Solem 1974

FRESHWATER CLAMS

Four groups of clams invaded freshwaters. By far the most conspicuous and diverse are the "unionids," 1 to 10 inches in length, comprising about 1000 species divided among several families, including one group (Family Aetheriidae) whose shells become cemented to the bottom by one valve. These are known as freshwater oysters (Fig. 1) and occur in scattered areas of South America, Africa, and India. Next in abundance are the fingernail clams of the Family Sphaeriidae. These are $\frac{1}{8}$ to $\frac{1}{2}$ inch in diameter bottom dwellers, often extremely abundant, and form a substantial portion of the food taken by many fish. Their young are brooded inside the gills of the

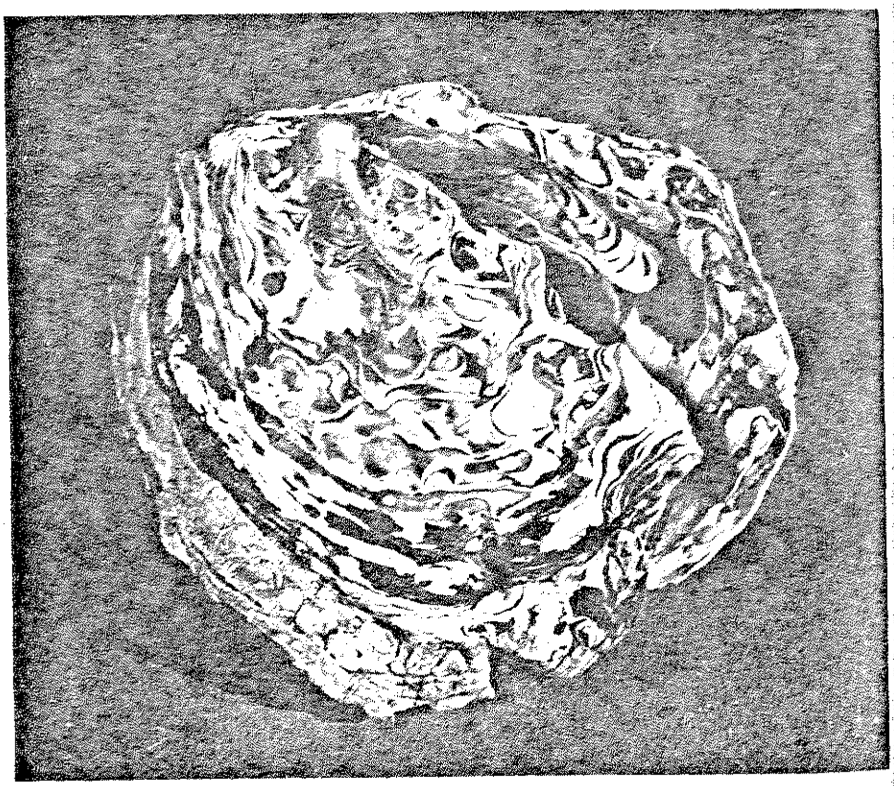

FIGURE 1. A freshwater oyster. *Acostaea,* from the Magdalena River of Columbia, South America. Length $3\frac{1}{2}$ inches.

adults and held there until they reach crawling size. Depending on the species, from 2 to 20 young may be present at any one time. Sphaeriids are found in most permanent bodies of freshwater, where they are occasionally accidentally transported by flying insects or on the feet of water birds.

Members of the Family Corbiculidae were originally absent from North America, although abundant on other continents. Some time in the late 1930s an Oriental species, *Corbicula manilensis,* was accidentally introduced into the United States. It has spread rapidly in the Western States and through much of the Tennessee River system, and will spread much further. At times dead shells can clog irrigation canals several feet deep. The fertilized eggs are brooded inside the gills of the parent and released as swimming young. During a short stage they float in the current, thus being widely dispersed, but soon settle to the bottom, sometimes briefly attached by a byssus, and eventually become burrowing filter feeders. If the floating larvae attach to the sides of water inlet pipes, they can easily grow and clog the pipes completely. In Europe and Asia, *Dreissena polymorpha,* a byssate veneroid clam with a swimming larval stage, has apparently rather recently made the transition from brackish to freshwater situations. It is causing problems similar to those resulting from the spread of *Corbicula.*

