of a power station. (A) Rate of impingement of adults dispersing downstream onto traveling screens in front of water intake embayments (shell length >10 mm). (B) Rate of retention of subadults (shell length = 1–7 mm) in a clam trap held on the substrate surface of the intake canal. (C) Juveniles suspended in the water-column (shell length <2 mm). Right vertical axis represents density of juveniles in the intake canal water column (solid circles connected by dashed lines). Left vertical axis is number of juveniles entrained daily with intake water (open circles connected by solid lines). Note that the adult and subadult clams display maximal downstream dispersal behavior during only two periods, March–May and September–November). Juveniles occurred in the water column throughout the year; peak juvenile water column densities occurred during reproductive periods and midwinter periods of low ambient water temperature. (From Williams and McMahon, 1986.)

TABLE IV The Effects of Temperature on the Percentage of Time Spent in Various Valve Movement Behaviors in Emersed Specimens of *Corbiucla fluminea*[a]

Temperature (°C)	*Time with valves closed* (%)	*Time with mantle edge exposed* (%)	*Time with mantle edge parted or attempting to burrow* (%)
15	29.5	65.8	4.7
25	51.2	43.5	5.3
35	90.5	9.1	0.4

[a] From Byrne *et al.* (1988).

by extending the foot tip, anchoring it with mucus, and pulling the body forward by pedal muscle contraction (Wu and Trueman, 1984). Juvenile *C. fluminea* crawl on hard subtrates in the same manner, while adults similarly crawl while lying on one of the valves (Cleland and McMahon, unpublished). Small specimens of *D. polymorpha* are active crawlers and can climb smooth vertical surfaces. They routinely discard their byssus and migrate to a new position for reattachment. Thus, juveniles migrate to deeper waters in the winter to avoid ice scour (Mackie *et al.,* 1989).

Freshwater bivalves also respond to external cues. Chief among these is valve closure in response to irritating external stimuli when detected by mantle edge and siphonal sense organs (Section II.B.6). Valve closure seals internal tissues from damage by external irritants. Almost all freshwater bivalves tolerate some degree of anaerobiosis (Section II.C.3). Thus, individuals exposed to irritants may keep the valves shut for relatively long periods until normal external conditions return. Valve closure occurs in response to heavy metals (Doherty *et al.,* 1987), chlorine, and other biocides (Mattice *et al.,* 1982; McMahon and Lutey, 1988), suspended solids (Aldridge *et al.,* 1987), and pesticides (Borcherding, 1992). This ability allows *C. fluminea* to avoid intermittent exposure to chlorination or other biocides, making chemical control of their fouling difficult (Mattice *et al.,* 1982). Valve closure in immediate response to mantle edge or siphonal tactile stimulation is a predator defense mechanism. Valve closure response in *D. polymorpha* is used to monitor water pollution in Europe (Borcherding and Volpers, 1994).

Freshwater bivalves have adaptive behavioral responses to prolonged emersion. Physiological adaptations were discussed in Section II.C.4. Here, behavioral responses are described in greater detail. When emersed, *C. fluminea* displays four major behaviors: (1) escape responses involving attempts to burrow; (2) valves gaped widely with mantle edges parted, opening the mantle cavity to the atmosphere; (3) valves narrowly gaped with mantle edges exposed, but cemented together with mucus; and (4) valves clamped shut. Behaviors (1) and (2) are never displayed more than 6% of time in air. Exposure of sealed mantle edges allows aerial gas exchange (Byrne *et al.,* 1988), but results in evaporative water loss. When valves are closed, water loss is minimized; but O_2 uptake ceases (Byrne *et al.,* 1988; McMahon and Williams, 1984). As temperature increases (Table IV) or relative humidity decreases, duration of mantle edge exposure decreases (McMahon, 1979b; Byrne *et al.,* 1988). Hence, behaviors associated with water loss are reduced in response to increased desiccation pressure. Indeed, relative humidities near zero or temperatures above 30–35°C induce continual valve closure (Byrne *et al.,* 1988) (Table IV), reducing water loss, but making individuals anaerobic. Similar behaviors occur in emersed unionoideans (Byrne and McMahon, 1994). Less emersion-tolerant unionoideans, like *P. grandis,* display high levels of mantle edge exposure (25–90% of time emersed) and high rates of water loss. More emersion-tolerant species, like *Uniomerus tetralasmus* and *Toxolasma parvus,* have reduced levels of mantle edge exposure behavior when emerged (<25% of time emersed). The extremely emersion-tolerant *U. tetralasmus* plugs the siphon openings with mucus to reduce water loss and spend little time with mantle edges exposed (Byrne and McMahon, 1994). Ability of emersed bivalves to adjust aerial respiratory responses to external dessication pressures is a complex behavior, requiring capacity to sense, integrate, and respond to external temperature and relative humidity levels and internal osmotic concentration.

Freshwater bivalves may also have circadian patterns of behavior. Both ion-uptake and O_2-consumption rates are greater during dark than light hours in unionoideans and *C. fluminea* (McCorkle *et al.,* 1979; Graves and Dietz, 1980; McCorkle-Shiley, 1982; Section II.C.2) indicative of circadian-activity patterns in feeding, reproduction, and burrowing. The density of juvenile *C. fluminea* in the water column increases during dark hours (McMahon, unpublished) suggesting that adults preferentially release juveniles at night.

Freshwater bivalves may have circadian burrowing cycles, retreating into sediments during light hours to avoid visual predators like fish and birds. The unionoideans, *Anodonta anatina* and *Unio tumidis,* displayed a diurnal activity rhythm with valves open for longer periods at night than during the day (Englund and Heino, 1994a). Similar diurnal valve movement behavior occurs in *D. polymorpha* (Borcherding, 1992).

2. Filter Feeding

a. Particle Capture Most freshwater bivalves feed by filtering suspended material from gill water flow (Section II.B.2) driven by lateral cilia located on each side of the filaments. Projecting laterally from each filament's leading edge are "cirri" made up of partially fused tufts of eulaterofrontal cilia occurring at intervals of 2–3.5 μm (Figs. 5A and 21). Eulaterofrontal cirri on adjacent filaments project toward each other forming a stiffened grid on which suspended seston (phytoplankton, bacteria, and fine detritus) is retained from water flow driven between the filaments by the lateral cilia. Filtering may also involve creation of eddies by cirri in which seston particles settle. Filtered particles range from 1 to 10 μm, with *D. polymorpha* and *C. fluminea* both able to filter smaller particles ($\leq$1.0 μm) than most other freshwater species (Fig. 22) (Jørgensen *et al.,* 1984; Paterson, 1984; Way *et al.,* 1990a; Silverman *et al.,* 1995). It has been claimed that a mucus net covering the gill is the primary filter. While the role of mucus in bivalve filtering is debated, there is little doubt that the dense mesh of the cirri could form an effective filter (Morton, 1983; Way, 1989). Particles are captured at the level of the cirri (Jørgensen, 1996), suggesting their involvement in filtration. However, adjacent cirri are separated by 2–3.5 μm, which until recently, made their mode of particle capture an enigma because filtered particles were much smaller than the intercirral distance. Two-particle capture mechanisms have been hypothesized: direct physical cirral filtration; or capture by water currents created by gill cilia (Silverman *et al.,* 1996a). Recent confocal microscopic examinations of living gill tissue of *D. polymorpha* (Silverman *et al.,* 1996a, 1996b) and marine mytilid mussels (Silverman *et al.,* 1999) support direct cirral particle capture as the main feeding mode.

The cirrus is composed of a pair of adjacent fused ciliary sheets aligned with inhalant water flow, extending from a single gill epithelial cell (Fig. 21D.b). Thirty-eight-to-42 cilia form the cirrus. Each cilium has a distinct basal "hinge" region (Fig. 21D.c) and a free distal end characterized by reduced numbers of microtubules. Cilia increase in length from the inhalant to the trailing edge of the cirrus (Fig. 21D.b). Cirral cilia move in unison on the hinge. When they reflex into the space between adjacent filaments, the free cirral cilia tips splay out into the inhalant current forming a filter of submicron dimensions (Fig. 21D.a) on which previously free-moving particles ($<$0.75 μm diameter) are trapped. When the cirrus is then flexed back over the leading edge of the filament, trapped particles are released (Silverman *et al.,* 1996a, 1996b, 1999) (Fig 21D.a), allowing them to entrain in mucus transported either ventrally or dorsally by filament frontal cilia (Beninger *et al.,* 1997) to specialized, ciliated food grooves on the ventral edges or bases of the demibranches depending on species (Figs. 2 and 5A–C). In the unionoidean, *Pyganodon cataracta,* particles and mucus transported by filament frontal cilia become entrained and concentrated in a mucus thread on reaching the ventral food grooves where they are carried anteriorly to the labial palps (Tankersley, 1996) (Figs. 5A and 21). The role of mucus in bivalve food particle transport is being debated Other investigators feel that ciliary-based, fluid-mechanical forces are primarily responsible for particle transport with mucus playing a minor role if any (Jørgensen, 1996). Frontal cirri similar to those of *D. polymorpha* occur in sphaeriid, unionoidean and corbiculacean bivalves (Fig. 21) (Way *et al.,* 1989) and marine bivalves (Beninger *et al.,* 1997) where they are presumed to similarly function in particle capture.

b. Sorting of Filtered Particles Mucus-entrained, filtered particles are carried anteriorly to the labial palps, paired triangular flaps on each side of the mouth (Figs. 2 and 4). The outer labial palp lies against the outer ventral side of the outer demibranch, and the inner palp, against the inner ventral side of the inner demibranch (Fig. 2). Palp epithelial surfaces facing away from the demibranches are smooth, while those adjacent to the demibranch have a series of parallel ridges lying obliquely to a ciliated oral groove formed in the fused dorsal junction of the inner and outer labial palps leading to the mouth (Morton, 1983). In the unionoidean, *P. cataracta,* the palps transfer the food-laden mucus thread from the ctenidial food groove directly to the mouth for ingestion (Tankersley, 1996). In marine eulammelibranch bivalves, the mucus thread becomes mechanically fluidized on the palp surface by a combination of grinding movements of the opposing palp surfaces, transport across the corrugated palp surface and chemical reduction in mucus viscosity. Fluidization, breaks the mucus thread into a fragmented, flocculent mucus–particle slurry prior to ingestion (Beninger *et al.,* 1997). After fluidization, the corrugated palp surface sorts filtered particles into those accepted for ingestion and those rejected. Generally, smaller particles are carried over the tops of palp corrugations by cilia to be deposited in the oral groove for ingestion. Denser, larger

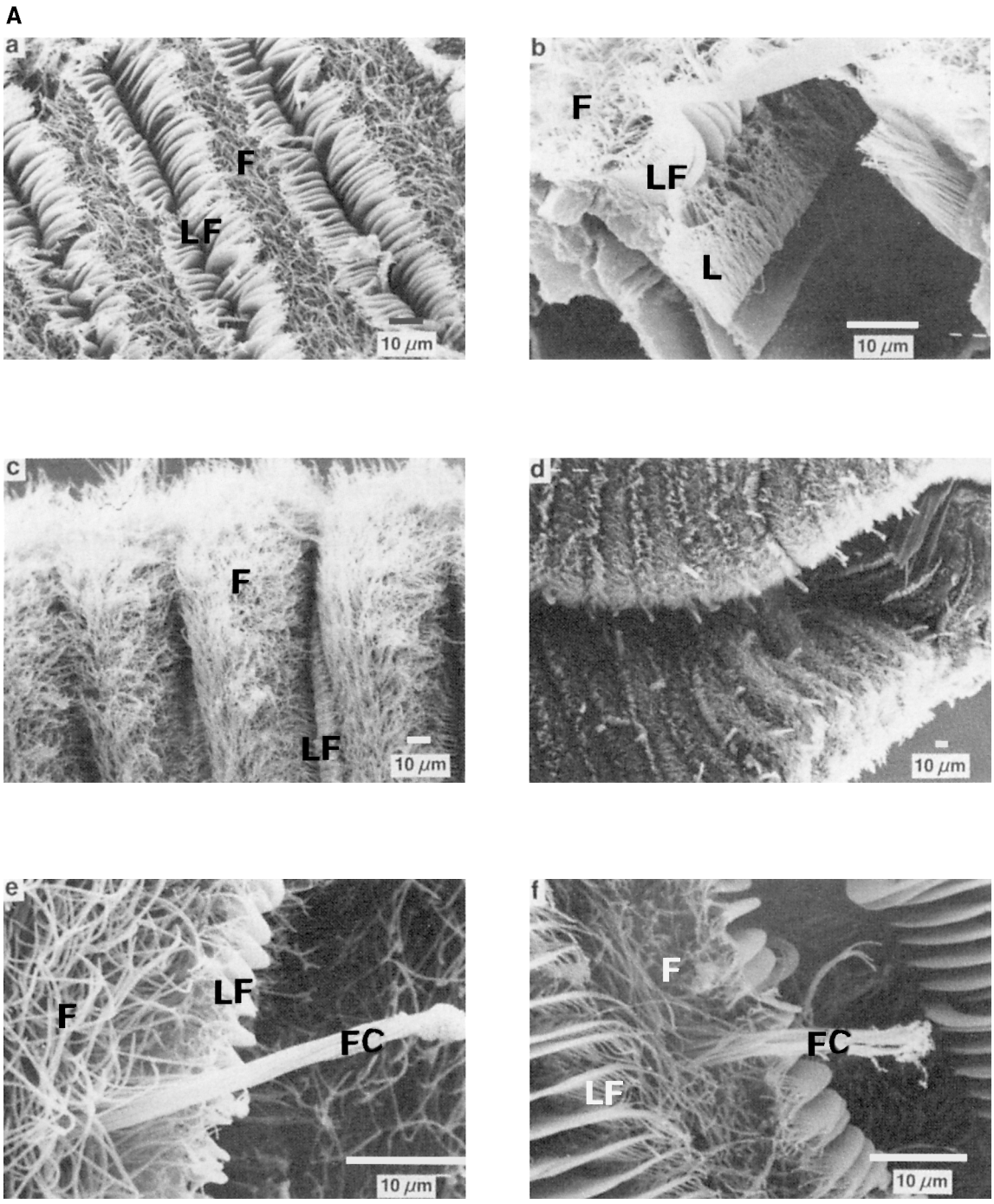

FIGURE 21 Scanning electron micrographs of the gill ciliation of representative freshwater bivalves. (A) *Musculium transversum* (Sphaeriidae): (a) arrangement of frontal and eulaterofrontal ciliation forming cirri on the leading edge of the gill filaments in the midgill region; (b) oblique view of a cross-sectional fracture of the gill showing frontal and eulataterofontal cilia forming cirri on the leading edge of the filament and lateral cilia on the side of the filament; (c) ciliation of the food groove on the ventral edge of the gill; (d) posterior portion of the outer (foreground) and inner (background) demibranchs of the gill; (e) a frontal cirrus formed from fused cilia emerging between the eulaterofrontal cirri and frontal cilia on the leading edge of a filament; (f) a frontal cirrus emerging from a band of frontal cilia. (B) *Corbicula fluminea* (Corbiculidae): (a) leading edge of a gill filament showing frontal cilia, eluatorofrontal cilia forming cirri, lateral cilia and frontal cirri; (b) high-magnification view of frontal cilia and eulateralfrontal cirri; (c) oblique view of a longitudinal fracture through the midgill region showing all four types of ciliation, including lateral cilia lining the sides of the gill filiament;

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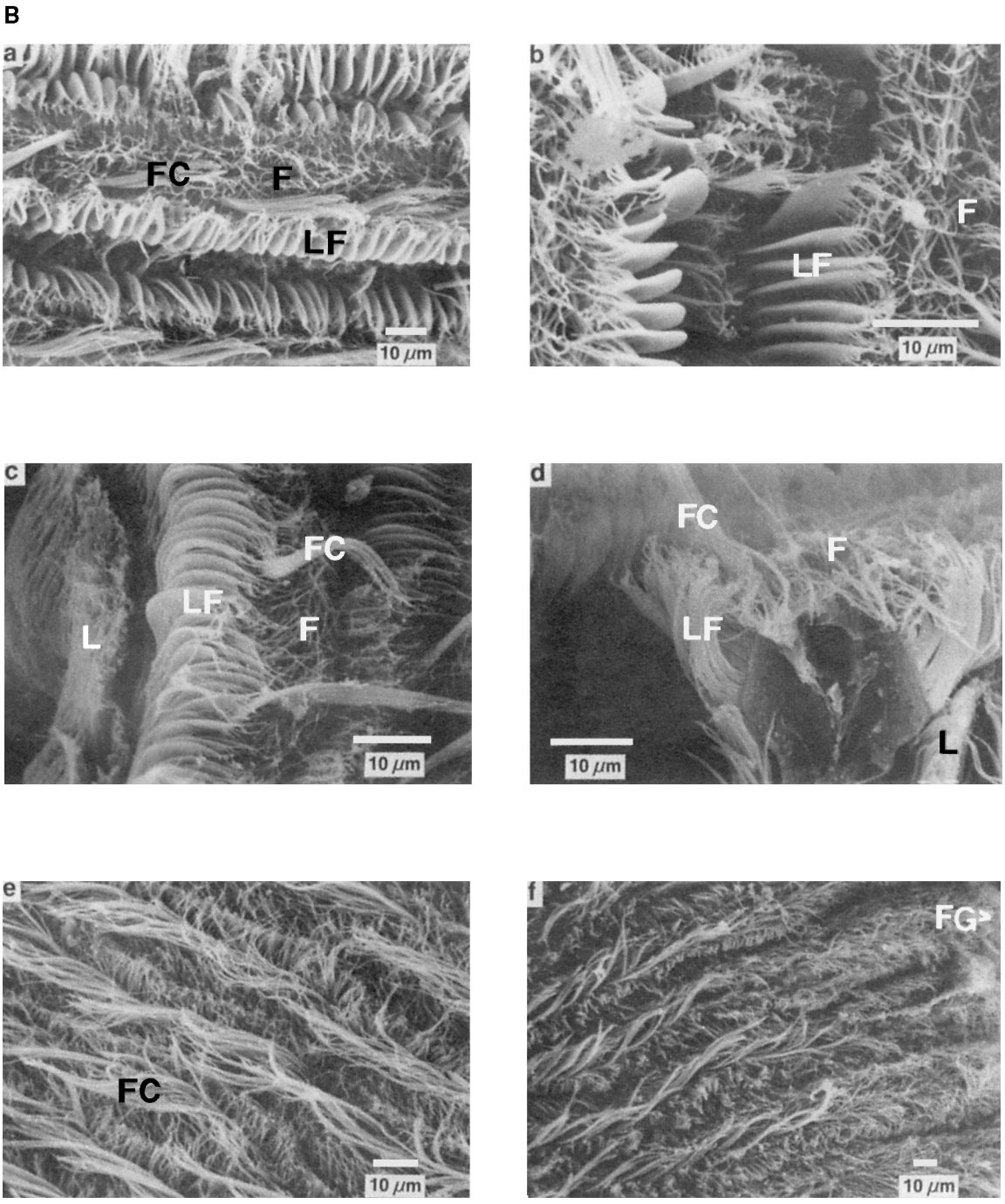

FIGURE 21 (Continued)
(d) crosssection of the midgill region showing the origin of the frontal cirrus; (e) lower region of the gill showing the presence of less well organized frontal cilia; (f) food groove region at the ventral edge of the inner demibranch; note loss of ciliary organization in food groove, including lack of frontal cirri. (C) *Obliquaria reflexa* (Unionoidea): (a) frontal cilia and eulaterofrontal cilia forming cirri on the leading edges of several gill filaments (500X); (b) high-power view showing lateral cilia on sides of the gill filaments between tracts of frontal cilia and eulaterofrontal cilia forming cirri on adjacent filaments. (D) *Dreissena polymorpha* (Dreissenoidea): (a) frontal cilia on the leading edge of a gill filament and some eulaterofrontal cirri reflexed into the space between adjacent filaments with the free, distal ends of their cilia splayed out to form the primary gill filtering mechanism and other cirri reflexed over the frontal cilia in a position in which they release particles captured from water flow between adjacent filaments to frontal cilia of the food groove; (b) detailed structure of a eulaterofrontal cirrus formed from two rows of opposed cilia fused basally, free at their distal tips, with a distinct

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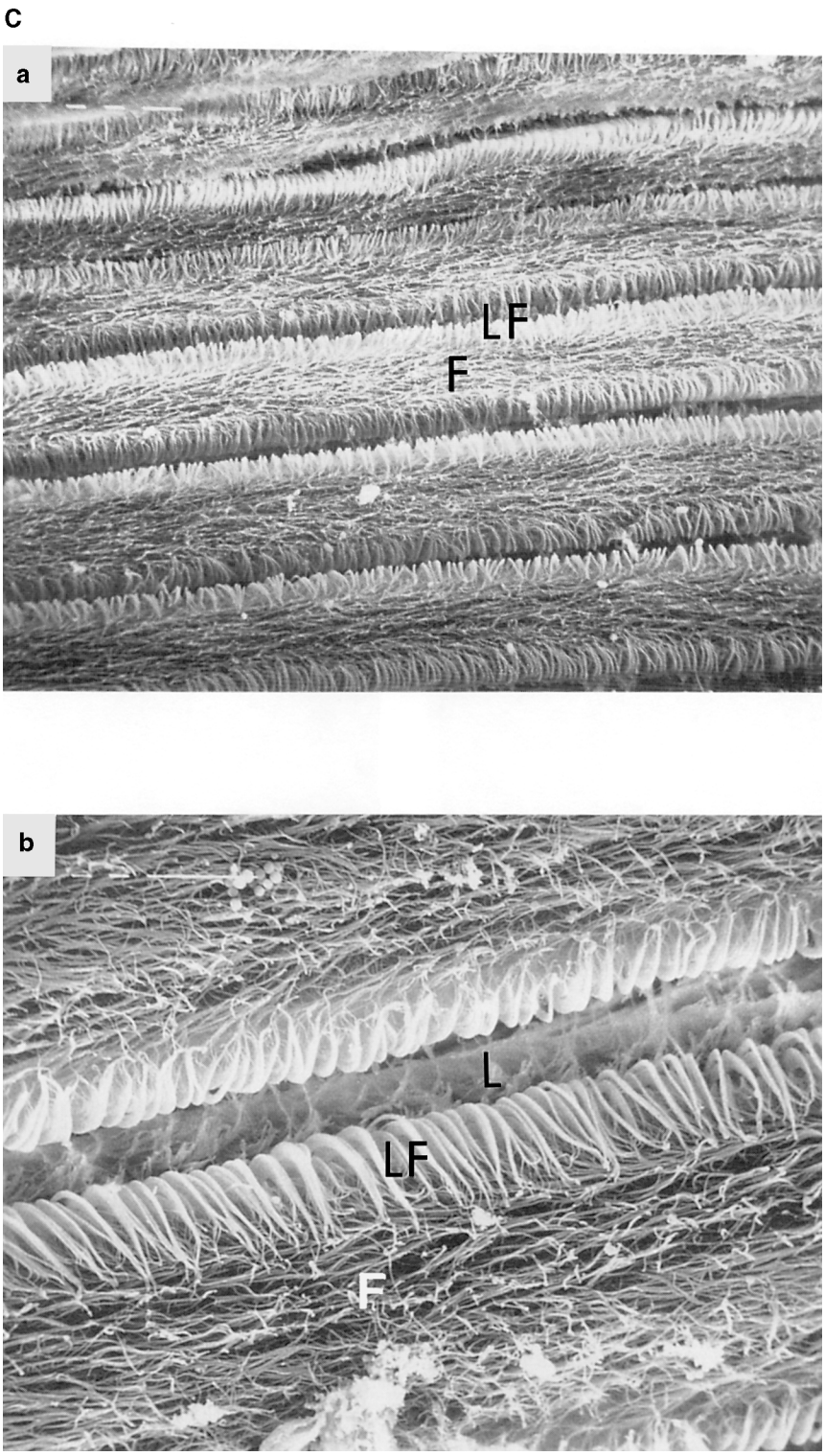

