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Patterns of freshwater bivalve global diversity and the state of phylogenetic studies on the Unionoida, Sphaeriidae, and Cyrenidae*

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Abstract. The objective of this paper is to review the current state of our knowledge of freshwater bivalve diversity and evolution in order to identify some of the “Great Unanswered Questions” in the field. Twenty-one bivalve families have been attributed to fresh waters, but only 16 actually live and reproduce in inland waterways. Of 1209 species of freshwater bivalves, 1178 (97%) belong to eight primary freshwater families: Unionidae, Margaritiferidae, Hyriidae, Mycetopodidae, Iridinidae, and Etheriidae (all Unionoida), Sphaeriidae, and Cyrenidae (both Veneroida). The remaining 31 species represent secondary freshwater lineages of predominantly brackish/marine bivalve families. The global geographical patterns of freshwater bivalve richness are discussed, and an appendix detailing the families, genera, and species of freshwater bivalves is provided.

Although the primary freshwater bivalve families represent at least three independent radiations from marine into inland aquatic habitats, these lineages have converged on similar adaptations to life in a flowing hypoosmotic medium. For example, all have abandoned broadcast spawning and planktonic veligers. Phylogenetic studies of the Unionoida, Sphaeriidae, and Cyrenidae have also converged on a suite of common challenges: outgroup issues, biased ingroup taxon and character sampling, and atypical modes of genetic inheritance that uncouple gene trees from species trees. The recent phylogenetic literature on the three primary radiations is reviewed, emphasizing areas in need of research. Ample opportunities exist in freshwater bivalve research but progress is hindered by the limited numbers of researchers and students in the field.

Key words: mussels, clams, species richness, life histories, convergent evolution

The modern polyphyletic assemblage of freshwater bivalves is of scientific, aesthetic, and practical interest. The Bivalvia (and indeed the Mollusca) originated in the oceans, but there have been repeated invasions of inland aquatic habitats (Gray 1988, Deaton and Greenberg 1991, Bogan 2008). These phylogenetically-independent bivalve lineages vary in the extent to which they have radiated and expanded away from coastal influences. Conversely, there are convergent evolutionary trends that lend general insights into biological transitions from marine to freshwater environments. Bivalves are major components of aquatic communities, and the ongoing global biodiversity catastrophe occurring in our fresh waters lends urgency to the study of these mollusks (Strayer 2006, Strayer and Dudgeon 2010, Dudgeon *et al.* 2011). Ironically, while some groups of freshwater bivalves are disproportionately suffering the brunt of aquatic habitat degradation (*e.g.*, freshwater mussels), others are catalyzing the decline as invasive species (*e.g.*, *Dreissena* Van Beneden, 1835, *Corbicula*

Megerle von Mühlfeld, 1811). The time is ripe for a synthesis of the State of the Science in order to highlight the unanswered questions about global freshwater bivalve diversity and evolution.

Identifying the “Great Unanswered Questions” in freshwater bivalve research is a subjective problem, dependent on the research bent of the inquirer as well as the scope of the venue. A variety of outstanding problems can readily be determined, and different malacologists would prioritize them differently. For example, what are the biotic and abiotic factors that determine freshwater bivalve diversity and abundance? (Strayer *et al.* 2004, Strayer 2008) How is anthropogenic habitat modification (including climate change) affecting freshwater bivalves? (Spooner and Vaughn 2008, Galbraith *et al.* 2010) What ecosystem functions do freshwater bivalves provide to aquatic communities? (Strayer *et al.* 1999, Vaughn and Hakenkamp 2001, Vaughn *et al.* 2004) What is the nature and extent of life history variation among freshwater bivalves?

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(Haag and Staton 2003, Barnhart *et al.* 2008) And, how has the evolutionary history of freshwater bivalves influenced their current diversity? As a systematist, I would argue that the last of these is the most fundamental because comprehensive answers to all the previous questions are predicated on an understanding of freshwater bivalve taxonomic diversity and evolutionary relationships. Although many biologists take it for granted, a phylogenetic classification is the bedrock theory upon which our interpretations of biological patterns and processes rest. The objective of this paper is to review current research on the diversity and phylogeny of freshwater bivalves, the lessons learned thus far, and some of the great questions remaining to be answered.

The foci herein will be the major freshwater bivalve radiations of the Unionoida, Sphaeriidae, and Cyrenidae (= Corbiculidae) (Fig. 1). These bivalves are colloquially known as freshwater mussels, pill/fingernail/pea clams, and Asian freshwater clams, respectively. However, many more bivalve taxa have been labeled as “freshwater,” and it is worth taking a step back to consider freshwater bivalves generally.

WHICH BIVALVES ARE THE FRESHWATER BIVALVES?

Specifying which bivalves are the “freshwater bivalves” is also a subjective problem, conditioned on which end of the salinity gradient one starts their examination. Marine (c. 35‰ salinity) and freshwater habitats (< 0.5‰) generally harbor distinctive assemblages of organisms, and as a result they are studied by largely independent research traditions. There is a substantial gap between these two poles, and among systematic malacologists there has been (and continues to be) a reluctance to own that gap. For marine biologists, “freshened” waters are fresh, and for freshwater biologists, brackish coastal waters are marine.

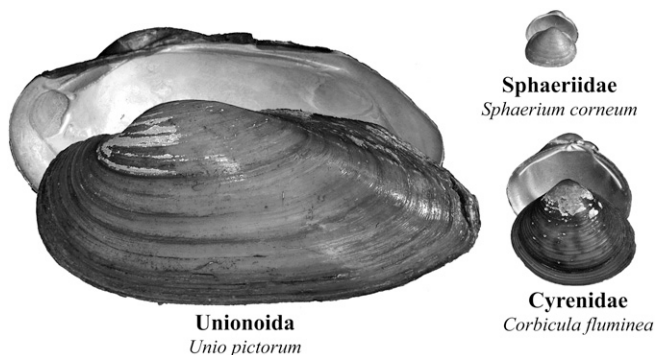


Figure 1. Exemplar species representing the Unionoida, Sphaeriidae and Cyrenidae. Specimens roughly natural size.

For example, Gray (1988: 10) regarded as freshwater any species that does not occupy “‘normal’ marine environments as defined by all objective criteria.” A similar definition was also applied by Hutchinson (1967). This diagnosis includes both truly freshwater taxa as well as those living in brackish oligohaline waters (up to and surpassing 20‰). Physiologically, the osmotic trough between fresh and marine waters is difficult to straddle. Adaptation to hypotonic habitats limits tolerance to higher concentrations, and marine osmoconformers typically lack the mechanisms to maintain their salt and water balance in dilute media (Pennak 1985, Deaton and Greenberg 1991). As a result, there is a distinctive brackish-water assemblage of bivalves that is neither fresh nor marine. I am looking at this question from the (literal) high ground, and for my discussion, I will regard as freshwater those bivalves capable of living and reproducing in inland waterways above coastal influences. Some freshwater bivalves are tolerant of oligohaline waters, but mere occurrence in fresh water does not a freshwater bivalve make.

Sixteen families have one or more species occupying inland fresh waters, and at least five more families are known from “freshened” oligohaline habitats (Hutchinson 1967, Gray 1988, Deaton and Greenberg 1991, Bogan 2008, and numerous references cited in the appendix). These 21 families and their patterns of global species richness in fresh waters are summarized in Table 1. The five brackish-water families are listed for the sake of completeness, having been previously attributed to fresh waters, but will not be discussed further. Eight families constitute the three primary bivalve radiations into fresh waters: Unionidae, Margaritiferidae, Hyriidae, Etheriidae, Mycetopodidae, and Iridinidae (all Unionoida), as well as Sphaeriidae and Cyrenidae (both Veneroida). The remaining eight families are herein regarded as secondary invasions. That is, typically brackish/marine families with occasional freshwater genera or species. Of the estimated 1209 freshwater bivalve species recognized in the recent literature (see the appendix for details), 1178 (97%) belong to the primary freshwater families (Table 1).

The two regional hotspots of freshwater bivalve richness are the Nearctic and Indotropical regions (Table 1). These two areas account for more than half of the species (684 spp., 57%), and both bivalve assemblages are dominated by the family Unionidae. The two most species-rich families worldwide are the Unionidae (681 spp., 57%) and the Sphaeriidae (227 spp., 19%), with each represented in all six regions. The other primary freshwater families show higher degrees of endemism to various regions (Table 1).

