Heard
1973

ANATOMICAL SYSTEMATICS OF FRESHWATER MUSSELS

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Abstract

Numerous conchological classifications of freshwater mussels [the Mutelacea ("Etheriidae," Mutelidae and Mycetopodidae) and Unionacea (Amblemidae, Hyrridae, Margaritiferidae and Unionidae)] have been promulgated over the past 150 years, yet only Modell (1942, *Arch. Molluskenk.*, 74: 161–191; 1949, *Ibid.*, 78: 29–48; 1964, *Ibid.*, 93: 71–126) suggested phylogenies based on shell features.

Aside from Simpson's (1900, *Proc. U.S. natn. Mus.*, 22: 501–1044) frequently erroneous accounts, inferred from similar shells of different nominal taxa, Ortmann (1910, *Nautilus*, 23: 114–120; 1911, *Ibid.*, 24: 103–108, 114–120, 127–131, pls. 6–7; 1912, *Ann. Carnegie Mus.*, 8: 222–365, pls. 18–20; 1921, *Mem. Carnegie Mus.*, 8: 451–668, pls. 34–48) presented the first, consistent anatomical groupings of freshwater mussels. He considered that species and genera should be defined by shell characters, but that higher taxa should be delineated by soft-part anatomy, larval aspects and duration of incubation. Ortmann's approach was extended and partially revised by Parodiz & Bonetto (1963, *Malacologia*, 1: 179–213) and Heard & Guckert (1970, *Ibid.*, 10: 333–355), and several animal phylogenies were proposed.

As noted by Heard & Guckert (1970, *op. cit.*), shell features are typically not correlated with animal characters, and the use of 1 set of criteria demonstrates extensive parallelism and/or convergence in the other. Recent availability of many anesthetized, fixed and preserved mussels from southeastern Asia and Africa has made possible a more critical analysis of animal features, and the findings indicate that more conservative characters may be associated with reproduction. This report summarizes a provisional scheme of relationships according to the variations found in the marsupial demibranchs. The genera cited are examples only and do not constitute a complete list of taxa showing specific conditions.

The most primitive marsupial condition is that of an irregular patchwork of discontinuous interlamellar connections in the tetragenous (all 4 demibranchs marsupial) Margaritiferidae (*Cumberlandia, Margaritifera*); a partial organization occurs in an oblique orientation of some of the connections in the middle of the demibranchs. Derived from that state, and present in the most primitive (*Gonidea, Megalonaias, Pilsbryoconcha, Pseudodon*) and in the more advanced (*Caelatura, Ensidens, Scabies*) Amblemidae, is one of vertically-oriented septa that are interrupted by perforations. This condition is also found in the endobranchous (only the inner 2 demibranchs marsupial) Hyriidae (*Castalia, Diplodon, Hyria, Hyridella, Prisodon*), primitive endobranchous Mutelidae (*Chelidonopsis arietina, Pseudospatha tanganyikensis*), endobranchous "Etheriidae" (*Etheria elliptica*) and in the primitive exobranchous (only the outer 2 demibranchs marsupial) Unionidae (*Cafferia, Hyriopsis, Physunio, Trapezoideus*). The most advanced amblemids (*Amblema, Plectomerus*), mutelids (*Aspatharia, Mutela*) and unionids (*Anodonta, Elliptio, Pleurobema, Unio*), as well as all investigated endobranchous mycetopodids (*Anodontites, Leila, Mycetopoda*), were derived by the fusion of the perforations. Furthermore, advanced groups of amblemids, mutelids, mycetopodids and unionids also evolved imperforate non-marsupial septa.

In addition to the change in number and location of the marsupia, and in the closure of the perforations in the marsupial and non-marsupial septa, there evolved a dimorphic spacing of the septa in unionaceans. Males, females and hermaphrodites of the most primitive Amblemidae are morphologically indistinguishable (as are margaritiferids) and can be identified only by examining the gonads; all 4 demibranchs in each sex possess perforated septa that are distantly-spaced. However, a dimorphism occurs in presumably all Hyriidae, advanced Amblemidae and all known Unionidae: the non-marsupial demibranchs (all 4 in males and some hermaphrodites, and 0 or 2 in females and some hermaphrodites) and non-marsupial parts of marsupial demibranchs retain distant septa (about 15 filaments between successive septa), whereas the marsupial septa are densely-spaced (about 3 filaments between successive septa). This condition apparently arose by the evolution of additional septa in the marsupia, at first relatively short (still evident) and subsequently increasing in height. In those groups displaying this dimorphism, it is usually possible (except for hermaphrodites) to determine the sex of an individual without examining the gonads. Inadequate information is available about the mutelacean septal spacing in "etheriids" and primitive mutelids, but the most advanced mutelids and all investigated mycetopodids, many of which are hermaphroditic, have distantly-spaced septa in all 4 demibranchs of all individuals.

If marsupial anatomy is used to delineate subfamilial taxa, one finds that each such group possesses both tachytictic (short-term, only in the Nearctic summer) and bradytictic (long-term, except in the Nearctic summer) incubation periods. For example, among the primitive amblemids with perforated, distantly-spaced marsupial and non-marsupial septa, *Gonidea, Pilsbryoconcha* and *Pseudodon* are tachytictic, whereas *Megalonaias* is bradytictic. The duration of incubation may thus be best employed, at least for convenience of communication, in a tribal concept.

