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# Freshwater bivalve (Unioniformes) diversity, systematics, and evolution: status and future directions

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# Freshwater bivalve (Unioniformes) diversity, systematics, and evolution: status and future directions

## Abstract

Freshwater bivalves of the order Unioniformes represent the largest bivalve radiation in freshwater. The unioniform radiation is unique in the class Bivalvia because it has an obligate parasitic larval stage on the gills or fins of fish; it is divided into 6 families, 181 genera, and ~800 species. These families are distributed across 6 of the 7 continents and represent the most endangered group of freshwater animals alive today. North American unioniform bivalves have been the subject of study and illustration since Martin Lister, 1686, and over the past 320 y, significant gains have been made in our understanding of the evolutionary history and systematics of these animals. Here, the current state of unioniform systematics and evolution is summarized, and suggestions for future research themes are proposed. Advancement in the areas of systematics and evolutionary relationships within the Unioniformes will require a resurgence of survey work and reevaluation of all taxa, especially outside of North America and Western Europe. This work will require collection of animals for shell morphology, comparative anatomy, and molecular analyses. Along with reexamination of described taxa, a renewed emphasis on the natural history, host-fish relationships, ecology, and physiology of these animals is needed. Traditional conchological and anatomical characters should be reevaluated, new character suites should be added, and new morphometric methods should be applied. The fossil record of freshwater bivalves should be carefully reviewed, and phylogenetic hypotheses including fossil taxa must be developed. We will have to expand our set of molecular tools to include or develop additional markers, such as single-copy nuclear genes and microsatellites. Examination of double uniparental inheritance of mitochondrial deoxyribonucleic acid (DNA) is providing new insights into the evolution of this order. Mitochondrial gene order differs among genera but is still to be explored. Expansion of our understanding of the evolutionary relationships and history of unioniform bivalves will provide a solid foundation to study the zoogeography of these rather sessile, obligate freshwater organisms. The unique natural history of unioniform bivalves provides a fertile area for testing and developing evolutionary theories, and, as our understanding of the systematics of these animals improves, a better understanding of the evolution of this expansive radiation in freshwater will develop.

## Keywords

Unioniformes, mussels, bivalves, macroinvertebrates, benthic, clams

## Disciplines

Evolution | Genetics | Marine Biology | Natural Resources Management and Policy | Terrestrial and Aquatic Ecology

## Comments

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## Freshwater bivalve (Unioniformes) diversity, systematics, and evolution: status and future directions

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**Abstract.** Freshwater bivalves of the order Unioniformes represent the largest bivalve radiation in freshwater. The unioniform radiation is unique in the class Bivalvia because it has an obligate parasitic larval stage on the gills or fins of fish; it is divided into 6 families, 181 genera, and ~800 species. These families are distributed across 6 of the 7 continents and represent the most endangered group of freshwater animals alive today. North American unioniform bivalves have been the subject of study and illustration since Martin Lister, 1686, and over the past 320 y, significant gains have been made in our understanding of the evolutionary history and systematics of these animals. Here, the current state of unioniform systematics and evolution is summarized, and suggestions for future research themes are proposed. Advancement in the areas of systematics and evolutionary relationships within the Unioniformes will require a resurgence of survey work and reevaluation of all taxa, especially outside of North America and Western Europe. This work will require collection of animals for shell morphology, comparative anatomy, and molecular analyses. Along with reexamination of described taxa, a renewed emphasis on the natural history, host-fish relationships, ecology, and physiology of these animals is needed. Traditional conchological and anatomical characters should be reevaluated, new character suites should be added, and new morphometric methods should be applied. The fossil record of freshwater bivalves should be carefully reviewed, and phylogenetic hypotheses including fossil taxa must be developed. We will have to expand our set of molecular tools to include or develop additional markers, such as single-copy nuclear genes and microsatellites. Examination of double uniparental inheritance of mitochondrial deoxyribonucleic acid (DNA) is providing new insights into the evolution of this order. Mitochondrial gene order differs among genera but is still to be explored. Expansion of our understanding of the evolutionary relationships and history of unioniform bivalves will provide a solid foundation to study the zoogeography of these rather sessile, obligate freshwater organisms. The unique natural history of unioniform bivalves provides a fertile area for testing and developing evolutionary theories, and, as our understanding of the systematics of these animals improves, a better understanding of the evolution of this expansive radiation in freshwater will develop.

**Key words:** Unioniformes, mussels, bivalves, macroinvertebrates, benthic, clams.

Freshwater bivalves of the order Unioniformes represent the largest bivalve radiation in freshwater. This diverse assemblage is divided into 6 families, 181 genera, and ~800 species (Table 1). These families are distributed across 6 of the 7 continents (Figs 1–6) and represent the most endangered group of freshwater animals alive today (Graf and Cummings 2006, Bogan 2008). This radiation is unique in the class

Bivalvia because its members display parental care via brooding of eggs and immature larvae, and the larvae are obligate parasites of fishes (Wächtler et al. 2001).

We have chosen to use the ordinal name Unioniformes Rafinesque, 1820 (Rafinesque 1820) rather than Unionoida Stoliczka, 1871 (Stoliczka 1871) following the suggestions of Starobogatov (1991). This ordinal name follows the ordinal-level suffix (-iformes) used in other animal groups (e.g., birds and fishes) and is used many times in the Russian literature. Use of Unioniformes removes the confusion of whether unionoid refers to the

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TABLE 1. List of freshwater bivalve families and number of genera and species in fresh water (Bogan, 2008).

Order	Family	Number of genera	Number of species
Arcoida	Arcidae	1	4
Mytiloida	Mytilidae	3	5
Unioniformes	Etheriidae	1	1
	Hyriidae	17	83
	Iridinidae	6	41
	Margaritiferidae	3	12
	Mycetopodidae	12	39
	Unionidae	142	620
Veneroida	Cardiidae	2	5
	Corbiculidae	3	6 <sup>a</sup>
	Sphaeriidae	8	196
	Dreissenidae	3	5
	Solenidae	1	1
	Donacidae	2	2
	Navaculidae	1	2
Myoida	Corbulidae	1	1
	Erodonidae	2	2
	Teridinidae	1	1
Anomalodesmata	Lyonsiidae	1	1
Total		209	1026

<sup>a</sup> The total number of species in the Corbiculidae is unknown at this time. The group is overdescribed based on shell variation

order (Unionoida) or superfamily (Unionoidea) when the term unionoid is used to discuss higher groups.

**A Review of the Study of Unioniform Bivalves**

*Freshwater mussel researchers*

Unioniform bivalves have been the subject of study since at least Aristotle and have been figured in the early printed volumes of Konrad Gesner (1553) (Fig. 7) and Olaus Magnus (1555). The earliest work illustrating unionids from North America is by Martin Lister (1685–1688), who figured unionid specimens from Virginia (Fig. 8). The current state of unioniform systematics and evolution is summarized here.