FIGURE 21 (Continued)
basal hinge on which the cirral cilia simultaneously flex between the interfilament space (food capture) and the frontal cilia on the leading edge of the filament (food release); (c) transmission electron micrograph showing details of the unique hinge on which cirral cilia flex between the interfilament space and the frontal cilia. Note lack of frontal cirri characteristic of the (A) Sphaeriidae, and (B) *Corbicula fluminea* in (C) unionoideans and (D) *Dreissena* Label key for figures A–C : F, frontal cilia; FC, frontal cirrus; L, lateral cilia, LF eulaterofrontal cirri; and FG, food groove. [Photomicrographs supplied by Tony Deneka and Daniel Hornbach (Macalester

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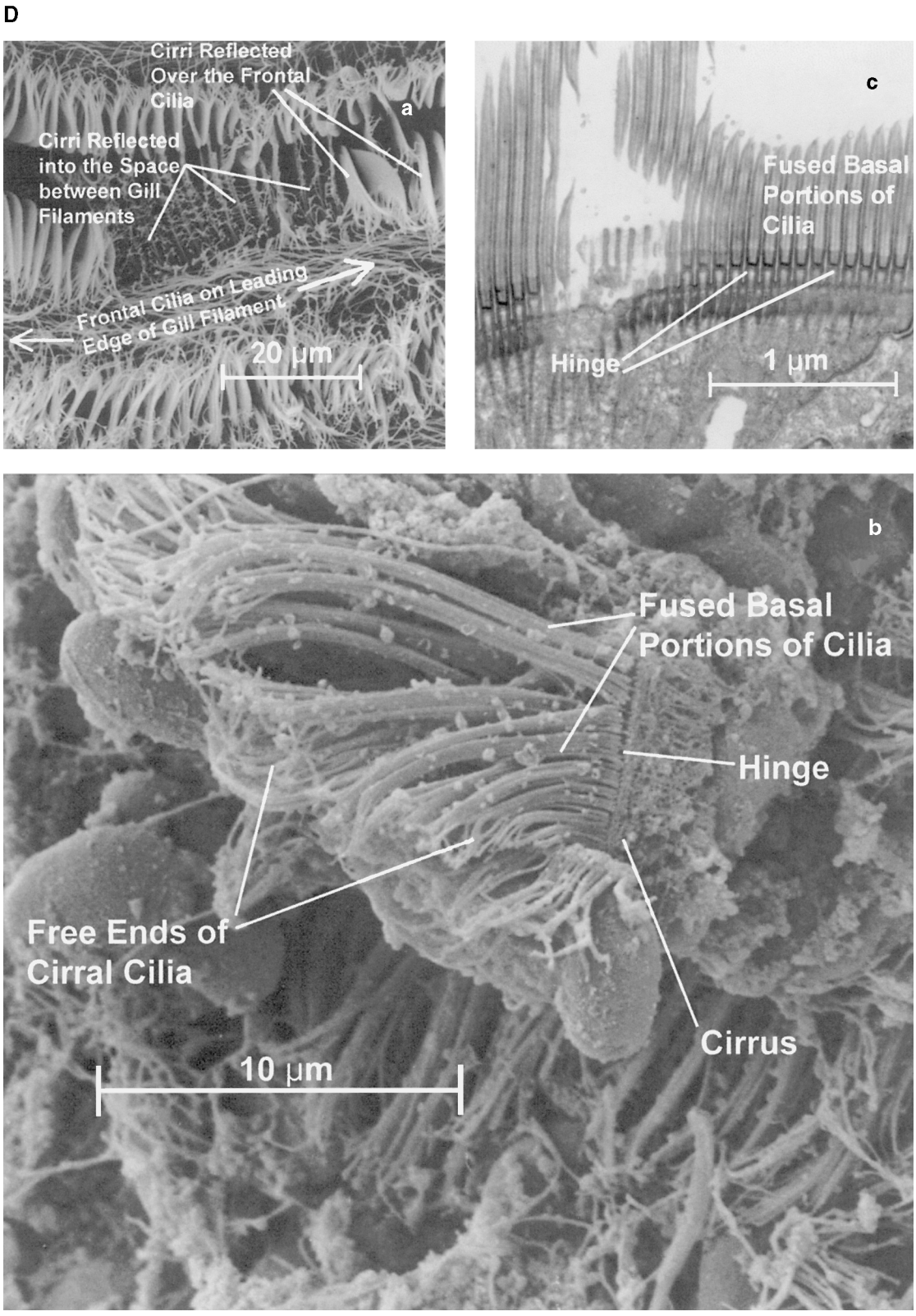


FIGURE 21 (Continued)

College), Carl M. Way (U.S. Army Corps of Engineers), and Harold Silverman and Thomas H. Dietz (Louisiana State University, Baton Rouge).]

particles fall between the corrugations where cilia carry them to the ventral edge of the palp to be bound in mucus and released onto the mantle as pseudofeces (pseudofeces are mucus-bound particles that have not been ingested) (Morton, 1983; Beninger *et al.,* 1997). Pseudofeces are carried by mantle cilia to the base of the inhalant siphon (Fig. 2), where they are periodically expelled with water forced from the inhalant siphon by rapid valve adduction (i.e., valve clapping) (Morton, 1983). The palp may also sort medium-sized particles. Smaller medium-sized particles tend to remain longer on corrugation crests than in intervening grooves, thus, reaching the oral groove for ingestion, while larger, medium-sized particles remain longer in the grooves leading to eventual rejection as pseudofeces. Thus, labial palp particle sorting may be primarily by particle size and, perhaps, density. The function of labial palps in particle sorting is being debated, palps appearing to have little if any sorting function in some species (Tankersley, 1996) and extensive sorting functions in others (Beninger *et al.,* 1997). Labial palp function in freshwater bivalves requires further study.

The width of palp corrugations and gill filaments can be adjusted by both muscular activity and distention of gill and palp blood sinuses, thus allowing active particle-size selection (Morton, 1983). When fed natural seston, the percentage of particles retained by the unionoidean, *Elliptio complanata,* declined linearly over a particle size range of 5 (nearly 100%) to $>10\mu$m (less than 10% retention), suggesting size selection (Paterson, 1984). Similar size selection for particles occurs in the sphaeriid, *Musculium transversum* (Way, 1989), and *C. fluminea* (Way *et al.,* 1990a). Some unionoidean species may select different algal types. In the same river pool, *Amblema plicata* ingested a greater proportion of green algae, a lower diversity of algal species, and different algal species than *Ligumia recta* (Bisbee, 1984). Interspecific differences in particle selection may allow some sympatric species to divide the feeding niche, avoiding competition, however, other unionoideans are nonselective in feeding and have high diet overlap between species.

c. Filtering Rate The filtering rate of bivalves can be computed as follows:

$$C = \frac{M}{t}\left(In\,\frac{C_0}{C_t}\right)$$

where M is the volume of suspension filtered, t the time, and Co and Ct the concentrations of filtered particles at time o and t, respectively (Jørgensen *et al.,* 1984). Filtration rates are elevated in *C. fluminea* compared to other freshwater bivalves. For a 25-mm shell length (SL) specimen, rate ranges from 300 to 2500 L/h depending on temperature and seston concentration (Foe and Knight, 1986b; Lauritsen, 1986b; Way *et al.,* 1990a). The filtering rate of *C. fluminea* fed natural seston concentrations was not significantly correlated with field water temperature (Long and McMahon, unpublished) and was independent of temperature between 20 and 30°C in the laboratory (Lauritsen, 1986b), suggesting capacity for temperature compensation of gill ciliary filtering activity. The filtration rate is also somewhat temperature independent in *Sphaerium striatinum* and *Musculium partumeium,* reaching maximal values during reproductive periods when water temperatures, were below midsummer maxima (Burky *et al.,* 1981, 1985a; Way *et al.,* 1981). Filtering rates in *D. polymorpha* are similar to those in *C. fluminea* (Lei *et al.,* 1996) and 2–4 times higher than those in sphaeriids and unionoideans (Kryger and Riisgård, 1988).

High particle concentrations reduce filtering rates (Burky *et al.,* 1985a; Way, 1989; Way *et al.,* 1990a; Lei *et al.,* 1996). Filtering rates in *S. striatinum* (Hornbach *et al.,* 1984a) and *M. partumeium* (Burky *et al.,* 1985a) were depressed at concentrations below natural seston, making particle ingestion nearly constant above a critical particle concentration. Thus, filtering may have be regulated to control ingestion rate. Particle concentrations within ambient seston concentrations do not affect filtering rate in *C. fluminea* (Mattice, 1979), ingestion rates increasing directly with concentration. However, filtration rate in *C. fluminea* declined three-fold with increasing particle concentration between 0.33 and 2.67 μl algal volume/L suggesting inhibition at very high concentrations, but increasing algal concentration over this range still resulted in a 3.5-fold rise in ingestion rate (Lauritsen, 1986b). Similar reduction in filtration rate at particle concentrations above natural seston levels occurs in the sphaeriid, *M. transversum* (Way, 1989). In contrast to *C. fluminea,* filtration rate of the unionoidean, *E. complanta,* was depressed by increasing natural seston concentrations (Paterson, 1984). Filtration rate differed among populations of *C. fluminea,* but ingestion rates were similar, suggesting regulation of the filtration rate to control ingestion rates (Way *et al.,* 1990a). In *D. polymorpha,* filtration rate was reduced when feeding on artificial plastic microspheres compared to natural seston. When filtering particles <1.5 μm in diameter, filtration rate decreased with decreasing particle concentration below a critical upper limit, and with decreasing temperature. Filtration rate was also affected by prior temperature acclimation (Lei *et al.,* 1996). Such data indicate that the seasonal and environmental filter-feeding responses of freshwater bivalves are species-specific and laboratory measurements of filtration rates are likely to be invalid unless carried out at natural seston concentrations and

sizes and with natural seston rather than artificial particles. Filter feeding and particle retention rates were depressed in gravid females of the unionoidean, *Pyganodon cataracta,* in which particle transport was slowed down and the ability to retain small particles (<6 μm) reduced, when the marsupial gills were distended with glochidia (Tankersley, 1996).

Suspended silt can inhibit filtering and consumption rates in freshwater bivalves, perhaps by overwhelming ciliary filtering and sorting mechanisms. High silt concentrations reduced filtering and metabolic rates in three unionoidean species whether exposure was infrequent (once every 3 h) or frequent (once every 0.5 h), suggesting interference with gill ciliary activity. Furthermore, individuals experiencing frequent exposure increased reliance on carbohydrate catabolism (Aldridge *et al.,* 1987), symptomatic of short-term starvation; perhaps, the basis of exclusion of unionoideans from habitats with high silt loads (Adam, 1986). In contrast, natural suspended sediment concentrations did not affect shell or tissue growth in *C. fluminea* (Foe and Knight, 1985), perhaps, accounting for its ability to colonize high-flow lotic habitats with greater suspended solids than tolerated by most unionoideans (Payne and Miller, 1987; Section III.A.). In contrast, growth in juvenile unionoideans is stimulated by small amounts of suspended silt in their algal food (Hudson and Isom, 1984), perhaps because juveniles (*Villosa iris*) may feed primarily on sediment interstitial water through the pedal gape, leading to ingestion of silt, microdetritus and bacteria, with little consumption of algae (Yeager *et al.,* 1994).

In smaller streams, where phytoplankton productivity may be low, most suspended organic matter is particulate organic detritus or heterotrophic bacteria and fungi (Nelson and Scott, 1962). While experiments are few, at least some freshwater bivalves efficiently filter suspended bacteria. *D. polymorpha* appears to extract particles of bacteria size (<1.0 μm in diameter) (Sprung and Rose, 1988, Fig. 22) as can *C. fluminea* (Silvermann *et al.,* 1995) with *D. polymorpha* and *C. fuminea* able to clear the bacterium, *Escherichia coli,* 30 and 3 times faster than the lotic unoinid, *Toxolasma texasiensis,* respectively. Increased capacity for bacterial filtration in *D. polymorpha* appears associated with its enlarged gill with a 100-fold greater density of cirri relative to *C. fluminea,* that of *T. texasiensis* has even fewer and smaller cirri than *D. polymorpha* or *C. fluminea* (Silverman *et al.,* 1995). Filter-feeding by *D. polymorpha* may significantly reduce bacterioplankton densities in the inner portion of Saginaw Bay, Lake Huron (Cotner *et al.*,). *Musculium transversum* (Way, 1989a) and some unionoidean species (Fig. 22) do not efficiently filter bacterial-size particles. Unionoideans appear specialized to filter larger particles, such as phytoplankton, detritus, protozoa, and even small zooplankton, such as rotifers (Singh *et al.,* 1991). In contrast, six unionoidean species adapted to lotic habitats where seston was dominated by bacteria and detritus could filter bacteria at significantly higher rates than three species adapted to lentic habitats where seston was dominated by phytoplankton. Lotic species had more complex cirri (>25 vs <16 cilia per cirral plate) and greater gill cirral density than lentic species, indicative of a filtering system better adapted for fine particle filtration (Silverman *et al.,* 1997) . Because bacteria and detrital particles may comprise most of the organic matter in some, particularly lotic, habitats, bacterial feeding warrants greater study in freshwater bivalves.

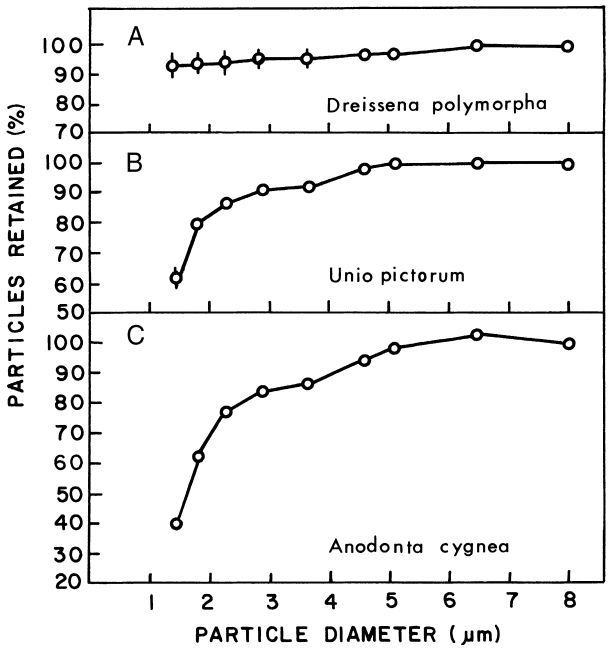


FIGURE 22 Relationship between the percentage of suspended particles retained by the gill filtering mechanism of freshwater bivalves and particle size, as particle diameter in micrometers. Horizontal axis for all figures is the percentage of total particles retained from suspensions passing over clam gill filtering systems in (A) *Dreissena polymorpha*, the unionoideans, (B) *Unio pictorum*, and (C) *Anodonta cygnea*. Vertical lines about points are standard deviations. Note that all three species efficiently retained particles of 2.5–8 μm diameter, equivalent to most unicellular algae, but only *D. polymorpha* efficiently retained bacteria-sized particles of 1 μm diameter. (Redrawn from Jørgensen *et al.*, 1984.)

d. Sediment Feeding At least some freshwater bivalves may supplement phytoplankton filter feeding by consuming organic detritus or interstitial bacteria from sediments. The infaunal habit of many *Pisidium* species suggests dependence on nonplanktonic food sources. Many pisidiids can efficiently filter small interstitial bacteria. They burrow continually through sediments with the shell hinge downward, drawing dense interstitial

water and bacteria through parted ventral mantle edges into the mantle cavity to be filtered on the gills (Lopez and Holopainen, 1987). Both *Pisidium casertanum* and *P. conventus* feed in this manner, filtering bacteria of smaller diameter (<1 μm) than most bivalves (Lopez and Holopainen, 1987) (Fig. 22). Filtering of rich interstitial bacterial flora may be associated with the reduced ctenidial surface areas and low filtration and metabolic rates of *Pisidium* species compared to *Sphaerium* or *Musculium* (Hornbach, 1985; Lopez and Holopainen, 1987). Similar interstitial bacteria and detritus feeding occurs in juvenile unionids (Yeager *et al.,* 1994). *M. transversum* uses its long inhalant siphon to vacuum detrital particles from the sediment surface (Way, 1989).

Pedal feeding on sediment organic detritus may be another important food source in some freshwater bivalves. Pedal feeding occurs in marine and estuarine bivalves (Morton, 1983; Reid *et al.,* 1992), but is little studied in freshwater species. *Corbicula fluminea* draws sediment detrital particles over the ciliated foot epithelium into the mantle cavity, where they accumulate in the food groove of the inner demibranch and are carried to the palps for sorting and ingestion (Way *et al.,*1990b; Reid *et al.,* 1992). Cellulose particles (40–120 μm in diameter) soaked in various amino acid solutions and mixed with sediments accumulated in the stomach of pedal-feeding *C. fluminea* (McMahon, unpublished). Thus, *C. fluminea* removed sediment organic matter at a rate of 50 mg/clam per day and doubled growth rates when allowed to pedal feed in addition to filter feeding (Hakenkamp and Palmer, 1999). Similar pedal feeding has been reported in *M. transversum* (Way, 1989) and in juvenile *Villosa iris* (Yeager *et al.,* 1994). Thus, pedal deposit feeding may be an important auxiliary feeding mode in freshwater and marine bivalves and may have important impacts on sediment organic dynamics (Hakenkamp and Palmer, 1999).

Pedal feeding may be more universal in freshwater species than previously suspected. In a stream *S. striatinum* population, only 35% of organic carbon assimilation occurred by filter feeding, leaving 65% to come from sediment detrital sources (Hornbach *et al.,* 1984b), presumably by pedal feeding. Other sphaeriid species reach highest densities in sediments of high organic content (Zbeda and White, 1985) or in habitats receiving organic sewage effluents, suggesting dependence on pedal deposit-feeding (Burky, 1983). Pedal deposit-feeding mechanisms may explain the extensive horizontal sediment locomotion of a number of freshwater bivalves (Section II.D), as it allows pedal contact with organic detritus.

3. Population Regulation

a. Abiotic Population Regulation Most of the information regarding regulation of freshwater bivalve populations is anecdotal. Fuller (1974) reviews factors affecting population density and reproductive success. Catastrophic abiotic factors causing reductions in bivalve populations are reviewed in Section III.B. Among these are silt accumulation in sediments of impounded rivers and in the water column during flooding. Silt interferes with gill filter feeding and gas exchange (Aldridge *et al.,* 1987; Payne and Miller, 1987) causing massive mortality in unionoidean populations (Adam, 1986, Section III.A). In contrast, many sphaeriids thrive in silty sediments (Burky, 1983; Kilgour and Mackie, 1988) associated with their utilization of sediment detrital food sources (Section III.C.2). Shell growth in *C. fluminea,* a silt tolerant species, can be temporarily inhibited by high turbidity (Fritz and Luz, 1986).

Temperature extremes also affect bivalve populations. *C. fluminea* tolerates 2°C (Mattice, 1979) to 36°C (McMahon and Williams, 1986b). Both cold-induced winter (Blye *et al.,* 1985; Sickel, 1986) and heat-induced summer kills (McMahon and Williams, 1986b) are reported for this species. The incipient upper lethal limit for *D. polymorpha* is 30°C, preventing its invadsion of many southern U.S. drainage systems (McMahon, 1996). Temperature limits for other NA bivalves are not as well known, but, on average, appear to be broader than either *C. fluminea* or *D. polymorpha* (Burky, 1983). Juvenile unionoideans are less temperature tolerant than adults (Dimock and Wright, 1993), suggesting that temperature limitation operates at the juvenile level in this group. Within the tolerated range, temperature may have detrimental effects on reproductive success. Sudden temperature decreases cause abortive glochidial release in unionoideans (Fuller, 1974), and temperatures above 30–33°C inhibit reproduction in *C. fluminea* (McMahon, 1999). Sphaeriid densities were reduced in midsummer by heated effluents (Winnell and Jude, 1982). Heated effluents may also stimulate bivalve growth, inducing early maturity and increasing reproductive effort. They can provide heated refugia in which cold-sensitive species may overwinter as in northernmost NA populations of *C. fluminea* (McMahon, 1999).

Low ambient pH can depauperate or extirpate bivalve populations. Bivalve populations have been extirpated by acid mine drainage (Taylor, 1985; Warren *et al.,* 1984). Highly acidic waters cause shell erosion and eventual death (Kat, 1982). Perhaps of more importance than pH in regulating freshwater bivalve populations are water hardness and alkalinity. Unionoideans do not occur in New York drainage systems with calcium concentrations <8.4 mg Ca/L (Fuller, 1974). In waters of low alkalinity, Ca concentrations may be too low for shell deposition; the lower limit for most freshwater bivalves being 2–2.5 mg Ca/L (Okland and Kuiper, 1982; Rooke and Mackie,

1984a). Growth and fecundity were suppressed in a *Pisidium casertanum* population in a low Ca concentration relative to that a higher Ca concentration (Hornbach and Cox, 1987). Waters of low alkalinity have little pH-buffering capacity, subjecting them to seasonal pH variation. This makes them particularly sensitive to acid rain, which detrimentally impacts bivalve faunae (Rooke and Mackie, 1984a). Shell Ca content is related to water Ca concentration. Of 10 Canadian freshwater bivalve species, two sphaeriids and one unionoidean displayed no relationship between shell Ca content and water Ca concentration, shell Ca content decreased with increased water Ca concentration in two sphaeriid species and increased with water Ca concentration in four sphaeriid and two unionoidean species (Mackie and Flippance, 1983b).

Lowering of water levels during dry periods induce bivalve mortality by exposing individuals to air. Such emersion caused near 100% mortality in *C. fluminea* populations (White, 1979) due to its poor desiccation tolerance (Bryne *et al.,* 1988). Many unionoidean species are relatively tolerant of emersion. When sympatric populations of nine unionoidean species, the sphaeriid *Musculium transversum,* and *C. fluminea* were emersed for several months, *M. transversum* and *C. fluminea* suffered 100% mortality while the unionoideans experienced only 50% mortality, because they either migrated downshore or resisted desiccation (White, 1979). Like *C. fluminea, D. polymorpha* is relatively emersion intolerant, particularly above 20°C (McMahon, 1996), restricting it to habitats with relatively stable water levels and making it unlikely to develop dense populations in variable level reservoirs.

Low environmental O_2 concentrations can be detrimental to freshwater bivalves. Continual eutrophication of Lake Estrom, Denmark, so reduced ambient profundal O_2 concentrations (0–0.2 mg O_2/L for three months) that massive reductions of sphaeriid populations ensued (Jonasson, 1984a, b), including hypoxia-tolerant species, such as *Pisidium casertanum* and *P. subtruncatum* in which the lower limit for aerobic respiration was 1.7 mg O_2/L (Jonasson, 1984b). Adult unionoideans are relatively hypoxia tolerant. Juveniles are more hypoxia sensitive, those of *Utterbackia imbecillis* and *Pyganodon cataracta* tolerating anoxia for less than 24 h (Dimock and Wright, 1993). Thus, restriction of unionoidean species to well oxygenated waters may be a juvenile rather than adult constraint.

Pollution is also detrimental to freshwater bivalves (reviewed by Fuller, 1974) including chemical wastes (Zeto *et al.,*1987), asbestos (Belanger *et al.,*1986a), organic sewage effluents (Gunning and Sutkkus, 1985; Neves and Zale, 1982; St, John, 1982), heavy metals (Belanger *et al.,* 1986b; Fuller, 1974; Lomte and Jabhav, 1982a; Grapentine, 1992), chlorine and paper mill effluents (Fuller, 1974), acid mine drainage (Taylor, 1985; Warren *et al.,* 1984) and PCBs (Grapentine, 1992). Potassium ions, even in low concentration (>4–7 mg K^+/liter), can be lethal to freshwater bivalves including *D. polymorpha* (Claudi and Mackie, 1993), excluding bivalves from watersheds where potassium is naturally abundant (Fuller, 1974).

b. Biotic Population Regulation There have been a few studies of biotic regulation of freshwater bivalve populations. Freshwater bivalves are host for a number of parasites. They are intermediate hosts for digenetic trematodes (Fuller, 1974). Such infections cause sterility in gastropods, and have been reported to induce sterility in the unionoidean, *Anodonta anatina,* allowing diversion of the mussel's energy stores from production of its gametes to production of trematode cercariae (Jokela *et al.,* 1993), reducing the mussel population's reproductive capacity. Parasitic nematode worms inhabit the guts of unionoideans (Fuller, 1974). The external oligochaete parasite *Chaetogaster limnaei* resides in the mantle cavities of unionoideans (Fuller, 1974), *C. fluminea* (Sickel, 1986) and *D. polymorpha* (Conn *et al.,* 1996). *Dreissena polymorpha* is host to a wide diversity of parasites (Malloy *et al.,* 1997), but their impacts on this species are unknown. All of these parasites probably contribute to the regulation of freshwater bivalve population densities, but the degree to which they do has received little experimental attention.

