

CHAPTER 1
INTRODUCTION
AND THE CURRENT STATE OF FRESHWATER MUSSEL AFFAIRS

The Unionoida, commonly known as freshwater pearly mussels or naiads, is a diverse order of bivalved mollusks. Comprised of over 150 genera and flung widely upon all continents except Antarctica, the Unionoida is a conspicuous member of the macrobenthos of the world's rivers and stable lacustrine habitats (Haas, 1969a). Over the last 20 years, there has been a renaissance in freshwater mussel study, especially in North America. Most of that research has dwelt on such topics as fine-scale, intra-drainage distribution patterns and life history traits relevant to applied conservation and propagation issues (see numerous references in Burch, 1975 and Watters, 1994b). This buzz of ecological work focusing on contemporary processes among freshwater mussels has tended to overlook freshwater mussel evolution and the role of historical processes on their current patterns of global morphological diversity and biogeography. This dissertation will present the results of investigations into different aspects of the evolution of the Unionoida. These studies drastically alter the story of freshwater mussel diversification found in the modern biological and paleontological literature. The objectives of this introductory chapter are (1) to provide the necessary background information on freshwater mussel biology by reviewing the pertinent aspects of their life history, classification, and distribution; and (2) to furnish the scientific framework for the analytical chapters that follow.

It is necessary to first orient ourselves on the Tree of Life. Although there has been some incongruence among molluscan classification schemes, most arrangements are

consistent with the Bivalvia split among two subtaxa: Protobranchia and Autobranchia (= Isofilibranchia + Pteriomorpha + Anomalodesmata + Heterodonta + Palaeoheterodonta). According to the current consensus (*e.g.*, Newell, 1969; Boss, 1982; Brusca & Brusca, 1990), the Unionoida belong to the latter in the subclass Palaeoheterodonta (**Table 1.1**). The Recent Palaeoheterodonta, however, receives only a single non-unionoid genus, the marine *Neotrigonia*. The divisions among the Autobranchia and the inclusion of the Unionoida among the Palaeoheterodonta have been based, traditionally, upon hinge morphology (Thiele, 1934; see **Appendix I**).

Freshwater Mussel Life History

As their common name implies, unionoids are confined to freshwater environments. In most other respects, the adult mussel behaves just as one would expect a clam to behave: freshwater mussels are sedentary filter feeders. The reproductive end of their life history, however, is truly extraordinary among the Bivalvia. Freshwater mussel larvae are parasitic, generally upon fishes. Exceptions have been reported wherein some species have completed metamorphosis without a host (Howard & Anson, 1923; Allen, 1924; Parodiz & Bonetto, 1963; Kondo, 1990), and one species, *Simpsonaias ambigua* (Say, 1825), is known to naturally infect *Necturus*, an amphibian (Howard, 1915; Clarke, 1985). Excellent reviews of the freshwater mussel life cycle can be found in Coker *et al.* (1921) and Kat (1984). However, as discussed in Graf (1998), these synopses tend to overlook the more subtle evolutionary consequences of the mussels' parasitic larval life-style.

Freshwater mussels are generally gonochoristic, although there are exceptions (van der Schalie, 1970; Hoeh *et al.*, 1996b). While broadcast spawning is typical for their marine counterparts (and other marine/aquatic invertebrates) (Brusca & Brusca, 1990), fertilization of unionoid ova occurs within the mantle cavity of the female. The

male ejects his sperm directly to the water, and these must be entrained in a female's respiratory current to reach their target. Interestingly, the sperm are packaged in spermatozeugmata (Edgar, 1965; Lynn, 1994; Waller & Lasee, 1997) — also known as “sperm spheres” (Ishibashi *et al.*, 2000). This is similar to the way sperm are packaged in brooding oysters (Ó Foighil, 1989). Spermatozeugmata presumably retard the dilution of the sperm in turbulent water.

The embryos are brooded within the interlamellar spaces of the females' ctenidial demibranchs (figured in Ortmann, 1911c). For the vast majority of species, the brooded embryos develop into parasitic larvae; however, the morphology can differ drastically among the major freshwater mussel taxa (Parodiz & Bonetto, 1963; Heard & Guckert, 1971). When ripe, the larvae are released to meet a host. The larvae generally reach their host passively (Lefevre & Curtis, 1910), although some genera, such as *Lampsilis*, have evolved morphologies and behaviors (reviewed in Kat, 1984; see also O'Brien & Brim Box, 1999) for attracting potential hosts to the female before she releases her brood.

It is while encysted in the gill or fin epithelium of a suitable host that the larva can complete its metamorphosis into a free-living juvenile (Lefevre & Curtis, 1910, 1912). That is, the mussel begins formation of its postlarval/juvenile shell and internal organs. When metamorphosis is complete, the unionoid uses its new foot to break free of the cyst, falls to the bottom, and takes on the habits of an adult bivalve. The juvenile freshwater mussel may sediment-feed for a period before its ctenidia are fully matured, and it can begin suspension feeding (Yeager *et al.*, 1994; Gatenby *et al.*, 1997).