The classification history of the Unioniformes begins with Linnaeus (1758), in which several unionoid species were lumped together with marine species into the genus *Mya*. Shortly thereafter, freshwater bivalve taxa recognized by Linnaeus were moved to new genera, and new classifications were proposed (e.g., Retzius 1788, Lamarck 1799).

Thomas Say (1817) wrote the first paper on mollusks by an American author and described both land and freshwater mollusks. Say (1818) erected the genus *Alasmidonta*. He was followed by Lamarck (1819), who published a paper describing 71 new taxa of unioni-



FIG. 1. Distribution of the Etheriidae. Modified from Bogan (2008).



FIG. 2. Distribution of the Hyriidae. Modified from Bogan (2008).

forms, some from North America, but did not illustrate them. C. S. Rafinesque also entered the fray with several short papers listing genera and species to be described. Rafinesque (1820) described 3 new subfamilies, 12 genera, and 68 species from the Ohio River basin. Barnes (1823) set the standard for describing and illustrating new species.

Isaac Lea, a wealthy lawyer and publisher in Philadelphia, established himself as the leading figure studying freshwater bivalves, and he was one of the first to attempt something approaching a global synthesis of freshwater mussels. He published 239 papers and described 851 modern and fossil bivalve taxa (Scudder 1885). His view of the classification of the Unionidae was published in the 4 editions of his synopsis (Lea 1836, 1838, 1852, 1870). Lea chose to keep all of the species in several genera and not to recognize other genera until the anatomies of all described species were known.

Timothy Conrad was born in Trenton, New Jersey, and held positions as a geologist and paleontologist. One of his early publications was a small volume describing new freshwater mollusk species from the southeastern USA (Conrad 1834). Conrad (1835–1840) attempted to produce a monograph of the family Unionidae. He is probably best remembered for his

attempt to correct the synonymy of unionoids presented by Lea in his synopsis (Conrad 1853). This paper angered Lea, who responded viciously to defend the priority of his named taxa (Lea 1854, 1872). A recently arrival to the USA in 1846, Louis Agassiz wasted little time in making contributions to North American freshwater malacology. In 1852, Agassiz, recognizing the generic diversity already described by Rafinesque, erected a number of new genera in the North American fauna (Agassiz 1852).

After the death of Isaac Lea in 1886, the Lea family approached Charles T. Simpson with a request to produce a 5<sup>th</sup> edition of Lea's synopsis (Lea 1870). Simpson was employed at the US National Museum as a staff scientist and had already published extensively on freshwater mussels. In 1900, Simpson published an expanded and modified version of Lea's ideas, producing a synopsis of the world unioniform bivalves (Simpson 1900). This volume was closely followed by his much-expanded descriptive catalog (Simpson 1914). His classification was based largely on the portion and the number of demibranches included in the marsupium, the portion of the demibranch(s) in which the female broods her larvae.

Arnold E. Ortmann was a student of famed zoologist Ernst Haeckel. Ortmann immigrated to the



FIG. 3. Distribution of the Iridinidae. Modified from Bogan (2008).

USA in 1894 and was hired as an invertebrate paleontologist at Princeton University. By 1900, Ortmann was a curator at the Carnegie Museum of Natural History, Pittsburgh, and would soon begin to publish papers on freshwater mussels. Ortmann described the anatomy of freshwater mussels and used these data for his revisions of Simpson's works (Ortmann 1912, 1919, 1921, 1923a, b, 1924a). These data were complemented by his faunal surveys in Pennsylvania and the southeastern USA (e.g., Ortmann 1909, 1913, 1918, 1924b, c, 1925, 1926). He expanded the concept that mussel shell shape was related to the location of the organism in the drainage (Ortmann 1920). Ortmann and Walker (1922), with the arbitration of H. A. Pilsbry, addressed some of the nomenclatural problems surrounding Rafinesque's freshwater bivalve names that had been ignored by Lea.

Lorraine Screven Frierson was another early author on freshwater mussels. Within the span of his malacological career, he published >50 papers on freshwater mussels. The most significant of these papers was a classification and annotated list of the freshwater mussels of North America that recognized some of Rafinesque's overlooked taxa (Frierson 1927). This paper was the last complete listing of the North American unioniform fauna after Simpson (1914) for >40 y.

Modell (1942, 1949, 1964) developed a classification of freshwater bivalves that focused on the umbonal sculpture but recognized some additional shell and soft-anatomy characters. He included the fossil record wherever possible and greatly expanded the higher classification of Unioniformes.

Parodiz and Bonetto (1963) produced a new higher classification for 5 of the 6 families of unioniforms that was based on larval stage: Unionacea (= Unionoidea) with glochidial larvae (Hyriidae, Margaritiferidae, Unionidae), and Mutelacea (= Etherioidea) with lasidial and haustorial larvae (Mutelidae [= Iridinidae] and Mycetopodidae). The larval stage of the Etheriidae was unknown, so it was not included in their classification scheme.

Haas (1969a) published the next major monograph covering the classification of the unioniform bivalves of the world. He followed the checklist of Frierson (1927) for the organization of the North American unioniform bivalves. Haas (1969b) wrote the unioniform section of the bivalve volume of the *Treatise on Invertebrate Paleontology*, using a slightly different classification.

Starobogatov (1970), working at the Zoological Institute, Russian Academy of Sciences, St. Petersburg, produced a survey of the freshwater mollusks of the world. He elevated a number of taxa, introduced a



FIG. 4. Distribution of the Margaritiferidae. Modified from Bogan (2008).

large number of higher taxa, and split many recognized groups. Starobogatov's classification appears to have been based on the earlier work of Modell. He subsequently revised and inflated the classification of the Margaritiferidae (Starobogatov 1995). Smith (2001) revised the classification of the Margaritiferidae based on his concepts of the anatomy and shell morphology. However, none of these early classification schemes is supported by further phylogenetic studies of morphological or genetic data.

During the last ½ of the 20<sup>th</sup> century, several state field guides to the freshwater bivalves were produced. These field guides varied in depth of coverage, but all provided an entrance into the study of this fauna (e.g., Florida: Clench and Turner 1956, Johnson 1972; Kansas: Murray and Leonard 1962; Illinois: Parmalee 1967; Louisiana: Vidrine 1993; Texas: Howells et al. 1996; Missouri: Oesch 1995; New York: Strayer and Jirka 1997; Tennessee: Parmalee and Bogan 1998). A field guide to the unionoid bivalves of the USA with a key and line drawings was produced for the Environmental Protection Agency as part of their series *Biota of Freshwater Ecosystems: Identification Manual* (Burch 1973). This field guide was subsequently modified and updated (Burch 1975).