Water mites of the family Unionicolidae, including *Unionicola* and *Najadicola,* are external parasites of unionoideans (Vidrine, 1990). Both mature and preadult mites are parasitic, attaching to gills, mantle, and the visceral epithelium (depending on species) (Mitchell, 1955; Chapter 16). Heavy mite infestations cause portions of the gills to be shed, abortion of developing glochidia, or even death (Fuller, 1974), perhaps making unionicolid mites a major regulator of unionoidean populations. The larval stage of the chironomid, *Ablabesmyia janta,* parasitizes the unionoidean gill filaments and may exclude unionicolid mites from the gills they infest (Vidrine, 1990).

Disease has been little studied. There is little evidence of viral or bacterial involvement in die-offs of *C. fluminea* (Sickel, 1986) or unionoideans (Fuller, 1974).

In some *C. fluminea* populations, massive die-offs (particularly of older individuals) occur after reproductive efforts (Aldridge and McMahon, 1978; McMahon and Williams, 1986a; Williams and McMahon, 1986), probably due to reductions in tissue energy reserves of postreproductive individuals (Williams and McMahon, 1989). Such postreproductive morality also occurs in sphaeriids (Burky, 1983).

TABLE V List of the Major Fish Predators of Freshwater Bivalves[a]

Family	*Genus and species*	*Common name*
Clupeidae	*Alosa sapidissima*	American shad
Cyprinidae	*Cyrinus carpio*	Common carp
Catostomidae	*Ictiobus bubalus*	Smallmouth buffalo
	Ictiobus niger	Black buffalo
	Minytrema melanops	Spotted sucker
	Moxostoma carinatum	River redhorse
Moronide	*Morone saxatilis*	Striped bass
Ictaluridae	*Ictalurus furcatus*	Blue catfish
	Ictalurus punctatus	Channel catfish
Centrarchidae	*Lepomis gulosus*	Warmouth
	Lepomis macrochirus	Bluegill
	Lepomis microlophus	Red-ear sunfish
Sciaenidae	*Aplodinotus grunniens*	Freshwater drum
Acipenseridae	*Acipenser fulvesens*	Lake sturgeon

[a] Data from Fuller (1974), McMahon (1983a), Robinson and Wellborn (1988), and Sickel (1986).

Predation may be the most important regulator of freshwater bivalve populations. Shore birds and ducks feed on sphaeriids and *C. fluminea* (Dreier, 1977; Paloumpis and Starrett, 1960; Smith *et al.,* 1986; Thompson and Sparks, 1977, 1978) and *D. polymorpha* (Mazak *et al.,* 1997). *C. fluminea* densities were 3–5 times greater in enclosures excluding diving ducks (Smith *et al.,* 1986). Water fowl feeding also significantly reduces *D. polymorpha* populations (Mackie and Schloesser, 1996). Crayfish feed on small bivalves including *C. fluminea* (Covich *et al.,*1981) and *D. polymorpha* (Mackie *et al.,* 1989), and, in some habitats, may regulate bivalve population densities. Fire ants (*Solenopis invicta*) prey on clams emersed by receding water levels. In additions, turtles, frogs, and the mudpuppy salamander *Necturus maculosus* all feed to a limited extent on small or juvenile bivalves (Fuller, 1974). Free-living oligochaetes prey on newly released glochidia (Fuller, 1974).

Perhaps the major predator of freshwater bivalves are fish. A number of NA fish are molluscivores (Table V). While most molluscivorous fish feed on small bivalve species or juveniles of larger bivalves (SL <7 mm), several routinely take large adults, including carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*) and freshwater drum (*Aplodinotus grunniens*). The latter species crushes shells with three massive, highly muscular pharyngeal plates, as do carp to a lesser extent. Bivalve prey size may be limited by the dimensions of the shell-crushing apparatus. Thus, 273–542-mm long *A. grunniens* did not take *D. polymorpha* with SL >11.4 mm, but, below this size, fish size and mussel size taken were not related. Thus, predation by *A. grunniens* is unlikely to control *D. polymorpha* populations (French and Love, 1995). In contrast, channel catfish swallow bivalves intact (J. C. Britton, personal communication). The majority of molluscivorous fish may limit predation to smaller bivalves because shells of larger individuals are too strong to crack or crush. The shell strength of *C. fluminea* increases exponentially with size [$\log_{10}$ force in newtons to crack the shell = $-0.76 + 2.31$ ($\log_{10}$ SL in mm)]; it is 6.5 times stronger than the very thick-shelled estuarine bivalve, *Rangia cuneata* (Fig. 23) (Kennedy and Blundon, 1983). Shell strength is directly correlated with shell thickness. In specimens with an SL of 20 mm, the 3.0 mm thick shell of the unionoidean, *Fusconaia ebena,* was more crush resistant than the 1.3 mm thick shell of *C. fluminea* which, in turn, was more crush resistant than the fragile 0.31 mm thick shell of *D. polymorpha.* The fragile shell of *D. polymorpha* makes it prone to predation by diving ducks, crayfish and fish relative other freshwater bivalves (Miller *et al.,* 1994).

Fish predation can deplete freshwater bivalve populations. Sphaeriid diversity and density increased in habitats from which molluscivorous fish were excluded (Dyduch-Falniowska, 1982). Robinson and Wellborn (1988) reported that, 11 months after settlement, densities of *C. fluminea* were 29 times greater in enclosures excluding fish. In contrast, exclusion of fish and turtles did not increase density or species richness of a combined unoinoidean and sphaeriid community in a cooling reservoir (Thorp and Bergey, 1981).

As fish are intermediate hosts for unionoidean glochidia, the size of fish host population can influence mussel reproductive success. Absence of appropriate fish hosts have caused extirpation of unionoideans in a number of NA aquatic habitats (Fuller, 1974; Kat and Davis, 1984; Smith, 1985a, b; Neves *et al.,* 1997; Vaughn, 1997; Section III. A.) and availability of fish hosts may regulate recruitment (Johnson and Brown, 1998). Indeed, restoration of host fish populations produced remarkable recoveries of some endangered unionoidean populations (Smith, 1985b). Thus, anthropomorphic activities reducing fish host population densities can result in destruction of unionoidean populations, making relationships between unionoideans and their glochidial host fish an important future management consideration for drainage systems and their fisheries to ensure continued health of their remaining unionoidean fauna (Watters, 1993; Neves, 1997).

Mammals prey on freshwater bivalves. Otters, minks, muskrats, and raccoons eat bivalves and may regulate populations of some species (Fuller, 1974). Raccoons and muskrats feed on *C. fluminea* and may account for reductions of adult clam densities in the shallow, near-shore waters of some Texas rivers, where

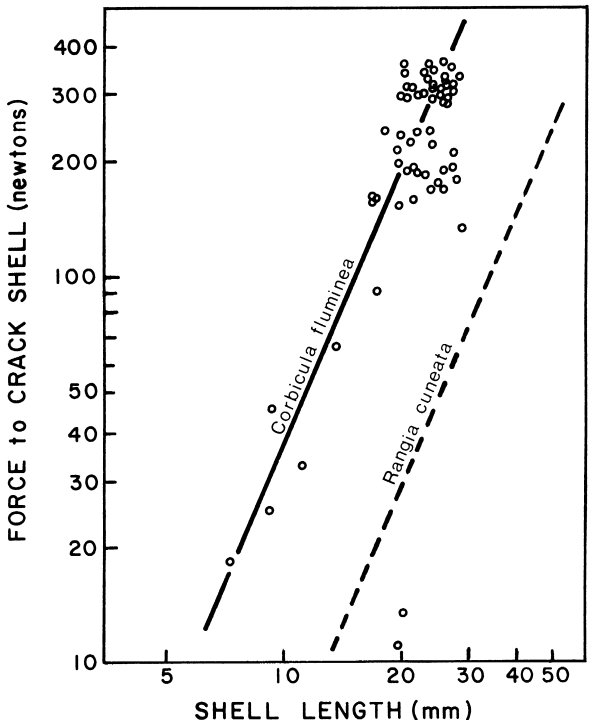


FIGURE 23 Shell strength of *Corbicula fluminea*. Solid line is the best fit of a geometric mean estimate of a least squares log–log linear regression, relating shell length (SL) to force required to crack the shell (open circles) as follows: Log_{10} force to crack the shell in newtons = $-0.76 + 2.31$ ($\log_{10}$ mm SL). Dashed line is the best fit of a similar log–log linear regression for the estuarine wedge calm, *Rangia cuneata,* as follows: $\log_{10}$ force to crack the shell in newtons = $-0.736 + 2.42$ ($\log_{10}$ SL in mm). *R. cuneata,* with the strongest shell of eight tested estuarine bivalve species, has a thicker shell than does *C. fluminea*. However, as the regression slope values for the two species are nearly equal, the elevated y-intercept for *C. fluinea* (-0.76 compared to -1.73 for *R. cuneata*) indicates that its shell is approximately an order of magnitude stronger. (Redrawn from Kennedy and Blundon, 1983.)

feeding sites are marked by thousands of opened shells (McMahon, unpublished observations). Even wild hogs root out and destroy shallow-water unionoidean beds (Fuller, 1974). Muskrats annually consummed 3% of individuals of *Pyganodon grandis* in a small Canadian lake, equivalent to 31% of the mussel's annual tissue production. They preferentially consumed larger mussels (shell length >55 mm), strongly affecting mussel population size–age structure, resulting in a biomass decline of large individuals, reducing the population's annual reproductive effort (Hanson *et al.,* 1989).

c. Competitive Interactions There have been no experimental evaluations of interspecific or intraspecific competition among freshwater bivalves; only anecdotal observations. Unionoidean or sphaeriid population declines coincident with establishment of *C. fluminea* have occurred in NA habitats (McMahon, 1999; Sickel, 1986). *C. fluminea* may detrimentally impact sphaeriid populations after invasion, but there is little evidence of major impacts of *C. fluminea* on NA unionoideans (Strayer, 1999b). Thus, *C. fluminea* had little impact on a Tennessee River unionoidean community, the *C. fuminea* population declining over time while unionid density remained stable (Miller *et al.,* 1992). Rather, habitats are first made inhospitable to indigenous unionoideans by channelization, dredging, over-fishing or other water management practices. *C. fluminea* is more tolerant of high flows, suspended solids, and silting caused by human activities in drainage systems, allowing it to rapidly colonize such disturbed habitants in which unionoideans have been reduced or extirpated (McMahon, 1999). In contrast, establishment of *C. fluminea* in drainage systems receiving minimal human interference has little effect on native bivalve populations (McMahon, 1999; Sickel, 1986), suggesting an inability of *Corbicula* to outcompete native unionoideans in undisturbed habitats. The impacts of *C. fluminea* on native, NA bivalves remains subject to debate (reviewed by Strayer, 1999b) and should be experimentally addressed.

In contrast to *C. fluminea,* there is clear evidence of direct negative impacts of *D. polymorpha* on NA unionoidean populations. *Dreissena polymorpha* byssally attaches to the posterior portions of unionoidean valves projecting above the substrate where they can reach densities which strip seston from the unionoidean's inhalant current, leading to its slow starvation. Extensive *D. polymorpha* infestations can cause unionoideans to be dislodged from the substrate, leading to death. *D. polymorpha* infestation has caused near complete extirpation of unionoideans from the lower Great Lakes and St. Lawrence River (Schloesser *et al.,* 1996; Strayer, 1999b). Interestingly, short-term brooding unionoideans (tribes Amblemini and Pleurobemini) appear less sensitive to zebra mussel impacts than long-term brooders (tribe Lampsilini and subfamily Anodontinae), perhaps due to their greater tissue energy reserves (Strayer, 1999b). Unionoidean populations in shallow (1 m), near-shore waters of western Lake Erie were less subject to *D. polymorpha* infestation than those at greater depths (Schloesser *et al.,* 1997), perhaps because wave-induced agitation inhibits byssal attachment (Clarke and McMahon, 1996b).

Dreissena polymorpha can have indirect impacts on N.A. bivalve communities. After *it* colonized the lower Hudson River in 1992, sphaeriid and unionoidean populations declined even though *D. polymorpha* did not attach to their shells. This decline resulted from a massive reduction in phytoplankton

density by *D. polymorpha* feeding, causing starvation of indigenous bivalves (Strayer, 1999b).

d. Density-Dependent Mechanisms of Population Regulation Factors directly impacting freshwater bivalve population densities may have secondary impacts associated with reduction in gamete fertilization through reduction of sperm concentration in the water column. Thus, egg fertilization in the marsupial gills of female *Elliptio complanata* was directly correlated with population density, fertilization failing completely at <10 adults/m^2 (Downing *et al.,* 1993).

Published experimental investigations of intraspecific, density-dependent, population regulation mechanisms in freshwater bivalves are also lacking. However, some evidence is available from descriptive field studies of *C. fluminea* and sphaeriids. In *C. fluminea,* extremely successful recruitment of newly settled juveniles occurred after adult population decimation (McMahon and Williams, 1986a, b); whereas, juvenile settlement is generally far less successful in habitats harboring dense adult populations. High adult density may prevent successful juvenile recruitment, thus preventing extensive juvenile–adult competition. This hypothesis was tested by enclosing adult *C. fluminea* at different densities in a lake harboring a dense *Corbicula* population. While adult density had no effects on adult or juvenile growth rates, it affected juvenile settlement. Settlement in enclosures without adults was 8702 juveniles/m^2. Maximal settlement (26,996 juveniles/m^2) occurred at 329 adults/m^2; and was least at the highest adult densities of 659 and 1976 clams/m^2, being only 8642 and 3827 juveniles/m^2, respectively (McMahon, unpublished data). Thus, adults of *C. fluminea* may inhibit juvenile settlement. Mackie *et al.,* (1978) found that high adult densities in *Musculium securis* caused significant reduction in the number of juveniles incubated, implying that intraspecific adult competition regulates reproductive effort. In addition, interspecific competition between *M. securis* and *M. transversum* caused reduction in reproductive capacity in the subdominant species, with species dominance dependent on habitat. While intraspecific density effects and interspecific competition may regulate *Corbicula* and sphaeriid populations, results may not be the same for highly K-selected unionoidean populations which require further study before the effects of thinning of mussel beds by commercial harvesters on juvenile recruitment and adult growth can be assessed.

4. Functional Role in the Ecosystem

Bivalves play important roles in freshwater ecosystems (reviewed by Strayer *et al.,* 1999a, b). Because they can achieve high densities and are filter feeders, they are important consumers of phytoplankton primary productivity. Unionoideans, with filtering rates on the order of 300 mL/g dry tissue/h (Paterson, 1984), can account for a large proportion of total consumption of phytoplankton productivity. As unionoidean densities range from 15 individuals/m^2 (Paterson, 1985) to 28 individuals/m^2 (Negus, 1966) and dry tissue standing crop biomasses from 2.14 g/m^2 (Paterson, 1985) to 17.07 g/m^2 (Negus, 1966), filtering by unionoidean communities could be as high as 15–122.9 L/m^2 per day. Thus, on an annual basis, a eutrophic lake unionoidean community filtered 79% of total lake volume, removing 92–100% of all suspended seston. However, even with such high cropping rates, high phytoplankton reproductive rates resulted in unionoideans reducing seston by only 0.44% (Kasprzak, 1986). While the unionoidean community accounted for only 0.46% of seston removed by all phytoplanktivorous animals in the lake, they made up 85% of its standing crop biomass. Their biomass contained a high proportion of the phosphorus load of the lake, limiting the quantity of phosphorus available for phytoplankton production. Similarly, the unionoidean community of Lake St. Clair ingested 13.5% of the total phosphorus load of the lake from May through October and deposited 64% of consumed phosphorus in the sediments, providing nutrients for rooted macrophytic vegetation and invertebrate deposit feeders (Nalepa *et al.,* 1991). *D. polymorphia* populations in five European lakes had an average dry weight biomass 38 times that of submerged macrophytes and average standing crop phosphorus and nitrogen contents 2.94 (range, 0.39–7) and 4.21 (range, 0.59–9.4) times that of submerged macrophytes, respectively, greatly reducing availability of these growth-limiting inorganic nutrients to the aquatic plant community (Stanczykowska, 1984). In the western basin of Lake Erie, *D. polymorpha* has become a major factor in phosphorus flux; its uptake of phosphorus and nitrogen potentially limiting phytoplankton growth and its low N:P excretion ratios (<20:1) potentially shifting phytoplankton community structure toward cyanobacteria (Arnott and Vanni, 1996).

Sphaeriids also have important impacts on lentic phytoplankton communities. The sphaeriid community of an oligotrophic lake comprised only 0.12% of total planktivore biomass and 0.2% of the bivalve biomass, but accounted for 51% of total seston consumption (Kasprzak, 1986). This probably resulted from their relatively high filtration rates and population productivity (Burky *et al.,* 1985a; Hornbach *et al.,* 1984a, b). In smaller lotic and lentic habitats, sphaeriids can consume a major portion of primary productivity. In a canal community dominated by sphaeriids (98% of planktivore biomass), they accounted for 96% of total

seston consumption (Krasprzak, 1986). A stream population of *S. straitinum* was estimated to filter 3.67 g organic C/m^2 per year or 0.0004% of seston organic carbon flowing over them (Hornbach *et al.,* 1984b). In contrast, filtration by a pond population of *M. partumeium* removed 13.8 g C/m^2 per year as seston (Burky *et al.,* 1985a). Based on the data of Burky *et al.,* (1985b), standing crop seston levels for the entire pond ranged annually between 46 and 550 g carbon. Average annual seston organic carbon consumption by the *M. partumeium* community was estimated to be roughly 3.9 g C per day, or 0.7–8.5% of total standing crop seston carbon per day. These data indicate that sphaeriid communities crop a significant portion of the primary productivity of their small lentic habitats.

With extremely high filtering rates and dense populations (McMahon, 1999), *C. fluminea* is potentially a major consumer of phytoplankton productivity. In the Potomac River, phytoplankton densities and chlorophyll a concentrations declined as it flowed over dense beds of *C. fluminea,* both measures falling 20–75% lower than upstream values; current phytoplankton levels in this river section are considerably lower than those prior to *C. fluminea* invasion. It was estimated that the *C. fluminea* population filtered the entire water column in the 3–4 day period required for it to pass the river reach where the population was most dense (Cohen *et al.,* 1984). Similar reduction in phytoplankton density of a lotic habitat by *C. fluminea* has been reported by Leff *et al.* (1990). Reductions in phytoplankton density and chlorophyll a concentration must have been due to clam filter feeding, particularly as discharge volume variation, zooplankton feeding, toxic substances, and nutrient limitations were not different from other river sections (Cohen *et al.* 1984). Similarly, Lauritsen (1986b) estimated that a *C. fluminea* population of 350 clams/m^2 in the Chowan River, NC, at an average depth of 5.25 m and clam filtering rate of 564–1010 mL/h, filtered the equivalent of the overlying water column every 1–1.6 days. At an average depth of 0.25 m, current flow of 18.5 m/min, and average clam filtering rate of 750 mL/h (Lauritsen, 1986b), the entire water column of the Clear Fork of the Trinity River flowing over a *C. fluminea* population with an average adult density of 3750 clams/m^2 was filtered every 304 m of river reach, or every 16 min (McMahon, unpublished observations). Such massive filtering of the water column by dense bivalve populations could keep seston concentrations at low levels and limit the energy available to other seston-feeding species. Consumption of the majority of primary productivity by dense bivalve populations and the accumulation of that production in large, relatively long-lived, predator-resistant adult clams may not only limit the inorganic nutrients available for primary productivity and the energy available to other primary consumers, but may also divert energy flow from higher trophic levels.

Bivalves, by filtering suspended seston, are water clarifiers and organic-nutrient sinks. When co-cultured with channel catfish, *C. fluminea* increased ambient water O_2 concentrations by reducing seston and turbidity levels (Buttner, 1986). Dense bivalve populations, by removing phytoplankton and other suspended material, increase water clarity, and, by binding suspended sediments into pseudofeces, accelerate sediment deposition rates (Prokopovich, 1969). Dense *D. polymorpha* populations clarify water which increases light penetration, stimulating the growth of rooted aquatic macrophytes (Mackie and Schloesser, 1996).

Such major ecological impacts by *D. polymorpha* have been observed in several locations in the lower Great Lakes, St. Lawrence River and Hudson River harboring dense mussel populations (reviewed by MacIsaac, 1996). In these habitats, *D. polymorpha* filtering increases water clarity. In the Hudson River, *D. polymorpha* filtered the equivalent of the entire water column every 1.2–3.6 days (Strayer *et al.,* 1999). Phytoplankton densities are most negatively impacted by *D. polymorpha* filtering in waters <1.85 m above mussel beds (MacIsaac *et al.,* 1999). Besides phytoplankton and small zooplankton, *D. polymorpha* filters suspended clay and silt particles and binds them into pseudofeces deposited in sediments (MacIsaac, 1996; Strayer *et al.,* 1999). Phytoplankton reductions by *D. polymorpha* have been extensive, ranging from 59 to 91% in portions of the Great Lakes (MacIsaac, 1996) and from 80 to 90% in the lower Hudson River, with mussels less efficiently removing diatoms than other smaller algae (Strayer *et al.,* 1999). Filter feeding by *D. polymorpha* can reduce bacterioplankton densities, but can also stimulate bacterioplankton growth through nutrient or organic carbon excretion (Cotner *et. al.,* 1995). Feeding by dense *D. polymorpha* populations appears to favor development of cyanobacteria blooms in some NA waters, perhaps due to reduction in N:P ratio, enhanced light penetration, greater buoyancy of cyanobacteria filaments, and/or chemical or mechanical inhibition of mussel filtering by cyanobacteria (MacIsaac *et al.,* 1996).

Zooplankton populations are reduced by *D. polymorpha* filtering. Small zooplankton such as rotifers and even *Dreissena* veligers can be directly filtered; rotifer density in western Lake Erie declining by 74% within 5 years of *D. polymorpha* colonization, while larger zooplankton species that avoid entrainment on the mussel's inhalant currents were relatively unaffected (MacIsaac, 1996). Similarly, zebra mussel

invasion brought about 80–90% reductions in rotifers, tintinnids, and copepod naupli densities in the lower Hudson River (Strayer *et al.,* 1999). Suppression of small zooplankton could reduce fish populations whose larvae utilize them as food and result in density increases of bacterioplankton on which small zooplankton feed (Strayer *et al.,* 1999). Increased water clarity and sediment nutrient levels appear to stimulate increased aquatic macrophyte growth in many areas colonized by *D. polymorpha,* favoring fish species associated with them over open-water species (MacIsaac, 1996). Increased macrophyte growth also appeared to favor associated invertebrate species, whose densities increased dramatically in the Hudson River after *D. polymorpha* colonization while deep-water benthic invertebrates concurrently declined (Strayer *et al.,* 1999). Thus, overall, *D. polymorpha* populations appear to divert resources from the pelagic zone and deep-water sediments to vegetated shallows and zebra mussel beds (Strayer *et al.,* 1999), leading to increases in benthic invertebrate abundance and diversity due to habitat structure enhancement among accumulated mussel shells and increased food supply, enhancement of physical habitat appearing to have the greatest impact (Botts *et al.,* 1996). Increased bentic invertebrate densities support density increases in fish populations feeding on them (MacIsaac, 1996; Ricciardi *et al.,* 1997; Stewart *et al.,* 1998; Strayer *et al.,* 1999), These post-colonization impacts of *D. polymorpha* are extensive, with almost all of 11 measured ecological variables being shifted by >50% after establishment of mussel populations in the lower Hudson River (Strayer *et al.,* 1999). Increased food availability, associated with feeding on *D. polymorpha,* may also be responsible for postzebra mussel colonization increases in diving-duck flock sizes and staging durations in several portions of Lake Erie (MacIsaac, 1996).

