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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater

Arthur E. Bogan

Abstract The term freshwater bivalve is very inclusive and not very informative. There are representatives of at least 19 families that have at least one representative living in freshwater. This suggests at least 14 different invasions of freshwater. At least nine families have small to large radiations in the freshwater environment: Corbiculidae, Sphaeriidae, Dreissenidae, and the unioniforme families: Hyriidae, Margaritiferidae, Unionidae, Etheriidae, Iridinidae, and Mycetopodidae. The unioniforme families contain at least 180 genera and about 800 species. This order is characterized by the unique parasitic larval stage on the gills, fins or the body of a particular host fish. This order of freshwater bivalves is suffering a very high rate of extinction, with about 37 species considered presumed extinct in North America alone. The level of endangerment and extinction facing these animals is primarily the result of habitat destruction or modification.

Keywords Bivalve · Etheriidae · Extinction · Freshwater mussel · Hyriidae · Iridinidae · Margaritiferidae · Mycetopodidae · Unionidae · Unioniformes

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Freshwater Animal Diversity Assessment

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Introduction

Freshwater bivalves provide a filtering service in rivers and lakes. Many species are often found in dense aggregations and filter out large quantities of blue–green algae, diatoms, bacteria, fine-particulate organic particles, as well as silt, absorb heavy metals and large organic molecules. All of the taxa included here are obligate freshwater organisms and spend their entire life cycle in freshwater.

Freshwater bivalves are not a monophyletic group and represent at least 19 families in three subclasses of bivalves. Most families are represented by only a few genera or species. Taxa with large radiations in freshwater include the Sphaeriidae, Corbiculidae, and the Order Unioniformes with 6 families, about 180 genera and about 800 species. Bivalves are mollusks without a head have a single foot enclosing the visceral mass, two pair of gills, and the sexes are typically separate. Each individual has two valves surrounding the body composed of calcium carbonate, either as calcite or aragonitic crystal structure. Unioniforme shells have aragonitic crystal structure.

The life history of freshwater bivalves is varied and depends on the family being discussed. Those species from primarily marine bivalve families have veliger

or brooded larvae (McMahon & Bogan, 2001). The unioniforme bivalves are unique among bivalves, having an obligate parasitic larval stage on the gills, fins or sides of a host fish (Wächtler et al., 2001).

Shell shape varies among the families reflecting partially their phylogentic history and partially the habitat in which they are living. Byssally attached mussels are often much thinner shelled than those species living buried in cobble and gravel substrates. Many of the species of the Unionforme families have heavy shells with a variety of surface sculpture that aid in stability in the substrate.

Most of the species in this group are infaunal organisms burrowing into substrates varying from sand to cobbles and gravel but a few species exploit the exposed hard surfaces by attaching to hard surfaces with byssal threads like blue mussels and the zebra mussels.

Species/generic diversity

Freshwater bivalves are found in 3 different subclasses, separated into 5 separate orders and divided among 19 families within the Class Bivalvia (Deaton & Greenberg, 1991) (Table 1). There are 206 recognized genera of freshwater bivalves, most families represented by only one to five genera. Species diversity in the Dreissenidae follows Rosenberg & Ludyanskiy (1994). Large bivalve radiations in freshwater have occurred in the Sphaeriidae and the six unioniforme families. The species diversity mirrors the diversity of genera with about 1026 species (Tables 1, 2). Once again the highest diversity is found in the Sphaeriidae and the six unioniforme families. Corbiculidae species are over described based on variable shell form, and indications are that there are only a few species (Brandt, 1974; Morton, 1979; Subba Rao, 1989). Generic and species counts were based on literature for Sphaeriidae (Burch, 1975; Mandahl-Barth 1988; Smith, 1992; Dreher Mansur 1993; Daget, 1998; Korniushin & Glaubrecht, 2002; Lee & Ó Foighil, 2003). Estimates of the generic and specific diversity were more difficult to compile for the unioniforme families, due to the variation in systematic philosophy, lack of overview data for areas of the world. We have chosen to ignore for purposes of this exercise the over-inflation of taxonomic levels by the Russian malacologist of the Starobogatov school. Total genera and species were based on major reviews and localized faunal accounts (Ortmann, 1912; Pilsbry & Bequaert, 1927; McMichael & Hiscock, 1958; Haas, 1969; Brandt, 1975; Liu, 1979; Mandahl-Barth, 1988; Subba Rao, 1989; Smith, 1992; Starobogatov 1995; Bonetto, 1997; Daget, 1998; Turgeon et al., 1998; Bogan and Hoeh, 2000; Smith, 2001; Walker et al., 2001; Huff, et al., 2004).

