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Robert T. Dillon
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1 · *Introduction*

The invasion launched by elements of the molluscan army upon fresh water has aptly been characterized as 'desultory' (Deaton and Greenberg 1991). Dozens of offensives seem to have taken place, sporadically timed over hundreds of millions of years, some ultimately carrying the works, others now witnessed only in the fossil record. The diversity of freshwater molluscs is vast. Yet it is my thesis here that in their interactions with the environment and with each other, freshwater molluscs share enough similarities that some intellectual profit may be gained by examining their ecology together.

We might begin with a brief overview of the forces (Tables 1.1 and 1.2). The larger freshwater bivalves belong to the order Unionoidea, an ancient group of six families whose fossil record extends to the Devonian period. They are distinguished by a parasitic larval stage that is unique among the Bivalvia. The best-known families are the Margaritiferidae and the highly diverse Unionidae, both worldwide. The hyriids of Neotropical and Australian regions are less studied, while the Neotropical mycetopodids, and the Ethiopian mutelids and etheriids, remain rather obscure.

The smaller infaunal freshwater bivalves belong to the superfamily Corbiculoidea. This is a somewhat younger group, generally hermaphroditic, with a fossil record beginning in the Jurassic and Cretaceous periods. The two corbiculoid families may represent separate invasions of fresh water (Park and O'Foighil 1998). Bivalves of the worldwide family Pisidiidae hold developing embryos for extended periods, ultimately releasing juveniles quite large in relation to their own bodies. The family Corbiculidae (restricted to old world tropics and subtropics until recently) release juveniles as smaller 'pediveligers'. The Dreissenoidea is much less diverse than the Unionoidea or Corbiculoidea, the freshwater *Dreissena* being restricted to the Ponto-Caspian basins until recently.

Table 1.1. *A classification of some of the genera of freshwater bivalves more commonly mentioned in this work*

Class Bivalvia

- Subclass Paleoheterodonta
- Order Unionoidea
  - Superfamily Unionacea
    - Family Margaritiferidae
        - *Margaritifera*
        - *Cumberlandia*
    - Family Unionidae
      - Subfamily Anodontinae
        - *Anodonta*
        - *Anodontoides*
        - *Cristaria*
      - Subfamily Ambleminae
        - *Amblema*
        - *Actinonaias*
        - *Elliptio*
        - *Fusconaia*
        - *Lampsilis*
        - *Unio*
        - *Villosa*
    - Family Hyriidae
        - *Diplodon*
        - *Hyridella*
  - Superfamily Etheriacea
    - Family Etheriidae
    - Family Mutelidae
    - Family Mycetopodidae

- Subclass Heterodonta
- Order Veneroidea
  - Superfamily Corbiculoidea
    - Family Corbiculidae
      - *Corbicula*
    - Family Pisidiidae
      - *Pisidium*
      - *Eupera*
      - *Sphaerium*
      - *Musculium*
  - Superfamily Dreissenoidea
    - Family Dreissenidae
      - *Dreissena*
      - *Mytilopsis*

Source: modified from Vaught (1989).

They doubtless represent yet another separate invasion from the sea (their oldest fossils are Eocene), retaining the overall aspect of edible marine mussels. By virtue of their ability to spin strong byssal attachment threads, they have occupied the epifaunal habitat not exploited by unionoids or corbiculoids. They have also retained a planktonic larval stage in their development.

Among the bivalves, adaptation to fresh waters does not seem to have been rare nor restricted to the unionoids, corbiculoids, and dreissenoids. Freshwater or brackish/freshwater species are to be found among the Arcidae, Mytilidae, Trapeziidae, Donacidae and Cardiidae, to name but a few families. Although quite interesting from many points of view, the

Table 1.2. *A classification of some of the gastropod genera more commonly mentioned in the present work*