The "unionids" are not only the largest in the number of species but biologically perhaps the most interesting. As is typical in the study of clams, their classification is hotly debated between those who depend mostly on the hinge structure and those who study the gills and reproductive systems. Something of a general consensus is emerging. There are distinctive larval types. When this is combined with variations in shell structure which correlate with major geographic areas, a logical and simple classification results:

SUPERFAMILY UNIONACEA

FAMILY MARGARITIFERIDAE (North America and Eurasia)
FAMILY AMBLEMIDAE (United States and Canada)
FAMILY HYRIIDAE (South America and Australasia)
FAMILY UNIONIDAE (worldwide)

SUPERFAMILY MUTELACEA

FAMILY MUTELIDAE (Africa)
FAMILY MYCETOPODIDAE (South America)

The split into two superfamilies is based on differences in how the clam larva functions. Unionids solved the problem of dispersal in a unique way, that is, by spending part of its larval stage as a parasite, usually on a fish.

In species with separate sexes, sperm are released into the water, frequently with the male individuals facing downstream. The females are facing upstream and the sperm is pumped into the inhalent siphon and passed into the gills. Eggs have been released into the "water tubes" inside the gill of the female, where fertilization takes place. The fertilized eggs are brooded inside the gills until they grow into a stage called a "glochidium" in the Unionacea (Fig. 2*e*). At this point the larvae are expelled from the exhalent siphon and drop to the bottom. They lie with their valves opening

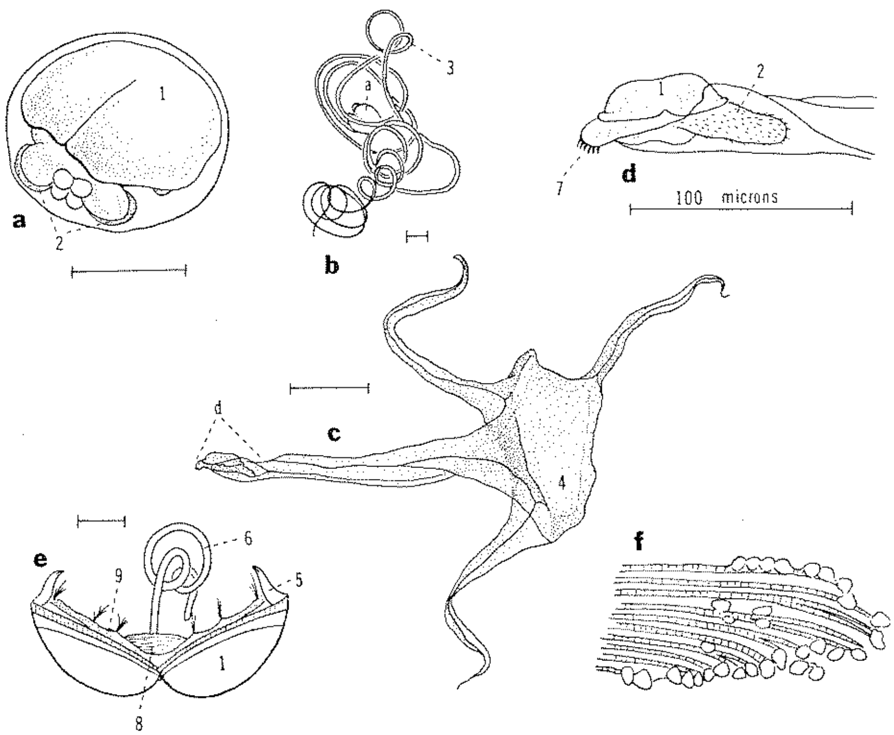

FIGURE 2. Larvae of freshwater unionid clams: (*a*) early haustorium of the African *Mutela bourguignati;* (*b*) later stage of the same species; (*c*) lasidium larva of the South American *Anodontites trapesialis forbesianus;* (*d*) detail of body structure in the same species; (*e*) glochidium larva of the Australian *Velesunio ambiguus;* (*f*) glochidia encysted on the gill of a fish, much enlarged and diagrammatic. Identified structures are larval shell (1), anterior lobe (2), haustoria (3), adhesive organ (4), larval tooth (5), filament (6), hooks (7), adductor muscle (8), and mantle edge (9). *a–b* after Fryer; *c–d* after Bonetto and Excurra; *e* after Parodiz and Bonetto; *f* modified from Lefevre and Curtis.