Phylogeny and historical processes

Our current understanding of the phylogeny of the bivalves is still developing. Higher level phylogenies have been developed for bivalves supporting the subclasses recognized on the basis of morphological characters. However, phylogenetic analyses at the family level are just developing. The overall phylogeny of the Order Unioniformes, a monophyletic group is still in a state of flux. Based on recent DNA analyses, the Margaritiferidae, Unioidae, Mycetopodidae, Iridinidae are all monophyletic. Hyriidae genera from South America and Australasia form monophyletic sister clades, but whose relationships to other unioniforme families is still uncertain (Graf, 2000; Hoeh, et al., 1998, 1999, 2001). Curole and Kocher (2002) based on DNA anlyses suggested the family Margaritiferidae branched off from the Unionidae at a minimum of 230 MYA and estimated the subclass Paleoheterodonta diverged from the rest of Bivalvia at approximately 500 MYA (Middle Cambrian).

Speciation in freshwater bivalves may be driven by separation of stream systems by vicariant events or separate invasions of freshwater. In the Unioniformes speciation may be tied to speciation in host fishes. There has been little discussion of the factors driving speciation in unioniforme bivalves.

Present distribution and main areas of endemicity

Diversity of freshwater bivalves across the main zoogeographic areas is extremely variable (Tables 1, 2; Fig. 1). A total of 19 families with 206 genera and an estimated 1026 species are reported from freshwater. Two main areas of diversity and endemism in freshwater bivalves are the southeastern United States and the Oriental region. This diversity is primarily in

Table 1 Total number of genera in families of freshwater bivalves with representatives found in freshwater

	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Subclass Pteriomorpha									
Order Arcoida									
Arcidae	0	0	0	0	1	0	0	0	1
Order Mytiloida									
Mytilidae	0	0	2	1(I)	1	0	0	0	3 (I)
Subclass Paleoheterodonta									
Order Unioniformes									
Etheriidae	0	0	1	0	0	0	0	0	1
Hyriidae	0	0	0	9	0	8	0	0	17
Iridinidae	0	0	6	0	0	0	0	0	6
Margaritiferidae[a]	3	2	0	0	1	0	0	0	3
Mycetopodidae	0	0	0	12	0	0	0	0	12
Unionidae[b]	26(I)	51(I)	6	20(I)	38(I)	1	0	0	142
Total Unionifomes	29	53	13	41	39	9	0	0	180
Subclass Heterodonta									
Order Veneroida									
Cardiidae	2	0	0	0	0	0	0	0	2
Corbiculidae	1	1(I)	1	2(I)	2	2	0	0	3
Sphaeriidae	4	4	3	5	2	2	2(I)	0	5
Dreissenidae	2	1(I)	1	0	0	0	0	0	3
Solenidae	0	0	0	0	1	0	0	0	1
Donacidae	0	0	2	0	0	0	0	0	2
Navaculidae	0	0	0	0	1	0	0	0	1
Order Myoida									
Corbulidae	1	0	0	0	0	0	0	0	1
Erodonidae	0	0	1	1	0	0	0	0	2
Teridinidae	0	0	0	1	0	0	0	0	1
Subclass Anomalodesmata									
Lyonsiidae	0	0	0	1	0	0	0	0	1
Total	40	59	23	51	47	13	2(I)	0	206

PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

(I) are taxa introduced outside of their native range

[a] The genus *Margaritifera* occurs in three regions

[b] The genus *Unio* occurs in two different regions

the Unionidae. The distribution of unioniforme families does not completely correspond to the standard zoogeographic regions (Fig. 2A–F).

Antarctic area

There are no known modern freshwater bivalves from Antarctica.

Oceanic Islands-Pacific area

There are two genera and two species of Sphaeriidae known as introduced species from Hawaii.