Standardization of the taxonomy and common names was initiated by the American Fisheries Society and the American Malacological Union supported by the Council of Systematic Malacologists Committee on Common and Scientific Names. This effort resulted in a peer-reviewed, standardized checklist of the common and scientific names of the land, freshwater, and marine mollusks of North America (Turgeon et al. 1988, 1998).

#### *Families of the Unioniformes*

The order Unioniformes is composed of 6 families, all of which have an obligate parasitic larval stage on either the gills, fins, or sides of host fish (Wächtler et al. 2001). The Hyriidae, Margaritiferidae, and Unionidae all have glochidial larvae, and Parodiz and Bonetto (1963) used this character as the basis for placing these families in the superfamily Unionoidea. The Iridinidae and Mycetopodidae have lasidial larvae, and Parodiz and Bonetto (1963) placed these families in the Mutelacea (= Etherioidea). Etheriidae were not discussed because their larval structure was unknown.

The Margaritiferidae and Unionidae have no mantle fusion that results in incurrent and excurrent apertures, whereas the other 4 families (Hyriidae, Etheriidae, Iridinidae, and Mycetopodidae) have



FIG. 5. Distribution of the Mycetopodidae. Modified from Bogan (2008).

some degree of fusion that results in, at least, a completely fused excurrent siphon and, often, a completely fused incurrent siphon (Ortmann 1912). This separation has been confirmed by recent phylogenetic work (Roe and Hoeh 2003, Graf and Cummings 2006, Walker et al. 2006a).

The Etheriidae, represented by a single genus and species, is a cemented freshwater oyster that lives in Africa and extreme northwest Madagascar (Pilsbry and Bequaert 1927) (Fig. 1). The larval stage of the Etheriidae is unknown. Formerly, this family was thought to contain 2 or 3 other genera (Yonge 1962, 1978, Mansur and da Silva 1990, Bonetto 1997). However, based on anatomy and deoxyribonucleic acid (DNA) sequence data, *Pseudomulleria dalyi* (Smith, 1898) from southern India was shown to belong to the Unionidae, and *Acostaea rivolii* (Deshayes, 1827) from the Rio Magdalena in Colombia was shown to belong to the Mycetopodidae (Arteaga-Sogamoso 1994, Bogan and Hoeh 2000).

The Hyriidae is a monophyletic group that contains 17 genera and has a distribution including South America (9 genera) and Australia, New Zealand, and New Guinea (8 genera) (McMichael and Hiscock 1958, Smith 1992, Walker et al. 2001) (Fig. 2). The mussels of this family brood developing glochidia only in the inner

gills, and the larvae bear a superficial resemblance to those of anodontine mussels in the Unionidae. The classification of hyriid genera is based almost completely on shell structures, and the genera in the Hyriidae tend to form sister clades that reflect their geographic distribution. The relationship of the Hyriidae to other unioniform families is still uncertain at this time (Hoeh et al. 1998, 1999, 2001, Graf and Cummings 2006). Walker et al. (2001) moved the genus *Haasodonta* from the Hyriidae to the Unionidae and made it the only representative of the Unionidae east of Wallace's Line.

The Iridinidae (+Mutelidae) has a lasidial larval stage (lasidium) and a secondary larval stage (haustorium) that attaches to the sides of fishes (Fryer 1961, Wächtler et al. 2001). The 6 genera of the Iridinidae are restricted to the Nile River basin and sub-Saharan Africa (Mandahl-Barth 1988, Daget 1998) (Fig. 3). The Iridinidae brood developing lasidia only in the inner gills, and one species is hermaphroditic (Walker et al. 2006b).

The Margaritiferidae contains 3 genera. The margaritiferid species are distributed across the Holarctic (Fig. 4), with a single representative in Morocco, North Africa (Van Damme 1984). This family has been considered the most primitive unionoidean family, and the shells of this family can be distinguished



FIG. 6. Distribution of the Unionidae. Modified from Bogan (2008).

readily by the presence of mantle attachment scars on the inside center of the shell. All 4 gills form the marsupium for brooding developing glochidia. Neither of the most recent classifications of the Margaritiferidae provided by Starobogatov (1995) and Smith (2001) is supported by current research using mitochondrial DNA sequence data (e.g., Huff et al. 2004).

The Mycetopodidae have a lasidial larval stage (lasidium) that attaches to the sides of host fish (Wächtler et al. 2001). This family contains 12 genera. It occurs in South America, and its range extends up the western side of Central America to west-central Mexico (Fig. 5). The Mycetopodidae brood the developing lasidia only in the inner gills.

The Unionidae contain ~142 genera. The family is found in North America (50), Europe (5), Africa, including extreme northwest Madagascar (11), and Asia (48), including one genus in New Guinea formerly placed in the Hyriidae (Walker et al. 2001) (Fig. 6). The 2 major unionid radiations are found in: 1) the south-eastern USA, including the Tennessee, Cumberland, and Mobile River basins (Parmalee and Bogan 1998, Williams et al., in press), and 2) Asia, extending from extreme eastern Iran, Afghanistan, Nepal, India, and Myanmar, east to Sumatra, Java, Borneo, the Philippine Islands, the Indo-Malay peninsula, China, and Japan,

and north to the Amur River of China and Siberia (Haas 1969a, Brandt 1974, Liu 1979, Đặng et al. 1980, Subba Rao 1989). These 2 areas represent the 2 oldest unundated or unglaciated regions of the world. The animals in this family use all 4 gills or the entire or restricted portions of the outer gill for the marsupium and brooding developing glochidia.

#### *Phylogenetic research*

The history of modern phylogenetic analysis relating to the Unioniformes most likely begins with the publication of Heard and Guckert (1970). Heard and Guckert (1970) reevaluated the classification for the North American Unionacea (Margaritiferidae and Unionidae) and proposed a classification based on several anatomical characters. Although not phylogenetic by today's standards, the paper was a point of departure for future analyses that used a more objective approach than previous works had used. Davis and Fuller (1981) used immunoelectrophoretic data to test the hypothesis put forward by Heard and Guckert (1970) and arrived at a more conservative view of the higher classification of North American unionoids. Allozyme electrophoresis also has been used for examination of more directed questions