Of the 31 secondary freshwater bivalve species, 26 (84%) have native ranges restricted to either Indotropical southeastern Asia or the Ponto-Caspian area of Palearctic Eurasia (Table 1). Sixteen Indotropical freshwater species belong to the families Mytilidae, Arcidae, and Pharidae, and there is even a

Table 1. Patterns of global species richness among freshwater bivalves. Brackish species are listed only to indicate those that have been previously attributed to fresh waters. See the appendix for references and other information. Primary freshwater families are shown in **bold**, and introduced species are in parentheses. Secondary freshwater species are those belonging to typically brackish/marine families. Geographical regions follow Graf and Cummings (2007).

Taxon	total	Nearctic	Neotropical	Afrotropical	Palaearctic	Indotropical	Oceania/Australasia
Mytilidae	5	0	(1)	0	(1)	5	0
Arcidae	5	0	0	0	0	5	0
Unionidae	681	295 (1)	94	38	46 (1)	218	2
Margaritiferidae	13	5	0	0	8	1	0
Hyriidae	75	0	44	0	0	0	31
Etheriidae	4	0	2	1	0	1	0
Mycetopodidae	43	0	43	0	0	0	0
Iridinidae	43	0	0	43	0	0	0
Cardiidae	3	0	0	0	3	0	0
Cyrenidae	92	(1)	4 (3)	4	13 (1)	72	2 (1)
Cyrenoididae				BRACKISH			
Dreissenidae	9	2 (2)	3	0	5 (1)	0	0
Sphaeriidae	227	41	59	33	54	29	27
Donacidae	2	0	0	2	0	0	0
Solenidae				BRACKISH			
Pharidae	5	0	0	0	0	5	0
Mactridae				BRACKISH			
Corbulidae	1	0	1	0	0	0	0
Erodonidae				BRACKISH			
Teredinidae				BRACKISH			
Pholadidae	1	0	0	0	0	1	0
TOTAL	1209	347	254	121	133	337	62
1° freshwater	1178	343	249	119	123	321	62
2° freshwater	31	4	5	2	10	16	0

wood-boring pholadid. These species represent active invasions of fresh waters from the sea by euryhaline lineages (Hutchinson 1967). The relatively high number of independent colonizations of Indotropical fresh waters has been attributed to the high diversity of brackish-water clades in the region, the shallow salinity gradients of tropical river estuaries, repeated changes in sea-level over geological time, and long-term climatic stability (Davis 1982, Deaton and Greenberg 1991). In the Black and Caspian seas, the Cardiidae and Dreissenidae represent passive radiations into brackish waters, as the closure of the Tethys Sea during the Cenozoic squeezed those families into freshened habitats (Gray 1988). Though typically brackish, a few species have managed to colonize adjacent lakes and rivers in the region. Notably, these two centers of origin have given rise to invasive freshwater bivalves like *Limnoperna fortunei* (Dunker, 1857) (Mytilidae) and *Dreissena polymorpha* (Pallas, 1771) (Dreissenidae) that have become pests in eastern Asia, South America and North America (Roberts 1990, Ram and McMahon 1996, Ricciardi 1998, Morton and Dinesen 2010).

POLYPHYLETIC ORIGINS

Traditionally, only two independent radiations of bivalves into fresh waters have been recognized, but recent phylogenetic work suggests at least three. All eight primary freshwater bivalve families had been arranged into only two superfamilies: “Unionacea” (freshwater mussels) and “Corbiculacea” (= Corbiculidae + Sphaeriidae) (Haas 1969, Keen and Casey 1969, Boss 1982). While cladistic studies have consistently resolved the monophyly of freshwater mussels (Graf and Cummings 2006), none have supported a sister relationship between the Cyrenidae (= Corbiculidae) and Sphaeriidae (Park and Ó Foighil 2000, Taylor *et al.* 2007). For all three lineages (*e.g.*, Unionoida, Sphaeriidae, and Cyrenidae), marine sister taxa (or the lack thereof) contribute to outgroup issues, especially with regard to the polarization of morphological transformations associated with adaptation to freshwater habitats.

The sister lineage to the Order Unionoida is the Australian marine genus *Neotrigonia* Cossmann, 1912 (Hoeh *et al.* 1998,

Giribet and Wheeler 2002), the sole living representative of the Order Trigonioidea (Newell 1969, Darragh 1998). These two orders comprise the extant Subclass Palaeoheterodonta (although alternative rankings and spellings have recently been offered by Bieler *et al.* (2010) and Carter *et al.* (2011)). Besides esoteric nucleic acid synapomorphies, they are united by a common hinge morphology and sperm ultra-structural characteristics (Healy 1989, Graf and Cummings 2006). However, unionoid monophyly is robust and uncontroversial only when the Recent palaeoheterodonts are considered, copious extinction having created a distinct phylogenetic gap. Precisely when the stem-groups of these clades diverged has yet to be fully elucidated. The prevailing hypothesis (based largely on shell morphology) is that freshwater mussels originally diverged from the Triassic Trigonodidae (= Pachycardiidae) (Newell and Boyd 1975), although the earliest fossils attributable to the crown-Unionoidea may be as late as the Jurassic (Skawina and Dzik 2011). This scenario renders the Paleozoic Archanodontoidea, Anthracosioidea, etc. as freshwater radiations independent from modern freshwater mussels (Weir 1969, Gray 1988).

Sphaeriid and cyrenid sister groups have not been as convincingly determined. An affinity between these two families had been assumed based upon similar shell morphologies, occurrence in fresh waters, and shared life history characters, such as direct development and parental care (Thiele 1934, Boss 1982). However, these hypothesized synapomorphies are actually a combination of veneroid plesiomorphies and homoplastic adaptations to life in flowing hypotonic waters (Park and Ó Foighil 2000). While we can be confident that the Sphaeriidae and Cyrenidae are not sister to each other, the actual sister group of neither is well understood. Taylor *et al.* (2007, 2009) sampled the widest array of heterodont families to date. They recovered (with little support) the Sphaeriidae as sister to a (Pholadoidea + Myoidea + Dreissenidae) clade, and *Corbicula fluminea* (Müller, 1774) (Cyrenidae) was placed in a well supported clade with *Glaucanome virens* (Linnaeus, 1767) (Glauconomidae) and *Cyrenoida floridana* Dall, 1901 (Cyrenoididae). These results confirmed the independent invasions of fresh waters by the Sphaeriidae and Cyrenidae but leave the higher taxonomy of both dangling in their own respective superfamilies. Furthermore, as will be explained below, current evidence in fact supports multiple separate freshwater radiations within the Cyrenidae.

Despite these questions regarding marine sister groups, the available phylogenetic work has succeeded in refining our hypotheses about the relationships among freshwater bivalve taxa. The Unionoidea (6 families), Sphaeriidae and Cyrenidae (plus each of the secondary lineages, Table 1) represent independent invasions of fresh waters by marine/brackish bivalve

clades. Further research that combines both morphological and molecular characters targeting the stems leading to these extant crown groups (as well as fossil taxa) will be necessary to bring their early evolution into focus. It is less the case that we lack the materials and theory to solve these problems and more that the will to do so has yet to be mustered.

CONVERGENCE OF LIFE HISTORY TRAITS

Fresh waters impose selection pressures distinct from those of marine habitats. These include not only the need for osmotic regulation in a dilute environment but also challenges associated with flowing water (Cummings and Graf 2009). Lotic habitats can be conceptualized as a one-dimensional unidirectional cline powered by gravity. The water, with its dissolved and suspended loads, inevitably falls back to sea level and oceanic conditions. For freshwater organisms, the stereotypical marine autobranch bivalve habits of broadcast spawning and metamorphosis through a planktonic veliger are maladaptive. Not only do flowing waters accelerate passive downstream dispersal away from favorable parental habitats, but hypoosmotic waters are also nutrient limiting (Needham 1930, Pennak 1985, Gray 1988). Despite their polyphyletic origins, shared selection pressures led all three primary radiations to converge on elimination of the planktonic larval stage and evolution of parental care.