Australasian area

The freshwater bivalve fauna of this region includes representatives of 4 families, 13 genera and 43

Table 2 Total number of species in families of freshwater bivalves with representatives found in freshwater

	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Subclass Pteriomorpha									
Order Arcoida									
Arcidae	0	0	0	0	4	0	0	0	4
Order Mytiloida									
Mytilidae	0	0	2	1(I)	2	0	0	0	5
Subclass Paleoheterodonta									
Order Unioniformes									
Etheriidae	0	0	1	0	0	0	0	0	1
Hyriidae	0	0	0	55	0	28	0	0	83
Iridinidae	0	0	41	0	0	0	0	0	41
Margaritiferidae	6	5	0	0	1	0	0	0	12
Mycetopodidae	0	0	0	39	0	0	0	0	39
Unionidae	86(I)	297(I)	32	85(I)	120	1	0	0	621
Total Unionifomes	92	302	74	179	121	29	0	0	797
Subclass Heterodonta									
Order Veneroida									
Cardiidae	5	0	0	0	0	0	0	0	5
Corbiculidae	[a]	2(I)	2	2(I)	[a]	[a]	0	0	6[a]
Sphaeriidae	34	45(I)	35	41	20	14	2(I)	0	196
Dreissenidae	5	2(I)	1	0	0	0	0	0	5
Solenidae	0	0	0	0	1	0	0	0	1
Donacidae	0	0	2	0	0	0	0	0	2
Navaculidae	0	0	0	0	2	0	0	0	2
Order Myoida									
Corbulidae	1	0	0	0	0	0	0	0	1
Erodonidae	0	0	1	1	0	0	0	0	2
Teridinidae	0	0	0	1	0	0	0	0	1
Subclass Anomalodesmata									
Lyonsiidae	0	0	0	1	0	0	0	0	1
Total	137	351	117	226	150	43	2	0	1026

PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

(I) are taxa introduced outside of their native range

[a] The total number of species in the genus is unkown at this time. The group is over-described based on shell shape variation

species. Diversity in the area is dominated by the Hyriidae with 8 genera and 28 species. Hyriids are restricted to Australia, Tasmania, New Zealand, New Guinea and the Solomon Islands. The number of species of Corbiculidae found in Australia is unknown but represented by an abundance of named shell shapes (Smith, 1992).

Palaearctic area

The diversity found in this region is dominated by the diversity of the Unionidae and Sphaeriidae with the remaining diversity contributed by six other families. Considering the vast area covered by this region, the diversity is not evenly distributed. Western Europe,

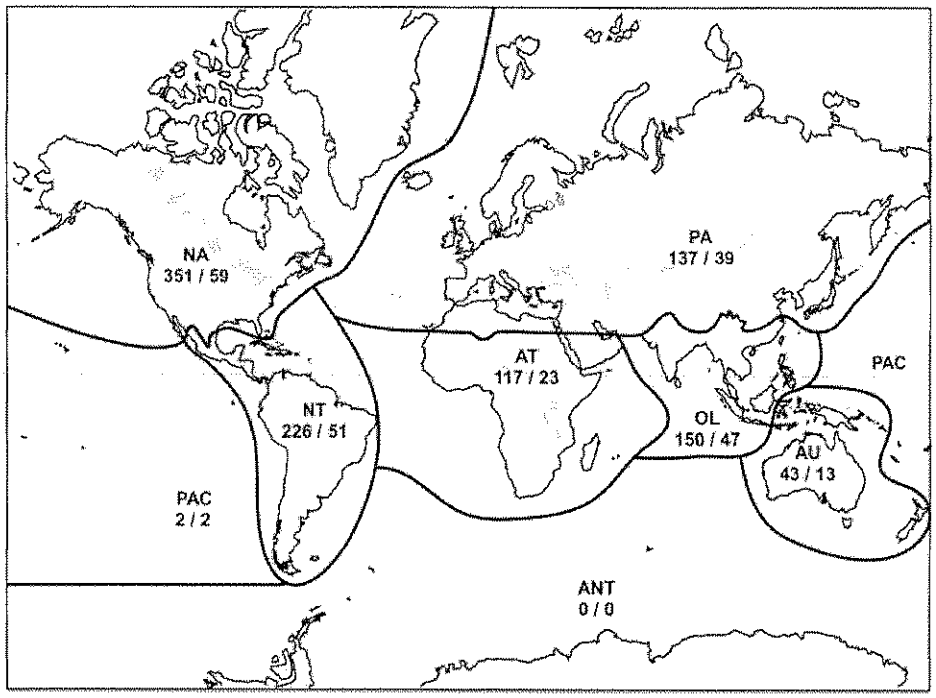

Fig. 1 Distribution of freshwater bivalvia species and genera (SP/GN) per zoogeographic region: ANT, Antarctica; AT, Afrotropical; AU, Australasia; NA, Nearctic; NT, Neotropical; OL, Oriental; PA, Palaearctic; PAC, Pacific Oceanic Islands, ANT, Antarctic