- Class Gastropoda
- Subclass Pulmonata
- Order Basommatophora
  - Family Acroloxidae
    - *Acroloxus*
  - Family Lymnaeidae
    - *Lymnaea*
    - *Pseudosuccinea*
    - *Galba*
    - *Myxas*
    - *Radix*
    - *Stagnicola*
  - Family Physidae
    - *Physa*
    - *Aplexa*
  - Family Planorbidae
    - *Planorbis*
    - *Anisus*
    - *Gyraulus*
    - *Armiger*
    - *Segmentina*
    - *Biomphalaria*
    - *Helisoma*
    - *Menetus*
    - *Planorbula*
    - *Promenetus*
    - *Bulinus*
  - Family Ancylidae
    - *Ancylus*
    - *Rhodacmaea*
    - *Ferrissia*
    - *Hebetancylus*
    - *Laevapex*

- Subclass Prosobranchia
- Order Archaeogastropoda
  - Superfamily Neritoidea
    - Family Neritidae
      - *Neritina*
      - *Theodoxus*
- Order Mesogastropoda
  - Superfamily Viviparoidea
    - Family Viviparidae
      - *Bellamya*
      - *Cipangopaludina*
      - *Viviparus*
      - *Campeloma*
      - *Tulotoma*
    - Family Ampullariidae
      - *Marisa*
      - *Pila*
      - *Pomacea*
- Superfamily Valvatoidea
    - Family Valvatidae
      - *Valvata*
    - Superfamily Rissoidea
    - Family Hydrobiidae
      - *Amnicola*
      - *Hydrobia*
      - *Potamopyrgus*
    - Family Bithyniidae
      - *Bithynia*
      - *Hydrobioides*
    - Family Micromelanidae
      - *Pyrgula*
    - Family Pomatiopsidae
      - *Oncomelania*
      - *Pomatiopsis*
      - *Tricula*
  - Superfamily Cerithioidea
    - Family Thiaridae
      - *Melanoides*
      - *Thiara*
      - *Pachymelania*
    - Family Melanopsidae
      - *Melanopsis*

Table 1.2 (*cont.*)

	Family Pleuroceridae
	Amphimelania
	Goniobasis
	Pachychilus
	Paludomus
	Brotia
	Juga
	Pleurocera
	Semisulcospira

Source: modified from Vaught (1989).

freshwater members of such primarily marine groups are at present too poorly known to have much impact upon our discussions here.

Most species of gastropods belong to what has for many years been called the subclass Prosobranchia, a universally distrusted collection of taxa not fitting into other groups (Ponder 1988b). They share a few (probably ancestral) characters: they breathe through gills, carry an operculum, and are usually gonochoristic and occasionally parthenogenetic, but only rarely hermaphroditic. Prosobranchs have invaded fresh waters on at least as many occasions as the number of their superfamilies listed in Table 1.2, plus twice again for minor groups (buccinids and marginellids) not treated in this volume. Most of the families are effectively worldwide in distribution: the neritids, viviparids, hydrobiids, pomatiopsids, and pleurocerids. The valvatids are restricted to the northern hemisphere, while the melanopsids and bithyniids were both restricted to the eastern hemisphere until recently. The thiarids and ampullariids are circumtropical, with distributions reaching to the subtropics.

As their name implies, snails of the subclass Pulmonata have lost their gills and now respire over the inner surface of their mantle, effectively a lung. The four major (and several minor) freshwater pulmonate families belong to the order Basommatophora, so named because their eyes are at the base of their tentacles. (The primarily terrestrial Stylommatophora have eyes at their tentacle tips.) They seem to have derived from a single ancient invasion of fresh water, dating at latest to the Jurassic period (Starobogatov 1970). Minor families (including the limpet-shaped Acroloxidae and two others not treated here) are held to be the most ancestral of the freshwater pulmonates, by virtue of anatomical detail (Hubendick 1978). The worldwide Lymnaeidae, with their rather ordinary looking, dextral shells of medium to high spire, are believed the next

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most ancestral. Members of the primarily holarctic Physidae are distinguished by their inflated shells coiled in a left-handed ('sinistral') fashion, quite unusual in the class Gastropoda. Members of the worldwide Planorbidae are also sinistral, but often planispiral. The members of the worldwide Ancylidae are limpet-shaped.