As freshwater clams filter suspended organic detritus and bacteria and consume sediment interstitial bacteria and organic detritus (Section III.D.2), they may be significant members of the aquatic decomposer assemblage. *Pisidium casertanum* and *P. corneum* feed primarily by filtering sediment bacteria (Lopez and Holopainen, 1987). Hornbach *et al.* (1982, 1984b) estimated that only 24–35% of energy needs of a population of *Sphaerium striatinum* were met by filter feeding, the remaining coming from sediment organic detritus. *C. fluminea* pedally feeds on sediment detritus (Reid *et al.,* 1992), impacting the decomposer community (Hakenkamp and Palmer, 1999). *Musculium transversum* utilizes its long inhalant siphon to vacuum organic detritus from the sediment surface (Way, 1989). The detritivorous habit of many freshwater bivalve species may divert primary productivity ordinarily lost to respiration of the detritivorous community back into bivalve tissue where it is made re-available to higher trophic levels.

The activity of freshwater bivalves may also directly affect habitat physical characteristics. Deposition of calcium in shells may reduce ambient Ca concentrations. In a *C. fluminea* population of 32 clams/m^2, annual fixation of shell $CaCO_3$ was 0.32 kg $CaCO_3/m^2$ per year (Aldridge and McMahon, 1978). At this rate, shell $CaCO_3$ fixation in a dense population of 100,000 clams/m^2 (Eng, 1979) could be 50–60 kg Ca CO_3/m^2 per year. Such rapid removal of calcium to shells accumulating in the sediments could reduce water hardness, particularly in lentic habitats (Huebner *et al.,* 1990). Seasonal cycles of shell growth could induce seasonal cycles in water Ca concentration, being greatest in winter when shell growth is minimal and least in summer when shell growth is maximal (Rooke and Mackie, 1984c). Bivalves can also affect solute flux between sediments and the water column. Unionoidean mussels enhanced release of nitrate and chloride and inhibited $CaCO_3$ release from sediments (Matisoff *et al.,* 1985). Dense sphaeriid populations can be the principal affectors of sediment dissolved O_2 demand, in cases reaching levels characteristic of semipolluted and polluted streams (Butts and Sparks, 1982). *D. polymorpha* and *C. fluminea* increase sedimentation rates, negatively or positively impact phosphate and nitrate fluxes between sediments and the water column, change the N:P ratio of the water column, clarify water, and change sediment physical make up by accumulation of their shells (Arnott and Vanni, 1996; Strayer *et al.,* 1999).

Small bivalves (sphaeriids, juvenile unionoideans, *D. polymorpha,* and *C. fluminea*) can be a major food source for third trophic level carnivores, including fish and crayfish (Section III.C.3). Bivalve flesh has a low caloric content, 3.53–5.76 kcal/g ash-free dry weight (Wissing *et al.,* 1982), reflecting low lipid:protein ratios. *C. fluminea* has tissue organic C:N ratios ranging from 4.9–6.1:1, indicative of a 51–63% of dry weight protein content (Williams and McMahon, 1989). High protein content makes bivalve flesh an excellent food source to sustain predator tissue growth.

Many freshwater bivalve populations are highly productive (particularly sphaerids, *C. fluminea,* and *D. polymorpha*), rapidly converting primary productivity into tissue energy available to third trophic level carnivores. Productivity values range from 0.019 g C/m^2 per year for a *Pisidium crassum* population to 10.3 g C/m^2 per year for a *C. fluminea* population (Aldridge and McMahon, 1978) and 75 g C/m^2 per year for a *D. polymorpha* population (Mackie and Schloesser, 1996); the average for 11 sphaeriid species and two species of *Corbicula* was 2.5 g C/m^2 per year (Burky, 1983). Other values include 12.8–14.6 g C/m^2 per

year for an Arizona *C. fluminea* canal population (computed from data of Marsh, 1985) and 1.07 g C/m^2 per year for a New Brunswick lake unionoidean population of *Elliptio complanata* (computed from data of Paterson, 1985).

Bivalves are generally more efficient at converting assimilated food energy into new tissue than most second trophic level aquatic animals because their sessile, filter-feeding habits minimize energy expended in food acquisition, allowing efficient transfer of energy from primary production to bivalve predators. Thus, bivalves can be important conduits of energy fixed by phytoplankton photosynthesis to higher trophic levels. However, such trophic energy transfer is mainly through smaller species and juvenile specimens, as large adults are relatively immune to predation (Section 3.C).

The measure of efficiency of conversion of assimilated energy absorbed across the gut wall into energy fixed in new tissue growth is net growth efficiency:

$$\% \text{ Net Growth Efficiency} = \frac{P}{A(100)}$$

where P is the productivity rate or rate of energy or organic carbon fixation into new tissue growth by an individual or population and A the assimilation rate or rate of energy or organic carbon assimilated by an individual or population. The greater the net growth efficiency of a second trophic level species, the more efficient its conversion of assimilated energy into flesh, and, therefore, the greater the potential for energy flow though it to third trophic level predators (reviewed by Russell-Hunter and Buckley, 1983; Holopainen and Hanski, 1986; Hornbach, 1985). Net growth efficiencies (Table III), are 9–79% in sphaeriids (average = 55%) and 58–89% in *C. fluminea,* indicating efficient conversion of assimilated energy into flesh compared to other aquatic second trophic level animals.

5. Bivalves as Biomonitors

Freshwater bivalves, particularly unionoideans *C. fluminea* and *D. polymorpha,* have characteristics such as long life spans, and growth and reproductive rates sensitive to environmental perturbation (Burky, 1983) that make them good biomonitors (Imlay, 1982). They can be held in field enclosures without excessive maintenance. Shell growth is sensitive to environmental variation and/or disturbance (Way and Wissing, 1982; Fritz and Lutz, 1986; Belanger *et al.,* 1986a, b; Way, 1988), and the valves remain as evidence of death, allowing mortality rates to be estimated. Shells can be marked by tags (Rosenthal, 1969; Young and Williams, 1983c), including floating tags tethered to the shell (Englund and Heino, 1994b), paint, or shell-etching (McMahon and Williams, 1986a).

Bivalves can be collected throughout the year and easily shipped alive long distances. Because large species stay in place (exception is *C. fluminea*), they experience conditions in the monitored environment throughout life (Imlay, 1982). Annual shell-growth increments allows determination of variation in heavy-metal pollutant levels over long periods by analysis of levels in successively secreted shell layers (Imlay, 1982). However, there is controversy regarding use of shell-growth rings to age unionoideans. Growth rings are produced annually in some species (Neves and Moyer, 1988), but not in others (Downing *et al.,* 1992). Large size allows analysis of pollutant levels in single individuals, and the wide geographical ranges of some species (Imlay, 1982) allow comparisons across drainage systems. Table VI indicates the types of pollutants and environmental perturbations monitored by freshwater bivalves. The broad distributions of *C. fluminea* and *D. polymorpha* in North America and their dense, readily collectible populations make them excellent biomonitors compared to unionoideans, many species of which have restricted distributions and/or are threatened or endangered (Section III.A).

D. Evolutionary Relationships

Sphaeriid, dreissenids, corbiculids, and unionoideans represent separate evolutionary invasions of freshwaters. Sphaeriids, dreissenids, and corbiculids fall in the order Veneroida, and unionoideans in the order Unionoida (Allen, 1985). The Veneroida became successful infaunal filter feeders though evolution of inhalant and exhalant siphons, allowing maintenance of respiratory and feeding currents while burrowed. Their eulamellibranch gills with fused filaments (Fig. 5) were a clear advancement over the primitive (i.e., filibranch) condition with separate gill filaments attached by interlocking cilia (Allen, 1985).

The family, Sphaeriidae, in the superfamily, Corbiculacea, with a long freshwater fossil history extending from the Cretaceous (Keen and Dance, 1969) has evolved along two major lines. The first, represented by *Pisidium,* involves adaptation to life in organically rich sediments by filtering interstitial bacteria (Lopez and Holopainen, 1987), making them dominant in profundal habitats. The second, represented by *Sphaerium* and *Musculium,* involves adaptation to life in small, shallow, lentic or lotic habitats subject to predictable seasonal perturbation, such as habitat-drying. Their adaptations include estivation during prolonged emergence (Section III.A). Like many of the Veneroida, the byssus is absent in adults of most species.

The superfamily Unionoidea, like the Sphaeriidae, has a long freshwater fossil history, extending from at

TABLE VI List of some Investigations Involving Utilization of Bivalves to Monitor Effects or Levels of Pollutants in Freshwater Habitats

Pollutant monitored	*Species utilized*	*Literature citations*
Arsenic	*Corbicula fluminea*	Elder and Mattraw (1984), Price and Knight (1978), Tatem, (1986)
Cadmium	Eight unionoidean species,	Price and Knight (1978)
	Anodonta anatina	Hemelraad *et al.* (1985)
	Anodonta cygnea	Hemelraad *et al.* (1985)
	Corbicula fluminea	Elder and Mattraw (1984), Graney *et al.* (1984), Price and Knight (1978), Tatem (1986)
Chromium	Eight unionoidean species	Price and Knight (1978)
	Corbicula fluminea	Elder and Mattraw (1984), Tatem (1986)
Copper	*Corbicula fluminea*	Annis and Belanger (1986), Elder and Mattraw (1984), Price and Knight (1978), Tatem (1986)
	Lamellidens marginalis	Hameed and Raj (1990)
Iron	*Corbicula fluminea*	Tatem (1986)
Lead	*Corbicula fluminea*	Annis and Belanger (1986), Elder and Mattraw (1984), Price and Knight (1978), Tatem (1986)
	Lamellidens marginalis	Hameed and Raj (1990)
Manganese	Eight unionoidean species	Price and Knight (1978)
	Corbicula fluminea	Elder and Mattraw (1984), Tatem (1986)
	Lamellidens marginalis	Hameed and Raj (1990)
Mercury	*Corbicula fluminea*	Elder and Mattraw (1984), Price and Knight (1978)
Nickel	*Lamellidens marginalis*	Hameed and Raj (1990)
Tin	Eight unionoidean species	Price and Knight (1978)
Zinc	*Anodonta* sp.	Herwig *et al.* (1985)
	Corbicula fluminea	Belanger *et al.* (1986b), Elder and Mattraw (1984), Foe and Knight (1986c)
	Lamellidens marginalis	Hameed and Raj (1990)
Asbestos	*Corbicula fluminea*	Belanger *et al.* (1986a, 1987)
Octachlorostyrene	*Lampsilis siliquiodea*	Elder and Mattraw (1984), Tatem (1986)
Polychlorinated	*Corbicula fluminea*	Elder and Mattraw (1984), Tatem (1986)
Biphenols (PCBs)	*Lampsilis siliquoidea*	Pugsely *et al.* (1985)
	Dreissena polymorpha	Fisher *et al.*1993
Pentachlorophenol (PCP)	*Dreissena. Polymorpha*	Borcherding (1992), Fisher *et al.* (1993)
Pesticides	*Corbicula fluminea*	Elder and Mattraw (1984), Hartley and Johnston (1983), Tatem (1986)
Sewage effluents	*Corbicula fluminea*	Foe and Knight (1986c), Horne and MacIntosh (1979), Weber (1973)
Power station effluents	*Corbicula fluminea*	Dreier and Tranquilli (1981), Ferris *et al.* (1988), Foe and Knight (1987), McMahon and Williams (1986b)
Natural waters	*Dreissena polymorpha*	Borcherding and Volpers (1994)
	Unio tumidus	Englund and Heino (1994a)
	Anodonta anatina	Englund and Heino (1994a)

least the Triassic (Haas, 1969). A long fossil history and tendency for reproductive isolation due to gonochorism and the parasitic glochidial stage (Section III.A) which allows sympatric speciation via new glochidial fish host acquisition (Graf, 1997) has led to extensive radiation, the Unionoidea being represented worldwide by 150 genera and a great number of species (Allen, 1985). Their origin remains unclear. Similarity of shell structure suggests a relationship to marine fossil species in the order Trigonoida (Allen, 1985). Like the majority of sphaeriids, adult unionoideans lack a byssus, which would be of no use in their infaunal habitats. They dominant the shallow regions of larger, relatively stable lentic and lotic habitats, particularly in stable sand–gravel sediments (Section III.A). The division of the superfamily, Unionoidea, into the presumed more primitive family, Margaritiferidae, and the more derived family, Unionidae, has been partially supported by mitochondrial DNA analysis of NA species. This study also supported the monophyly of the NA unionoidean subfamilies Anodontinae and Ambleminae and tribe Pleuorblemini, but provided only weak support for the

tribe Lampsilini (Lydeard *et al.,* 1996). Further molecular studies are needed to elucidate the complex phylogeny of the Unionoidea, including analysis of species outside of North America.

The Sphaeriidae and Unionoidea, with long freshwater fossil histories, have evolved distinct niches. While both occur in stable habitats, the majority of sphaeriids inhabit smaller ponds and streams or the profundal regions of lakes, and the majority of unionoideans inhabit stable sediments of shallow portions of larger rivers and lakes (Sections III.A and III.B).

C. fluminea entered freshwater only in recent (Pleistocene) times (Keen and Casey, 1969), making it unlikely to complete effectively with sphaeriids or unionoideans whose long fossil histories have allowed them to become highly adapted to their preferred stable freshwater habitats. Indeed, *C. fluminea* does not appear to seriously impact native NA bivalves in undisturbed freshwaters (McMahon, 1999; Section C.3). Rather, it is adapted for life in unstable habitats—subject to periodic catastrophic perturbation, particularly flood-induced sediment disturbance—which are generally unsuitable for sphaeriids or unionoideans (Section III.A). Among its adaptations to high-flow habitats are: (1) capacity for rapid burrowing; (2) a strong, heavy, concentrically sculptured, inflated shell; and (3) juvenile retention of a byssal thread—all of which allow maintenance of position in sediments (Vermeij and Dudley, 1985). Additionally, its high fecundity, elevated growth rate, early maturity, and extensive capacity for dispersal (Section III.B) allow it to colonize habitats from which other bivalves have been extirpated and rapidly recover from catastrophic population reductions. Thus, *C. fluminea* evolved a niche in unstable, disturbed habitats not utilized by sphaeriids or unionoideans, having evolved from an estuarine *Corbicula* ancestor inhabiting similar environments in the upper, near-freshwater portions of estuaries (Morton, 1982).

The superfamily Dreissenacea, containing *D. polymorpha,* while superficially resembling marine mytilacean mussels (order Mytiloida), is placed in the Veneroida because of its advanced eulamellibranch ctenidium. Adult dreissenaceans retain an attachment byssus, considered a primitive condition. In contrast, the mytiliform shell with its reduction of the anterior valves and anterior adductor muscle, is a derived adaptation to an epibenthic niche characterized by byssal attachment to hard surfaces (Allen, 1985; Mackie and Schloesser, 1996). *D. polymorpha* probably evolved from an estuarine dreissenacean ancestor of the genus *Mytilopsis*. As with *C. fluminea,* its fossil record indicates a recent, Pleistocene introduction to freshwaters (Mackie *et al.,* 1989). Also, like *C. fluminea, D. polymorpha* appears to have successfully colonized freshwaters because its niche (i.e., an epibenthic species attached to hard substrates) is not occupied by infaunal, burrowing sphaeriids or unionoideans, thus minimizing competition with these more advanced groups.

Freshwater bivalves have characteristics that are uncommon in comparable marine species. Most shallow-burrowing marine species are gonochoristic with external fertilization and free-swimming planktonic veligers. A planktonic veliger is nonadaptive in lotic freshwater habitats, as it would be carried downstream before settlement, eliminating upstream populations. Thus, the planktonic veliger stage is suppressed in sphaeriids, which brood embryos in gill marsupia and release large, fully formed juveniles ready to take up life in the sediment. In unionids, eggs are retained in gill marsupia and hatch into the glochidium, whose parasitism of fish hosts allows upstream as well as downstream dispersal and permits release of well-developed juveniles into favorable habitats (Section III.B). Even the recently evolved *C. fluminea* has suppressed the planktonic veliger stage of its immediate estuarine ancestors (Morton, 1982), producing a small, but fully formed juvenile whose byssal thread allows immediate settlement and attachment to the subtrate. Retention of external fertilization and a free-swimming veliger in *D. polymorpha* are primitive characteristics reflecting its recent evolution from an estuarine ancestor.

Downstream veliger dispersal would preclude *D. polymorpha* from establishing populations in high-flow lotic habitats, unless upstream impoundments provide replacement stock. In fact, in Europe and Asia, this species is most successful in large, lentic or low-flow lotic habitats such as canals or large rivers (Mackie *et al.,* 1989). Serial impoundment of rivers has provided lentic refugia for this species in otherwise lotic drainages, facilitating its invasion of NA waters (Mackie and Schloesser, 1996).

Another common adaptation in freshwater species is hermapharoditism with a capacity for self-fertilization. Hermaphroditism makes all individuals in a population reproductive, allowing rapid population expansion during favorable conditions. Hermaphroditism allows sphaeriids to re-establish populations after predictable seasonal perturbation and *C. fluminea,* along with its high fecundity, to rapidly re-establish populations after catastrophic habitat disturbance. It makes both sphaeriids and *C. fluminea* invasive, as the introduction of a single individual can found a new population. In contrast, the gonochorism of most unionoideans and *D. polymorpha* limits their invasive capacity, reflected by their stable, relatively undisturbed habitats. Hermaphroditism occurs in only seven species within three subfamilies of NA Unionoidea (Hoeh *et al.,* 1995) with widely different habitats and reproductive traits. Selection pressures for evolution of hermaphroditism within these species have not been elucidated.

Finally, unionoideans and sphaeriids have different shell morphologies relative to comparable shallow-burrowing marine bivalves. Freshwater species generally do not have denticulated or crenulated inner-valve margins, extensive radial or concentric shell ridges, tightly sealing valve margins, well-developed hinge teeth, overlapping shell margins, or uniformally thick, inflated, strong shells to the degree displayed by shallow-burrowing marine species (Vermeij and Dudley, 1985). These shell characteristics allow shallow-burrowing marine species to maintain position in unstable substrates and/or resist shell cracking or boring by large predators common in marine habitats. Lack of such structures in unionoideans and sphaeriids reflects their preference for stable sediments and the general absence of effective predators on adult freshwater bivalves; certainly there are no shell-boring predators of NA freshwater species. Indeed, the shells of freshwater unionoideans display considerably less nonlethal, predator-induced damage than shallow-burrowing marine species (Vermeij and Dudley, 1985). While retention by *C. fluminea* of a thick, extremely strong shell (Kennedy and Blundon, 1983; Miller *et al.,* 1992), lacking pedal and siphonal gapes, with a well-developed hinge, shell inflation, and concentric ornamentation, may represent a primitive condition, it allows this species to inhabit sediments too unstable to support unionoideans or sphaeriids. Such primitive characteristics reflect similar adaptations in the immediate estuarine ancestor of this recently evolved freshwater species. In contrast, the thin, fragile shell of *D. polymorpha* (Miller *et al.,* 1992) may have evolved due to byssal attachment of the species to hard substrates where the shell is not subject to damage from unstable sediments.

IV. COLLECTING, PREPARATION FOR IDENTIFICATION, AND REARING

A. Collecting

Small sphaeriid clams are best collected by removing sediments containing clams with: (1) a trowel or shovel (shallow water); and (2) a long-handled dip net or shell scoop with a mesh of <0.35 mm (moderate depths) or by Ekman, Ponar, or Peterson dredges (deeper water), the heavier Ponar and Peterson dredges being better in lotic habitats. Drag dredges must have sediment catch bags of small mesh (1 mm or less). Use of scuba is also an effective means of collecting sphaeriids. Larger sphaeriids species can be separated from fine sediments with a 1-mm mesh sieve, but a 0.35-mesh is required for smaller specimens. Fragile sphaeriids should be separated from sediments by gentle vertical agitation of the sieve at the water surface to prevent shell damage. Coarse material should be removed prior to sieve agitation to avoid shell breakage. Exceptionally small, fragile species can be collected by washing small quantities of sediment into settlement pans, specimens being revealed after sediments settle and the water clears.

Ekman, Ponar, or Peterson dredges are best for quantitative samples of sphaeriids, because they remove sediments from under specific sediment surface areas. Quadrat frames can be placed on the bottom (Miller and Payne, 1988) and all surface sediments within the frame collected for sorting. Such frames can be utilized in shallow or deeper waters (the latter in conjunction with scuba equipment). Drag dredging at specified speeds for known intervals allows partial sample quantification. Core sampling devices consisting of tubes driven into the substrate to specific depths can yield both accurate estimates of sphaeriid density and sediment depth distributions. Core samplers sample only a small surface area, thus are best utilized with dense populations and/or repetitive sampling.

Low densities of some unionoidean populations make their collection difficult. Where populations are dense, shoveling sediments through a sieve allows collection of a broad range of sizes and age classes (Miller and Payne, 1988). As unionoideans are larger than sphaeriids, sieve mesh sizes of 0.5–1 cm may be appropriate unless recently settled juveniles must be collected. In less dense, shallow-water populations, hand-picking using a glass-bottomed bucket to locate specimens can often suffice. In turbid waters and/or soft sediments (sand or mud), shell rakes may be utilized. Hand-picking and shell rakes can select larger, older individuals. In shallow, turbid water, using hands and fingers to systematically feel for mussels buried in soft sediments can be effective, but selects larger individuals and can lead to cut fingers. On rocky or boulder bottoms, unionoideans generally accumulate in crevices or near downstream bases of large rocks. Here, only hand-picking (in conjunction with scuba techniques in deeper water) is effective. Unionoideans may also be collected by drag or brail dredges. Mussel brails (often used by commercial shellers) consist of a bar with attached lines terminating in blunt-tipped gang hooks. When dragged over unionid beds, mussels clamp the valves onto the hooks allowing them to be brought to the surface.

Quantitative sampling of unionoideans can be accomplished with quadrats, along with scuba in deeper waters (Isom and Gooch, 1986; Miller and Payne, 1988; Waller *et al.,* 1993). Only heavy Ponar and Peterson dredges bite deeply enough into the substrate to take large unionoidean species. In sparse populations, errors in density estimates can result from the small surface areas that these dredges sample, requiring numerous samples to improve accuracy. Drag dredges sample larger areas and may be partially quantitative,

but generally do not provide accurate estimates. A skimmer dredge collected 62.3% of mussels in its path, but resulted in 10% mortality of thin-shelled species (Miller *et al.,* 1989) Unionoideans may also be collected during natural or planned water level drawdowns (White, 1979) by collecting either emersed individuals or those migrating downshore and accumulating at the water's edge.

In a comparative study of sampling, quadrat sampling provided the most accurate analysis of a unionoidean community, but was difficult and expensive to carry out in deeper waters, where systematic sampling by scuba produced the best results (Isom and Gooch, 1986). In a comparison of the accuracy of quadrat and qualitative timed searches for unionoideans, it was found that timed searches overestimated large species, highly sculptured species and those whose shells protruded from the substrate, while underestimating buried, small, smooth-shelled species. In contrast, quadrat sampling tended to underestimate rare species and total number of species unless a large number of quadrats were sampled (Vaughn *et al.,* 1997). Extensive sampling may be required to find rare species, particularly if their population densities need to be assessed; thus, time and funding limitations may prevent accurate assessment of presence/absence and population densities of rare unionoideans (Kovalak *et al.,* 1986; Vaughn *et al.,* 1997). Accurate sampling of rare unionoidean species is required for their effective management and conservation. As many NA unionoidean species are endangered, one should ascertain the status of any species before permanently removing specimens from their natural habitats. Take only dead shells or, if absolutely necessary, a few living specimens for identification.

C. fluminea is easily collected because it occurs in high densities, prefers shallow waters, and is easily identified. Individuals can be separated from sediments with a 1-mm mesh sieve. Qualitative samples are best obtained by shovel or drag dredge (Williams and McMahon, 1986) and quantitative samples by quadrat frame (Miller and Payne, 1988), or Peterson (Aldridge and McMahon, 1978) or Ekman dredges (Williams and McMahon, 1986). In rock or gravel substrates, *C. fluminea* are best taken by hand, hand trowel, or shovel; collected sediments should be passed though a coarse mesh sieve to separate specimens. In fast-flowing streams, specimens of *C. fluminea* accumulate in crevices or behind the downstream sides of large rocks.