Russia, the trans-Caucasus region and Siberia have a rather limited diversity including representatives of seven families from the area but the greatest diversity in the Unionidae occurs in the eastern region extending from the Amur River basin in the north to southern China, including the Yangtze River basin (Wu, 1998). The diversity of the Unionidae in Western Europe and the region east to the Trans-Caucasus and south to Israel is limited to 6 genera while the Yangtze River basin has 14 genera.

Afro-tropical area

Nine families represented by 23 genera and 117 species are reported from sub-Saharan Africa and the Nile River. Two families with 2 genera and 4 species of freshwater unioniforme bivalves have been reported for Madagascar. Two families, Iridinidae and the Unionidae account for the greatest amount of the generic and species level diversity in this area.

Oriental area

This region's freshwater bivalve fauna is represented by 8 families, 47 genera and 150 species. This fauna can be broken into two separate components, one on the Indian plate extending from extreme eastern Iran east through Pakistan, Afghanistan, India and Bangladesh, and western Myanmar. Southern India is home to two monotypic endemic genera, one a cemented Unionidae (Subba Rao, 1989). The second faunal component extends from Myanmar east down the Malay Peninsula to Java, Borneo, the Philippines, Thailand, Laos, Cambodia, Vietnam, and southern China.

Nearctic area

The Nearctic freshwater bivalve fauna is globally the most diverse with 5 families, 59 genera and 302 species. The greatest diversity of freshwater bivalve genera and species occurs in this area followed by the Oriental region, especially in the Mekong River basin (Brandt, 1974). This diversity is the result of the high level of diversity of the Unionidae of the southeastern United States with 42 genera of and 271 species (e.g., Neves et al., 1998).

Neotropical area

The fauna of this area is diverse with 9 families, 51 genera and 226 species. The freshwater bivalve fauna