Most freshwater pulmonates carry an air bubble in their mantle cavity, which they replenish periodically at the surface, and which they use to regulate their buoyancy. This allows many species to exploit warm, eutrophic habitats where dissolved oxygen may be quite low. Some (especially smaller, cold-water) species do not seem to surface-breathe, however, and their mantle cavities are found to be filled with water. Pulmonates typically have much lighter shells than prosobranchs, and lack an operculum. Other major, although less immediately apparent, pulmonate distinctions include radulae with many small, simple teeth per row and reproductive hermaphroditism.

Authors have sometimes held that the freshwater environment is more harsh than the marine environment (Macan 1974). Temperature fluctuation is typically more extreme in fresh waters, and freezing more likely. Water levels and current speeds are more unpredictable in fresh waters than in the ocean, as is the chemical composition of the medium. Given that all classes of molluscs evolved in the sea, and all share the same broad body plan, it is not surprising that their freshwater representatives, although quite diverse, display some broad points of resemblance.

Osmoregulatory adaptation is one area of striking similarity. Marine molluscs generally conform to sea water, osmotically equivalent to a 0.56 M solution of NaCl. Freshwater molluscs have evolved much lower body fluid concentrations, the equivalent of about a 0.040–0.070 M NaCl solution for gastropods, and 0.020–0.040 M for bivalves. The osmolalities of freshwater bivalves are among the lowest recorded for any animal (Pynnönen 1991, Dietz *et al.* 1996). By way of comparison, freshwater crustaceans, insects, and fish all generally show osmolalities in excess of 0.100 M as NaCl.

Fresh waters are extremely variable in their ionic concentration, but typically range about the order of 0.005 M NaCl, very much lower than any of the figures cited above. So since molluscan tissues are highly permeable to water, freshwater molluscs nevertheless have substantial osmoregulatory chores to perform. Their overall strategy involves active transport of ions from the medium and production of copious urine hypo-osmotic to their hemolymph. Reviews of water balance and excretion in the freshwater molluscs have been offered by Machin (1975), Burton (1983), Little (1981, 1985), Dietz (1985), and Deaton and Greenberg (1991).

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Active transport of Na^+, Ca^{+2}, and Cl^-, even against sharp concentration gradients, has been documented in all groups of freshwater molluscs. It is not certain whether the process may be localized (the gills are often mentioned) or whether all body surfaces are involved. Ions may also be exported as required to maintain electrical balance, as for example H^+ or NH_3^+, may be exchanged to balance Na^+ uptake, and HCO_3^- exchanged for Cl^- (Byrne and Dietz 1997). Voluminous urine is produced by ultrafiltration of haemolymph across the heart wall of freshwater molluscs into the pericardial cavity, where it is conducted to the kidney. The lining of the kidney resorbs Na^+ and Cl^-, and perhaps Ca^{+2} and K^+ as well.

Osmotic regulation in the reverse direction, balancing salt concentrations higher in the environment than in the organism, is unknown in the Mollusca. Thus the process of adaptation to fresh waters seems to be irreversible. Although some freshwater mollusc populations can be found tolerating low salinities, none has apparently recolonized the sea.

I am not aware of any direct estimates of the energetic cost of osmoregulation in freshwater molluscs. But a wealth of indirect evidence (reviewed in Chapter 8) suggests that in many waters of the earth, the price of osmoregulation may be so high as to limit the success of molluscan colonists. It also seems possible that adaptation to fresh water is at least partly responsible for the suppression of the larval dispersal stages so common in marine molluscs. With their high surface-to-volume ratios and reduced shells, planktonic larvae may simply be unable to gather enough fuel to fire the machinery necessary for osmotic balance. With few exceptions, all freshwater molluscs pass their larval stages in the egg, or enfolded within their parents.

This brings to the fore a second point of general similarity over all groups of freshwater molluscs. They are poor dispersers in an environment notably difficult to colonize. The directionality of freshwater flow is in some places powerful, and in other spots negligible. But without exception, all successful molluscan colonists of fresh waters have adapted to directional flow at some point in their evolutionary history. Osmoregulatory barriers are certainly not the only conceivable explanation for the general absence of a conventional larval stage from the life history of freshwater molluscs. Their turbulent medium interferes with the external union of egg and sperm. Planktonic larvae are swept away.