and closing until they die or come into contact with a fish or salamander. Each clam species has at most a few species that it can parasitize. Frequently only one or two species will be acceptable to the larva. The few lucky larvae clamp onto the gills or body of their host, encyst, and remain as parasites for usually 10 to 20 days, but sometimes as long as six months (Fig. 2*f*). During this time the fish can swim quite a distance. Eventually the larva drops off the gill, sinks to the bottom, and transforms into a juvenile about $\frac{1}{100}$ inch long.

Details differ enormously from species to species, but this basic pattern of a parasitic stage on a fish or salamander characterizes the unionid type clams. It is a wasteful method of reproducing, since only a tiny fraction of the shed "larvae" can hope to encounter a fish body or gill. Once attached, something may eat that fish while the larvae are encysted, or when they fall off they may land on unsuitable bottom. Enormous numbers of larvae must be produced. One study estimated there were 74,000 to 129,000 larvae in a single gravid clam, with a maximum count of 2,225,000 larvae in a specimen of *Leptodea fragilis*. Despite these huge numbers, another study showed that less than 9% of the fish examined were parasitized, although over 30 species of clams were present in that river. There were from 1 to 416 parasites on any single fish, with a maximum of six clam species represented.

Mature females in one group of North American unionids, members of the genus *Lampsilis*, have accessory flaps on the mantle and dark eyespots near their base. Whenever glochidia are ready to be shed, these flaps (Fig. 3) are moved up and down in a way that is characteristic for each species. Undoubtedly this movement would tend to delay settling of the expelled glochidia to the bottom, while to the human eye the appearance of the moving flaps is like that of a small hovering fish. Experimental results were inconclusive, but if a host fish was attracted by these flapping movements, it would be certain to become parasitized by the glochidia.

Since the parasite period of the larva is so important to the dispersal and continued existence of the freshwater unionids, the presence of major differences in the types of larvae has great significance in understanding the evolutionary history of this group. The three larval types are the "haustorium" larva of the Mutelidae, the "lasidium" larva of the Mycetopodidae, and the "glochidium" larva of the Unionacea. The two former types were only discovered and confirmed (respectively) in the 1960s. Far more data are available concerning the glochidium type, known from the mid-1800s, which can be hooked or hookless, with or without the central filament (Fig. 2*e*, 6). The "haustorium" begins as a globular object with anterior ciliated lobes (2) and some posterior hooks (Fig. 2*a*, 7). It fastens to the outside of a