Both the Sphaeriidae and freshwater members of the Cyrenidae exhibit parental care in the form of ovovivipary (or in some cases euvivipary), and they forgo a planktonic larval stage in favor of direct development (*i.e.*, crawl-away juveniles). These species are hermaphroditic and capable of self-fertilization (Cummings and Graf 2009). Minute juveniles and adult sphaeriids (< 2 cm) are capable of avian dispersal and are thus adept at colonizing isolated lentic habitats and ephemeral water-bodies (Rees 1965, Mackie 1979). Species of the Unionoidea likewise brood their larvae in the females' ctenidial demibranchs, and they have a larval stage that is not planktonic but parasitic upon freshwater fishes (or, in one case, an amphibian) (Kat 1984, Watters 1994). It is while the larvae are encysted in the gill or fin epithelium of their host that they undergo metamorphosis to a free-living juvenile, and this is also the major dispersal stage of the life cycle (Graf 1997). Freshwater mussels are typically large (often exceeding 20 cm) and gonochoristic in addition to having this complex life cycle, and as such they are poor colonizers without over-land vagility. The nuances in how these independent radiations have adapted to the opportunities of freshwater life have influenced global diversity patterns. For example, few freshwater mussel genera have ranges extending across regional boundaries (Table 1), whereas sphaeriid genera are largely cosmopolitan.

It is noteworthy that neither parental care nor direct development are common among the secondary radiations of freshwater bivalves. For example, *Dreissena polymorpha*, *Mytilopsis leucophaeata* (Conrad, 1831), and *Limnoperna fortunei* retain plesiomorphic external fertilization and planktonic veligers (Morton 1977, Siddall 1980, Nichols 1996). This hints at the relative recentness of their occupation of fresh waters. It also goes to explaining their success as invasive species, their microscopic larvae capable of stowing-away in ships' ballast water (Johnson and Padilla 1996, Ricciardi 1998).

PHYLOGENETIC PATTERNS WITHIN THE MAJOR PRIMARY RADIATIONS

The phylogenetic patterns within the Unionoida, Sphaeriidae and Cyrenidae have received relatively more research than their respective positions among the Bivalvia, but results to date are compromised by: 1) outgroup issues, 2) incomplete taxon sampling, and 3) character conflict. Below, I briefly review the state of phylogenetic studies on each of the three major radiations of freshwater bivalves. While it is true that evolutionary studies of all three groups would benefit from more robust phylogenetic results, a number of interesting patterns have emerged that emphasize the value of freshwater bivalves for addressing broader evolutionary and ecological problems.

Unionoida

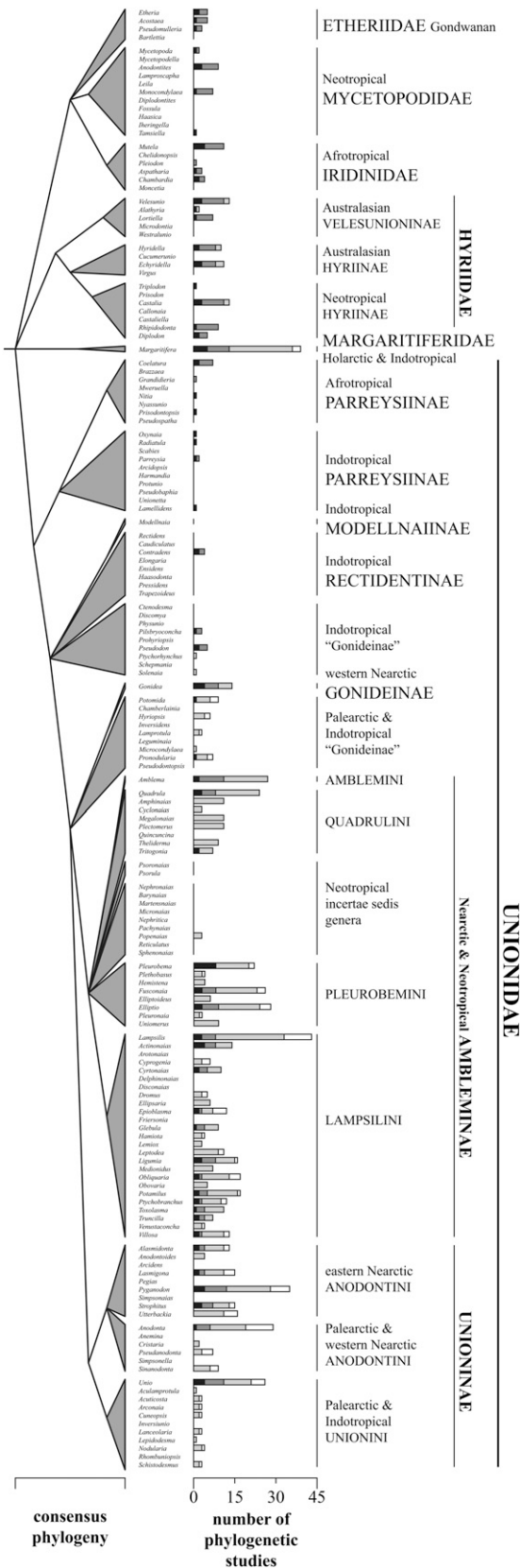
The phylogeny of the Unionoida has received a good deal of attention, but biased sampling and conflicting results limit the utility of this research. The pattern of taxon sampling bias is illustrated in Fig. 2. I surveyed the recent literature (98 articles, too numerous to cite) and tallied the number of times each freshwater mussel genus was included in a phylogenetic or phenetic analysis. This is depicted by the maximum extent of the column next to each genus name. The next tier (represented by light gray) indicates the number of phylogenetic studies that analyzed representatives of at least three different family-group level taxa. That is, analyses with at least minimal taxon sampling to test the monophyly of families, subfamilies or tribes. Dark gray shows the number of phylogenetic studies with ≥ 3 families, testing the basal branching order of freshwater mussels. Finally, the short black bars also represent studies with ≥ 3 families but with multiple uses of the same data omitted (as indicated by Genbank accession numbers; <http://www.ncbi.nlm.nih.gov/genbank/>). The bias in taxon sampling is evident. While there have been many studies of freshwater mussel evolutionary relationships, relatively few taxa have been applied to determine family-group level relationships. Some clades, such as Unionini, Anodontini, Lampsilini, Pleurobemini, Quadrulini, Amblemini and Margaritiferidae, are frequently represented in phylogenetic studies. These taxa in-

clude well-sampled eastern North American and European genera. Conversely, tropical taxa such as the Rectidentinae and Parreysiinae have been largely neglected. The relationships among the tropical lineages of freshwater mussels remain Great Unanswered Questions in malacology.

The history of freshwater mussel classification has been recently reviewed elsewhere (Roe and Hoeh 2003, Graf and Cummings 2006, Bogan and Roe 2008), and the cladistic relationships among the families of the Unionoida will be the focus of my discussion. The subfamilies and tribes of the Unionidae are beyond the scope of this review. The key insight from Figure 2 can be seen in the differences between the dark gray bars (number of studies testing inter-familial relationships) and the black bars (omitting multiple uses of the same character data). Not only have relatively few taxa been engaged to test hypotheses of higher-level freshwater mussel relationships, but the tendency has been to reanalyze too much of the same data. As a result, our knowledge of freshwater mussel evolution is biased by both limited sampling and false replication.

Furthermore, repeated re-analyses of similar data sets have yielded conflicting results. Figure 3 summarizes the results of the 13 phylogenetic studies that have included representatives of at least three freshwater mussel families. Conflict among these analyses is evident, with the most contentious issues being the monophyly of the Unionidae, the monophyly of the Etheriidae, and the sister group of the Hyriidae. However, the alternative phylogenies among these studies are, in general, poorly supported. These problems have been attributed to the unsuitability of mitochondrial DNA to recover Mesozoic divergences and have been discussed in detail elsewhere (Graf and Cummings 2006, Hoeh *et al.* 2009, Graf and Cummings 2010). To date, a fine example has been set of how *not* to resolve the family-group level relationships among the Unionoida.