The general suppression of the larval stage in the freshwater Mollusca has yielded a large group of obligately aquatic organisms that do not swim. Some groups (e.g. the unionoids) have evolved unique solutions to this problem. But on a fine spatial scale, freshwater molluscs appear generally immobile, helpless to avoid predators, parasites, or the ecologist's sampling device. On a coarse geographic scale, one must figure high the likelihood that freshwater mollusc distributions derive from vagaries of chance colonization.

Fretter and Graham (1964) pointed out that hermaphroditism seems to be more common in freshwater molluscs than in those that inhabit the sea. This third point of general similarity may be a consequence of the second, that their dispersal capabilities are so poor. 'Reproductive assurance,' the certainty that all simultaneous hermaphrodites can find at least one partner (themselves), has for years been a leading hypothesis for the origin of hermaphroditism (Heath 1977). I would strengthen Fretter and Graham's generalization a bit by adding that it seems to me that asexual reproduction is more common in freshwater than in marine molluscs. Not only can hermaphroditic pulmonate snails and corbiculoid bivalves self-fertilize, they often do. Parthenogenesis has evolved three times in freshwater prosobranchs, but not in their marine ancestors.

The success that freshwater molluscs have enjoyed, together with their relative immobility, constitute for me the most persuasive arguments for a unified treatment of their ecology. Bivalves and gastropods, pulmonates and prosobranchs, are easier to sample than just about any other animal. A biologist need only walk to the creek bank, or row to mid lake, and drop his or her sampling gear, and the molluscs below are as helpless as ferns. But in contrast to the situation in plants, a biologist can fairly assume that the molluscs inhabiting any patch of sampled habitat are not entirely a function of a passive process, for molluscs are not rooted. They could leave if they wished. Study of population biology or community ecology is thus greatly facilitated.

In the two chapters that follow, emphasis will often come to rest upon the undeniable biological diversity of freshwater molluscs. Touching on the broad themes of habitat, diet, and reproduction in filter-feeding and grazing organisms, the reviews of Chapters 2 and 3 will traverse most of the territory of benthic ecology. But the common elements of the biology of freshwater molluscs will be featured in the six chapters that form the body of this book. A general life history model is developed in Chapter 4, the consequences of competition, predation, and parasitism explored in Chapters 5–7, and all this material is placed into a general community-ecological context in Chapters 8 and 9.

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2 · *Bivalve autecology*

In this chapter we will review a few of the basic attributes of the biology of freshwater bivalves. Although filter feeding might at first seem a relatively simple process, closer examination shows a wide discrepancy between the particles in the medium (often largely inorganic) and the food actually assimilated (diatoms, green and blue-green algal cells, bacteria, and organics both dissolved and suspended). Our discussion of bivalve feeding will be divided into sections on particle retention, ingestion, and assimilation. There is some large-scale diet and habitat specialization in bivalves; *Pisidium* seems to have become adapted to filter waters from within the sediments, sometimes deep in the profundal zone, and *Dreissena* has colonized the hard bottoms. But in general, we will see that all bivalve populations seem to live in about the same habitat and eat about the same food at the same time. In light of the evidence that large populations of bivalves may substantially depress the concentration of suspended particles in even the largest lakes and rivers, the potential for food limitation and both intra- and interspecific competition must be acknowledged.

The freshwater bivalves are quite diverse in their modes of reproduction. We will see that unionoids are gonochoristic (although their mechanisms of sex determination are unclear) with widespread hermaphroditism. Their adaptation to hold developing larvae (‘glochidia’) and impose them parasitically upon fish hosts constitutes one of the more interesting natural history sagas of which I am aware. The corbiculoids are generally hermaphroditic and often self-fertilize, although dioecious populations are common in some groups, and brooding or delayed release of juveniles is again the rule. Thus in the freshwater bivalves we will find examples of both great biological unity and striking biological diversity.