To counteract the inefficiency of their complicated life cycle, freshwater mussels tend to live for long periods — decades to over a century in some cases (Ziuganov *et al.*, 1994; Bauer, 2001). While the parasitic aspect of freshwater mussel reproduction certainly drives microevolutionary phenomena (Graf, 1998), an important macroevolutionary consequence of this interaction (*i.e.*, reliance upon freshwater fishes for not only survival but also dispersal) is that the Unionoida is (and apparently always

has been) constrained to freshwater. The mussels have no overland vagility (Graf, 1997b) and little opportunity or tolerance for marine dispersal (Sepkoski & Rex, 1974; Atrill *et al.*, 1996; but see discussions in Kat, 1983 and Strayer, 1987). Thus, the Unionoida is a strictly continental clade.

The basic reproductive information summarized in the preceding paragraphs is widely known, and it has been recapitulated or figured in the introductory chapters of many handbooks on freshwater mussels (*e.g.*, Oesch, 1984; Cummings & Mayer, 1992; Parmalee & Bogan, 1998). While a detailed knowledge of the specific life cycle (*i.e.*, duration, hosts) for many species is wanting, the scuttle for life history information has tended to overshadow, in recent years, evolutionary studies of freshwater mussel natural history. This is unfortunate as freshwater mussels present many interesting phylogenetic and biogeographic patterns.

Freshwater Mussel Classification

The most recent, comprehensive treatments of the Unionoida were those of Haas (1969a, b), and those two different perspectives — diversity and stratigraphy — upon the same topic illuminate a wealth of unexplored relationships, distributions, and other historical, evolutionary patterns. The Recent global diversity, continental ranges, and paleontological stratigraphy based on Haas's work are presented in **Table 1.2**. Graphic representations of the taxonomic and geographic diversity of the Unionoida are shown in **Figure 1.1**. The taxonomic 'arrangement' (*sensu* Wiley, 1980) has been updated to be consistent among the numerous available systems (see below) and is explained in greater detail in **Appendix II**.

The general consensus, based on various malacological schools of taxonomy (*e.g.*, Simpson, 1900, 1914; Ortmann, 1910a, 1911a, b, 1912b, 1921a; Frierson, 1927; Modell, 1942, 1949, 1964; Morrison, 1956, 1973; McMichael & Hiscock, 1958; Pain &

Woodward, 1961; Parodiz & Bonetto, 1963; Haas, 1969a, b; Heard & Guckert, 1971; Davis & Fuller, 1981; Boss, 1982; Korniushev, 1998), is that the Unionoida is composed of six families: Margaritiferidae, Unionidae, Hyriidae, Iridinidae, Mycetopodidae, and Etheriidae. While there seems to be widespread agreement upon the recognition of these taxa (reviewed in **Appendix II**), there is confusion regarding their precise generic composition and phylogeny.

The diagnoses of these six families are generally based on soft-anatomical and life history characters. Although other malacologists at other times (*e.g.*, Simpson, 1900, 1914; Modell, 1942, 1949, 1964) have relied more heavily upon shell morphology, it is the influence of Arnold E. Ortmann's (1909-1924) malacological-vs.-conchological perspective that has persisted into the modern era of freshwater mussel systematics (*i.e.*, Haas, 1969a, b; Heard & Guckert, 1971; Davis & Fuller, 1981). While there have been disagreements regarding the details of the family-level arrangement of the Unionoida, a meaningful consensus can be derived (**Table 1.2**).

The Unionidae, Margaritiferidae, and Hyriidae have, in recent decades, been associated as the Superfamily Unionoidea based upon their shared possession of glochidium-type parasitic larvae (Parodiz & Bonetto, 1963). Glochidia are small (60-350 μm), bivalved larvae (**Figure III.3**). Besides the morphological differences among the glochidia of the three families, the Unionidae, Margaritiferidae, and Hyriidae are readily distinguishable based upon their adult anatomy (Ortmann, 1911a, 1912b, 1921a; Heard & Guckert, 1971).

The Unionidae is the most diverse and widespread family of freshwater mussels, with over 670 species in roughly 120 genera (**Table 1.2 & Figure 1.1**). This taxonomic and geographic diversity has led to ample infra-familial classification (see Modell, 1942 or Pain & Woodward, 1968, for example). The most recent re-analysis of the system of the Unionidae is that of Davis & Fuller (1981). Most subsequent considerations (*e.g.*, Lydeard *et al.*, 1996; Parmalee & Bogan, 1998) have agreed that the numerous unionid

tribes should be divided among two subfamilies, Anodontinae (**Figure 1.2**) and Unioninae (**Figures 1.3-6**). The classification of the Unionidae is discussed in more detail in **Appendix II**, and the morphology of the Unionoida in general is described in **Appendix III**.

Three morphological characters have been used to diagnose the Unionidae:

- (1) the presence of a supra-anal aperture,
- (2) what is known as a ‘slightly incomplete’ diaphragm dividing the inhalant from the exhalent chambers of the mantle cavity, and
- (3) possession of either a tetragenous or ectobranchous marsupial arrangement.