This lack of phylogenetic resolution is unfortunate because freshwater mussels could be exemplar taxa for addressing broad-scale hypotheses of evolutionary, ecological, genetic, and other biological processes. However, even with a solid unionoid phylogeny, some important problems in freshwater bivalve evolution might remain intractable applying only the comparative method. For example, both parasitic larval morphology and the arrangement of the marsupial demibranchs have historically been regarded as essential characters for classification (Ortmann 1912, Heard and Guckert 1971, Davis and Fuller 1981). While phylogenetic work to date has been sufficient to reject the simplicity of the traditional arrangement (Fig. 3), the lack of parental care and retention of a planktonic larval stage in *Neotrigonia* (Ó Foighil and Graf 2000) renders the well-supported sister group to the Unionoida useless for polarizing transformations among the states of these key characters. A similar problem obtains for interpreting the morphology of *Margaritifera* Schumacher,



1816. Traditionally, the Margaritiferidae has been regarded as the basal unionoid family, and the lack of both posterior mantle fusion and well developed interlamellar septa were regarded as symplesiomorphies shared with *Neotrigonia* (Smith 1980). The discovery that the Margaritiferidae is nested within the crown Unionoida renders this reconstruction of character transformation ambiguous (Graf 2002). If the lack of those characters among *Margaritifera* species is plesiomorphic, posterior mantle fusion and interlamellar septa are homoplastic among the other families. Alternatively, those characters may be synapomorphies of the Unionoida that are reversed in the Margaritiferidae. Graf and Cummings (2006) found these two scenarios equally parsimonious.

The combination of phylogenetic ambiguity and out-group issues is further exemplified in the study of doubly-uniparental inheritance (DUI) of mitochondria by Walker *et al.* (2006). DUI seems to be widespread among the Bivalvia, but it has been most commonly reported among mytilids and freshwater mussels (Theologidis *et al.* 2008, Doucet-Beaupré *et al.* 2010, and references cited therein). Interestingly, DUI is apparently absent from the (*Etheriidae* + *Mycetopodidae* + *Iridinidae*) clade as well as *Neotrigonia* (Walker *et al.* 2006). How one interprets the history of DUI among freshwater mussels depends upon the position of the Hyriidae. If the hyriids (DUI+) are the basal branch of the Unionoida, then the (Et + My + Ir) clade (DUI-) represents the loss of a separate paternally inherited lineage of mitochondria. But, if the (Et + My + Ir) clade is basal, then the absence of DUI could simply be retention of the plesiomorphic condition from *Neotrigonia* and the other heteroconchs (DUI-). The absence of a robust phylogeny of freshwater mussel families hampers study of the origin and maintenance of mitochondrial heteroplasmy, which likely has broader implications than freshwater bivalve phylogeny (*e.g.*, Tuppen *et al.* 2010).

At this moment, the classification of the Unionoida, the richest clade of freshwater bivalves, teeters in precarious position. The family-group level classifications of many genera, especially those from the tropics, rely on 1) a traditional non-cladistic interpretations of morphological similarities that molecular phylogenetic analyses have shown to be homoplastic

Figure 2. Taxonomic bias in published phylogenetic studies of the Unionoida. See text for explanation. The consensus phylogeny is based on the analyses of Graf and Cummings (2006) and Whelan *et al.* (2011), and the classification proposed by Bieler *et al.* (2010). Graph bars depict the number of published phylogenetic and/or phenetic analyses that included a representative of each genus. White/maximum extent: all studies; light gray: studies including ≥ 3 different family-group level taxa; dark gray: studies including ≥ 3 families; black: ≥ 3 families, but omitting multiple uses of the same sequence data. [Author's Note: Complaining that the genus names are too small to read is missing the tree for the leaves.]

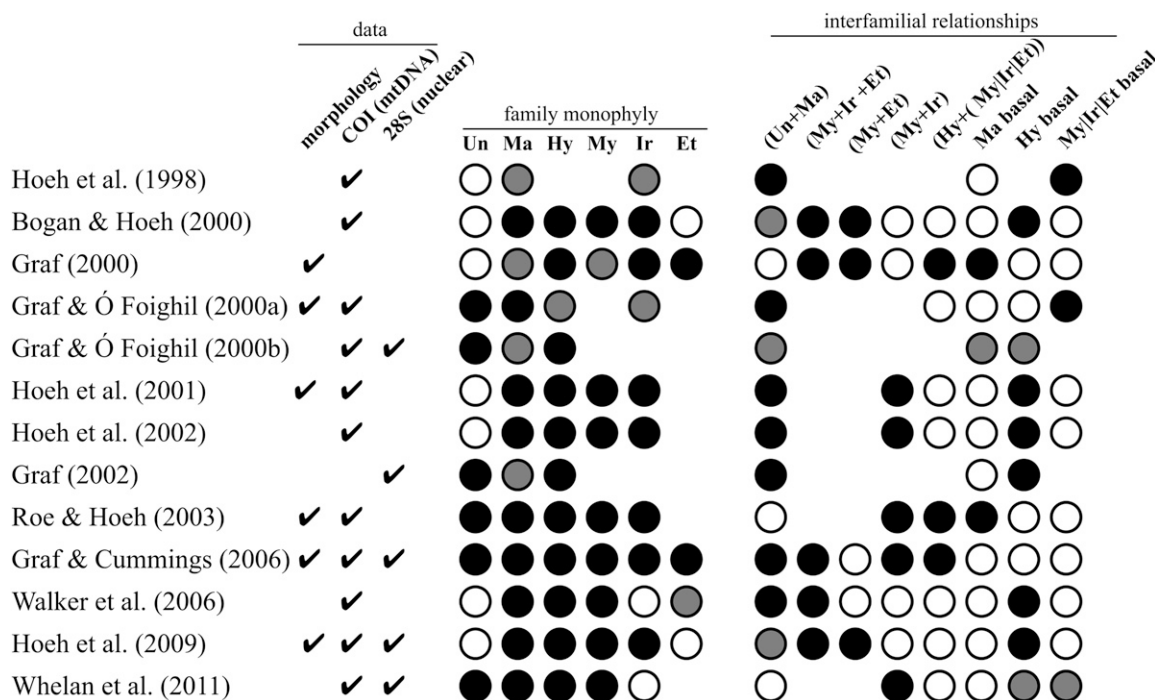


Figure 3. Summary of results from phylogenetic studies testing relationships among freshwater mussel families. Family names for Unionidae, Margaritiferidae, Hyriidae, Mycetopodidae, Iridinidae and Etheriidae are abbreviated by their first two letters. Black circles: relationship/monophyly supported; white circles: relationship/monophyly not supported; gray circles: insufficient sampling or ambiguous results.

and 2) conflicting phylogenetic studies based on biased taxon and character sampling (Figs. 2 and 3). The principle area of agreement among the analyses so far is that the Folmer *et al.* (1994) fragment of cytochrome oxidase subunit I (COI) is not equal to the task of resolving freshwater mussel families (Graf and Cummings 2006, Hoeh *et al.* 2009, Whelan *et al.* 2011). That gene, the most commonly applied to date (Fig. 3), suffers saturation due a combination of conservatism in amino acid sequence and redundancy in the genetic code. This realization after more than a decade of research provides not only 20/20 hindsight to assess previous analyses but also insight into solving these problems. Simply put, we need not only more slowly evolving markers but also targeted taxon sampling to explicitly test the monophyly of freshwater mussel taxa and the relationships among them. These same lessons will need to be applied to the problem of relationships among the subfamilies of the Unionidae (Campbell *et al.* 2005, Whelan *et al.* 2011). Given the species-richness, geological age, and zoogeographical conservatism of the Unionoida, patterns of vicariance among well-resolved freshwater mussels clades could be valuable for testing macroevolutionary process hypotheses such as the chronology of tectonic events or hydrological evolution on a continental scale. Given the rates of extinction among freshwater mussels (Haag 2009) and the multitude of threats facing fresh waters

(Strayer and Dudgeon 2010, Dudgeon *et al.* 2011), resolving the supra-generic relationships of the Unionoida is time-critical and among the most pressing problems in freshwater malacology.

Sphaeriidae

The Sphaeriidae are biologically quite distinct from the Unionoida, although some of the same syndrome of analytical problems have compromised our understanding of their phylogenetic relationships. The Sphaeriidae is less species-rich than the Unionoida (227 spp., Table 1) and traditionally represented by only five genera: *Sphaerium* Scopoli, 1777, *Musculium* Link, 1807, *Pisidium* Pfeiffer, 1821, *Eupera* Bourguignat, 1854 and *Byassanodonta* d'Orbigny, 1846 (Dreher-Mansur and Meier-Brook 2000). As described above, the small size of fingernail, pill and pea clams and their life history traits make them extraordinary colonizers. For example, as pointed out by Cummings and Graf (2009), sphaeriid diversity is higher in the formerly glaciated areas of North America than in the south. These clams are capable of dispersing to favorable habitats across drainage divides. As such, populations of the Sphaeriidae are commonly found in isolated lentic environments, too unstable to support a diverse freshwater mussel community. Although morphological and molecular studies of sphaeriid phylogeny are incongruent, both reveal

complimentary evolutionary trends for adaptation to ephemeral habitats.