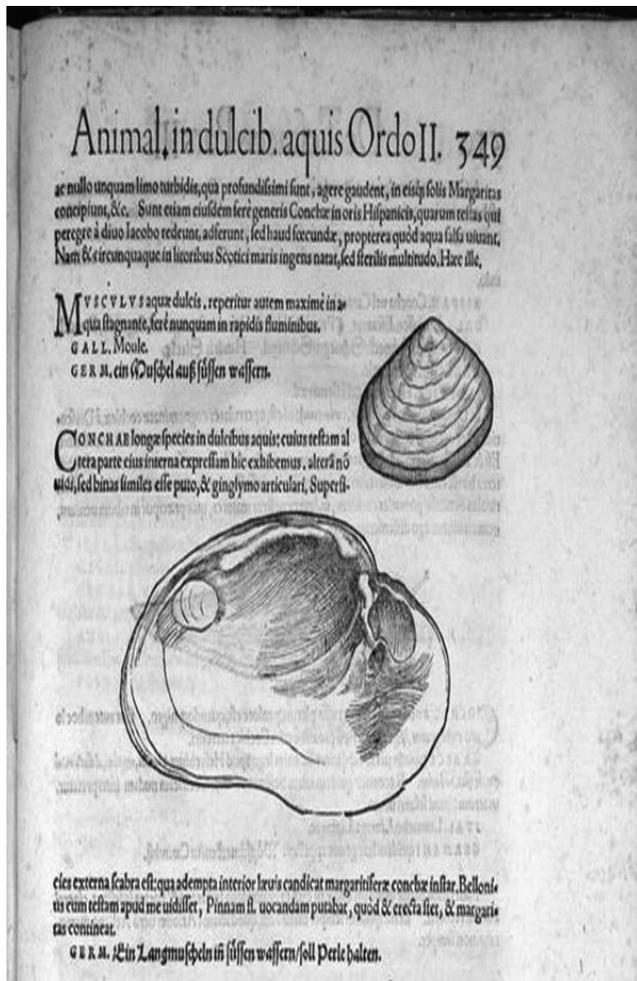


FIG. 7. Illustration of *Margaritifera* from Konrad Gesner (1553).

(e.g., Mulvey et al. 1997, Kandl et al. 2001, Curole et al. 2004). Nucleic acids also have been used to examine the relationships between various groups of freshwater mussels. Restriction fragment length polymorphisms (RFLP) have been used in combination with DNA sequence analyses (Kandl et al. 2001). Various authors have used DNA and ribosomal ribonucleic acid (rRNA) sequences to compare relationships of unioniform bivalves, with varying results. The most commonly used genes in unioniform analyses have been: 1) cytochrome *c* oxidase subunit 1 (CO1) (e.g., Hoeh et al. 1998, Roe and Lydeard 1998, Graf 2000, Graf and O’Foighil 2000a, Lydeard et al. 2000, Hoeh et al. 2002, Huff et al. 2004, Mock et al. 2004, Campbell et al. 2005, Graf and Cummings 2006, Walker et al. 2006a); 2) cytochrome *c* oxidase II (CO2) (e.g., Curole and Kocher 2005, Walker et al. 2006b); 3) histone (H3) (Huff et al. 2004); NADH dehydrogenase (ND1) (e.g., Serb et al. 2003, Campbell et al. 2005, Serb 2006); 4) 18S rRNA

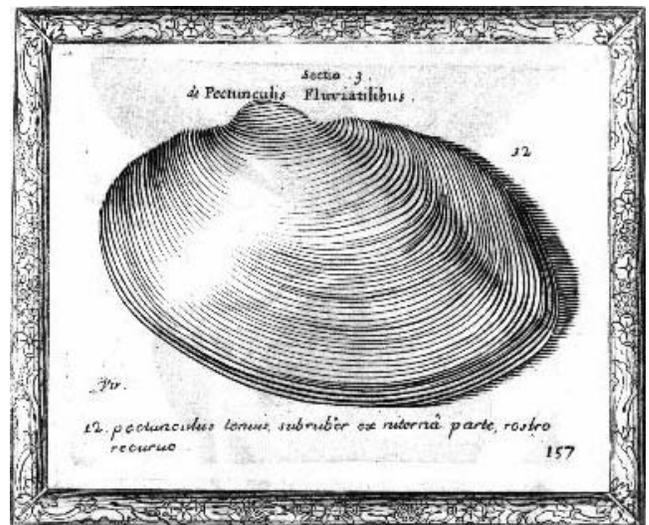


FIG. 8. Illustration of freshwater mussel from Virginia (Lister 1686).

(Huff et al. 2004); 5) 16S rRNA (e.g., Lydeard et al. 1996, Mulvey et al. 1997, Lydeard et al. 2000, Kandl et al. 2001, Campbell et al. 2005); and 6) 28S ribosomal DNA (rDNA) domain 6 (Rosenberg et al. 1994) and domain 2 (e.g., Graf and O’Foighil 2000b, Graf 2002, Huff et al. 2004). Some authors also have used a combination of gene sequences to test hypotheses about unioniform relationships (e.g., Roe et al. 2001, Campbell et al. 2005, Graf and Cummings 2006, Serb 2006), and a few have combined morphological data with DNA sequence data (e.g., Hoeh et al. 2001, Roe and Hoeh 2003, Graf and Cummings 2006). Only one study of mitochondrial gene order has been published for a freshwater mussel. Serb and Lydeard (2003) sequenced the mitochondrial genome of the unionid *Lampsilis ornata* and compared their data with an unpublished genome (Genbank #AB055625) of another unionid, *Inversidens japonensis*, from Japan.

A consensus appears to be emerging that there are 2 superfamilies of unioniform bivalves, the Unionoidea and the Etherioidea, which contain 2 (Unionidae and Margaritiferidae) and 4 (Etheriidae, Iridinidae, Hyriidae, and Mycetopodidae) families, respectively. The position of one family, the Hyriidae, within the order is somewhat unclear, although it appears to be the most basal branch on the phylogenetic tree.

Doubly uniparental inheritance (DUI) is the unusual condition where both male and female mitochondrial genomes are transmitted to offspring. In DUI, female bivalves have the female genome in the gonads and all somatic tissues, whereas males have the female genome in all somatic tissues but the male genome

in testicular tissue. DUI of mitochondria has been identified in 2 orders of marine bivalves: Mytiloida (Skibinski et al. 1994, Zouros et al. 1994, Hoeh et al. 1996) and Veneroida (Passamonti and Scali 2001). It was first recognized as occurring in Unioniformes by Hoeh et al. (1996) and Liu et al. (1996).

Male mitochondrial genomes accrue substitutions at higher rate than female mitochondrial genomes (Krebs 2004, Walker et al. 2006b), and in the Unioniformes, male mitochondria have an extension of the cytochrome oxidase II gene (Curole and Kocher 2005, Walker et al. 2006b) not seen in the female genome. Divergence of the female and male genome sequences ranges from 28 to 34%, and this split is suggested to have begun ~450 million years before present, with a minimum divergence time of ~213 million years before present (Curole and Kocher 2002, 2005).

The distribution of DUI in the Unioniformes was examined by Walker et al. (2006b), and evidence of the male genome was found in specimens representing Hyriidae, Margaritiferidae, and Unionidae but was absent from representatives of Etheriidae, Iridinidae, and Mycetopodidae. The Etheriidae, Iridinidae, and Mycetopodidae form a unique clade with Unionidae and Margaritiferidae as sister taxa, and the Hyriidae are the basal clade on the tree (Walker et al. 2006b). No evidence for the presence or absence of DUI was found in *Neotrigonia*, the sister taxon to the Unioniformes. At this time, the origin or subsequent loss of DUI cannot be resolved. As a result, 2 opposing scenarios explain the gain or loss of DUI based on the latest trees (Walker et al. 2006b).