A supra-anal aperture is formed by a short, pallial fusion dorsal to the excurrent aperture. This fusion creates a third opening and is the only fusion of the left and right lobes of the mantle among the Unionidae (with the exception of where the lobes are joined beneath the umbo). The absence of fusion of the mantle is considered primitive among the Bivalvia (Waller, 1998).

The absence of pallial fusion between the incurrent and excurrent apertures contributes to the incomplete nature of the diaphragm dividing the infrabranchial/inhalant and suprabranchial/exhalent chambers of the posterior mantle cavity. However, the diaphragm is only ‘slightly incomplete’ (Davis & Fuller, 1981) since the isolation of these two chambers is accomplished by the ctenidia. The ascending lamellae of the inner demibranchs of the ctenidia are fused to each other behind the foot, and the ascending lamellae of the outer demibranchs are fused to the mantle along their entire length. Thus, without *actual* fusion, the lobes of the mantle between the incurrent and excurrent apertures are brought into contact.

The parasitic glochidia are often brooded in only a portion of the females’ two pairs of demibranchs. Sometimes only the outer pair of demibranchs serve as marsupia (ectobranchy), or only the inner pair (endobranchy), or, in other cases, all four (tetrageny). Among the Unionidae, most genera use either just the outer demibranchs for

brooding, or they use all four. There are, however, rare exceptions of endobranchous unionids (Kondo, 1984, 1990). The marsupial arrangement of the demibranchs has been considered of prime importance for classification within the Unionidae, as well as for the Unionoidea generally (Ortmann, 1912b; Heard & Guckert, 1971).

The nearly unanimous assumption has been that the Margaritiferidae (**Figure 1.7**) are primitive among the Unionoidea based upon the relatively simple morphology of its constituent genera (Heard & Guckert, 1971; Heard, 1974; Davis & Fuller, 1981; Lydeard *et al.*, 1996). For the most part, the family has been diagnosed by its *lack* of characters. Margaritiferids lack pallial fusion dorsal to the excurrent aperture, and, thus, they have no supra-anal aperture. The diaphragm dividing the infra- from the suprabranchial chamber is grossly incomplete, without posterior fusion of the ascending lamellae of the outer demibranchs to the adjacent mantle in addition to the absence of fusion between the incurrent and excurrent apertures. Limited separation of the infra- from the suprabranchial chamber is accomplished by ‘diaphragmatic septa’ emanating from the walls of the mantle cavity (Smith, 1980).

In contrast, the Hyriidae (**Figure 1.8**) exhibit several elaborations to the unionid condition (Ortmann, 1921a). The diaphragm is complete, achieving separation of the infra- from the suprabranchial chambers not only through fusion of the ctenidia (to each other and to the mantle) but also by fusion of the left and right mantle lobes in-between the incurrent and excurrent apertures. The hyriid marsupium occupies only the inner demibranchs; thus, the Hyriidae is exclusively endobranchous. Also in contrast to the Unionidae, the pallial fusion dorsal to the excurrent aperture is complete. That is, rather than re-opening to produce a supra-anal aperture, the postero-dorsal margin is closed. The adult morphology of the Hyriidae is similar to that of the Iridinidae, Mycetopodidae, and Etheriidae, but those latter three families are widely considered to comprise the second unionoid superfamily, the Etherioidea.

Whereas the Unionoidea possess glochidia, the parasitic larval form of the Etherioidea is known as a lasidium. Lasidium larvae, like glochidia, are also small (85-150 μm), but they are of a wholly different morphology. The lasidia are univalved, non-calcareous, and possess a conspicuous posterior ribbon. Parodiz & Bonetto (1963), after examining the freshwater mussels of South America, identified larval morphology (glochidium vs. lasidium) as the essential character with which to divide the Unionoidea, and their scheme has been followed ever since (Haas, 1969a, b; Heard & Guckert, 1971; Boss, 1982).

The adult morphology of the etherioidean families is less variable than among the families of the Unionoidea. The soft-anatomy of the Mycetopodidae (**Figure 1.9**) is very similar to that described above for the Hyriidae, with the exception that there is usually no pallial fusion dorsal to the excurrent aperture (Parodiz & Bonetto, 1963; Boss, 1982). The three genera of the Etheriidae are of like morphology to the mycetopodids, the former family differing principally in their cementing habit and consequently asymmetrical valves (**Figure 1.9**) (Heard & Vail, 1976a).

The last unionoid family, the Iridinidae (**Figure 1.10**), shares several adult anatomical characters with the Mycetopodidae, Etheriidae and Hyriidae (Unionoidea):

- (1) larval brooding is done in the inner pair of demibranchs (endobranchy),
- (2) the diaphragm is complete, formed by fusion among the ctenidia and the lobes of the mantle, and
- (3) pallial fusion above the excurrent aperture is complete.

These points of posterior pallial fusion are further developed in the Iridinidae than among hyriids. Iridinids generally possess siphons that are similar to those described among many veneroid genera, and these siphons are often complete with pallial sinuses (Bloomer, 1932; Heard & Dougherty, 1980).