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THE FAMILIES OF THE PEARLY FRESHWATER MUSSELS

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Brooks, in 1875, reporting on North American "*Unio*" (actually Amblemidae), may have been the first to indicate the true story of the development and relationships of the pearly freshwater mussels. He reported that the shell nucleus develops first as an undivided, saddle-shaped structure on the middle of the slightly elongate embryo. This stage corresponds to the lasidium and the haustorium larva of the Mycetopodidae and the Mutelidae. In other words this first stage corresponds to the Mutelacea. Because the embryonic shell is later divided into two distinct valves, the glochidium larva of the Unionacea is considered more advanced. I consider the Unionacea more advanced than the Mutelacea.

The Mutelacea possess the lasidium type of larvae, with the strong development of anterior pallial processes of the mantle, which are in effect attachment processes that grow into the host tissues in a mucus blister on the surface of the host fish. When these larvae are completely mature, they break off their attachment stalks and leave the fish hosts to begin their adult lives. This Superfamily contains the families Mutelidae, Etheriidae, Mycetopodidae and Acostaeidae.

The Family MUTELIDAE, whose haustoria larvae are incubated in the inner gills only, are African. *Spatha, Mutela,* and a few other genera belong here.

The Family ETHERIIDAE (the "freshwater oysters" of the larger African Rivers) are distinct because they are cemented to rocks, or other shells in rapid water. Characteristically they show blistered, greenish nacre. In spite of being attached, they have retained both anterior and posterior adductor muscles. The occurrence of eggs in the inner gills of the females of the *Etheria* mussels indicates their relationship with, and derivation from, the unattached mutelid mussels of the same region.

The Family MYCETOPODIDAE of South America, are gravid in the inner gills only, with the lasidia larvae described first by Von Ihering. These lasidia larvae also attach in a mucus "blister" to the skin of the fishes, then when mature, break off the attachment stalk to start juvenile adult life. One genus, *Anodontites,* is living as far northward as Vera Cruz, Mexico. *Bartlettia* mussels are only modified *Anodontites* hooked into firm (rocky ?) bottoms, but are not cemented on. Most of the Mycetopodidae possess markedly greenish nacre.

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Another Family, the ACOSTAEIDAE, living in the Magdalena River System, are the "South American freshwater oysters". The shells of *Acostaea* are cemented to rocky bottoms, but unlike the "African freshwater oysters", they are modified in the adult to retain only one (the posterior) adductor muscle. Their unblistered greenish colored nacre is so obviously similar to the nacre of the Mycetopodidae from the same region, that I consider them most closely related.

The Unionacea reproduce by means of glochidia larvae, distinctly bivalved from the later embryonic stages onward. With many other characters involved, there is more apparent divergence and/or convergence in this complex of Families. They may have developed from more than one original ancestral stock. This Superfamily contains the Families Margaritiferidae, Hyriidae, Unionidae, Amblemidae and Pseudomulleridae.

The MARGARITIFERIDAE stand alone, not directly in the ancestral line of any other Family. They have retained the most primitive gill structures, with diagonal, incomplete gill septa, and incomplete separation of the siphonal openings. Their very small glochidia, borne in all four gills, are parasitic on the gills of fishes. The very few species are relict, with one species circumpolar, and a very few others southward in southeast Asia, and southeast North America. The only two highly sculptured members of this Family are known from North Vietnam, West of Canton, China, in the Pearl River System, and from the southern United States (southern Alabama and Louisiana).

The HYRIIDAE carry their lop-sided, subtriangular, hooked glochidia in the inner gills only. In South America, *Tetraplodon (Hyria)* and other genera including the widespread *Diplodon* have been studied extensively by Bonetto and other authors. The glochidia larvae of the hyriid mussels are normally parasitic on the external surfaces (fins, tail, etc.) of their host fishes. Bonetto has indicated that some species of *Diplodon* may have secondarily dropped the parasitic stage on fishes and metamorphose directly. With identical characters by definition, this Family must also include the genera and species of the Australian Region often called the Hyridellidae, etc.. It seems there are two Austral Regions, populated by surviving members of the Hyriidae, while mussels we consider more highly specialized moved in behind them, both in Asia and in America.