Feeding and digestion

Digestive anatomy

Although morphological details are quite various in the diverse taxa of freshwater bivalves, in broad outline the digestive anatomy in typical unionoids, *Corbicula* and *Dreissena* can be discussed together (Morton 1983). The posterior margin on the mantle of these taxa is modified into an incurrent siphon fringed by sensory tentacles and a smaller, more dorsal excurrent siphon nearby. The term 'siphon' may be somewhat misleading, for these structures are very short and sometimes indistinct, more like holes than tubes. In fact, the posterior mantle of margaritiferid mussels does not form distinct siphons at all, although the path of water flow is the same as in other unionoids. Specialized batteries of cilia on the gills draw water slowly into the mantle cavity, along with any suspended particles not so large as to irritate the tentacles or other sensory devices, moving it anteriorly. Most bivalves have a second, longer set of cilia or cirri on the gills, the 'laterofrontals', acting either as mechanical particle filters or as modulators of fluid mechanical processes capturing particles (Jorgensen 1983). The movement of particles after their entrapment on the gills has been nicely illustrated by Huca *et al.* (1982), for the South American hyriid *Diplodon*, and by Avelar (1993) for the mycetopodid *Fossula*. Filtered water is expelled back posteriorly, often with increased force, presumably to minimize the likelihood of refiltration.

The pattern of water flow described above is the most common in bivalves generally. The corbiculoids have a pair of short, fairly elaborate, well-differentiated posterior siphons. The siphons of *Sphaerium* are fused into a proper tube and may extend 50–100% of the animal's shell length. But interestingly, *Sphaerium* and *Musculium* are apparently also able to take in water through the mantle margin some distance from the siphons.

The unusual manner by which *Pisidium* feeds has attracted a good deal of attention (Mitropolskij 1966a,b, Meier-Brook 1969, Holopainen 1985). Unlike most other bivalves, these little clams often do not maintain direct contact with the water column. They bury beneath the surface and then move through the substrate with umbo down, drawing a current through the ventral mantle margin (rather than the posterior) and ejecting excurrent water and pseudofaeces through the posterior siphon. So although water flow may loop about inside the mantle cavity in a path at least as elaborate as that seen in typical bivalves (Lopez and Holopainen

1987, Holopainen and Lopez 1989), filtered water is not expelled into the same region from which unfiltered water is drawn. The adaptive value of this water flow pattern to a bivalve living below the sediments in a lake is fairly apparent. Water circulation would be negligible in such an environment, so that an individual *Pisidium* would be in danger of refiltering its own medium if it had two siphons side-by- side, as in the usual arrangement. By this reasoning, one would predict that in general, bivalves of any taxon inhabiting more lentic habitats would need some sort of adaptation to minimize refiltration, for example well-developed siphons that may be directed in opposite directions. And one can understand why the margaritiferid mussels, with no siphons at all, might be restricted to areas where good water circulation occurs naturally.

In the last several decades, biologists have become aware that because of the mechanical properties of water, small aquatic organisms experience their environments quite differently from larger ones. Water is effectively more viscous to a small organism and much more difficult to move. In addition to the cilia on its gills, *Pisidium* apparently has rows of cilia on its foot to help it move the syrupy water. So even setting aside microhabitat choice, one would not be surprised to see unidirectional water flow in any very small bivalve. Churchill and Lewis (1924) reported that siphons have not developed in unionid juvenile mussels at 0.2–2.0 mm length, and that incurrent water passes through the anterior mantle of the mussel, about where the foot protrudes. Yeager and colleagues (1994) have described pedal-sweep feeding behaviours in *Villosa* recently shed from their hosts.

In all freshwater bivalves, mucus and particles trapped on the gill are moved forward toward the labial palps by yet a third set of specialized cilia. The palps convey material to the mouth, dropping any excess onto the mantle for expulsion as ‘pseudofaeces’. A short oesophagus leads to an elaborate stomach, with typhlosoles, grooves, ciliated regions, and a rotating crystalline style regulating the flow of mucus and food. Among other functions, the style is a primary source of digestive enzymes. Material is either moved into digestive diverticulae, where digestion seems to be largely intracellular, or to intestine and anus.

Commonly, then, the particles assimilated are only a subset of those ingested, and the particles ingested are only a subset of those retained. If any competition for food occurs between bivalves, it is for particles retained, but a bivalve’s health and success are a function of the particles assimilated. In a discussion of bivalve feeding, it is important to keep the