#### *Anatomical and morphological research*

The basic anatomy of unioniform bivalves was studied during the late 19<sup>th</sup> and early 20<sup>th</sup> centuries, but it is largely ignored today (but see Kraemer 1967, 1978, 1984, Smith 1980, 1983, 1986, 2000, Haggerty et al. 1995, 2005, Garner et al. 1999, Haggerty and Garner 2000, Henley et al. 2007). A comprehensive overview of the basic anatomy, physiology, and biology of freshwater mussels is provided by McMahon and Bogan (2001). Information on glochidia is usually limited to shell size and shape (Hoggarth and Gaunt 1988, Hoggarth 1993, 1999). However, a good illustrated summary of unioniform larval structures and their biology is presented by Wächtler et al. (2001). Many unionid species use a variety of host fish (Watters 1994), but most of the information is based on laboratory infested species. Some of the lampsiline genera have mantle modifications that function as fish lures or attractants (Kraemer 1970). Many also produce conglutinates of various shapes and sizes, which often

mimic fish food items (e.g., Hartfield and Hartfield 1996, Hartfield and Butler 1997, Watters 1999, 2002).

#### *Paleontological research*

The fossil record of unioniforms arguably reaches back into at least the Upper Devonian, depending on what is admitted as representing a unioniform bivalve (Haas 1969b). The early fossil record includes Archanodontidae of the Devonian, Anthracosiidae of the Carboniferous, and finally, Unionoidea in the Triassic and Jurassic periods. The fossil record for western North America is quite good or, at least, abundant in the Cretaceous. White (1883) summarized the western fossil species and concluded that the diverse modern fauna of the Mississippi River basin was derived from the Late Cretaceous fauna of western North America. White's opinion concerning the origins of modern North American freshwater mussels was echoed by Russell (1934), and Davis and Fuller (1981) continued to subscribe to this idea. Watters (2001), noting some of the problems with generic assignment of fossil specimens, summarized the unioniform fossil record and dissented from the opinion that all modern freshwater mussels were related to forms from the Cretaceous.

The fossil record of Unioniforms east of the Mississippi River is rather meager and begins with the Devonian Archanodontidae in Pennsylvania and New York. Diversity appears in the Triassic with the recognition of fossils assigned to the families Mycetopodidae, Hyriidae, and Unionidae. Assignment of these shells to modern families was based upon shell shape and umbonal sculpture. A major gap occurs in the fossil record for eastern North America until the Miocene of Texas and Louisiana. Florida is home to a few Pliocene unioniform taxa. The early Pleistocene unioniform fauna is rather sparsely represented for the earliest part of the epoch, but representation increases with decreasing age (Bogan et al. 1989, Bogan and Grady 1991, Bogan and Portell 1995). The Pleistocene fauna of the eastern USA is summarized by Bogan and Grady (1991).

At the present time, there are no phylogenies for the fossil unioniform bivalves. Classifications that incorporate fossil taxa (Haas 1969a, b, Starobogatov 1970) do exist, but no rigorous phylogenies have been developed for the Unioniformes below the family level. The fossil record of freshwater bivalves is in need of careful review, and a phylogeny should be developed. A framework for the classification of fossil bivalves already exists (Carter et al. 2000). However, evidence of rampant convergence in shell morphology (e.g., Ortmann 1912,

Prashad 1931) would have to be addressed to develop robustly supported phylogenetic hypotheses.

### Future Directions

We have attempted to summarize the current state of unioniform systematic and evolutionary studies. Freshwater mussels are considered to be one the most endangered groups of organisms in the world (Vaughn and Taylor 1999, Lydeard et al. 2004), and the field of systematics has an important role to play in their conservation by providing a general evolutionary framework within which data from other biological research can be organized and communicated. The purpose of the rest of our paper is to highlight areas of study that we think are necessary to further our understanding of freshwater mussels. Advancement of our knowledge of the Unioniformes in the areas of systematics and evolution will require a renewal of effort in already established areas of research, reviewed earlier here, and a concerted effort aimed at the development and application of new tools. A high degree of overlap exists among several of the subjects treated. This overlap is, in part, a consequence of the primacy of evolutionary theory in understanding and explaining the biological world. Phylogenetic trees constitute hypotheses of descent and character change over time. All attributes of the organisms of interest can, in theory, be incorporated into these hypotheses, and the results can be used to study a variety of phenomena, including character evolution, biogeography, and host-parasite co-evolution. This interconnectivity of the many aspects of evolutionary studies means that advances in one area have the potential to enhance understanding in one or more other areas. For example, renewed effort with well-established techniques in the areas of natural history and biotic surveys could provide much needed information on reproductive behaviors, host use, timing of reproductive events, and habitat use for many species of mussel. This type of basic information represents the raw material for evolutionary studies and is necessary for thorough studies on specific topics, such as evolution of reproductive traits (Lydeard et al. 1996, Graf and O'Foighil 2000b) and host-attracting behaviors (Zanatta and Murphy 2006), and it supplies additional characters for phylogenetic analyses. As our understanding of the systematics of these animals improves, a better understanding of the evolution of this expansive radiation in freshwater mussels will develop, and this understanding will inform our efforts to conserve them.

### Global diversity

An informal survey of the literature indicates that the geographic foci of published studies on freshwater mussels are highly biased toward the fauna of North America and Europe. These 2 regions are the subject of 62% and 19% of the literature but constitute only 43% and 10% of global freshwater mussel diversity, respectively. All other faunas are underrepresented, some dramatically so, in the literature relative to their diversity. For example, Asia is the subject of 8% of published studies but contains 23% of the known freshwater mussel diversity, whereas the Neotropics are the topic of 6.5% of studies but are home to 12% of mussel species.

The paucity of studies from the Old and New World tropics and Asia reflects our lack of knowledge of the faunas of these areas. This fact, coupled with an increasing pace of industrial and agricultural development (Collins et al. 1996, Ndulu and O'Connell 1999) in these regions, underscores the need for a renewed effort to undertake systematic and evolutionary studies in these underrepresented regions. Reevaluation of all taxa, especially outside of North America and Western Europe, and their relationships to each other and North American taxa should be a high priority for freshwater mussel research. A recently renewed interest in the global diversity of freshwater mussels has resulted in a resurgence in revisionary taxonomic works (e.g., Graf and Cummings 2006). Taxonomic works of this magnitude are critical for developing a complete picture of freshwater mussel diversity, and they set the ground work for more geographically focused studies.