There have been two separate approaches to sphaeriid phylogeny, and these are exemplified by the strictly molecular analysis of Lee and Ó Foighil (2003) and the morphology-based study of Korniusshin and Glaubrecht (2002). Several other studies (e.g., Cooley and Ó Foighil 2000, Dreher-Mansur and Meier-Brook 2000, Lee 2004, Korniusshin and Glaubrecht 2006) are roughly consistent with one or the other of these, and comparison of the alternative cladograms shown in Fig. 4 will be the focus of my discussion. Both trees support the traditional subfamilial arrangement: the Neo- and Afrotropical Euperinae (= *Eupera* + *Byssanodontia*) sister to the cosmopolitan Sphaeriinae. In general, the hypothesized relationships of the Sphaeriinae run anti-parallel to each other in the two studies. Lee and Ó Foighil (2003) recovered the traditional *Pisidium* as a grade at the base of the subfamily, and *Musculium* was nested among the species of *Sphaerium*. Korniusshin and Glaubrecht (2002) reported the opposite pattern, with a monophyletic *Pisidium* and a paraphyletic basal grade composed of *Sphaerium* and *Musculium*. At the species-level there is some congruence, with some closely related species occurring together on both topologies, but there seems to be a similar degree of incongruence among other species groups (Fig. 4). Both sets of authors proposed novel genus-group level classifications of the Sphaeriinae, but the unresolved conflicts seem to cancel each other out. With the exception of demoting *Musculium* to a subgenus of *Sphaerium*, the traditional generic classification of the Sphaeriidae remains in common usage.

Lee and Ó Foighil (2003) and Korniusshin and Glaubrecht (2002) have interpreted different trends in sphaeriid evolution from their respective preferred phylogenies (Fig. 4). The morphological tree of Korniusshin and Glaubrecht (2002) is consistent with a hypothesized trend toward miniaturization among the Sphaeriidae (Meier-Brook 1970). Sphaeriid species are small, typically less than 2 cm. Whereas *Sphaerium* species like *S. rhomboideum* (Say, 1822) and *S. striatinum* (Lamarck, 1818) (near the basal branches of the morphological tree) tend to be at the larger end of this size range, derived species of *Pisidium* may be 2–3x smaller (Clarke 1973). Correlated with smaller size is a concomitant reduction in various organ systems such as the ctenidia, stomach, and shell hinge (Korniusshin and Glaubrecht 2002).

Lee and Ó Foighil (2003) emphasized the increase in complexity in morphology and behaviors associated with ovovivipary. Based on their strictly molecular phylogeny (Fig. 4), the plesiomorphic condition of the Sphaeriidae is synchronous brooding in an unmodified marsupial inner demibranch. That is, a clutch derived from a single spawning event is brooded within the interlamellar spaces of the inner demibranchs, as seen in *Eupera*. In the Sphaeriinae, however, the marsupium is modified to hold this clutch within a specialized

brood sac. The brood sac is derived from the descending filaments of the inner demibranch and serves to provide extra-ooegonial nourishment to the clutch (i.e., euvivipary) (Korniusshin and Glaubrecht 2002). Whereas *Eupera* species produce large (500 μm), yolky eggs, sphaeriine species get away with smaller eggs (50 μm) with less yolk. Among the various *Pisidium* lineages, each marsupial demibranch harbors a single brood sac. The *Sphaerium* (+ *Musculium*) clade is diagnosed by asynchronous/sequential brooding. In these species, marsupia bear multiple brood sacs derived from separate spawning events (Cooley and Ó Foighil 2000).

While the two phylogenies in Fig. 4 are largely irreconcilable, these hypothesized trends in sphaeriid evolution are not necessarily mutually exclusive. Reduction in adult size and asynchronous brooding could both be adaptations for rapid reproduction. Smaller size can shorten generation times, and asynchronous brooding likely lowers the energy threshold that must be achieved before spawning (Cooley and Ó Foighil 2000). Both of these trends perhaps explain the success of sphaeriids in colonizing ephemeral freshwater habitats that exclude other bivalves.

Sphaeriids also have odd systems for reproduction and genetic inheritance that apparently contribute to their dispersal abilities. An area of promising research in this regard is the problem of genome duplication (Petkevičiūtė *et al.* 2007, Stunžėnas *et al.* 2011). Among the several species that have been examined, polyploidy is the rule, with chromosome numbers ranging to above 200 and ploidy levels as high as 13n (Lee 1999). Evidence for genome duplication comes not only from karyotype studies (Petkevičiūtė *et al.* 2007) but also the presence of paralogous copies of typically single-copy nuclear genes (Lee and Ó Foighil 2002). These paralogues diverged early in sphaeriine evolution, and highly polychromosomal nuclei have been discovered throughout the various lineages of *Pisidium* and *Sphaerium* (+ *Musculium*). Among bivalves, polyploidy is uncommon but observed in numerous sphaeriid species, *Lasaea* Leach, 1827 (Ó Foighil and Thiriott-Quévieux 1991) and *Corbicula* (Lee *et al.* 2005). In the latter genera, polyploidy is associated with asexuality, but Lee (1999) has confirmed spermatogenic meiosis for *Sphaerium striatinum* ($2n \times n = 152$). Only three sphaeriine species are known to be diploid: *Sphaerium corneum* (Linnaeus, 1758), *S. rhomboideum*, and *S. solidum* (Normand, 1844). But, 2n numbers differ among species and populations (30–44), and these taxa occur in different clades (Fig. 4). Parsimony optimization leads to the conclusion that diploidy is a derived homoplastic condition among the Sphaeriinae, but this interpretation runs counter to prevailing theory: polyploidy is regarded as a derived condition among animals and plants (Futuyma 2005). The equally unsatisfactory alternative is that polyploidy is common among the Sphaeriidae due to parallel independent origins. The nature of chromosomal inheritance