D. polymorpha is best collected by scuba with manual removal, using quadrat frames for quantification, because of its byssal attachment to hard surfaces and its preference for deeper waters (<1–2 m). Ripping of individuals from the byssus damages their tissues, thus the byssus should be cut with a knife or sharp trowel before removal. Juveniles can be collected after they have settled on settlement blocks or submerged buoys set out during the reproductive season. Ekman, Ponar, Peterson, and drag dredges are generally not suitable for collection of attached epibenthic species such as *D. polymorpha,* but they can be used for populations on soft or semisoft benthic substrates (Hunter and Baily, 1992).

Juveniles of sphaeriids and *C. fluminea* can be surgically removed from brood sacs or collected from sediments after release with a fine mesh sieve (mesh size <0.35 mm). Juvenile *C. fluminea* can also be obtained by release from freshly collected, gravid adults left in water for 12–24 h (Aldridge and McMahon, 1978). Planktonic *C. fluminea* juveniles and *D. polymorpha* veligers may be taken with a zooplankton net towed behind a boat or held in current flow. Their densities may be assessed by passing known volumes of water through a zooplankton net. Plankton net mesh size for collection of *C. fluminea* juveniles should be <200 μm and $\lesssim$40 μm for all planktonic stages of *D. polymorpha,* including the trochophore. Recently settled juveniles of unionoideans may be sieved from sediments. Glochidia can be surgically removed from demibranchs of gravid females or encysted glochicia taken from the fins, pharyngeal cavity, or gills of their fish hosts (for a list of unionoidean fish hosts, see Watters, 1994b).

B. Preparation for Identification

To preserve bivalves, larger individuals should first be narcotized or relaxed, allowing tissues to be preserved in a lifelike state and preservatives to penetrate tissues through gaped shell valves. Live bivalves placed directly in fixatives clamp the valves, which prevents preservative penetration. There are a number of bivalve relaxing agents (Coney, 1993; Araujo *et al.,* 1995), including alcoholized water (either 3% ethyl alcohol by volume with water or 70% ethyl alcohol added slowly, drop by drop, to the medium until bivalves gape), chloroform added slowly to the medium, methol crystals (one level teaspoon per liter, scattered on the water surface), propylene phenoxetol and phenoxetol BPC (5 mL of product emulsed with 15–20 mL of water, added to water containing bivalves or introduction of a droplet equal to 1% of holding water volume), phenobarbitol added in small amounts to the holding medium, magnesium sulfate (introduced into holding medium over a period of several hours to form a 20–30% solution by weight), magnesium chloride (7.5% solution by weight), and urethane.

None of these agents works equally well with all species. Laboratory tests of narcotizing agents against

C. fluminea revealed propylene phenoxetol to be the only agent capable of relaxing this species for experimental surgery, and allowing recovery on return to fresh medium (Kropf-Gomez and McMahon, unpublished). Heating bivalves to 50°C for 30–60 min causes most species to relax and gape widely, but is lethal. In larger specimens, wooden pegs or portions of matchsticks forced between the valves prior to fixation allows preservative penetration of tissues.

The best long-term preservative for freshwater bivalves is 70% ethyl alcohol (by volume with water). Specimens may be initially fixed in 5–10% formaldehyde solutions (by volume with 40% formaldehyde solutions) for 3–7 days. But formaldehyde is acidic and dissolves the calcareous portion of shells unless pH-neutralized by the addition of powdered calcium carbonate ($CaCO_3$) to make a saturated solution, 5 g of powdered sodium bicarbonate ($NaHCO_3$) per liter, or 1.65 g of potassium dihydrogen orthophosphate and 7.75 g disodium hydrogen orthophosphate per liter (Smith and Kershaw, 1979). After 3–7 days in formaldehyde, specimens should be transferred to 70% ethyl alcohol for permanent preservation. Addition of 1–3% glycerin (by volume) to alcohol preservatives keeps tissues soft and pliable (Smith and Kershaw, 1979). Smaller species (shell length <15 mm) generally do not require relaxation. Tissues to be utilized in microscopy should be preserved in gluteraldehyde or Bouin's solution.

Shells can be cleaned with a mild soap solution and soft brush. Organic material can be digested from shell surfaces by immersion in a dilute (3% by weight with water) solution of sodium or potassium hydroxide at 70–80°C, thereafter, removing remaining organic matter with a soft brush. For dry-keeping, the shell periostracal surface should be varnished or covered with petroleum jelly to prevent drying, cracking, and/or peeling. Numbers identifying collection and specimen can be marked on the inner shell surface with India ink.

In order to remove soft parts from living bivalves, immerse them in water at >60°C and remove tissues after valves fully gape. Separated flesh can be fixed in 70% alcohol. For fragile sphaeriids, flesh is best removed with the tip of a fine needle, manipulating specimens with a fine brush. Shells should be dried in air at room temperature, not in an oven; heat causes shells to crack and their periostracum to crack and peel.

Both soft tissue and shell characteristics are utilized in the identification of freshwater bivalves, so both must be preserved for species identification. For unionoideans, *C. fluminea,* and *D. polymorpha,* most diagnostic taxonomic characteristics can be seen by eye or with a 10 × hand lens. For sphaeriids, a dissecting microscope with at least 10–30 × power or a compound microscope is required (Ellis, 1978). Anatomical details are best observed on dry shells or soft tissues immersed in water.

Identification of recently released juvenile bivalves is difficult and may require preparation of stained slide whole mounts. Glochidia are best identified by removal from a gravid adult of an identified species as are juvenile sphaeriids. Only the juveniles of *C. fluminea* and larval stages of *D. polymorpha* are routinely found in the plankton. The juvenile of *C. fluminea* (Fig. 15A) is easily recognizable, and can be readily separated from the pediveliger of *D. polymorpha* by the presence of a fully formed foot, lack of a velum and a D-shaped shell while the foot is formed only in the pediveliger stage of *D. polymorpha* which has an umbonal shell (Nichols and Black, 1994). The planktonic veliger of *D. polymorpha* is clearly distinguishable by its ciliated velum, lack of a foot and D-shaped shell (Nichols and Black, 1994; Fig. 15C). The glochidia of many unionoidean species have specific fish species hosts (Watters, 1994b), whose identification will assist glochidial identification. Identification of glochidia without knowledge of the host fish or species of origin is extremely difficult, characters such as presence/absence of attachment hooks or threads and glochidial size may allow assignment to a family or subfamily, but may be unreliable even at these higher taxonomic levels (Bauer, 1994).

C. Rearing Freshwater Bivalves

For artificial rearing of freshwater bivalves, water in holding tanks should be temperature-regulated. Adequate aeration, filtration, and ammonia removal systems are required, as some species have low hypoxia and ammonia tolerances (Byrne *et al.* 1991a, 1991b).

As unionoideans and *C. fluminea* are filter phytoplankton, they require a constant supply of filterable food to remain healthy and growing. The best artificial food appears to be algal cultures. When fed monoalgal cultures of the green algae, *Ankistrodesmus* and *Chlorella vulgaris* or the cyanobacteruim, *Anabaena oscillariodes,* assimilation efficiencies in *C. fluminea* were 47–57% and net growth efficiencies, 59–78%, making them excellent food sources for this species (Lauritsen, 1986a).

Artificial diets do not appear to be as successful as algal cultures in maintaining *C. fluminea* growth. When fed either ground nine-grain cereal, rice flour, rye, bran, brewers' yeast, or artificial trout food, small *C. fluminea* (5–8 mm SL) starved on all but nine-grain cereal, the latter supporting little tissue growth. Supplementing these grain diets with live green algae (*Ankistrodesmus* sp.) greatly enhanced tissue growth, but the greatest growth occurred on pure *Ankistrodesmus* cultures (Foe

and Knight, 1986b). *C. fluminea* fed mixed cultures of the green algae *Pedinomonas* sp., *Ankistrodesmus* sp., *Chlamydomonas* sp., *Chorella* sp., *Scenedesmus* sp., and *Selenastrum* sp. had maximal growth when mixtures did not include *Selenastrum,* which was toxic to this species. Greatest tissue growth occurred in clams fed mixed cultures of all five remaining algal species. Growth declined with number of algal species in feeding cultures; feeding with two algal species resulting in starvation (Foe and Knight, 1986b). Thus, artificial bivalve culture appears to be best supported on mixed algal diets, but certain toxic algal species must be avoided.

Temperature also affects bivalve growth rate. When 5–8 mm SL specimens of *C. fluminea* were fed mixed algal cultures of *Chamydomonas, Chlorella,* and *Ankistrodesmus* at 10^5 cells/mL, assimilation efficiencies were maximal at 16 and 20°C (48–51%). Tissue growth was maximal at 18–20°C and became negative (tissue loss) at ≥30°C (Foe and Knight, 1986a), suggesting 18–20°C to be an ideal culture temperature for this species and, perhaps, other NA bivalves. In algae-fed cultures of *D. polymorpha,* growth was maximal at 15°C and suppressed at 20°C (Walz, 1978b). However, tissue growth in a natural population of *C. fluminea* increased up to 30°C (McMahon and Williams, 1986a), indicating that artificial culture systems are not equivalent to field conditions in supporting bivalve growth. In this regard, excellent tissue growth in *C. fluminea* was supported by algal cultures produced by several days' exposure to sunlight of water taken from the natural habitat of the clam to increase its algal concentration (Foe and Knight, 1985). Thus, ideal culture conditions for unionoideans and *C. fluminea* would appear to be a 20°C holding temperature and feeding with natural algal assemblages whose growth has been promoted with inorganic nutrients and exposure to sunlight; maximal growth being achieved in *D. polymorpha* under the same conditions at 15°C.

Specimens of *C. fluminea, D. polymorpha* and unionoideans may be held for long periods in the laboratory without feeding. *C. fluminea* survived 154 days of starvation at room temperature (22–24°C) while sustaining tissue weight losses ranging from 41 to 71% (Cleland *et al.,* 1986). Similarly, I have held unionoideans in the laboratory for many months without feeding. Samples of *D. polymorpha* experienced 100% mortality after being held in the laboratory without feeding for 166, 514, and 945 days at 25, 15, and 5°C, respectively (Chase-Off and McMahon, unpublished data). Thus, maintenance at low temperature (<10°C) greatly prolongs the time bivalves may be held in good condition without feeding.

C. fluminea has never been reared successfully to maturity or carried through a reproductive cycle in artificial culture, although field-collected, nongravid adults released juveniles after four months in laboratory culture (King *et al.,* 1986). The glochidium stage makes unionoideans difficult to rear in the laboratory as it requires encystment in a fish host for successful juvenile metamorphosis, but it can be accomplished (Young and Williams, 1984a). Application of an immunosuppressant agent has allowed glochidial transformation to juveniles on nonhost fish where they would otherwise be rejected by the immune system of the host fish (Kirk and Layzer, 1997). Glochidia of several unionoidean species have been transformed into juveniles *in vitro* in a culture medium containing physiologic salts, amino acids, glucose, vitamins, antibiotics, and host fish plasma (Isom and Hudson, 1982). Juvenile *utterbackia imbecillis* and *Epioblasma triquetra* have been successfully cultured in a medium of river water exposed to sunlight for 1–4 days to enhance algal concentration. Addition of silt enhanced juvenile growth in both species, while feeding artificial, mixed cultures of three algal species resulted in starvation (Hudson and Isom, 1984), an observation supported by recent studies suggesting that juvenile unionoideans feed primarily on interstitial water drawn from sediments through the pedal gape, such that silt and associated microdetritus and bacteria may be their main ingested food source (Yeager *et al.,* 1994).

Many sphaeriid species can be easily maintained in simple artificial culture systems. Ease of artificial culture in this group may relate to their feeding on sediment organic detritus (Burky *et al.,* 1985b; Hornbach *et al.,* 1984b) and interstitial bacteria (Lopez and Holopainen, 1987), making use of algal cultures as a food source unnecessary. Hornbach and Childers (1987) maintained *Musculium partumeium* through successful reproduction in beakers with 325 mL of filtered river water, without sediments, on a diet of 0.1 mg of finely ground Tetra Min© fish food/clam per day. The first generation in this simple culture system survived 380–500 days, a life span equivalent to the natural population (Hornbach *et al.,* 1980). Similarly, Rooke and Mackie (1984c) maintained 20 adult *Pisidium casertanum* in a 6-L aquaria with sediments for 35 weeks without feeding, suggesting that individuals fed on sediment bacteria or organic deposits.

Live molluscs rapidly remove dissolved calcium from culture media (Rooke and Mackie, 1984c), thus calcium levels in holding media should be augmented by the addition of $CaCO_3$. The ease with which sphaeriids can be artificially cultured makes them ideal for laboratory microcosm experiments. Ideal culture conditions appear to include provision of natural sediments, a source of calcium (i.e., ground $CaCO_3$), and finely ground food of reasonable protein content, such as aquarium fish food or brewers' yeast, which may be directly assimilated by clams or support the

growth of interstitial bacteria upon which they feed (Lopez and Holopainen, 1987).

V. IDENTIFICATION OF THE FRESHWATER BIVALVES OF NORTH AMERICA

A. Taxonomic Key to the Superfamilies of Freshwater Bivalvia

There are five bivalve superfamilies with freshwater representatives in North America. Of these the Unionoidea, Corbiculoidea, and Dreissenoidea contain the true freshwater species and comprise the vast majority of freshwater bivalve fauna. The remaining two superfamilies, Cyrenoidea and Mactroidea, each contain one brackish water species that can extend into freshwater coastal drainages and so are included here. In North America, the Dreissenacea is represented by two introduced freshwater species and an estuarine species. The Corbiculoidea includes 36 native and five introduced species in six genera; the Unionoidea are composed of 278 native species and 13 subspecies in 49 genera (Turgeon *et al.*, 1998). Separate taxonomic keys are provided here for the latter two supperfamilies.

1a. Shell hinge ligament is external 2

1b. Shell hinge ligament is internal 4

2a(1a). Shell with lateral teeth extending anterior and posterior of true cardinal teeth (Fig. 1), shells of adults generally small (<25 mm in shell length, shell thin and fragile; exceptions are the genera *Polymesoda* and *Corbicula*) ..... superfamily Corbiculoidea [See Section V.B.]

2b. Shell without lateral teeth extending anterior and posterior of cardinal teeth 3

3a(2b). Shell hinge with two cardinal teeth and without lateral teeth; shell thin and fragile, 12–15 mm long with small umbos; *Cyrenoida floridana* (Dall) (extends from brackish into coastal freshwater drainages in Florida) ..... superfamily Cyrenoidea

3b. Shell without true cardinal teeth, when present, lateral teeth only occur posterior to usually well-developed pseudocardinal teeth (Fig. 1), pseudocardial teeth absent or vestigial in some species; Shells of adults are generally large (>25 mm in shell length) ..... superfamily Unionoidea [See Section V.C.]

4a(1b). Hinge with anterior and posterior latoral teeth on either side of cardinals; Shell massive, adults 25–60 mm shell length, obliquely ovate; *Rangia cuneata* (Gray) (extends from brackish into coastal freshwater drainages from Delaware to Florida to Veracruz, Mexico) ..... superfamily Mactroidea

4b. Hinge without teeth; shell mytiloid in shape, anterior end reduced and pointed, hinge at anterior end, posterior portion of shell expanded, anterior adductor muscle attached to internal apical shell septum, attached to hard substrates by byssal threads ..... superfamily Dreissenoidea 5

5a(4b). Periostracum bluish brown to tan without a series of dorsoventrally oriented black zigzag markings, anterior end hooked sharply ventrally, ventral shell margins not distinctly flattened over entire ventral side of valves; restricted to brackish water habitats. *Mytilopsis leucophaeata* (Conrad) (extends into coastal freshwater drainages from New York to Florida to Texas and Mexico) ..... *Mytilopsis*

5b. Periostracum light tan and often marked with a distinct series of black vertical zigzag markings; anterior portion of shell not ventrally hooked, ventral shell margins can be flattened, restricted to freshwaters, *Dreissena polymorpha* (Pallas) (Fig. 24); (a European species introduced into the Great Lakes in Lake St. Clair and present by December 2000 throughout the Great Lakes, the St. Lawrence River and the Mississippi Drainage. and Dreissona bugensis Andrusov now in lakes Erie and Ontario, the Erie-Barge Canal and the St. Lawrence River ..... *Dreissena*

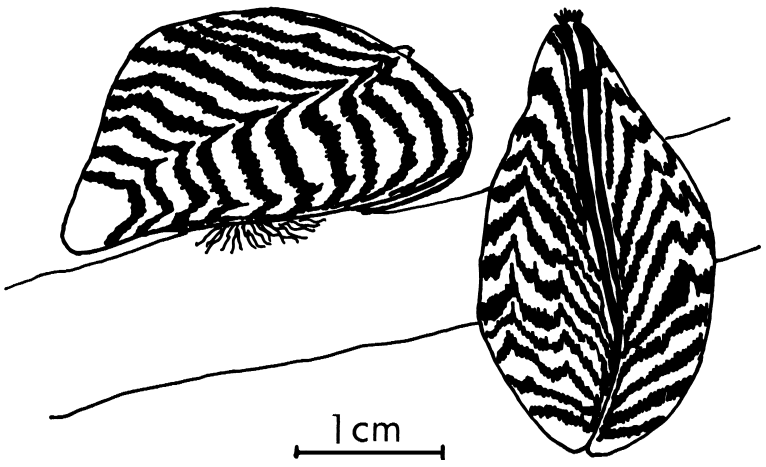


FIGURE 24 The external morphology of the shell of the zebra mussel, *Dreissena polymorpha*.

B. Taxonomic Key to the Genera of Freshwater Corbiculacea

This key is based on the excellent species key for North American freshwater Corbiculoidea by Burch (1975a) with additional material from Clarke (1973) for the Canadian Interior Basin, and Mackie *et. al.* (1980) for the Great Lakes. The Corbiculoidea have ovate, subovate, or trigonal shells with lateral hinge teeth anterior and posterior to the cardinal teeth. All North American species expect *Corbicula fluminea* are in the family Sphaeriidae. The family designation Pisidiidae has also been commonly applied to this group, but the International Commission of Zoological Nomenclature (ICZN) placed the Sphearriidae (Name number 573) on the Offical List of Family Names (Opinion 1331) in 1985; hence, Sphaeriidae is used as the family designation in this key and the rest of the chapter. In North America, the Sphaeriidae comprise the dominant bivalve fauna in small, often ephemeral ponds, lakes, and streams, the profundal portions of lakes and in silty substrates. Identification is generally based on shell morphology, but requires, in some cases, soft tissue morphology.

1a. Shells large (maximum adult shell length >25 mm), thick, lateral teeth serrated .....family Corbiculida 2

1b. Shells generally small (maximum shell length <25 mm), thin, lateral teeth smooth.....family Sphaeriidae 4

2a(1a). Maximum adult shell length generally <50 mm, shell ornamented by distinct, concentric sulcations, anterior and posterior lateral teeth with many fine serrations, simultaneous hermaphrodites, massive numbers of small (length <0.3 mm) developmental stages (>1000) incubated directly in inner demibranchs, released juveniles (<5 mm SL) anchor to substratum with a single mucilaginous byssal thread (Fig. 25).....*Corbicula* 3

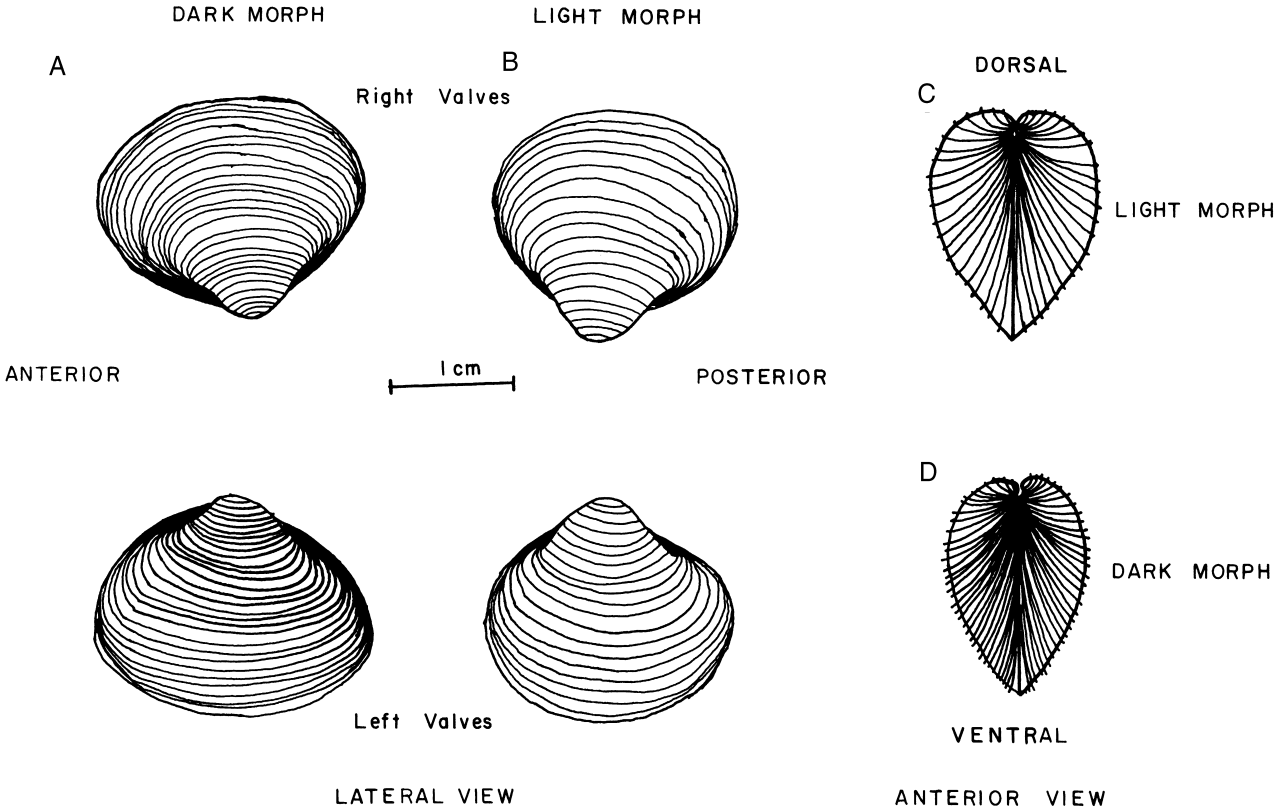


FIGURE 25 External morphology of the shell valves of the light-colored shell morph (*Corbicula fluminea*) and dark-colored shell morph (*Corbicula* sp.) of the North American *Corbicula* species complex. (A) Right and left valves of *Corbicula* sp. (dark-colored morph). (B) Right and left valves of *C. fluminea* (light-colored morph). (C) Anterior view of the shell valves of *C. fluminea* (light-colored morph). (D) Anterior view of the shell valves of *Corbicula* sp. (dark-colored morph). Note the distinguishing shell characteristics of these two species. *C. fluminea*, the light-colored morph, which is widely distributed in North America (Fig. 11), has a more nearly trigonal shell, taller umbos, a greater relative shell width and more widely spaced concentric sulcations than does *Corbicula* sp., the dark-colored morph, that is limited to spring-fed, alkaline, lotic habitats in the southwestern United States (Fig. 11). The dark-colored shell morph also has a dark olive green-to-black periostracum and deep royal blue nacre, while the light-colored shell morph has a yellow green-to-light brown periostracum and white-to-light blue or light purple nacre.