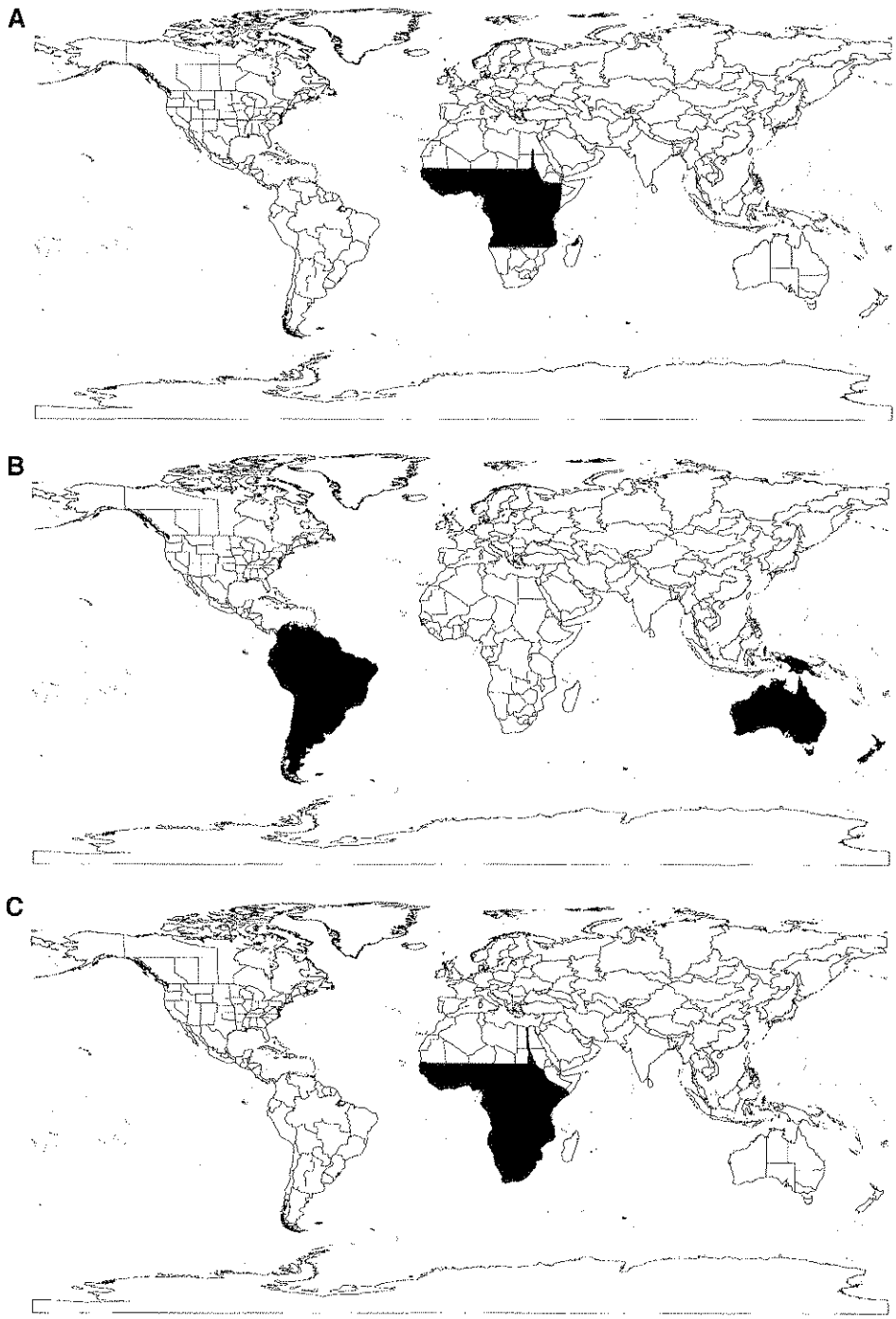

Fig. 2 (**A**) Distribution of Etheriidae, (**B**) Distribution of Hyriidae, (**C**) Distribution of Iridinidae, (**D**) Distribution of Margaritiferidae, (**E**) Distribution of Mycetopodidae, (**F**) Distribution of Unionidae

of this region is poorly known and has not been synthesized recently. The Hyriidae and Mycetopodidae along with the Sphaeriidae account for the majority of the diversity in South America. One genus of Mycetopodidae extends northward through Central America to west Central Mexico. The Unionidae in the Neotropical Area account for 20 genera and 85 species, but are only found in the area from Central Mexico south to Panama and are absent from South America.