### Natural history

Advances in the field of molecular phylogenetics have increased the ability of relatively untrained nonmalacologists to conduct evolutionary studies on freshwater mussels. Molecular data have great potential to resolve both phylogenetic relationships and population-level differentiation, but it cannot be forgotten that it is the diversity of natural histories, behaviors, and shell morphologies that stimulated interest in these organisms in the first place. Natural-history facts, such as host-fish use, reproductive behavior, and morphology of adults and glochidia, are important characteristics that are the evolutionary novelties and raw material for evolutionary studies. Unfortunately, much of this type of information is lacking for many North American species and most of the other unioniform faunas worldwide. A recent publication on the reproductive behavior of *Unio crassus* (Vicentini 2005) illustrates this point. Vicentini

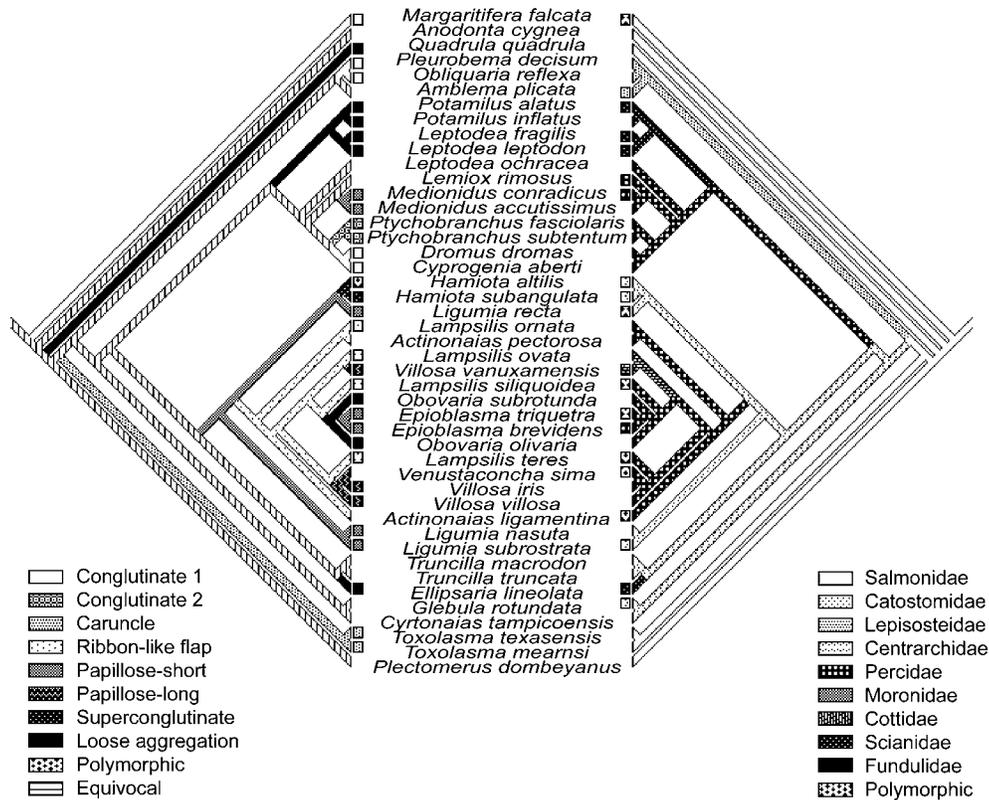


FIG. 9. Phylogenetic hypotheses for the Lampsilini illustrating the evolution of lure types (A) and host use (B) (modified from Roe 1999). Branches are coded to reflect different character states. See Roe (1999) for detailed descriptions of characters.

(2005) published a description of how fully gravid *U. crassus* females crawl up the bank of the stream when ready to release their glochidia larvae. The females keep the incurrent aperture submerged and the excurrent aperture above the surface of the water, and they release a stream of water that contains mature glochidia. Vicentini (2005) speculated that this mode of release increased the distance the larvae traveled before sinking to the bottom and that the disturbance at the water surface might attract the attention of suitable host fishes, thereby improving the chances for larvae to encounter a host. The unique reproductive behavior of *U. crassus* had been almost totally unnoticed since the species was first described ~200 y ago, despite the fact that it was once one of the most common species of unionid in central Europe, one of the most densely populated areas in the world.

Data on characters, such as host use and reproductive behavior, can be combined with other data to construct phylogenetic hypotheses for how such complex character traits evolved. For example, Roe (1999) examined the evolution of lures in conjunction with DNA sequence data for a single mitochondrial gene (16S rRNA) in the freshwater mussel tribe Lampsilini. In addition, Roe (1999) coded host-fish

use by family for the same group of mussels and traced the evolution of these 2 characters on the resulting phylogeny (Fig. 9). The molecular/morphological phylogeny, although weakly supported, indicates a possible correlation between visual predators (Centrarchidae and Percidae) and the evolution of visual lures to attract host fishes. Roe (1999) made no explicit test for correlated evolution between hosts and lures (e.g., Harvey and Purvis 1991), and the data set lacks host information for many species of mussel. These missing data led to numerous possible reconstructions of the evolution of host use within the Lampsilini, and more complete data sets clearly are required to develop robust hypotheses for the evolution of traits in this group. The results of Roe (1999) and other recent studies (Graf and O'Foighil 2000b, Zanatta and Murphy 2006) illustrate the potential of resolved well-supported phylogenies to aid in our understanding of character evolution in freshwater mussels. We encourage freshwater malacologists to investigate and publish findings on the natural history of freshwater mussels. As this information accumulates, data sets that will yield robust phylogenetic hypotheses on which to examine the evolution of these characters can be developed.