2b. Maximum adult shell length generally >50 mm, shell ornamentation of many fine, closely spaced concentric striations, embryos not incubated in demibranchs, dioecious, periostracum deep brown in color, three cardinal teeth, estuarine, restricted to brackish waters in the tidal portions of rivers. *Polymesoda caroliniana* (Bosc) (Virginia to northern Florida to Texas).....*Polymesoda*

3a(2a). Shell nacre white with light blue, rose, or purple highlights, particularly at shell margin, muscle scars of same color intensity as rest of nacre, periostracum yellow to yellow-green or brown with outer margins always yellow or yellow-green in healthy, growing specimens, shell trigonal to ovate, umbos inflated and distinctly raised above dorsal shell margin, shell length : shell height ratio ≈1.06, shell length : shell width ratio ≈1.47, shell height : shell width ratio ≈ 1.38, concentric shell sulcations widely spaced, 1.5 sulcations/mm shell height (Hillis and Patton, 1982); introduced in the early 1900s, it has spread throughout drainage systems of the United States and coastal northern Mexico (Fig. 11), the "light-colored shell morph" of *Corbicula* or Asian clam (Fig. 25B, C).*Corbicula fluminea* (Müller)

3b. Shell nacre uniformly royal blue to deep purple over entire internal surface, muscle scars more darkly pigmented than rest of nacre, periostracum dark olive green to black, edges of valves in healthy, growing specimens not yellow or yellow-green, shell more ovate and laterally compressed with umbos less inflated and less distinctly raised above the dorsal shell margin than in *C. fluminea*, shell length : height ratio ≈1.15, shell length : width ratio ≈ 1.65, shell height : width ratio ≈ 1.43, concentric shell sulcations narrowly spaced, particularly at umbos, 2.1 sulcations/mm shell height (Hillis and Patton, 1982); introduced, distribution limited to highly oligotrophic, permanent, spring-fed, calcium carbonate-rich streams in the southwestern United States (Britton and Morton, 1986); (Fig. 11). Called the dark-colored shell morph of *Corbicula*, its taxonomic status is uncertain, electrophoretic (Hills and Patton, 1982; McLeod, 1986) and physiological evidence (Cleland *et al.*, 1986) suggest it to be distinct from *C. fluminea* (Fig. 25A, D) .....*Corbicula* sp.

4a(1b). Both inhalant and exhalant mantle cavity siphons present and well developed, umbos lie anterior of center.....5

4b. Only exhalant mantle cavity siphon present, inhalant siphon either absent or formed as a slit in the posterior-ventral mantle edges, umbos posterior of center, generally small, shell length 0.5–12 mm, embryos in inner demibranch held in thick-walled sacs, each with individual chambers for embryos, no byssal gland, 24 species widely distributed in North Amercia; for species identifications and distributions see Burch (1975a) (Fig. 26A).....subfamily Pisidiinae *Pisidium*

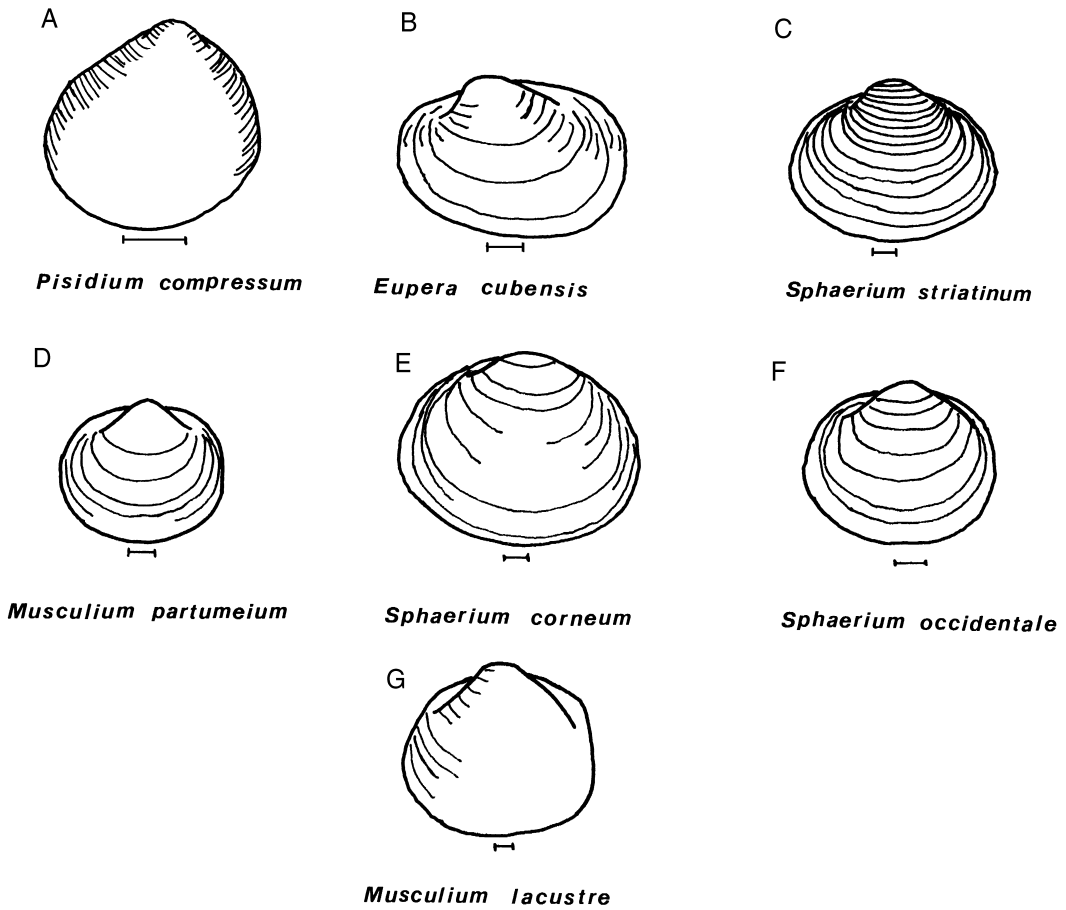


FIGURE 26 Diagrams of the external morphology of the left shell valve of species representative of the North American genera of the freshwater bivalve family, Sphaeriidae. Size scaling bar is 1-mm long.

5a(4a). Inhalant and exhalant mantle cavity siphons partially fused, embryos incubated in inner demibranchs in thin-walled longitudinal pouches, no byssal gland, shell with two cardinal teeth in each valve, without external mottling.....subfamily Sphaeriinae 6

5b. Inhalant and exhalant siphons not fused, embryos develop in individual chambers formed between inner and outer lamellae of inner demibranchs, functional byssal gland present, only one cardinal tooth in each shell valve, with external, mottled pigmentation, *Eupera cubensis* (Prime) (Atlantic coastal plain drainages from southern Texas to North Carolina, Caribbean Islands) (Fig. 26B) ....subfamily Euperinae *Eupera*

6a(5a). Shell sculptured with relatively coarse or widely spaced striae (≤8 striae/mm in middle of shell), shell relatively massive and strong, *Sphaerium simile* (Say) (Southern Canada from New Brunswick to British Columbia, south from Virginia to Wyoming, *S. striatinum* (Lamarck) (Canada from New Brunswick to the upper Yukon River, throughout the United States, Mexico, and Central America), *S. fabale* (Prime) (Southern Ontario to Georgia and Alabama) (Fig. 26C) .....*Sphaerium*

6b. Shell relatively thin, often fragile, with many fine, narrowly spaced striae (≥12 striae/mm in middle of shell) 7

7a(6b). Shell of adults <8 mm in length 8

7b. Shell of adults >8 mm in length 9

8a(7a). Posterior valve margin at near right angle to dorsal margin, shells roughly rhomboidal, umbos large and distinctly elevated above dorsal shell margin, *Musculium partumeium* (Say) (United States and southern Canada), *M. transversum* (Say) (Canada and the United States east of the continental divide, extending into Mexico), *M. securis* (Prime) (Nova Scotia to British Columbia southwestern Northwest Territories in Canada, United States except for southwest) (Fig. 26D).....*Musculium*

8b. Posterior and dorsal margins rounded or forming an obtuse angle, shells ovate, *Sphaerium corneum* (Linnaeus) (introduced from Europe, localities in southern Ontario and Lakes Champlain and Erie), *S. nitidum* Westerlund (distribution is holarctic, northern Canada to northern United States), *S. occidentale* (Prime) (Canada from New Brunswick to southeastern Manitoba, northern United States south to Florida, west to Utah and Colorado) (Fig. 26 E, F).....*Sphaerium*

9a(7b). Umbos large, distinctly elevated above the dorsal shell margin.....10.

9b. Umbos small, indistinctly elevated above the dorsal shell margin, *Sphaerium corneum* (Linnaeus), (introduced, localities in Ontario, Lakes Champlain and Erie) (Fig. 26E) .....*Sphaerium*

10a(9a). Shell rounded, umbos not prominent, *Sphaerium occidentale* (Prime) (New Brunswick to southeastern Manitoba, northern United States south to Florida in the east and Utah and Colorado in the west) (Fig. 26F) .....*Sphaerium*

10b. Posterior end of shell truncate, shell rhomboidal, umbos prominent, *Musculium lacustre* (Müller) (From treeline in Canada south throughout all but southwestern United States into central America) (Fig. 26G).....*Musculium*

C. Taxonomic Key to the Genera of Freshwater Unionoidea

The Unionoidea make up the large bivalve fauna (shell length >25mm) of permanent freshwater lakes, rivers, and ponds. North America has the richest and most diverse unionoidean fauna in the world, including 278 species and 13 recognized subspecies in 49 genera in the Unionidae and five species in two genera in the Margaritiferidae. The taxonomy used here follows Turgeon *et al.* (1998) with the addition of Johnson (1998), and Williams and Fradkin (1999). Unionoidean taxonomy remains very uncertain because intraspecific and interpopulation variation often makes identification and systematics difficult. Unionoidean bivalve shells lack true cardinal teeth and, when present, lateral teeth occur only posterior to pseudocardinal teeth (Fig. 1). Figure 27 displays shell-shape outlines and external shell ornamentations referred to in these taxonomic keys.

The key in the first edition of this chapter, as well as many of the major keys to freshwater bivalves (Walker, 1918; Clench, 1959; Burch, 1975b; Clarke, 1973), relied on the integrated use of important anatomical structures and shell characters to identify unionoidean bivalves. However, most field biologists do not have the luxury of having a fully gravid female in hand for identification, but more likely, a dead shell or valve. Several colleagues have commented that one can only use a key containing anatomical characters to key out a shell when you already know what the animal is. Several state keys (e.g., Parmalee, 1967; Watters, 1995; Oesch, 1984; Strayer and Jirka, 1997) have provided keys to shells of species occurring within the political boundaries of a particular state. North America is considered to consist of those river systems and lakes north of, and including, the Rio Grande Basin and the rest of the boundary with Mexico. This key is artificial and the key is divided into four sections corresponding to geographical provinces to facilitate identification. The four sections are: Gulf Coast, including Florida; Mississippi River Basin, including the Interior Basin of Canada; the area west of the Rocky Mountain divide; and the Atlantic Coast. These subdivisions are a simplification of the 12 faunal provinces recognized by Parmalee and Bogan (1998). Table VII lists

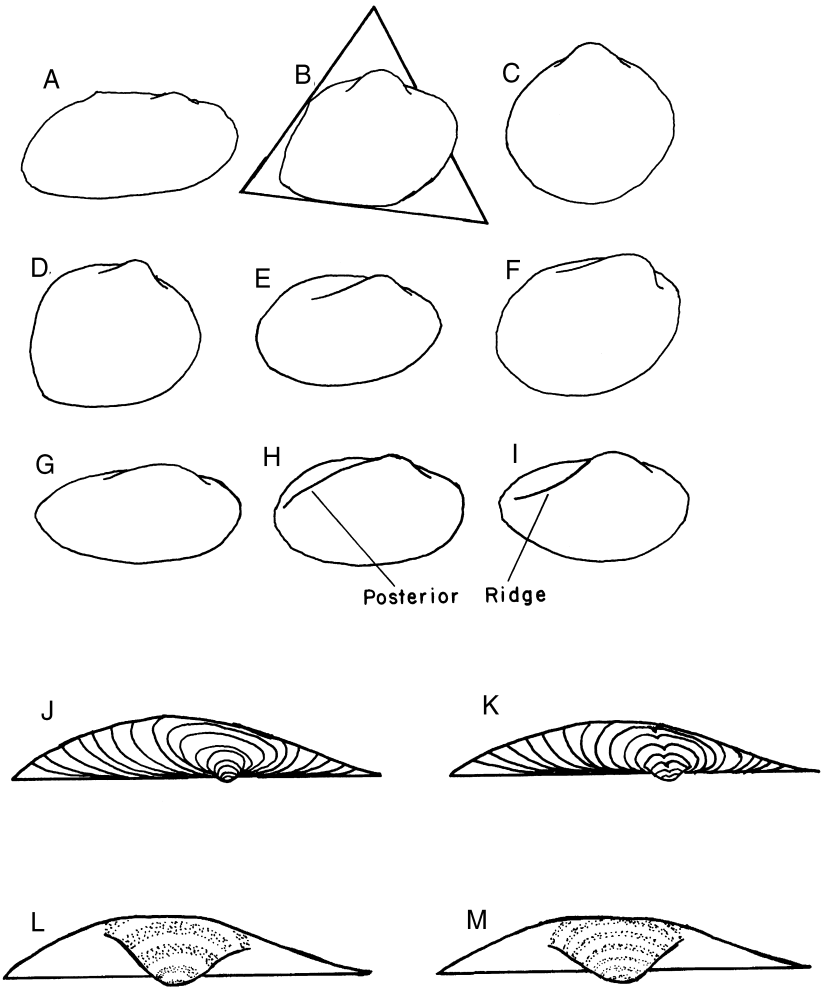


FIGURE 27 Illustrations of the diagnostic shell features or characters used for taxonomic identification in Section V.C. Shell-shape descriptions: (A) rhomboidal; (B) triangular or trigonal; (C) round; (D) quadrate; (E and F) oval or ovoid; and (G) elliptical. Posterior shell-ridge morphology: (H) posterior ridge convex; and (I) posterior ridge concave. Concentric ridge structures of umbos: (J) single-looped concentric ridges; (K) double-looped concentric ridges; (L); coarse concentric ridges; and (M) fine concentric ridges. (Redrawn from Burch, 1975b.)

the genera found in each of these four sections. This geographical approach allows a biologist to focus only on those genera actually occurring in their region and ignores the rest of the diversity (*e.g.*, west of the Rocky Mountains has only three genera: one Margaritiferidae and two Unionidae). We have attempted to provide a logical and clear key to the unionoidean genera of North America based solely on shell characters. The valve or pair of valves to be identified is assumed for the purposes of this key to be adults. Identification of very small juvenile shells and small adult specimens can be difficult. Landmarks, structures and shell shape are based on complete shells. We have attempted to use obvious characters, but many of them require familiarity with unionoidean shell morphology and the range of variation in each of these characters. Strayer and Jirka (1997; p. 28) stated the problem most clearly when they said, "Keys based on shell characters are inevitably filled with vague, subjective terms, are frustrating for beginners to use, and misidentify many shells." They have finally put into print what most malacologists have said: "**Users should know that if they rely solely on this key, they will misidentify many shells.**" (Strayer and Jirka, 1997; p. 28). There is no substitute for comparing the specimen to be identified with other identified specimens in a museum collection or specimens that have had their identification verified by a specialist. This key is an introduction to the genera of North American unionoideans. Each couplet which contains a genus, also lists some of the species in that genus which should key out to that cou-

TABLE VII List of Unionoidean Genera by Geographic Area Used in the Key

	Pacific coast	*Atlantic coast*	*Gulf coast*	*Interior basin*
Margaritiferidae	*Margaritifera*	*Margaritifera*	*Margaritifera*	
				Cumberlandia
Unionidae				*Actinonaias*
		Alasmidonta	*Alasmidonta*	*Alasmidonta*
			Amblema	*Amblema*
	Anodonta	*Anodonta*	*Anodonta*	*Anodonta*
		Anodontoides	*Anodontoides*	*Anodontoides*
			Arcidens	*Arcidens*
				Arkansia
				Cyclonaias
				Cyprogenia
			Cyrtonaias	
			Disconaias	
				Dromus
			Ellipsaria	*Ellipsaria*
		Elliptio	*Elliptio*	*Elliptio*
			Elliptoideus	
			Epioblasma	*Epioblasma*
		Fusconaia	*Fusconaia*	*Fusconaia*
			Glebula	
	Gonidea			
				Hemistena
		Lampsilis	*Lampsilis*	*Lampsilis*
		Lasmigona	*Lasmigona*	*Lasmigona*
				Lemiox
		Leptodea	*Leptodea*	*Leptodea*
		Lexingtonia		*Lexingtonia*
		Ligumia	*Ligumia*	*Ligumia*
			Medionidus	*Medionidus*
			Megalonaias	*Megalonaias*
			Obliquaria	*Obliquaria*
			Obovaria	*Obovaria*
				Pegias
			Plectomerus	*Plectomerus*
				Plethobasus
		Pleurobema	*Pleurobema*	*Pleurobema*
			Popenaias	
			Potamilus	*Potamilus*
			Ptychobranchus	*Ptychobranchus*
		Pyganodon	*Pyganodon*	*Pyganodon*
			Quadrula	*Quadrula*
			Quincuncina	*Simpsonaias*
		Strophitus	*Strophitus*	*Strophitus*
		Toxolasma	*Toxolasma*	*Toxolasma*
			Tritogonia	*Tritogonia*
			Truncilla	*Truncilla*
		Uniomerus	*Uniomerus*	*Uniomerus*
		Utterbackia	*Utterbackia*	*Utterbackia*
				Venustaconcha
		Villosa	*Villosa*	*Villosa*
Total	3	18	37	43

plet. This list of species is not complete, but is representative of the species in the genus with the listed set of characters. Two genera are a source of much confusion, *Elliptio* and *Pleurobema*. The South Atlantic Slope *Elliptio* species complex has yet to be worked out. Johnson (1970) lumped a considerable number of taxa, which may, in fact, be valid species. The Gulf Coast *Pleurobema* species complex is the other major area of confusion. There are a large number of named taxa, but it is not clear at the present time which is a valid species and which is part of a cline. This group is still in need of further work. We would recommend that, to identify

specimens to the species level, the user move to a key for the state or province in which he/she is working. These volumes will give detailed descriptions, keys and figures of the species occurring in your local area (e.g., Florida: Clench and Turner, 1956; Johnson, 1972; Tennessee: Parmalee and Bogan, 1998; Louisiana: Vidrine, 1993; New York: Strayer and Jirka, 1997; Illinois: Parmalee, 1967; Missouri: Oesch, 1984; and Ohio: Watters, 1995). A detailed list by state of freshwater bivalve literature can be found in Williams *et al.* (1993).

1a. Origin of shell is from west of the Rocky Mountains 4

1b. Shell is not from this area 2

2a. (1b) Origin of shell is from the Atlantic Coast of North America 6

2b. Shell is not from this area 3

3a. (2b) Origin of shell is from the Mississippi River Basin....26

3b. Origin of shell is from the Gulf Coast of North America....89

West of the Rocky Mountains

4a. (1a) Shell has lateral muscle scars [small pits for the attachment of mantle muscles to the shell], typically dark periostracum, relatively thick shell with pseudocardinal and lateral teeth ....*Margaritifera falcata* (Fig. 11.28B)

4b. Shell lacks lateral muscle scars, periostracum typically not dark and hinge teeth reduced or absent 5

5a. (4b) Shell has a very strongly developed posterior ridge, reduced hinge teeth, occurs from British Columbia to central California, east to Nevada and Idaho ....*Gonidea angulata* (Fig. 28U)

5b. Shell lacks the sharp posterior ridge, lacks any evidence of hinge teeth ....*Anodonta* [in part] [*A. beringiana, A. californiensis, A. dejecta, A. kennerlyi, A. nuttalliana, A. oregonensis*] (Fig. 28F)

Atlantic Coast

6a. (2a) Shell has lateral muscle scars, typically dark periostracum, relatively thick shell with pseudocardinal teeth and lateral teeth ....*Margaritifera margaritifera* (Fig. 28B)

6b. Shell lacks lateral muscle scars, periostracum may not be dark, hinge teeth present or absent 7

7a. (6b) Shell with hinge teeth absent or greatly reduced 8

7b. Shell with pseudocardinal teeth present, with or without lateral teeth 12

8a. (7a) Umbo not projecting above the hinge-line ....*Utterbackia* [in part] [*U. imbecillis*] (Fig. 28AW)

8b. Umbo projecting above the hinge-line 9

9a. (8b) Beak sculpture double looped (Fig. 27), shell uniformly thin....*Pyganodon* [in part] [*P. cataracta*] (Fig. 28AN)

9b. Beak sculpture consists of concentric bars 10

10a. (9b) Nacre usually orange in the beak cavity, pseudocardinal tooth area represented by a thickening near the umbo, ventral shell margin uniform thickness ....*Strophitus* [in part] [*S. undulatus*] (Fig. 28AR)

10b. Nacre bluish or white, hinge plate uniformly thin, teeth or swellings absent, ...11

11a. (10b) Ventral margin with a prominent thickened area along the anterior ventral magin below the pallial line, *Anodonta* [in part] [*A. implicata*] (Fig. 28F)

11b. Ventral margin not as above, shell elongate, Anodontoides [in part] [A. ferussacianus, restricted to the Susquehanna and Hudson River basins] (Fig. 28G)

12a. (7b). Shell with lateral teeth absent or reduced, neither functional nor interlocking ....*Alasmidonta* [in part] [*A. varicosa*, *A. marginata susquehannae*, *A. undulata*] (Fig. 28D)

12b. Shell truncated, with well-developed lateral teeth 13

13a. (12b) Right valve with two lateral teeth, small, rare ....*Alasmidonta* [in part] [*A. heterodon*] (Fig. 28D)

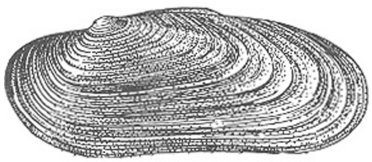
13b. Right valve with one lateral tooth 14

14a. (13b) Shell with spines on the umbo and down on to the disk of the shell 15

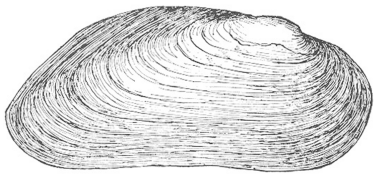
14b. Shell lacks any evidence of spines 16

15a. (14a) Shell thick and may be large ....*Elliptio* [in part] [shell from the Altamaha River Basin, Georgia, *Elliptio spinosa,* or the Tar/Neuse River Basin, North Carolina *Elliptio steinstansana*] (Fig. 28P)

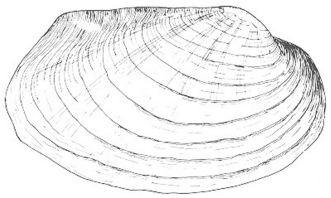
15b. Shell small and from the James River Basin, Virginia ....*Pleurobema collina* (Fig. 28AJ)