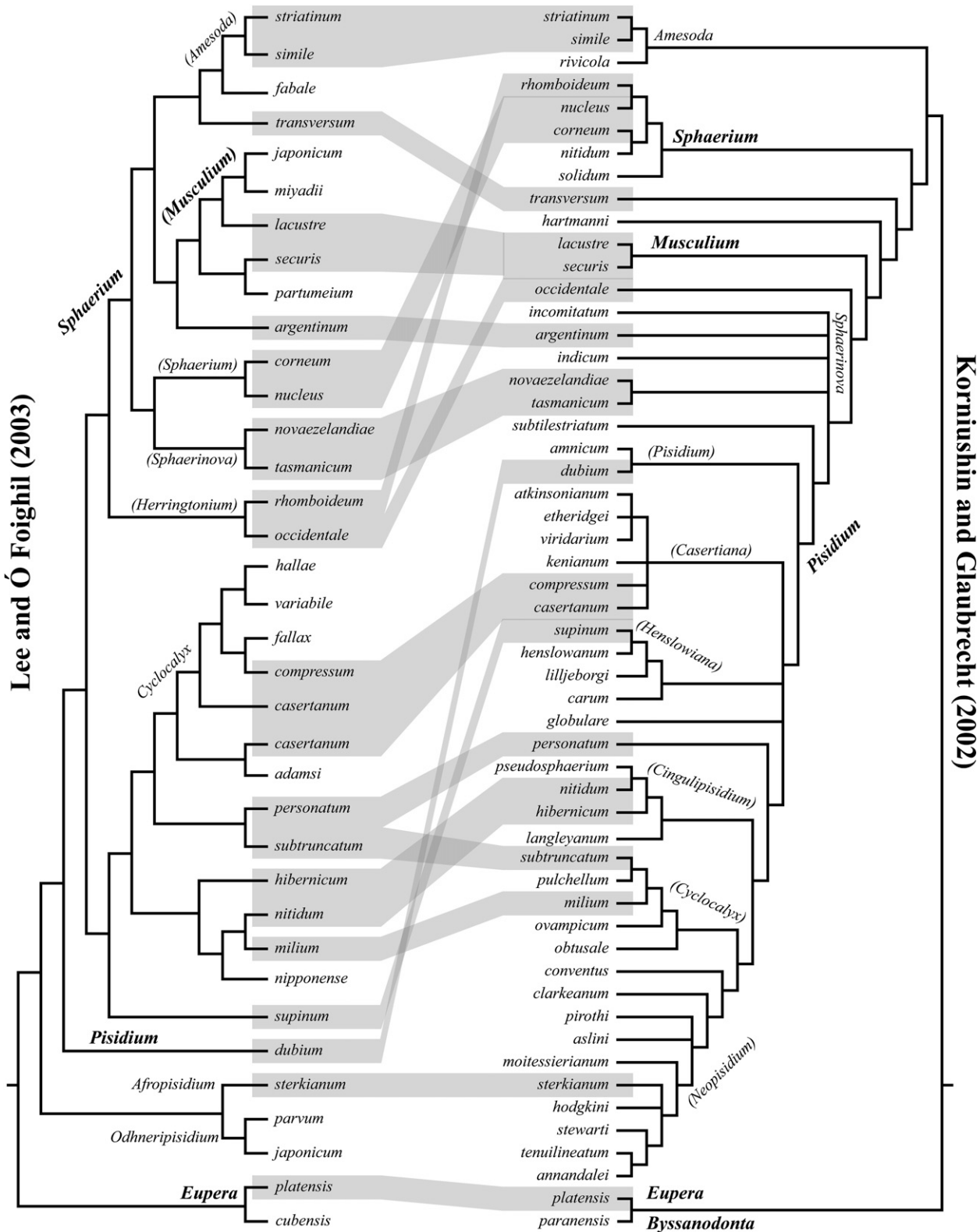


Figure 4. Comparison of molecule- and morphology-based phylogenies of the Sphaeriidae (Korniusshin and Glaubrecht 2002, Lee and Ó Foighil 2003). Traditional genera are shown in bold. Gray highlighting connects identical species in the two studies.

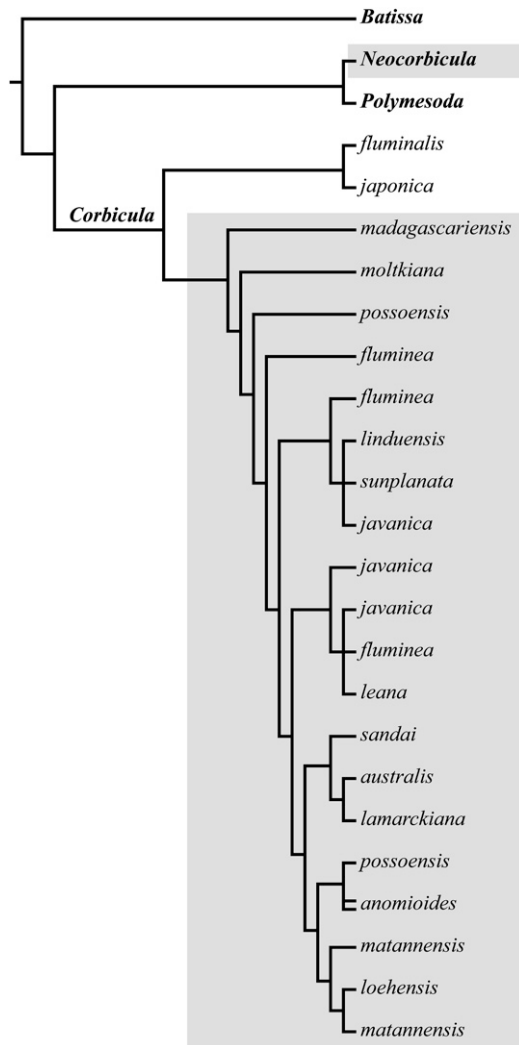


Figure 5. Phylogeny of the family Cyrenidae (Glaubrecht *et al.* 2006). Gray highlighting indicates freshwater taxa.

and the evolution of ploidy-levels in the Sphaeriidae is one of the most interesting unanswered questions among the freshwater bivalves.

The lack of a single phylogeny of the Sphaeriidae based on a combination of morphological and molecular characters undermines our understanding of freshwater bivalve evolution as well as questions of broader significance, such as the evolution of polyploidy and asexuality. And, the reliance upon cyrenids (*e.g.*, *Corbicula*, *Neocorbicula* Fischer, 1886) as outgroups to polarize morphological transformations has surely biased interpretation of trends in sphaeriid evolution. Among freshwater bivalves, the level of attention garnered by the Sphaeriidae is disproportionate to their diversity. While research to date has revealed surprising complexity among

these minute bivalves — manifest in their life history variation, mechanisms of genetic inheritance, and adaptive radiation into ephemeral freshwater habitats — a great deal of work remains to place the Sphaeriidae in a broader evolutionary context.

Cyrenidae (= Corbiculidae)

The Cyrenidae (formerly the Corbiculidae, Bieler *et al.* 2010) is perhaps best known for the invasive species *Corbicula fluminea* (Müller, 1774). In North America, this freshwater clam was first discovered in British Columbia in the 1920s and has since spread to occupy (and, in many places, dominate) freshwater habitats over much of the continent (McMahon 1982). *Corbicula* is also an invasive nuisance in Palearctic and Neotropical waterways (Beasley *et al.* 2003, Sousa *et al.* 2008, Rosa *et al.* 2011). Less attention has been paid to the > 80 other species of the genus in its native range in Eurasia and the Afrotropics, not to mention *Neocorbicula* in South America (Table 1). Indeed, the prevailing paradigm — challenged by multiple modern molecular analyses — has been that the global *Corbicula* is represented by only two widespread species (Morton 1986, Kijviriyia *et al.* 1991). The Cyrenidae differs from the other primarily freshwater families for retaining several marine/brackish genera like *Polymesoda* Rafinesque, 1820, *Batissa* Gray, 1853 and *Villorita* Griffith and Pidgeon, 1833 (see the appendix). Because of this, the Cyrenidae has the potential to be a model taxon for the general study of bivalve radiations into inland environments.

Efforts to resolve cyrenid phylogeny have been hampered by the independent evolution of nuclear and plastid genomes, but research to date supports multiple separate invasions of fresh water habitats. Several recent attempts have been made to recover the phylogeny of *Corbicula* using mitochondrial DNA, generally in the context of placing the invasive haplotypes among those of native Asian taxa (*e.g.*, Siripattawan *et al.* 2000, Lee *et al.* 2005, Pigneur *et al.* 2011). This work was significant for discovering multiple invasive lineages where the previous literature had recognized only a single species, *C. fluminea*. The most extensive sampling of the genus in its native range comes from Glaubrecht *et al.* (2003, 2006). Their topology derived from analysis of cytochrome oxidase subunit I (COI) mtDNA is shown in Fig. 5. Though sampling within *Corbicula* and the Cyrenidae is sparse, these data reveal two separate invasions of fresh waters from marine/brackish lineages. Neotropical *Neocorbicula* shares a more recent common ancestor with *Polymesoda* than with the Asian freshwater lineages of *Corbicula*. The basal lineage of *Corbicula* is represented by brackish-water species (*C. fluminalis* (Müller, 1774) and *C. japonica* Prime, 1867), with the remainder comprising a freshwater clade. Unlike the freshwater bivalve taxa discussed above, morphologically similar marine/brackish sister taxa are available to

polarize character transformations associated with adaptation to life in fresh waters.

The independent transitions to fresh water habitats are associated with convergent evolution of vivipary. Whereas marine/brackish taxa like *Polymesoda* and *Corbicula japonica* retain the plesiomorphic autobranch bivalve mode of broadcast spawning and planktonic veligers, *Neocorbicula* and freshwater *Corbicula* species brood their larvae within the interlamellar spaces of their demibranchs (Ituarte 1984, Morton 1985, Korniusshin and Glaubrecht 2003). In these freshwater lineages, offspring are released as crawl-away juveniles. A notable exception is *C. sandai* Reinhardt, 1878 from Lake Biwa, Japan. This species is oviparous and larvae immediately settle following liberation from their egg case (Hurukawa and Mizumoto 1953). Such a partial reversal in a lentic species circumstantially supports the hypothesis that parental care and direct development are adaptations to life in flowing water.