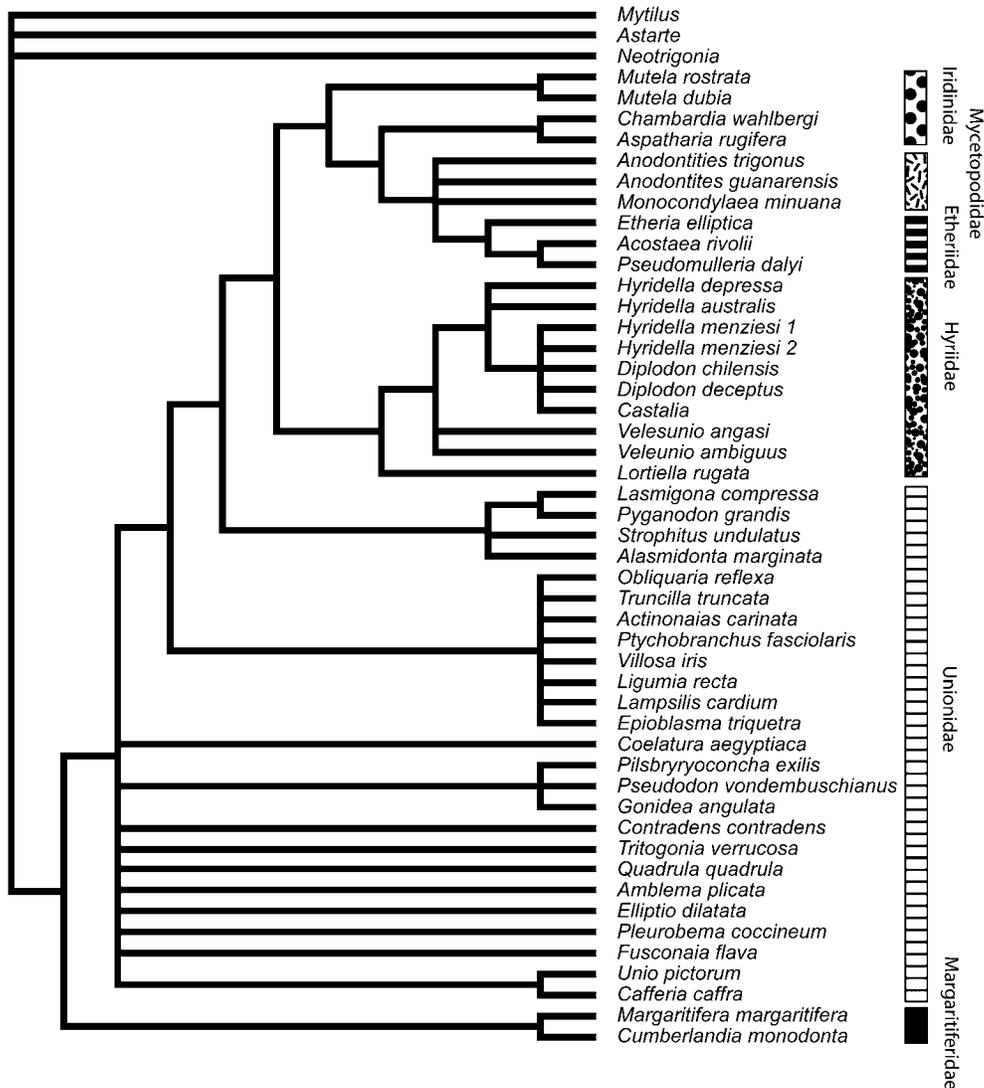


FIG. 10. Strict consensus of >30,000 most-parsimonious trees of 126 steps recovered by Graf and Cummings (2006) from analysis of 59 morphological characters.

*Anatomical and morphological research*

One of the apparently more intractable problems for systematists who study freshwater mussels is the development of morphology-based data sets that can produce well-supported phylogenetic hypotheses. The most recently published study (Graf and Cummings 2006) used 59 morphological characters, including conchological, soft anatomical, larval, and life-history traits, analyzed separately and together with molecular characters. The data compiled by Graf and Cummings (2006) arguably represent the most complete morphological data set for the Unioniformes to date. Their morphology-only consensus tree (Fig. 10) includes several unresolved or paraphyletic groups, including the Unionidae, Iridinidae, and Mycetopodi-

dae. The authors concluded that the lack of basic anatomical and reproductive data was one of the serious problems retarding advances in the systematics of freshwater mussels. The recent plethora of molecular-based phylogenetic studies has increased our knowledge of the systematics of freshwater mussels, but without an equal and concomitant treatment of morphological characters, the work of establishing a well-resolved phylogeny of freshwater mussels will remain uncompleted. We, the intellectual descendents of Arnold Ortmann and Charles Simpson, have failed to advance the field of freshwater mussel systematics as much as could have been possible because we abandoned the study and development of the morphological characters that were used to erect the classifications of our predecessors—classifications that

are largely still in use today. This unfortunate state of affairs can be rectified through a renewed effort to study and describe the morphology of freshwater mussels. Such studies could include phylogenetic analyses of discrete characters, *sensu* Graf and Cummings (2006), and geometric morphometric analysis of continuous variables, such as shapes and surfaces (Adams et al. 2004). Geometric morphometric characters have the potential to allow examination of morphological characters that have, to date, confounded freshwater malacologists because of the variability they exhibit. Geometric morphometric methods use statistical inference, as do traditional morphometric methods. However, traditional morphometric methods measure simple distances or angles, whereas geometric morphometric methods retain the geometry of the objects under study and allow quantification of features that cannot be measured using traditional landmarks. Such methods have the potential to enable quantitative discrimination between species of freshwater mussel that are notoriously difficult to distinguish (e.g., *Quadrula*, *Elliptio*, etc.). In addition, geometric morphometric methods have the potential to allow examination of ontogenetic change within a species by capturing the shape and surface features at various stages of development from juvenile to adult and by more accurately quantifying the degree and type of morphological convergence caused by environment between distinct lineages. Last, geometric morphometric methods provide an additional way to include fossil taxa with recent species in analyses designed to clarify the evolutionary history of freshwater mussels and test hypotheses concerning the origins of Holocene freshwater mussels.

#### *Paleontology*

The views that fossils are a boon or a bane to understanding the phylogenetic history of recent organisms have both been advanced with equal stridency (e.g., Simpson 1961, Ax 1987). Donoghue et al. (1989) compared the results of including vs excluding fossil information in a review of the importance of fossil taxa to phylogenetic reconstruction. They found that the inclusion of fossils is *required* (emphasis ours) for obtaining the true phylogeny of the group of interest and that, furthermore, fossil taxa should be incorporated into phylogenetic studies from the outset of project design and should not be included only as part of a post-hoc analysis. Compared to many taxonomic groups, freshwater mussels have a fairly robust fossil record that includes >200 named species (Haas 1969b, Watters 2001), and they have the potential for a well-resolved phylogenetic history.

Several authors have published descriptions of fossil mussels from North America (see *Paleontological research* section), and Watters (2001) provided an excellent summary of the paleontological history of freshwater mussels in North America. Members of this diverse fossil assemblage have been assigned to several different unioniform families (Hyriidae, Mycetopodidae, and Mutelidae) that are not included in the Holocene fauna of the continent (Watters 2001). The presence of these Gondwanan faunal elements in North America as early as the Triassic has strong implications for the evolutionary history of the Unioniformes, and yet, no attempt has been made to objectively test the taxonomic assignments of earlier workers (e.g., Pilsbry, in Wanner 1921, Parodiz 1968).