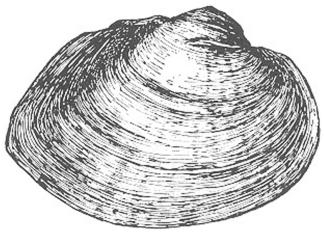
A. Cumberlandia monodonta



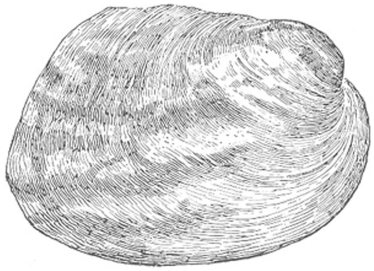
B. Margaritifera margaritifera



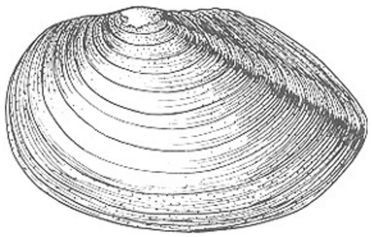
C. Actinonaias ligamentina



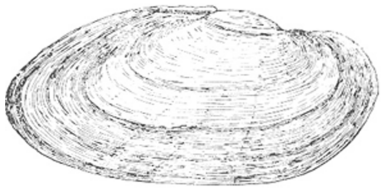
D. Alasmidonta undulata



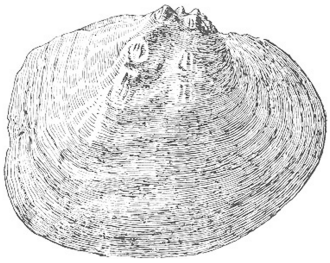
E. Amblema plicata



F. Anodonta sp.

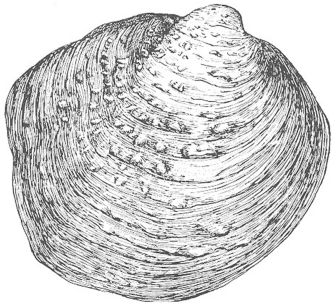


G. Anodontoides ferussacianus

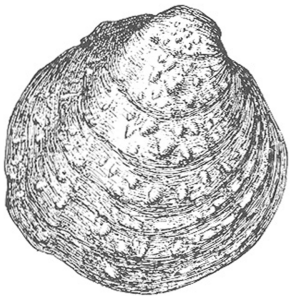


H. Arcidens confragosa

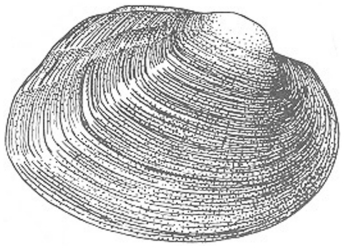
I. Arkansia wheeleri



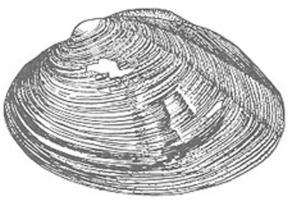
J. Cyclonaias tuberculata



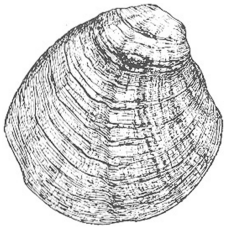
K. Cyprogenia stegaria



L. Cyrtonaias tampicoensis

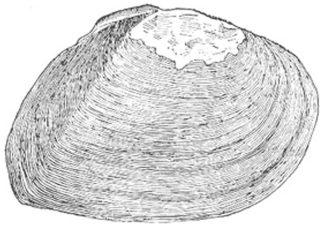


M. Disconaias discus

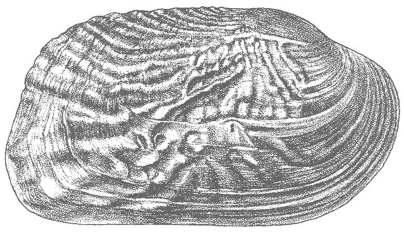


N. Dromus dromas

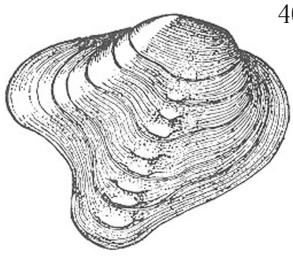
O. Ellipsaria lineolata



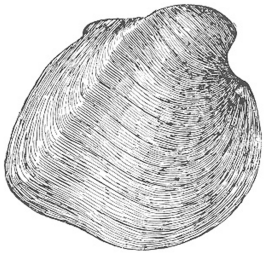
P. *Elliptio crassidens*



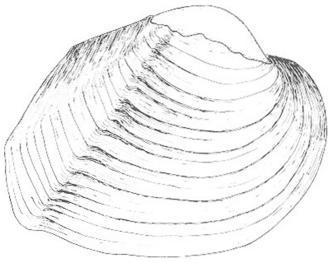
Q. *Elliptoideus sloatianus*



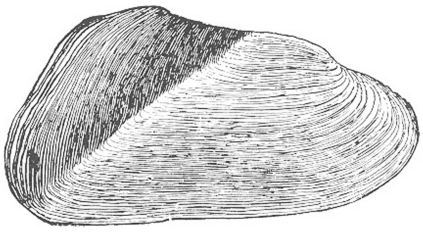
R. *Epioblasma flexuosa*



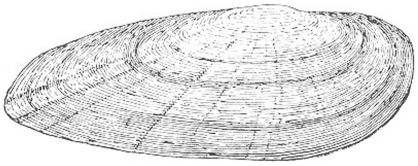
S. *Fusconaia flava*



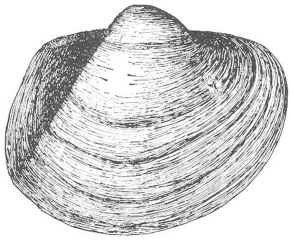
T. *Glebula rotundata*



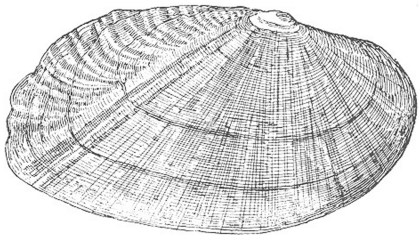
U. *Gonidea angulata*



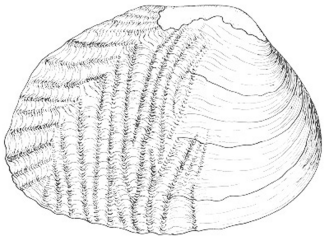
V. *Hemistena lata*



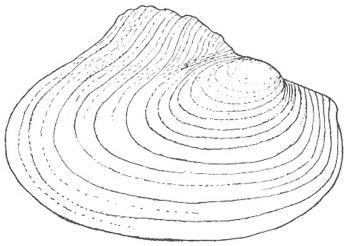
W. *Lampsilis ovata*



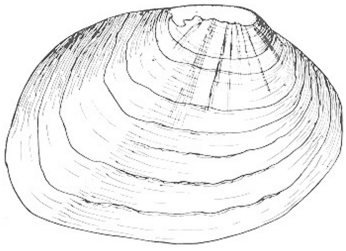
X. *Lasmigona costata*



Y. *Lemiox rimosus*



Z. *Leptodea fragilis*



AA. *Lexingtonia dolabelloides*

FIGURE 28 Diagrams of the external morphology mostly of right valves of the shell of species representative of the North American genera of the freshwater bivalve superfamily, Unionoidea (Figs. 28A–AY). Figures B–E, G–K, N, P, R–AC, AE–AG, AI, AJ, AL–AQ, AR–AU, reprinted with permission of Mrs. W.T. Edmondson from W.T. Edmondson (1959); Figures Q, AW, reprinted with permission of J.B. Burch from Burch (1973); Figures A, F, L, M, AD, AH, AK, AX, AY, reprinted with permission from the *Treatise on Invertebrate Paleontology*, courtesy of The Geological Society of America and the University of Kansas, © 1969.

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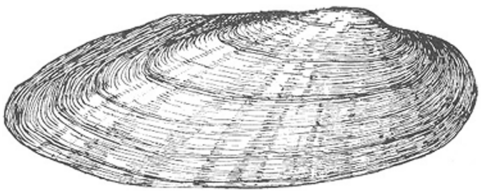
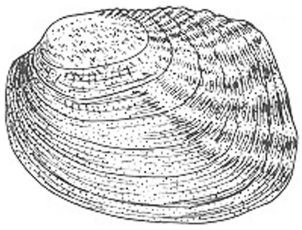


AB. *Ligumia recta*

AC. *Medionidus conradicus*

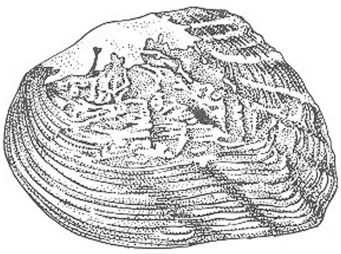


AD. *Megalonaias nervosa*

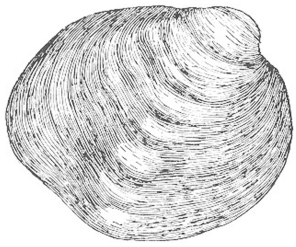
AE. *Obliquaria reflexa*

AF. *Obovaria retusa*

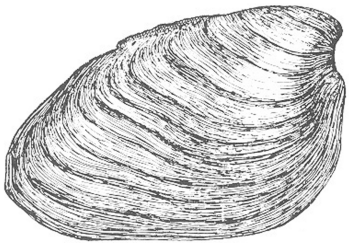
AG. *Pegias fabula*



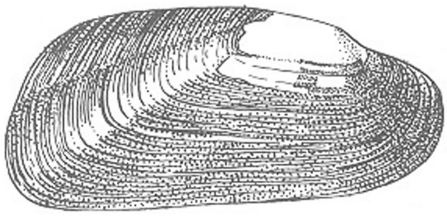
AH. *Plectomerus dombeyanus*



AI. *Plethobasus cyphyus*



AJ. *Pleurobema clava*

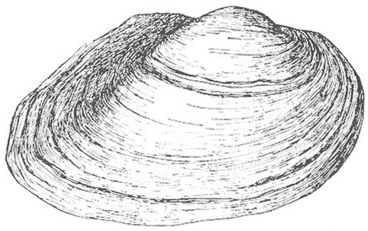


AK. *Popenaias popei*

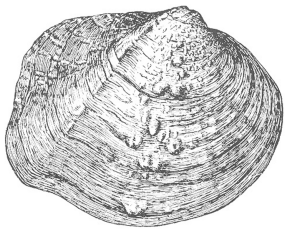
AL. *Potamilus alatus*

AM. *Ptychobranchus fasciolaris*

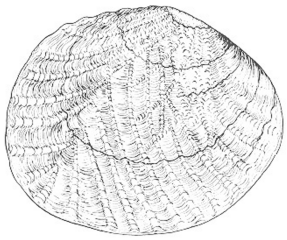
FIGURE 28 (Continued)



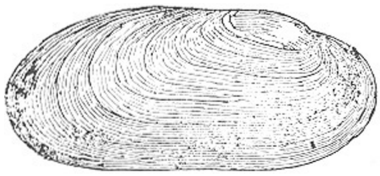
AN. *Pyganodon grandis*



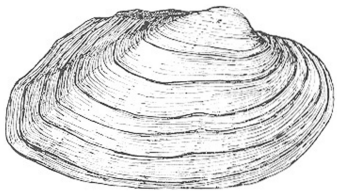
AO. *Quadrula quadrula*



AP. *Quincuncina infucata*

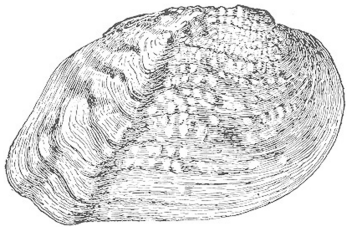


AQ. *Simpsonaias ambigua*

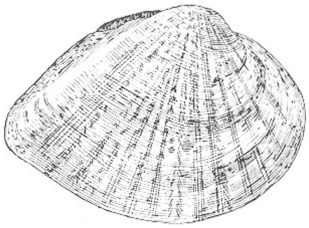


AR. *Strophitus undulatus*

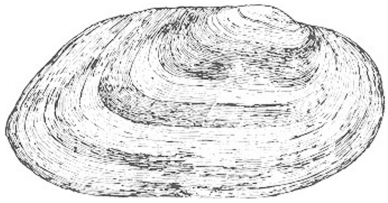
AS. *Toxolasma texasiensis*



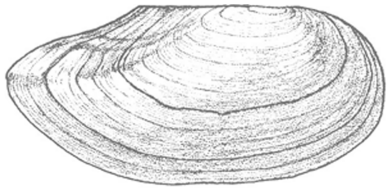
AT. *Tritogonia verrucosa*



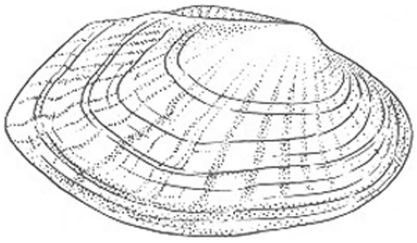
AU. *Truncilla truncata*



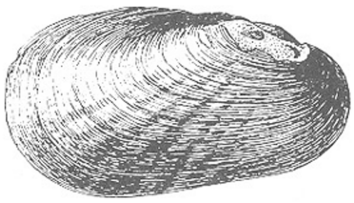
AV. *Uniomerus tetralasmus*



AW. *Utterbackia imbecillis*



AX. *Venustaconcha ellipsiformis*



AY. *Villosa villosa*

FIGURE 28 (Continued)

16a. (14b) Hinge line in left valve with an additional small interdental or accessory tooth, giving the appearance of three pseudocardinal teeth, shell more or less compressed, shell shape rhomboid, periostracum dark green with numerous green rays, beak sculpture consists of prominent bars .....*Lasmigona* [in part][*L. decorata, L. robusta*, *L. subviridis*](Fig. 28X)

16b. Left valve without extra interdental tooth 17

17a. (16b) Shell shape rectangular to broadly triangular 18

17b. Shell shape oval, round or rhomboid.....19

18a. (17a) Shell is from the James River Basin, Virginia .....*Lexingtonia subplana* (Fig. 28AA)

18b. Shell is from an area extending from the Roanoke River Basin south to the headwaters of the Savannah River Basin..... .....*Fusconaia masoni* (Fig. 28S)

19a. (17b) Shell shape rhomboid or rectangular 20

19b. Shell shape oval or round 23

20a. (19a) Shell usually more than twice as long as high 21

20b. Shell usually less than twice as long as high.....25

21a. (20a) Nacre color white, shell inflated, ...22

21b. Nacre color typically some shade of purple, but ranges from white to salmon to purple.....*Elliptio* [in part] [this genus contains basically three shell shapes, narrow and elongate: the *Elliptio lanceolata* complex; rectangular with various degrees of inflation: the *Elliptio complanata* complex; those shells with short shell length, not too tall and inflated: the *Elliptio icterina* complex] (Fig. 28P)

22a. (21a) Periostracum unrayed, shell thick, posterior end angled, periostracum mat or fuzzy, rectangular in shell shape, *Uniomerus carolinana* (Fig. 28 AV)

22b. Periostracum rayed in juveniles, posterior end tapered to a point in middle of posterior margin, periostracum not mat, *Ligumia nasuta* (Fig. 28AB)

23a. (19b) Adult shell typically <40 mm in length, with a fuzzy or mat textured dark periostracum .....*Toxolasma* [in part] [*T. pullus*] (Fig. 28AS)

23b. Adult shell >40 mm in length, lacking the pronounced fuzzy periostracum 24

24a. (23b) Shell shape oval to elongate oval, periostracum very shiny to mat with rays .....*Lampsilis* [in part] [*L. cariosa*, *L. dolabraeformis*, *L. radiata*, *L. splendida*] (Fig. 28W)

24b. Shell shape oval, periostracum dull yellow, without rays or with fine rays all over the shell, found in or near tidewater, nacre often a salmon color .....*Leptodea* [in part] [*L. ochracea*] (Fig. 28Z)

25a. (20b) Periostracum light colored with numerous green rays, shell relatively thin, oval to elongate oval, bladelike pseudocardinal teeth .....*Villosa* [in part] [*V. delumbis*, *V. villosa*, *V. vibex*] (Fig. 28AY)

25b. Periostracum dark to black, shell thick, no green rays, shell shape oval to round.....*Villosa* [in part] [*V. constricta*] (Fig. 28AY)

Mississippi River Basin

26a. (3a) Shell with lateral muscle scars on the inside center of the valve .....*Cumberlandia monodonta* (Fig. 28A)

26b. Shell lacking any evidence of lateral muscle scars 27

27a. (26b) Shell not as above, lacking lateral teeth or all evidence of any hinge teeth 28

27b. Shell with both pseudocardinal and lateral teeth present 34

28a. (27a) Shell with pseudocardinal teeth, but lacking lateral teeth 29

28b. Shell with greatly reduced or totally lacking both pseudocardinal and lateral teeth 30

29a. (28a) Shell <25 mm, typically periostracum eroded off with periostracum restricted to narrow strip on shell margin, beak sculpture heavy bars extending down on the disk of the shell, restricted to the upper Cumberland and upper Tennessee River basins ....*Pegias fabula* (Fig. 28AG)

29b. Shell not small, periostracum not eroded or erosion restricted to the umbo, beak sculpture consists of heavy bars, widespread in the Mississippi River Basin.....*Lasmigona* [in part] [*L. costata, L. complanata*] (Fig. 28X)

30a. (28b) Shell with pseudocardinal tooth consisting of a slight swelling or knob, lateral tooth consisting of a rounded ridge, beak cavity copper colored, umbo centrally located .....*Strophitus undulatus* (Fig. 28AR)

30b. Hinge teeth completely absent 31

31a. (30b) Umbonal area of shell projects above the plane of the hinge line 32

31b. Umbo level with hinge line or below the level of the hinge line 33

32a. (31a) Umbo elevated well above the hinge line, shell shape variable, ranging from oval, elliptical to rhomboid, beak sculpture consists of double loopedridges (Fig. 27) with projections on the bottom of the loop.....*Pyganodon* [in part] [*P. grandis*] (Fig. 28AN)

32b. Umbo projecting only slightly above the hinge line, shell elongated, inflated, beak sculpture consists of 3 or 4 fine sharp concentric ridges.....*Anodontoides ferussacianus* (Fig. 28G)

33a. (31b) Shell shape round to circular, compressed, beak sculpture consists of 4–5 pairs of broken irregular double looped ridges.....*Anodonta* [in part] [*A. suborbiculata*] (Fig. 28F)

33b. Shell shape elongate, inflated, dorsal and ventral margins nearly straight and parallel, beak sculpture consists of 5–6 fine irregular concentric ridges.....*Utterbackia* [in part] [*U. imbecillis*] (Fig. 28AW)

34a. (27b) Shell with sculpture on the external shell surface.....35

34b. Shell with no plications, undulations, ridges, pustules or nodules.....55

35a. (34a) Shell with prominent pustules or nodules and/or undulations, plications or ridges.....36

35b. Shell with only prominent, well-defined pustules, knobs or nodules.....46

36a. (35a) Shell with undulations, ridges, or plications, no pustules or nodules on the surface.....37

36b. Shell with undulations, ridges or plications and pustules on the disk or umbonal area.....44

37a. (36a) Shell with undulations, plications, ridges restricted to the posterior slope.....38

37b. Shell with undulations, plications, ridges not restricted to the posterior slope.....41

38a. (37a) Shell shape rectangular to oval, slablike, compressed, left valve with an accessory dentacle posterior to pseudocardinal teeth.....*Lasmigona* [in part] [*L. costata*](Fig. 28X)

38b. Shell shape more elongate, lacks the accessory dentacle.....39

39a. (38b) Shell elongate, inflated with a blue to blue-green nacre color, restricted to the Tennessee and Cumberland River basins.....*Medionidus* [in part] [*M. conradicus*] (Fig. 28AC)

39b. Shell elongate, inflated, nacre not as above.....40

40a. (39b) Shell thin, posterior slope steeply angled to moderately angled.....*Alasmidonta* [in part] [*A. marginata*] (Fig. 28D)

40b. Shell thicker, posterior slope rounded, posterior ridge rounded, restricted to the Tennessee and Cumberland River Basins.....*Ptychobranchus* [in part] [*P. subtentum*] (Fig. 28AM)

41a. (37b) Shell shape rectangular, with a distinct posterior ridge, purple nacre, open and shallow beak cavity.....*Plectomerus dombeyanus* (Fig. 28AH)

41b. Shell without a distinct posterior ridge, typically white nacre.....42

42a. (41b) Shell thick, compressed, maximum shell length <50 mm, low plications or wrinkles restricted to the posterior slope and posterior ventral margin of the shell, this species restricted to the Tennessee River Basin.....*Lemiox rimosus* (Fig. 28Y)

42b. Shell not as above.....43

43a. (42b) Shell variably inflated, shell shape round to quadrate, heavy pseudocardinal teeth, deep compressed beak cavity, sculpture consists of typically three well-developed ridges or undulations running across the shell from anterior of the umbo to the posterior ridge, widespread in the Mississippi River Basin.....*Amblema plicata* (Fig. 28E)

43b. Shell somewhat inflated, shell shape quadrate, or approaching oval, pseudocardinal teeth curved, heavy sculpturing on the posterior half of the shell, species is restricted to the Red River Drainage in Oklahoma and the Ouachita River Drainage in Arkansas.....*Arkansia wheeleri* (Fig. 28I)

44a. (36b) Shell elongate with a well-developed diagonal posterior ridge.....*Tritogonia verrucosa* (Fig. 28AT)

44b. Shell shape not elongate, lacking well-defined posterior ridge.....45

45a. (44b) Well-developed plications running across the shell and pustules on the disk and umbonal area.....*Megalonaias nervosa* (Fig. 28AD)

45b. Plications not well developed and wavy, not straight, plications on posterior slope, two rows of pustules or knobs on umbo.....*Arcidens confragosa* (Fig. 28H)

46a. (35b) Pustules distributed across most of the shell.....47

46b. Pustules restricted to a single or double row.....50

47a. (46a) Pustules covering most of the shell, purple nacre, beak cavity deep and compressed..... *Cyclonaias tuberculata* (Fig. 28J)

47b. Pustules covering most of the shell, nacre color white to pink not purple.....48

48a. (47b) Pustules consistently small, with a shallow sulcus down the center of the disk, nacre white.....*Cyprogenia* [in part] [*C. stegaria* in the Ohio, Tennessee and Cumberland rivers; *C. aberti* in Arkansas, Oklahoma] (Fig. 28K)

48b. Pustules generally larger, and often of variable size and shape.....49

49a. (48b) Disk of the shell usually with a broad green stripe running down the disk of the shell with a variable number of pustules, varies from a very few to covering most of the shell, nacre color mostly white, beak cavity deep and open not compressed ..... *Quadrula* [in part] [*Q. pustulosa*] (Fig. 28AO)

49b. Disk of shell without a broad green stripe, consistently covered with a large number of pustules, nacre color often pink, salmon or white, beak cavity open and shallow..... *Plethobasus* [in part] [*P. cooperianus*] (Fig. 28AI)

50a. (46b) Pustules forming two distinct rows.....51

50b. Pustules or nodules forming a single row.....52

51a. (50a) Two rows of pustules with one row on the posterior ridge, shell thick ..... *Quadrula* [in part], [*Q apiculata,* this species has small pustules in the sulcus between the two rows of pustules; *Q. nodulata*, this species lacks a sulcus between the rows of pustules and may only have very few pustules; *Q. quadrula*; *Q. fragosa,* this species has a well-developed wing posterior to the umbo] (Fig. 28AO)

51b. Radiating row of knobs, shell inflated, thin to relatively thick, umbo high and full, pseudocardinal teeth compressed, not curved; beak sculpture consists of irregular nodules forming two loops which continue down and across most of the shell in two radiating rows, [mostly in small and juvenile shells] pustules fuse, become elongate and form plications, plications on the posterior slope of adults..... *Arcidens confragosus* (Fig. 28H)

52a. (50b) The single row of pustules or knobs restricted to the posterior ridge..... *Quadrula* [in part] [*Q. cylindrica*, with pustules on the posterior ridge while *Q. cylindrica strigillata* of the upper Tennessee River Basin has small pustules over most of the shell as well as pustules on the posterior ridge.] (Fig. 28AO)

52b. The single row of pustules or knobs forming a single row down the center of the disk.....53

53a. (52b) Pustules large, located in a row down the center of the shell and limited to about three pustules on each valve ..... *Obliquaria reflexa* (Fig. 28AE)

53b. Pustules more numerous, but still in a centrally located row 54

54a. (53b) Pustules usually wider than tall, shell periostracum a waxy yellow color ..... *Plethobasus* [in part] [*P. cicatricosus, P. cyphyus*] (Fig. 28AI)

54b. Pustules rather small, running down the centerline of the disk, but interrupted by a well-defined, raised ridge running around the shell like a growth line, restricted to the Tennessee and Cumberland River drainages ..... *Dromus dromas* (Fig. 28N)

55a. (34b) Shell with a well-developed dorsal wing projecting above the hinge line, the wing usually posterior of the umbo, but some species may also have an anterior wing [some older shells, such as in *Leptodea fragilis*, maybe lacking the dorsal wing].....56

55b. Shell without a well-developed dorsal wing.....58

56a. (55a) Hinge teeth thin pseudocardinal teeth compressed, thin and not projecting perpendicular to the axis of the hinge line ..... *Leptodea* [in part] [*L. fragilis, L. leptodon*] (Fig. 28Z)

56b. Well-developed dorsal wing.....57

57a. (56b) White nacre, thick-shelled ..... *Lasmigona* [in part] [*L. complanata*] (Fig. 28X)

57b. Purple nacre, thin-to-thick shelled, may be inflated..... *Potamilus* [in part] [*P. alatus, P. purpuratus*] (Fig. 28AL)

58a. (55b) Shell shape round 59

58b. Shell shape not round 68

59a. (58a) Shell compressed, shell shape round 60

59b. Shell not compressed, but more inflated, shell shape round, oval.....61

60a. (59a) Shell compressed, shape nearly circular, without lateral teeth ..... *Lasmigona* [in part] [*L. complanata*] (Fig. 28X)

60b. Shell compressed, with lateral teeth, steep posterior slope, shell thick with well-developed hinge teeth, periostracum light yellow with interrupted rows of green chevrons..... *Ellipsaria lineolata* (Fig. 28O)