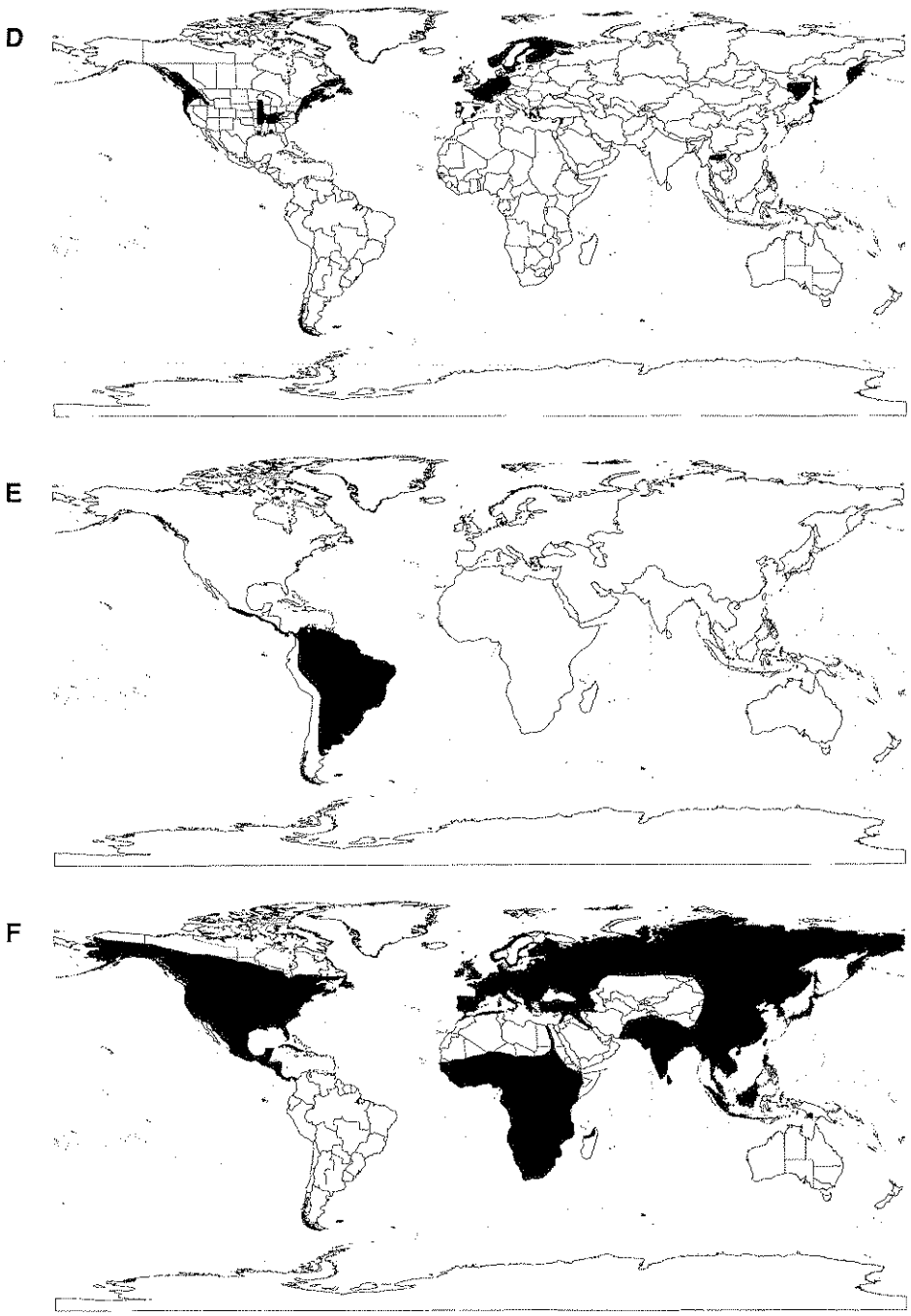

Fig. 2 continued

Human related issues

In various areas of the world, freshwater bivalves are a supplemental food source. The status of freshwater faunas is only incompletely known, but for freshwater mollusks it is declining (Bogan, 1993; Bogan, 1998; Lydeard et al., 2004). This decline is well documented for the very diverse freshwater molluscan fauna of the southeastern United States and suggested for the rest of the world (Bogan 1993; Neves et al., 1998; Lydeard et al., 2004). The consensus is the most dramatic cause of the declines and extinctions of freshwater bivalves is habitat modification and destruction. This can be due to the effects

of dams, canalization, changes in water depth, due to flow changes and changes in fine particle deposition (silt and sand). These modifications affect not only the freshwater mussels, but also the fish they rely on for the unioniforme mussel's parasitic life stage. Additional impacts include water withdrawal for industry and irrigation, and pollution, including the creation of impervious areas within the watershed, due to urbanization and road building.

The freshwater bivalve fauna of Africa and South America is poorly known and there is still much confusion around the number of species recognized. As pointed out in Lydeard et al. (2004), the basic surveys of invertebrate animals are "critically important, particularly in poorly inventoried areas, if managers are to determine appropriate locations for conservation efforts." Taxonomic studies go hand in hand with these surveys.

Brackish water bivalves

Many families of marine bivalves have a few representative genera or species that have invaded brackish water but have not made it into freshwater habitats. Representatives of at least 27 bivalve families are found in brackish water: Anomiidae, Arcidae, Cardiidae, Corbiculidae, Corbulidae, Cyrenoididae, Cultellidae, Donacidae, Dreissenidae, Glauconomidae, Gryphaeidae, Isognomonoidae, Limidae, Lyonsiidae, Lucinidae, Mactridae, Mesodesmatidae, Mytilidae, Ostreidae, Pharidae, Pholadidae, Psammobiidae, Tellinidae, Teredinidae, Trapezidae, Ungulinidae, and Veneridae (Deaton & Greenberg, 1991; P. Mikkelsen, Personal communication).

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