The Family UNIONIDAE includes mussels that

reproduce by means of triangular, hooked glochidia carried only in the outer gills of the gravid females. These glochidia are normally shed in strings of mucus trailing along the bottom. Chance contact by fish of an appropriate species results in the glochidia being clamped (hooked) onto the fin or tail edge, followed by encystment, and successful parasitism and metamorphosis to the juvenile mussel. The typical genus *Unio* is living from Europe eastward across Asia to China. Other relatives are known from Asia. On the other hand this Family is represented in North American waters only by members of the Subfamily Anodontinae. These North American mussels, as well as all other Anodontinae differ from the typical Unioninae by the partial reduction of, or the complete loss of, the hinge teeth.

The AMBLEMIDAE, the most highly specialized free-living Unionacea, produce hookless glochidia, usually of elongate shape, with short hinge lines. Their glochidia are normally parasitic on the gills of fishes. Some are gravid (carry the glochidia) in all four gills; some in the full length of the outer gills; the most highly specialized in only a part of the outer gills. With one exception, members of the typical Subfamily Ambleminae do not show any sexual dimorphism of the shells. In Africa, Asia, and America, genera of the Ambleminae include some of the smallest and thinnest, as well as the largest and thickest - shelled pearly freshwater mussels known.

The more specialized subfamily Lampsilinae shows permanent modification of the marsupial portions of the outer gills, and a corresponding permanent modification of the shells of the females, resulting in sexual dimorphism of the adult shells.

The necessity of parasitism on the gills of the host fish species has led to a variety of "bait - mechanisms" that serve to induce fish to "mouth" the glochidia, and so enable the glochidia to reach the gill filaments, to be there encysted and undergo their larval metamorphosis. In United States waters, the crimson glochidia of *Fusconaia* species, and the white glochidia of *Pleurobema* and other related genera may be shed in packages (conglutinates) resembling pink or white (flat) worms lying on the bottom. *Cyprogenia* has been recorded as shedding the conglutinates entire; resembling coiled red worms, which are avidly "eaten" by fish. *Ptychobranchus* ejects entire conglutinates which resemble in size, shape, and color, newly hatched fish embryos. A "tasty" morsel to attract predator fish species.

The mantle margins ventral to the siphons, of some of the Lampsilinae of North America, show "fish - bait" structures. The genus *Toxolasma* has small caruncles, which move like "twiddling thumbs" and attract small and/or young fish to eat the "wriggling red worms". *Ligumia* and *Villosa* have papillae that resemble worms of various types. The mantle margins of *Villosa amygdala* from southern Florida possess varicolored brown and green papillae that together resemble a caterpillar that has fallen into the water and is lying on the bottom.

The extreme "fish - bait" structure and mechanism is shown by *Lampsilis* species. The females have an eye-spotted, minnow-like mantle flap below the siphons. These specially innervated flaps move and resemble the intermittent jerking of a wounded minnow. This occurs when the glochidia are ripe in the late spring and the females are "up-ended" in the bottom, thereby fully showing this action. The host fish gets a mouthful of glochidia (burst out of the edge of the marsupia) when it attempts to eat the "wounded minnow".

Another extreme is shown by the blue or white "flags" of certain *Plagiola* species, which may be visible seven metres away in the clear water over the shallows, in their glochidia shedding season. *Plagiola rangiana* Lea was known to local fisherman as the "White Mouth" when it was described 133 years ago.

The Family PSEUDOMULLERIDAE is the third "freshwater oyster" family in the world. *Pseudomulleria* is living in certain rivers of southern India. The juvenile mussel starts as a small bilaterally symmetrical bivalve, then is attached, and changes to retain only one adductor muscle between the asymmetrical attached and free valves of the adult mussel. The general appearance, especially of the nacre of *Pseudomulleria,* is so different from the green nacre of *Acostaea* of South America that they should not be considered members of the same Family. Only examination of the marsupial gills and of the glochidia of *Pseudomulleria* can prove from which other Family of the Unionacea they have been modified.