61a. (59b) Umbo central or nearly central in the dorsal margin.....62

61b. Umbo anterior of the center of the shell 65

62a. (61a) Broad green ray extending from the umbo down only a short distance onto the disk of the shell..... *Quadrula* [in part] [*Q. pustulosa* without pustules] (Fig. 28AO)

62b. No broad green ray 63

63a. (62b) Shell with a raised ridge one quarter of the distance from the umbo running around the shell parallel with the growth lines. Restricted to the Tennessee and Cumberland River basins ..... *Dromus dromas* (Fig. 28N)

63b. Shell without a raised ridge 64

64a. (63b) Shell surface smooth, without a broad central sulcus .....*Obovaria* [in part] [*O. jacksoniana*, from the Mississippi River embayment shell somewhat more oval than round; *O. retusa*, nacre color white; nacre color purple inside the pallial line, white outside of the pallial line; *O. subrotunda*, shell round, thick shelled, nacre typically white but some populations with deep purple.] (Fig. 28AF)

64b. Shell with broad shallow-to-pronounced sulcus, fine green rays, shallow beak cavity, well-developed hinge teeth, female shells with a swollen, extended or expanded portion of the posterior slope and posterior ventral margin of the shell..... *Epioblasma* [in part] [*E. capsaeformis*, *E. florentina florentina*, *E. florentina walkeri*, *E. lewisi*, *E. flexuosa*, *E. biemarginata*, *E. stewardsoni*, *E. propinqua*, *E. torulosa torulosa*, *E. torulosa gubernaculum*, *E. torulosa biloba, E. sampsoni*] (Fig. 28R)

65a. (61b) Beak cavity deep compressed .....*Fusconaia* [in part][*F. subrotunda*, *F. ebena*] (Fig. 28S)

65b. Beak cavity shallow and open.....66

66a. (65b) Restricted to the Tennessee River Basin, shell with green rays at least on the umbo area with a thick shell, heavy lateral teeth, very shallow sulcus or missing, shallow-to-no beak cavity .....*Lexingtonia dolabelloides* (Fig. 28AA)

66b. Not restricted to the Tennessee River Basin, but widespread 67

67a. (66b) Long axis of the main pseudocardinal teeth parallel with the lateral teeth, umbo anterior .....*Obovaria* [in part, *O. olivaria*] (Fig. 28AF)

67b. Teeth not as above, shell wedge shaped to triangular or approaching square with or without a central sulcus, nacre white to deep pink .....*Pleurobema* [in part] [*P. rubrum*, *P. sintoxia*] (Fig. 28AJ)

68a. (58b) Shell shape not oval.....69

68b. Shell shape oval to oblong.....85

69a. (68a) Shell shape rectangular, triangular, square with sulcus.....70

69b. Shell shape elongate, two-to-four times longer than high.....75

70a. (69a) Beak cavity deep.....71

70b. Beak cavity shallow or broad and open 72

71a. (70a) Shell shape rectangular, with green rays on the umbo .....*Fusconaia* [in part] [*F. flava*, *F. cuneolus*, *F. cor*, *F. ozarkensis*, *F. barnesiana* has a shallow beak cavity but belongs with this group] (Fig. 28S)

71b. Shell shape triangular to broadly triangular.....*Pleurobema* [in part] [*P. cordatum, P. plenum*] (Fig. 28AJ)

72a. (70b) Posterior slope not very sharp or rounded, covered with lines of green chevrons .....*Truncilla* [in part; *T. truncata*, *T. donaciformis*] (Fig. 28AU)

72b. Posterior slope very sharp or steep 73

73a. (72b) Shell thin, inflated, abruptly truncate posteriorly, posterior slope lighter colored than the rest of the shell ..... *Alasmidonta* [in part] [*A. marginata*; shell thin, shell shape elongate, posterior slope not a steep sharp angle, headwaters of the Little Tennessee River in western North Carolina, *A. raveneliana*; streams of the upper Cumberland River Basin, *A. atropurpurea*] (Fig. 28D)

73b. Shell thin to thick, inflated posterior slope steep shell thick, shell shape rectangular.....74

74a. (73b) Females with posterior slope inflated into a marsupial swelling, males evenly rounded posterior ridge and not inflated posterior ridge, nacre white .....*Epioblasma* [in part] [*E. triquetra* wide spread, *E. arcaeformis* extinct and formerly restricted to the Tennessee and Cumberland River basins.] (Fig. 28R)

74b. Posterior margin not modified into a marsupial swelling, nacre purple.....*Elliptio* [in part] [*E. crassidens*] (Fig. 28P)

75a. (69b). Thin shelled.....76

75b. Thick shelled 79

76a. (75a) Shell compressed, very thin, periostracum rayed, nacre iridescent except for a purple wash in the open beak cavity ....*Hemistena lata* (Fig. 28V)

76b. Shell inflated.....77

77a. (76b) Hinge teeth thin, periostracum rayless, adult shell length <50 mm .....*Simpsonaias ambigua* (Fig. 28AQ)

77b. Periostracum usually rayed, adult shell length >50 mm 78

78a. (77b) Shell hinge thin, usually heavily rayed.....*Villosa* [in part] [*V. iris* complex, *V. taeniata*] (Fig. 28AY)

78b. Shell yellow, plain or rayed.....*Lampsilis* [in part] [*L. teres, L. rafinesqueana, L. siliquoidea, L. virescens*] (Fig. 28W)

79a. (75b) Shell compressed 80

79b. Shell inflated.....82

80a. (79a) Adult shell length <40 mm, rayed, compressed, widespread, ...*Villosa* [in part] [*V. fabalis*] (Fig. 28AY)

80b. Adult shell length >40 mm 81

81a. (80b) Shell hinge massive, curved, nacre white, periostracum with interrupted green rays .....*Ptychobranchus* [in part] [*P. fasciolaris, P. occidentalis*] (Fig. 28AM)

81b. Hinge lighter, straight, nacre purple to white, periostracum typically unrayed .....*Elliptio* [in part] [*E. dilatata*] (Fig. 28P)

82a. (79b). Adult shell length <55mm

82b. Adult shell length >55mm

83a. (82a). Periostracum olive green with numerous rays *Villosa* [in part] [*V. trabalis,* restricted to the Tennessee River Basin above Muscle Shoals and the upper Cumberland River basin, inflated, white nacre, *V. perpurpurea*, upper Tennessee River Basin, inflated, purple nacre] (Fig. 28AY)

83b. Periostracum ranges from greenish to black without rays *Toxolasma* [in part] [T. lividus, purple nacre, *T. parvus* white nacre, *T. texasiensis* white to salmon nacre] (Fig. 28AS)

84a. (82b) Shell inflated, periostracum rayless, posterior shell margin comes to a blunt point ventrally, coarse concentric beak sculpture opening posteriorly .....*Uniomerus* [*U. tetralasmus, U. declivus*] (Fig. 28AV)

84b. Shell inflated, periostracum rayed as a juvenile, becoming dark brown to black as an adult, posterior shell margin comes to a point in middle of posterior margin, nacre white to white with purple wash in umbo area .....*Ligumia* [*L. nasuta, L. recta, L. subrostrata*] (Fig. 28AB)

85a. (68b) Shell shape oval 86

85b. Shell shape oblong.....87

86a. (85a) Shell shape oval, inflated, rayed, thin to thick shell, posterior ridge rounded or sharp, nacre variously white to pink or salmon .....*Lampsilis* [in part] [*L. cardium*, *L. fasciola*, *L. ovata*, *L. reeviana*, L. *rafinesqueana*, *L. higginsi*, *L. abrupta*] (Fig. 28W)

86b. Shell shape elongate oval .....*Villosa* [in part] [*V. taeniata*, interrupted broad green rays, restricted to the Tennessee and Cumberland River basins; in the following three species males are oval while female shells have a truncate posterior margin, *V. vanuxemensis*, purple nacre, restricted to the Tennessee River Basin and the central Cumberland River Basin, *V. ortmanni*, restricted to Kentucky, *V. lienosa*, variously colored nacre] (Fig. 28AY)

87a. (85b) Shell shape oblong, inflated to globose, unrayed.....*Potamilus* [in part] [S-shaped, very compressed hinge line, very inflated and thin shelled *P. capax*; inflated, black shiny periostracum and purple nacre *P. purpuratus*] (Fig. 28AL)

87b. Shell shape oblong, inflated but not globose 88

88a. (87b) Adult shell length <70 mm, shell shape elliptic to oblong, thick shelled, nacre white with a tinge of salmon to coppery color in center of the shell, shallow beak cavity, rayed, with those rays on the posterior slope thick and wavy .....*Venustaconcha ellipsiformis* (Fig. 28AX)

88b. Adult shell length >70 mm, shell shape oblong to oval, thin to thick shelled, nacre white to iridescent, beak cavity broad and open, moderately deep, usually rayed but rays on posterior slope not thin or wavy .....*Actinonaias* [*A. pectorosa*, thin shelled, restricted to the Tennessee and Cumberland River basins; *A. ligamentina*, widespread and typically thick shelled.] (Fig. 28C)

Gulf Coast

89a (3b) Shell with lateral muscle scars in the interior center of the valve .....*Margaritifera* [in part] [*M. hembeli*, *M. marrianae*] (Fig. 28B)

89b. Shell without lateral muscle scars in the interior center of the valve 90

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92a. (91a) Shell with pseudocardinal tooth consisting of a slight swelling or knob, lateral tooth consisting of a rounded ridge, beak cavity copper colored, umbo centrally located .....*Strophitus* [in part] [*S. subvexus*, *S. connasaugaensis*] (Fig. 28AR)

92b. Shell with pseudocardinal tooth thin, reduced and compressed, umbo projecting only slightly above the hinge line, shell elongated, inflated, beak sculpture consists of 3–4 fine, sharp, concentric ridges .....*Anodontoides* [in part] [*A. radiatus*] (Fig. 28G)

93a. (91b) Umbo elevated well above the hinge line, shell shape variable, ranging from oval, elliptic or rhomboid, beak sculpture consists of double looped with projections on the bottom of the loop .....*Pyganodon* [in part] [*P. grandis*] (Fig. 28AN)

93b. Umbo level ridges with hinge line or below the level of the hinge line 94

94a. (93b) Shell shape round to circular, compressed, beak sculpture consists of 4–5 pairs of broken irregular double looped ridges..... .....*Anodonta* [in part] [*A. suborbiculata, A. heardi*] (Fig. 28F)

94b. Shell shape elongate, inflated dorsal and ventral margins nearly straight and parallel, beak sculpture consists of 5–6 fine irregular concentric ridges.....*Utterbackia* [in part] [*U. imbecillis, U. peggyae, U. peninsularis*] (Fig. 28AW)

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95b. Shell without plications, undulations, ridges, pustules or nodules.....109

96a. (95a) Shell with pustules or nodules and/or undulations, plications or ridges.....97

96b. Shell with only pustules, knobs or nodules.....105

97a. (96a) Shell with undulations, ridges, or plications, but not pustules or nodules on the surface.....98

97b. Shell with undulations, ridges or plications and pustules on the disc or umbonal area.....103

98a. (97a) Shell surface with undulations, plications, ridges restricted to the posterior slope.....99

98b. Shell surface with undulations, plications, ridges not restricted to the posterior slope.....101

99a. (98a) Shell shape round to oval, slablike, compressed, left valve with an accessory dentacle posterior to pseudocardinal teeth plications occur on dorsal wing.....*Lasmigona* [in part] [*L. complanata*] (Fig. 28X)

99b. Shell shape more elongate, lacks the accessory dentacle.....100

100a. (99b) Shell inflated with a blue to blue-green nacre color.....*Medionidus* [in part] [*M. accutissimus, M. mcglameriae, M. parvulus, M. penicillatus, M. simpsonianus, M. walkeri*] (Fig. 28AC)

100b. Shell inflated, nacre not as above, shell thin, posterior slope steeply angled to moderately angled.....*Alasmidonta* [in part] [*A. triangulata, A. wrightiana*] (Fig. 28D)

101a. (98b) Shell shape rectangular, with a distinct posterior ridge, purple nacre, open and shallow beak cavity.....*Plectomerus dombeyanus* (Fig. 28AH)

101b. Shell shape round to rectangular, without a distinct posterior ridge.....102

102a. (101b) Shell thick, compressed, low plications or wrinkles on posterior slope and undulations and ridges on the disk of the shell, nacre with a central white area and a peripheral purple band, restricted to the Apalachicola and Ochlockonee River basins.....*Elliptoideus sloatianus* (Fig. 28Q)

102b. Shell variably inflated, shell shape round to quadrate, heavy pseudocardinal teeth, deep compressed beak cavity, sculpture consists of three to five well-developed ridges or undulations running across the shell from anterior of the umbo to the posterior ridge, nacre color white to iridescent.....*Amblema* [in part] [*A. plicata, A. neislerii, A. elliotti*] (Fig. 28E)

103a. (97b) Shell shape elongate, with a well-developed diagonal posterior ridge.....*Tritogonia verrucosa* (Fig. 28AT)

103b. Shell shape not elongate, lacking well-defined posterior ridge.....104

104a (103b). Shell shape round to quadrate, lacking well-defined posterior ridge, has well developed plications running across the shell and pustules on the disk or umbonal area.....*Megalonaias nervosa* (Fig. 28AD)

104b. Plications not well developed and wavy, not straight, plications on posterior slope, two rows of pustules or knobs on umbo.....*Arcidens confragosa* (Fig. 28H)

105a. (96b) Pustules distributed across most of the shell.....106

105b. Pustules restricted to a single or double row.....107

106a. (105a). Adult shell length <60 mm, sculpture fine, shell oval to elongate oval, pustules and chevrons.....*Quincuncina* [*Q. infucata, Q. burkei* restricted to the Choctawhatchee River Basin; *Q. mitchelli* from the Rio Grand, Guadalupe, Colarado and Brazos rivers in Texas] (Fig. 28AP)

106b. Adult shell length not restricted to <60 mm, pustules covering most of the shell, nacre color white to pink, not purple, with a variable number of pustules, from a very few to pustules covering most of the shell, nacre color mostly white, beak cavity deep and open, not compressed.....*Quadrula* [in part] [*Q. petrina, Q. houstonensis, Q. couchiana, Q. aurea, Q. asperata*] (Fig. 28AO)

107a. (105b) Pustules or nodules large, forming a single row down the center of the disk, and limited to about three pustules on each valve.....*Obliquaria reflexa* (Fig. 28AE)

107b. Pustules forming two distinct rows especially on the umbonal area.....108

108a. (107b) Two rows of pustules, with one row on the posterior ridge, shell thick.....*Quadrula* [in part] [*Q apiculata,* has small pustules in the sulcus between the two rows of pustules; *Q. nodulata* lacks a sulcus between the rows of pustules and may only have very few pustules; *Q. quadrula, Q. rumphiana*] (Fig. 28AO)

108b. Radiating rows of knobs, shell inflated, thin to relatively thick, umbo high and full, pseudocardinal teeth compressed, not curved, beak sculpture consists of irregular nodules forming two loops which continue down and across most of the shell in two radiating rows.....*Arcidens confragosus* (Fig. 28H)

109a. (95b) Shell with a well-developed dorsal wing projecting above the hinge line, the wing usually posterior of the umbo [see Fig. 30] but some species may also have an anterior wing [some older shells such as in *Leptodea fragilis* may be lacking the dorsal wing] 110

109b. *Shell without a well-developed dorsal wing* 111

110a. (109a) *Pseudocardinal teeth moderately heavy, projecting perpendicular to the axis of the hinge line, purple nacre thin to thick shelled, may be inflated* ..... *Potamilus* [*P. inflatus, P. purpuratus*] (Fig. 28AL)

110b. Pseudocardinal teeth compressed, thin and not projecting perpendicular to the axis of the hinge line ..... *Leptodea* [*L. fragilis, L. amphichaenus*] (Fig. 28Z)

111a. (109b) Shell shape round 112

111b. Shell shape not round 117

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112b. Shell not compressed, round to oval 113

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113b. Umbo anterior of the center of the dorsal margin of the shell 116

114a. (113a) Broad green ray extending around the umbo down only a short distance onto the disk of the shell ..... *Quadrula* [in part] [*Q. asperata* without pustules] (Fig. 28AO)

114b. No broad green ray 115

115a. (114b) Shell surface smooth, without a broad central sulcus ..... *Obovaria* [in part] [*O. jacksoniana, O. unicolor*] (Fig. 28AF)

115b. Shell with broad, shallow to pronounced sulcus, fine green rays, shallow beak cavity, well developed hinge teeth, female shells with a swollen, extended or expanded portion of the posterior slope and posterior ventral margin of the shell ..... *Epioblasma* [in part] [*E. penita, E. metastriata, E. othcaloogensis*] (Fig. 28R)

116a. (113b) Beak cavity deep compressed ..... *Fusconaia* [in part][*F. ebena, F. succissa*, *F. escambia*] (Fig. 28S)

116b. Beak cavity shallow and open, shell shape wedge shaped to triangular or approaching square with or without a central sulcus, nacre white to deep pink ..... *Pleurobema* [in part] [*P. marshalli*] (Fig. 28AJ)

117a. (111b) Shell shape not oval 118

117b. Shell shape oval 130

118a. (117a) Shell shape triangular, square to rectangular, with sulcus 119

118b. Shell shape elongate, tapered posteriorly, two to four times longer than high 123

119a. (118a) Beak cavity deep 120

119b. Beak cavity shallow or broad and open 121

120a. (119a) Shell shape rectangular with green rays on the umbo ..... *Fusconaia* [in part] [*F. cerina*] (Fig. 28S)

120b. Shell shape triangular to broadly triangular ..... *Pleurobema* [in part] [*P. taitianum*] (Fig. 28AJ)

121a. (119b) Posterior slope rounded, not very steep, covered with lines of green chevrons ..... *Truncilla* [in part] [*T. cognata, T. macrodon, T. truncata*, *T. donaciformis*] (Fig. 28AU)

121b. Posterior ridge very sharp, posterior slope steep 122

122a. (121b) Shell thin, inflated, abruptly truncate posteriorly, posterior slope lighter colored than the rest of the shell ..... *Alasmidonta* [in part] [*A. triangulata*] (Fig. 28D)

122b. Shell thin to thick, inflated posterior slope steep shell thick, shell shape rectangular, posterior margin not modified into a marsupial swelling, often tapering posteriorly, nacre varies pale salmon to purple ..... *Elliptio* [in part] [*E. crassidens*] (Fig. 28P)

123a. (118b). Thin shelled 124

123b. Thick shelled 126

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124b. Shell inflated 125

125a. (124b) Hinge thin, periostracum usually heavily rayed ..... *Villosa* [in part] [*V. nebulosa* complex, *V. villosa, V. vibex*] (Fig. 28AY)

125b. Hinge not thin, periostracum yellow, plain or rayed.....*Lampsilis* [in part] [*L. teres, L. straminea, L. hydiana, L. bracteata*] (Fig. 28W)

126a. (123b) Shell compressed 127

126b. Shell inflated.....128

127a. (126a) Hinge massive, curved, nacre white, periostracum with interrupted green rays..... *Ptychobranchus* [in part] [*P. greeni*] (Fig. 28AM)

127b. Hinge thinner, straight, nacre purple to white, periostracum typically unrayed.....*Elliptio* [in part] [*E. arctata, E. arca*] (Fig. 28P)

128a. (126b) Rayed as a juvenile becoming dark brown to black as an adult, tapered to a point in middle of posterior margin, nacre white to white with purple wash in umbo area, *Ligumia* [*L. recta, L. subrostrata*] (Fig. 28AB)

128b. Shell unrayed

129a. (128b) Adult shell length >50mm, bluntly pointed posterior ventrally, coarse concentric beak sculpture seeming to radiate from a single point, *Uniomerus* [in part] [*U. tetralasmus, U. declivus*] (Fig. 28AV)

129b. Adult shell length 50 mm, bluntly rounded or squared off posteriorly, concentric beak sculpture in form of bars or ridges, angled up posteriorly *Toxolasma* [in part] [T. parvus, T. texasiensis] (Fig. 28AS)

130a. (117b) Shell shape oval.....131

130b. Shell shape oblong.....133

131a. (130a) Posterior half of the pseudocardinal tooth divided into several parallel vertical ridges (Fig. 29), thick shelled, inflated, periostracum dark brown to dark olive .....*Glebula rotundata* (Fig. 28T)

131b. Pseudocardinal tooth not divided into vertical ridges as above.....132

132a. (131b) Shell shape oval, inflated, rayed, thin-to-thick shell, posterior ridge rounded or sharp, nacre variously white to pink or salmon .....*Lampsilis* [in part] [*L. ornata, L. binominata*] (Fig. 28W)

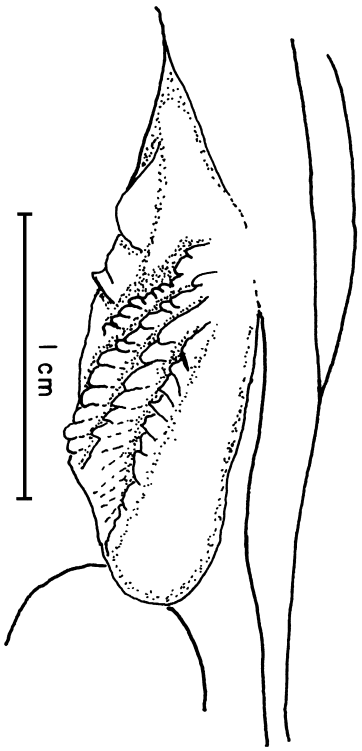

FIGURE 29 Structure of the posterior pseudocardinal teeth of the right valve of *Gelbula rotundata*. Note that the posterior pseudocardinal teeth are deeply divided into parallel, vertical, plicate lamellae, a tooth arrangement uniquely characteristic of this species. (Redrawn from Burch, 1975b.)

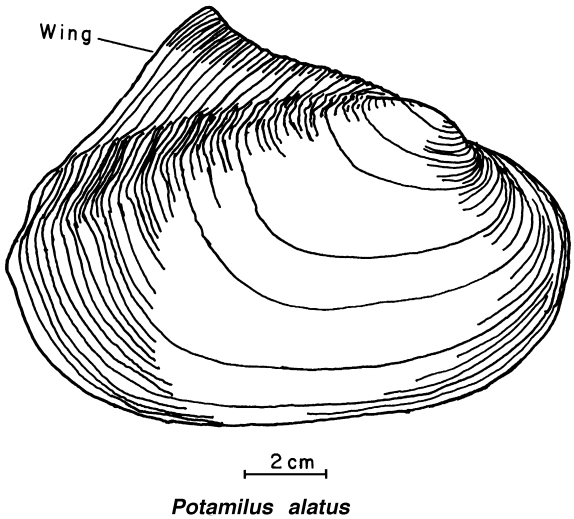

FIGURE 30 Right shell valve of the unionid, *Potamilus alatus*, showing the thin, extensive dorsal projection of the shell posterior to the umbos forming a "wing" whose presence or absence is a diagnostic characteristic valuable for identification of a number of unionid species. (Redrawn from Burch, 1975b.)

132b. Shell shape elongate, oval.....*Villosa* [in the following two species male shells are oval while female shells have a truncate posterior margin, *V. vanuxemensis umbrans*, purple nacre, restricted to the upper Coosa River Basin, V. *lienosa*, variously colored nacre] (Fig. 28AY)

133a. (130b) Shell shape oblong, inflated to globose, unrayed.....*Potamilus* [in part] [*P. amphichaenus*, P. *purpuratus*] (Fig. 28AL)

133b. Shell shape oblong, inflated, but not globose.....134

134a. (133b) Shell shape elongate oval, shell relatively thin to thick, compressed, pseudocardinal teeth compressed, thin, lateral teeth long, beak cavity shallow, periostracum tan to brown, with dark brown rays posteriorly, restricted to the Rio Grande Basin in Texas.....*Disconaias* [in part] [*D. salinasensis, D. conchos*] (Fig. 28M)

134b. Shell shape oval, moderately thick shell, inflated, beak cavity relatively deep, periostracum dull/shiny, red-brown to brown, juveniles with faint rays, Brazos River to Rio Grande Basin, Texas.....*Cyrtonaias tampicoensis* (Fig. 28L)

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