The mtDNA phylogeny of *Corbicula* species in Fig. 5 conflicts with the current taxonomy of the genus. Notice, for example, that specimens identified as *C. fluminea* are not recovered as monophyletic. This is possibly attributable to morpho-species circumscriptions that pre-date modern preferences in evolutionary species concepts. However, recent research has demonstrated that *Corbicula* species-trees can be uncoupled from maternally inherited mitochondrial DNA gene-trees by androgenetic clonal reproduction (Hedtke *et al.* 2008). Multiple *Corbicula* species have been discovered to be polyploid (*e.g.*, triploid or tetraploid), with biflagellate unreduced sperm (Komaru *et al.* 1997, Siripattawan *et al.* 2000, Korniusshin 2004). As simultaneous hermaphrodites, these species can self-fertilize. However, the maternal nuclear DNA of the ovum is ejected and replaced by that from the sperm. Offspring thus derive their plastid genomes from the ovaries but their nuclear genomes come from the testes. Hedtke *et al.* (2011) demonstrated that occasional out-crossing among *Corbicula* species can lead to the hijacking of nuclear genomes by parasitic sperm and the origin of new androgenetic lines. Mitochondrial gene-trees in *Corbicula* depict the phylogenetic history of germ-line cytoplasm, obscuring species-trees resulting from horizontal transfer of the nuclear genome and paternally-derived phenotypes.

Resolving the phylogeny of the Cyrenidae will require a combined-evidence approach utilizing not only mitochondrial and nuclear markers and morphology but also more sophisticated phylogenetic methodologies that incorporate reticulation/lateral transfer among taxa (de Vienne *et al.* 2007, Abby *et al.* 2010). The cyrenid freshwater bivalves are particularly interesting for their 1) parallel radiations into freshwater habitats and 2) identifiable marine/brackish sister taxa sharing conchological, soft-anatomical, and physiological homologies useful for phylogeny reconstruction. In this regard, evolutionary study of the Cyrenidae has the potential

to elucidate the biological mechanisms exploited by bivalves to colonize inland habitats, useful not only for understanding the invasion biology of *Corbicula* itself but also other nuisance species at the interface between marine and freshwater environments (*e.g.*, *Dreissena*, *Limnoperna* Rochebrune, 1881, *Potamocorbula* Habe, 1955). The complex evolutionary history of the Cyrenidae is surely one of the Great Unanswered Questions on the evolution of freshwater bivalves.

CONCLUSIONS

Recurring challenges among phylogenetic studies of the freshwater bivalves include outgroup issues, incomplete ingroup sampling, and atypical processes of genetic inheritance. Each of these challenges is an opportunity for significant research. While the several phylogenetic studies discussed above have been adequate to dismantle the traditional arrangements of the Unionoidea, Sphaeriidae, and Cyrenidae, work to date has yet to produce a natural classification with a firm cladistic foundation. This has partly to do with the difficulty of rooting these derived freshwater radiations among the marine bivalves. In the case of the Sphaeriidae, a clear bivalve outgroup for polarizing morphological transformations is as yet unavailable. However, even after the heterodont phylogeny is better resolved, the problem of homology between adaptations to fresh waters (*e.g.*, parental care and lack of a planktonic veliger) and the plesiomorphic marine bivalve states will remain. This is the case with the Unionoidea. Although *Neotrigonia* is well supported as the extant sister lineage to freshwater mussels, its morphology, behavior, and development are of no value for polarizing ingroup variation in parasitic larval type and the arrangements of the marsupial demibranchs. Unfortunately, these are the characters that have traditionally been the most useful for diagnosing freshwater mussel families. The “outgroup problem” is perhaps less of an issue for the Cyrenidae since the brackish/marine sister lineages to the freshwater clades occur in the same family.

Ingroup sampling in all three primary freshwater bivalve clades has been largely serendipitous. The advent of cheap DNA sequencing and rapid tree-searching algorithms in the 1990s led to a paradigm shift in freshwater bivalve systematics, and the major results have been rejection of long-held traditional views of bivalve evolution and acceptance that bivalve classification is not as simple as was once thought. In the vacuum of phylogenetic ignorance, advancement could be achieved by applying the taxa and characters that were merely available. Knowing what we do now, resolving the basal branching patterns of these freshwater bivalve clades will require targeted sampling to address specific hypotheses of monophyly and synapomorphy. This review has highlighted

some fruitful areas for phylogenetic research, in terms of both taxon and character sampling. In the next phase of cladistic studies of the Unionoida, Sphaeriidae, and Cyrenidae, transformative results will come from those who think globally about freshwater bivalve evolution.

In addition to these taxon and character sampling issues (not unique to freshwater bivalves), each of the primary freshwater bivalve clades exhibits mechanisms of genetic inheritance that defy biological dogma: doubly-uniparental inheritance of mitochondrial in the Unionoida, genome duplication in the Sphaeriidae, and androgenetic reproduction in the Cyrenidae. All three cases have resulted in species trees confounded by incongruent gene trees. These phenomena undermine the application of textbook theories of animal genetics to the problem of freshwater bivalve evolution, but they are also invitations to explore new frontiers and develop novel approaches to phylogeny reconstruction. While taxonomic resolution is its own reward, the effort to discover the relationships among the freshwater bivalve lineages has implications beyond systematic malacology.

At a more fundamental level, study of freshwater bivalves — like that of so many invertebrates — is hindered by the often cited “taxonomic impediment.” Simply put, too few researchers are training too few students in the methods of comparative biology. It was striking to me in researching this review how few lab groups are addressing the phylogeny of the primary freshwater bivalve radiations. In order to provide the biodiversity expertise needed by conservation biologists and resource managers to document, understand and mitigate the tide of extinction in freshwater ecosystems, the dwindling field of systematic malacology is going to need to pick up the pace. Until relatively recently, much of the necessary data were confined to natural history museums and their libraries, limiting by inertia access to specimens and literature. Fortunately, ongoing biodiversity informatics initiatives such as GBIF (<http://www.gbif.org/>) and BHL (<http://www.biodiversitylibrary.org/>), and even the rapid electronic pace of modern interlibrary loan, have changed all that. However, without the people to identify the problems and to do the work to solve them, these specimen and literature data will serve no purpose — and inertia will give way to entropy. It is my hope that this brief synthesis of freshwater bivalve diversity and evolution has both highlighted some of the Great Unanswered Questions in the field and articulated the value of trying to answer them.

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Appendix. *Species, genera and families of freshwater bivalves.* Twenty-one families of the Bivalvia have been attributed to fresh waters (see text), but there has been an insufficient distinction between those that inhabit inland waterways and those that merely occur in “freshened” habitats. The following lists the taxa attributed to fresh water, and those marked with a dagger (†) are herein regarded as freshwater bivalves. These data are summarized in Table 1. Valid species, synonymies and geographical range information can be found on the MUSSEL Project Web Site (<http://www.mussel-project.net/>).

Family MYTILIDAE

† *Brachidontes arcuatulus* (Hanley, 1844). — Distribution: Indochina. *Brachidontes* Swainson, 1840 is a typically marine/intertidal genus with > 30 species (Brandt 1974).

† *Limnoperna fortunei* (Dunker, 1857) = *L. siamensis* (Morelet, 1875) = *L. supoti* Brandt, 1974 = *L. coreana* Park and Choi, 2008. — Distribution: southeastern Asia; introduced to Brazil, Japan, etc. *Limnoperna* Rochebrune, 1881 is a typically brackish water genus of 9 species (Brandt 1974, Ricciardi 1998, Kimura *et al.* 1999, Beu 2006).

L. securis (Lamarck, 1819) = *Xenostrobus securis*. — Distribution: brackish, Australia and New Zealand; introduced to Japan.

Mytella charruana (d’Orbigny, 1842). — Distribution: brackish, Neotropical; introduced to Florida. *Mytella* Soot-Ryen, 1955 is a typically marine/intertidal genus of 5 species (Olsson 1961, Keen 1971, Boudreaux and Walters 2006).

M. maracaibensis Beauforthuy, 1967. — Distribution: brackish, Lake Maracaibo, Venezuela.

† *Sinomytilus harmandi* (Rochebrune, 1881). — Distribution: Mekong Basin, southeastern Asia. *Sinomytilus* Theile, 1934 is a poorly known, exclusively freshwater genus (H. Adams 1870, Brandt 1974, Morton and Dinesen 2010).

† *S. morrisoni* Brandt, 1974. — Distribution: Mun River (Mekong), Thailand.

† *S. swinhoei* (H. Adams, 1870). — Distribution: Yangtze River, China.

Family ARCIDAE

† *Scaphula celox* Benson, 1836. — Distribution: lower Ganga Basin, India. *Scaphula* Benson, 1834 is a freshwater genus in a typically marine family (Ghosh 1922, Brandt 1974, Janaki Ram and Radhakrishna 1984, Subba Rao 1989, Nesemann *et al.* 2003).