Rigorous phylogenetic analyses that incorporate fossil freshwater mussels along with Holocene species (*sensu* Donoghue et al. 1989) would allow assessment of higher-level assignments of fossil taxa and would provide a test of the hypothesis that North America was once home to every major extant lineage of freshwater mussel. One of the potential outcomes of such work would be a more complete classification that identifies fossil mussels as members of extant groups. An additional benefit of such studies would be the ability to develop estimates of fossil-calibrated divergence times for lineages of mussels once the ancestors of modern taxa have been identified using the methods developed by Huelsenbeck et al. (2001), Sanderson (2002), and others. These types of studies would eventually lead to greater understanding of when and where the various radiations of freshwater mussels have taken place in the past and would shed additional light on the mode and tempo of the evolution of the myriad of adaptations exhibited by this group. The recent announcement of determination of the collagen protein sequence from the bones of a 68-million-year-old *Tyrannosaurus rex* (Asara et al. 2007) holds some promise for inclusion of molecular characters of fossil freshwater mussels in future data sets. However, until such time, joint study of fossil taxa and recent species in a phylogenetic context will have to rely on the use of morphological characters.

#### *Molecular tools*

The advent of polymerase chain reaction analyses and the ability to sequence DNA have revolutionized phylogenetics (Kim 2001). The revolution has continued with larger and larger molecular data sets generated by an increasing number of laboratories. Data sets based on organelle genomes are no longer uncommon (GenBank currently lists sequences for 1204 mitochondrial genomes), and the increasing

number of organismal whole genomes will lead to the discovery of novel molecular markers that can be used to develop better estimates of phylogenetic history. Malacologists have not yet been able to benefit from this molecular largesse to the same degree as other taxonomic specialists. The current list of 25 whole genomes in GenBank includes 4 animals, 5 plants, 9 fungi, and 7 protists. To a large degree, market forces drive the choice of organisms for sequencing of genomes. Other than classic model organisms, existing whole genomes in GenBank represent important agricultural crops or are disease agents. Those researchers who work on taxonomic groups that are even distantly related to an organism with a sequenced genome have available numerous candidate nuclear genes with which they can explore the utility for phylogenetic construction. However, the pot of genetic gold at the end of the molecular rainbow is in sight for malacologists. Of 339 whole-genome projects listed in GenBank as pending or in assembly, 3 are mollusks (the freshwater snail *Biomphalaria glabrata*, the sea slug *Aplysia californica*, and the marine clam *Spisula solidissima*). Until such time as these and other molluscan genomes are available, freshwater mussel biologists must make use of existing published markers for freshwater mussels and explore the utility of markers designed for other groups.

At present, data for 2 mitochondrial genomes exist for members of the Unionidae, yet recently published phylogenies of freshwater mussels still use the same 3 markers (first subunit of the COI, 16S rRNA, and ND1) developed over a decade ago. With the caveat that there are limitations to the use of mitochondrial markers for phylogenetic reconstruction, much of the utility of the 37 gene regions (Serb and Lydeard 2003) of the mitochondrion has yet to be explored for freshwater mussels. The resolution and branch-support values for published phylogenies of freshwater mussels are, to some degree, a testament to the relatively small portion (<16%) of the mitochondrial genome that has been used to date. Mitochondrial gene sequences might have limited phylogenetic utility, at least for higher-level studies, but mitochondrial gene order might prove to be an informative phylogenetic character within the Unioniformes. At present, the complete mitochondrial genome has been sequenced and published for 1 freshwater mussel (Serb and Lydeard 2003).

A concerted effort to identify single-copy nuclear genes for the generation of unionoid phylogenies is required if the field of unioniform systematics is to advance. Several studies have used noncoding regions, such as the 18S and 28S ribosomal regions of the nuclear genome, but these regions are evolving too

slowly to be of much use for phylogenetic analysis of freshwater mussels. More variable nuclear sequences, such as the internal transcribed spacer regions, appeared to be more promising (e.g., King et al. 1999), especially for lower-level studies, but recent evidence indicates that these DNA regions are heteroplasmic in many taxa (e.g., Parkin and Butlin 2004), and therefore, they are not good candidates for phylogenetic reconstruction, at least in some lineages (Serb 2006). Some recent use has been made of the histone genes for molluscan systematics (Giribet and Distel 2003, Huff et al. 2004), but the small number of nucleotides and the relatively conserved nature of the region mean that these genes provide few phylogenetically informative sites. We desperately need to expand our set of tools to include or develop additional markers such as single-copy nuclear genes. Such markers are critical for developing well-supported phylogenetic hypotheses for worldwide freshwater mussel fauna.

Friedlander et al. (1992) published a list of 14 promising nuclear genes for phylogenetic analysis. A number of these have been used for phylogenetic studies that have included molluscs (see Anderson et al. [2004] for a brief review), but none has been included in a study that has focused on freshwater mussels.

#### Zoogeography

The unique natural history of unioniform bivalves provides a fertile area for testing and developing evolutionary theories, including zoogeography. Freshwater mussels are mostly sessile, largely dependent upon a host during their larval stage for dispersal, and they exhibit a high degree of endemism. Unioniform mussels also are confined to freshwater systems, and their fossil record indicates that their origins date back to at least the early Mesozoic. All of these factors combine to make freshwater mussels excellent subjects for biogeographic studies. The Gondwanan distribution of several major lineages (Hyriidae, Iridinidae, and Mycetopodidae) and largely Laurasian distribution of the remaining families (Unionidae, Margaritiferidae) imply that the breakup of Pangea at the close of the Jurassic included several vicariant events that are reflected in the current distribution of the Unioniformes. Some work has been conducted on zoogeography using freshwater mussels at smaller scales in Europe (e.g., Machordom et al. 2003) and North America (Roe et al. 2001, Kelly and Rhymer 2005, Elderkin et al. 2007), but much additional work remains to be done.

Areas of study involving the zoogeography of the Unioniformes include subjects as diverse as climate

change and patterns of species diversity. For example, the distribution of freshwater mussels appears to contradict one of the major trends in species diversity observed in other organisms, i.e., that species diversity increases closer to the equator (Wiens and Donoghue 2004). The reason for this pattern in mussel diversity, which does not seem to follow patterns observed in other taxa, is a zoogeographic question that is probably tied to the origins of this diverse and fascinating group of invertebrates. Scientists increasingly concur that climate change is occurring. Whether anthropogenic or not, changes in global climate raise questions about the conservation of many organisms that have reproductive cycles tied to environmental cues, such as seasonal changes in temperature (e.g., Root et al. 2000), and will undoubtedly pose challenges to the conservation of many freshwater mussel taxa. Understanding the differences in the numbers and types of mussel species along latitudinal or other geographic gradients, such as temperature, has the potential to help us manage and preserve unioniform mussels.

In conclusion, the freshwater malacological community has made great strides in understanding the life history, distribution, and ecology of unioniform bivalves, but we have really only laid the groundwork for the future. Exploration of new genetic data sources must continue, and new methods of describing the shells and the anatomy of freshwater mussels must be developed. However, the importance of collecting basic natural-history information cannot be overstated. The study of systematics and evolution is an historical endeavor and one that seeks to integrate various sources of data to develop hypotheses that are then subjected to further tests. Only by fostering research along the many diverse lines of interest in freshwater mussels will we begin to see real progress toward a more complete understanding of them.

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