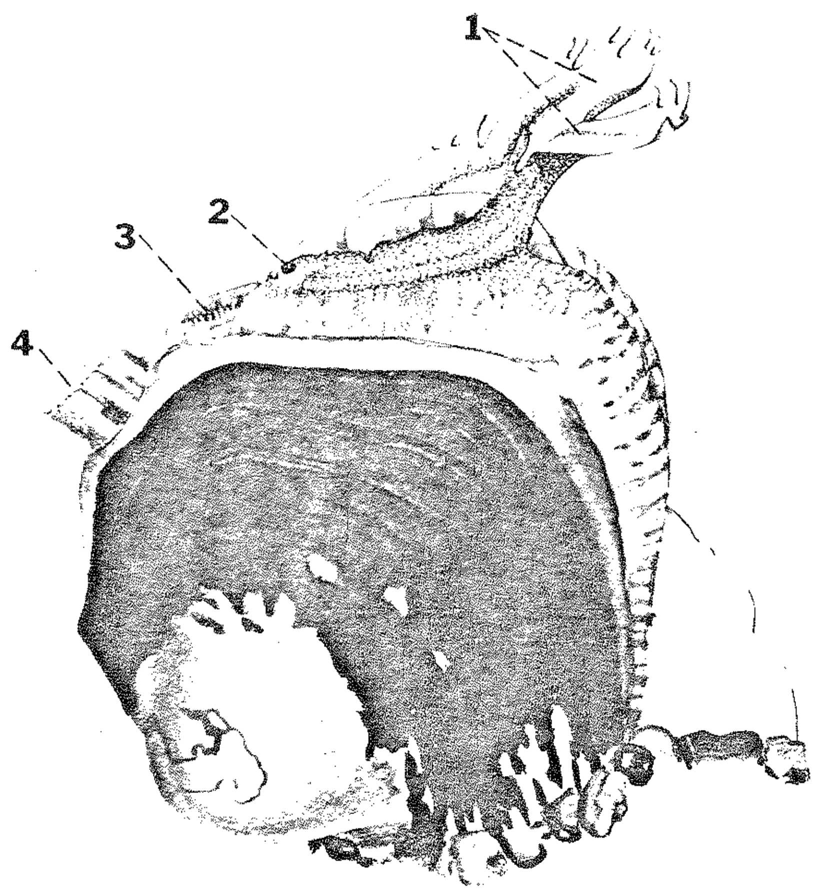

FIGURE 3. Mantle flaps in *Lampsilis siliquoidea* from Arkansas. Identified structures are mantle flaps (1), eyespot (2), inhalent siphon (3) and exhalent siphon (4). Courtesy of Louise Kraemer.

fish, then grows two long tubular "haustoria" (3) that penetrate the tissues of the fish, bind the larva to it, and also serve as a conduit through which fish body juices can be sucked (Fig. 2*b*). The haustorium larva is much larger than the lasidium found in the South American Mycetopodidae. The latter (Fig. 2*c, d*) has a very short body with anterior ciliated lobes (2), caplike shell (1), and posterior hooks (2), but this is attached to an enormous adhesion organ (4) which is used in attaching and encysting. Whether the difference between the glochidium that has two valves when released and the haustorium-lasidium single shell type is significant or merely indicates that the glochidium is retained for a longer period in the female clam is unknown. What is important is that the parasitic larvae of the unionid clams show major differences in structure and mode of functioning.

For unionids to reproduce, both fish and clams must be present. If a clam is put into water without the proper fish, no reproduction is possible. But if a heavily parasitized fish is accidentally carried to a body of water that lacks clams, then a new population of clams can start. Because of their large size and close ties to a fish host, unionids are found mainly in larger bodies of isolated waters or in streams and rivers. Rarely are they found in small ponds. Life history studies of commercially valuable unionids have shown that they may take 7 to 12 years to reach usable size. The total life span is uncertain, although a European species, *Margaritifera margaritifera,* has been aged at 116 years.

As mentioned above, the Eastern United States contained about half of the known unionid species. At the fabled "Mussel Shoals" of the Tennessee River in northern Alabama, before Wilson Dam was constructed, over 70 species of clams lived together. A few headwater streams of the Tennessee-Ohio system still have places where 30 species are found, but the vast majority of shoal dwellers have vanished or are on their way to extinction. Some clam species are adapted to living in the main river channels, and are still abundant, unless killed by pollution. Until World War II they were harvested for cutting into "pearl buttons," but the age of plastics ended this use. In later years the clam fishery was revived. Many Ohio, Tennessee, and Mississippi River species are collected, ground, and tumbled into small pellets, and then shipped to Japan. Inserted into the soft tissue of a living pearl oyster, in a few years they may become the center (nucleus) of a strung cultured pearl that will be exported to the United States.

The best general account of freshwater clams in English remains that given in Baker's *Fresh Water Mollusca of Wisconsin,* but useful identification manuals for several states are listed in Appendix B.

FRESHWATER SNAILS

Many groups of snails have colonized freshwater habitats. The archaeogastropod Family Neritidae, mesogastropods in abundance, and one of the pulmonate superorders, the Basommatophora, are primarily freshwater, but do have some marine and a few semiterrestrial species.