† *S. deltae* Blanford, 1867. — Distribution: lower Ganga Basin, India.

† *S. minuta* Ghosh, 1922. — Distribution: eastern Thailand peninsula.

† *S. nagarjunai* Janaki Ram and Radhakrishna, 1984. — Distribution: Krishna River, India.

† *S. pinna* Benson, 1856. — Distribution: Burma and Thailand.

† **Family UNIONIDAE** (681 species). — Distribution: North and Central America, Eurasia, Africa. Information about species richness of freshwater mussel families can be found in Graf and Cummings (2007) and Bogan (2008).

† **Family MARGARITIFERIDAE** (13 species). — Distribution: Holarctic.

† **Family HYRIIDAE** (75 species). — Distribution: South America, Australasia.

† **Family ETHERIIDAE** (4 species). — Distribution: South America, Africa, southeastern Asia.

† **Family MYCETOPODIDAE** (43 species). — Distribution: South America.

† **Family IRIDINIDAE** (43 species). — Distribution: Africa.

Family CARDIIDAE. — The Limnocardiiinae occurs in Ponto-Caspian brackish/marine waters. A few species are found in waters of low salinity (< 5 ppt) (Zhadin 1965, Starobogatov *et al.* 2004, Slugina 2006, Munasyypova-Motyash 2006, Kantor *et al.* 2010).

† *Adacna laeviuscula* (Eichwald, 1829) = *A. fragilis* Milachewitch, 1908. — Distribution: fresh/brackish, Black and Caspian Seas.

A. vitrea (Eichwald, 1829) = *A. glabra* Ostroumoff, 1905 = *A. minima* Ostroumoff, 1905 = *A. sidorovi* (Starobogatov, 1974). — Distribution: brackish, Caspian and Aral Seas.

Didacna Eichwald, 1838 (8 species). — Distribution: brackish, Caspian Sea.

† *Hypanis plicata* (Eichwald, 1829) = *H. relicta* (Milachewitch, 1916) = *H. regularis* (Starobogatov, 2004). — Distribution: fresh/brackish waters of the Black and Caspian Seas. The two other species of *Hypanis* Eichwald, 1838 are strictly brackish.

† *Monodacna colorata* (Eichwald, 1829). — Distribution: rivers and reservoirs, Black Sea Basin. *Monodacna* Eichwald, 1838 is a typically brackish genus of 8 species.

Family SOLENIDAE

Neosolen aquaedulcioris Ghosh, 1920 = ? *Solen delesserti* Sowerby, 1874. — Distribution: brackish, Indo-Pacific. *Neosolen* Ghosh, 1920 is regarded as a monotypic brackish water genus (Ghosh 1920, Subba Rao 1989).

Family PHARIIDAE

† *Novaculina andamanensis* Preston, 1918. — Distribution: Andaman Islands, India. *Novaculina* Benson, 1830 is a freshwater genus in a typically marine family (Brandt 1974, Subba Rao 1989).

† *N. chinensis* Liu and Zhang, 1979. — Distribution: Lower Yangtze, China.

† *N. gangetica* Benson, 1830. — Distribution: Ganga River, India and Bangladesh.

† *N. siamensis* Morlet, 1889. — Distribution: Thailand.

† *Pharella waltoni* Brandt, 1974. — Distribution: Thailand. *Pharella* is a typically brackish/marine genus of 7 species (Brandt 1974).

Family DONACIDAE

Galatea Bruguière, 1797 = *Egeria* de Roissy, 1805 (11 species). — Distribution: brackish, eastern Atlantic, West Africa (Daget 1998).

† *Iphigenia centralis* (Germain, 1904). — Distribution: Niger River. *Iphigenia* Schumacher, 1817 is a typically brackish water genus of 7 species (Daget 1998).

† *I. laevigata* (Gmelin, 1791). — Distribution: lower segments of rivers, Senegal to Congo.

Family SPHAERIIDAE. — The Sphaeriidae is strictly freshwater (Bogan 2008, and numerous local revisions).

† *Eupera* Bourguignat, 1854 (34 species). — Distribution: tropical Americas and Africa.

† *Byassanodonta paranensis* d'Orbigny, 1846. — Distribution: Parana Basin, South America.

† *Pisidium* Pfeiffer, 1821 (133 species). — Distribution: global.

† *Sphaerium* Scopoli, 1777 = *Musculium* Link, 1807 (59 species). — Distribution: global.

Family PHOLADIDAE

† *Lignopholas fluminalis* (Blanford, 1867). — Distribution: India, Burma and Borneo. *Lignopholas* Turner, 1955 is a typically brackish/marine genus of 4 species (Turner and Santhakumaran 1989).

Family TEREDINIDAE

Nausitora dunlopei (Wright, 1864). — Distribution: brackish, Indo-Pacific. *Nausitora* Wright, 1864 is a brackish/marine genus of 6 species (Turner 1966).

Psiloteredo healdi (Bartsch, 1931). — Distribution: brackish, Caribbean, Lake Maracaibo. *Psiloteredo* Barsch, 1922 is a brackish/marine genus of 3 species (Turner 1966).

Family CORBULIDAE

† *Anticorbula fluvialilis* (H. Adams, 1860) = *Guianadesma sinuosum* Morrison, 1943. — Distribution: Amazon Basin (Simone 1999, 2006).

Potamocorbula amurensis (Schrenck, 1861). — Distribution: brackish, northwestern Pacific; introduced to San Francisco Bay. *Potamocorbula* Habe, 1955 is a brackish/marine genus of 9 species (Carlton *et al.* 1990).

Family ERODONIDAE

Erodona mactroides (Bosc, 1802). — Distribution: brackish, temperate southwestern Atlantic estuaries (Carcelles 1941, Pérez *et al.* 2010).

Family DREISSENIDAE

† *Congeria kusceri* Bole, 1962. — Distribution: subterranean, Balkins (Stepien *et al.* 2001).

† *Dreissena bugensis* (Andrusov, 1897). — Distribution: rivers and estuaries in the Black Sea Basin; introduced to North America. *Dreissena* is a fresh and brackish water genus of 7 species (Rosenberg and Ludyanskiy 1994, Gelembiuk *et al.* 2006).

† *D. caputlacus* Schütt, 1993. — Distribution: Tigris-Euphrates.

† *D. carinata* (Dunker, 1853). — Distribution: Lake Ohrid.

† *D. polymorpha* (Pallas, 1771). — Distribution: Europe; introduced to North America.

† *Mytilopsis leucophaeata* (Conrad, 1831). — Distribution: brackish and freshwater, Gulf of Mexico, Atlantic U.S.A.; introduced to Europe. *Mytilopsis* Conrad, 1857 is a fresh and brackish water genus of 6 species (Olsson 1961, Marelli and Gray 1985, Simone 2006, Kennedy 2011).

† *M. lopesi* (Alvarenga and Ricci, 1989). — Distribution: Amazon Basin.

† *M. sallei* (Récluz, 1849). — Distribution: Caribbean, South America.

† *M. trautwineana* (Tryon, 1866). — Distribution: Pacific South America; introduced to Caribbean.

Family MACTRIDAE

Tanysiphon rivalis Benson, 1858. — Distribution: brackish, Gangetic Delta, India and Bangladesh (Subba Rao 1989).

Family CYRENIDAE = CORBICULIDAE

† *Corbicula* Megerle von Mühlfeld, 1811 (88 species). — Distribution: mostly freshwater, temperate/tropical Asia and Africa, widely introduced (Prashad 1924, 1928a, b, 1929, 1930, and numerous local revisions).

Batissa Gray, 1853 (3 species), *Villorita* Griffith and Pidgeon, 1833 (3 species), and *Geloina* Gray, 1842 (3 species). — Distribution: brackish, Indo-Pacific (Brandt 1974, Morton 1984, 1989, Subba Rao 1989).

† *Neocorbicula* Fischer, 1886 (4+ species). — Distribution: Central and South America. The diversity of *Neocorbicula* is likely under-estimated (Marshall 1924, 1927, Baker 1930, Simone 2006).

Polymesoda Rafinesque, 1820 (17 species). — Distribution: brackish, tropical eastern Pacific, western Atlantic (Olsson 1961, Keen 1971).

Family CYRENOIDIDAE

Cyrenoida de Joannis, 1835 (6 species). — Distribution: brackish, tropical Americas, West Africa (Dall 1903, Olsson 1961, Daget 1998).