Various familial-group and even some generic-group mussels with perforated marsupial septa and a common period of incubation display several kinds of beak sculpture as well as different forms of hinge dentition. Consequently, attempts to analyze fossil shell material present severe difficulties in interpreting phylogenetic affinities, and also zoogeographic relationships. Nevertheless, the animal approach emphasized here shows some distributional patterns.

Margaritiferids, the most primitive mussels, are Holarctic in occurrence and are interpreted as phylogenetic relicts with a contracted range. The most primitive amblemids and unionids range from southeastern Asia to Africa, with a few biogeographical and phylogenetic relicts occurring in North America; the most advanced amblemids and unionids are found in the Nearctic and Palearctic regions. The known hyriids, all presumably comparatively primitive, live in the Australian and Neotropical regions. In the Mutelacea, the very poorly known Recent "etheriids" comprise 1 monotypic genus each in Africa, India and South America, although this assemblage may constitute a composite of mussels of different groups; mutelids are known only from Africa, and mycetopodids are confined to South and Central America.

The primitive amblemids are considered to have given rise to the Mutelidae and "Etheriidae": *Etheria* in Africa and, by way of the eastern Palearctic, to the advanced amblemids of North America (where *Gonidea* and *Megalonaias* occur as relicts). The primitive unionids presumably also migrated across the Bering land bridge into North America, where they evolved into more advanced groups (*Strophitus* and *Uniomerus* persisting as relicts). The Australian hyriids could also have arisen from the primitive amblemids of the Oriental Region. The South American hyriids may have been derived from Oriental amblemids (or hyriids?) that dispersed over an eastern Palearctic-Nearctic route, or from the Australian hyriids through paleantarctic dispersal or perhaps by continental drift. Somewhat similarly, the Neotropical mycetopodids may have been derived from the African mutelids either by way of Ethiopian-Palearctic-Nearctic-Neotropical connections, continental drift or by paleantarctic dispersal.

COMPARATIVE REPRODUCTION IN VIVIPARID SNAILS

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Abstract

The objective of this study, yet in progress, on viviparid reproductive anatomy and seasonal reproductive cycles is to better delineate generic and specific features, and thus to present a basis for the study of other nominal taxa in the family. These snails are ideal subjects for comparative reproductive studies because they are dioecious, sexually dimorphic with respect to the male right tentacle which serves as the copulatory organ, and ovoviviparous, incubating the developing young in the pallial oviduct. The original information presented here was obtained from northern Florida populations of *Campeloma geniculum* (Conrad), *Lioplax pilsbryi* Walker and *Viviparus georgianus* (Lea).

Reproductive systems. Although other malacologists have previously described viviparid reproductive systems in general, there is confusion concerning the identity and function of accessory organs in both males and females. Detailed comparative information is lacking, and little has been done to evaluate the usefulness of anatomical characters in taxonomic and systematic interpretation.

The male system has the same basic organization in all 3 species: testis, proximal vas deferens, seminal vesicle, distal (=pallial) vas deferens, prostate gland and the penial-tentacular complex. What is here termed the seminal vesicle has previously been called the prostate gland, and what is here termed the prostate gland has been considered to be the distal vas deferens (cf. Baker, 1928, *The Fresh Water Mollusca of Wisconsin, Part* 1, *Gastropoda,* Wisc. Acad. Sci., Arts Lett., Madison, Wisc.; van der Schalie, 1965, *Occ. Pap. Mus. Zool., Univ. Mich.,* (611): 1-15). Differences between the 3 taxa occur in the relative size, location and shape of these 6 organs.

The female system consists of an ovary, proximal oviduct, accessory glands and pallial oviduct (= "brood sac"). Again, differences between the 3 taxa occur in the relative size, location and shape of these organs. The identity and specific functions of the accessory glands are unclear. In *Campeloma geniculum* and *Viviparus georgianus,* 2 large glands occur posteriorly and ventrally, respectively, to the brood sac. The larger gland has been identified as the albumen gland (cf. Ankel, 1925, *Senckenbergiana,* 6: 1-12; Baker, 1928, *op. cit.;* Mattox, 1938, *J. Morphol.,* 62: 243-261) and the smaller one as the seminal receptacle or spermatheca (Baker, 1928, *op. cit.;* van der Schalie, 1965, *op. cit.*) or a "shell gland" (Mattox, 1938, *op. cit.*). Histological sections of these 2 glands from *C. geniculum* and *V. georgianus* reveal differences in histological organization, yet presumably mature spermatozoa occur in both glands. In *Lioplax pilsbryi,* only 1 gland is distinct, located at the posterior end of the brood sac. However, the posterior wall of the brood sac appears to be more glandular in nature than in the other 2 species, although histological sections of *L. pilsbryi* females have not yet been made to verify this possibility. In addition, the brood sac in all 3 species appears to have walls that vary in thickness according to different phases of the reproductive cycle. The walls are thick (and glandular?) during incubation of young in early stages of development, but very thin when large shelled developing young are incubating.

Reproductive cycles. Previous life history studies on Nearctic viviparids were conducted by Van Cleave & Altringer (1937, *Amer. Natur.,* 71: 167-184) on *Campeloma rufum* (Haldeman), Medcof (1940, *Can. J. Res.,* 18: 165-172) on *C. tannum,* Mattox, Van Cleave & Chambers (1935, *Amer. Midl. Natur.,* 16: 913-920) on *Lio-*