Global diversity of gastropods (Gastropoda; Mollusca) in freshwater

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Abstract The world's gastropod fauna from continental waters comprises ~4,000 valid described species and a minimum of 33–38 independent lineages of Recent Neritimorpha, Caenogastropoda and Heterobranchia (including the Pulmonata). The caenogastropod component dominates in terms of species richness and diversity of morphology, physiology, life and reproductive modes and has produced several highly speciose endemic radiations. Ancient oligotrophic lakes (e.g., Baikal, Ohrid, Tanganyika) are key hotspots of gastropod diversity; also noteworthy are a number of lower river basins (e.g., Congo, Mekong, Mobile Bay). But unlike many other invertebrates, small streams, springs and groundwater systems have produced the most speciose associations of freshwater

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gastropods. Despite their ecological importance in many aquatic ecosystems, understanding of even their systematics is discouragingly incomplete. The world's freshwater gastropod fauna faces unprecedented threats from habitat loss and degradation and introduced fishes and other pests. Unsustainable use of ground water, landscape modification and stock damage are destroying many streams and springs in rural/pastoral areas, and pose the most significant threats to the large diversity of narrow range endemics in springs and ground water. Despite comprising only ~5% of the world's gastropod fauna, freshwater gastropods account for ~20% of recorded mollusc extinctions. However, the status of the great majority of taxa is unknown, a situation that is exacerbated by a lack of experts and critical baseline data relating to distribution, abundance, basic life history, physiology, morphology and diet. Thus, the already considerable magnitude of extinction and high levels of threat indicated by the IUCN Red List of Threatened Species is certainly a significant underestimate.

Keywords Phylogeny · Taxonomy · Biogeography · Endemicity · Radiations · Life history · Fossil record · Biomonitoring · Disease transmission · Conservation

Introduction

The Mollusca is an extraordinarily varied phylum—with estimates of 80,000–100,000 described species

and total diversity possibly as high as 200,000, they are second only to arthropods in species richness. The largest molluscan classes—Gastropoda and Bivalvia—have repeatedly and successfully colonized continental ("fresh") waters. Freshwater gastropods are found on every continent except Antarctica and in nearly all aquatic habitats including rivers, lakes, streams, swamps, underground aquifers and springs, as well as temporary ponds, drainage ditches and other ephemeral and seasonal waters. Most live submerged, and many are specialized for particular habitats—aquatic vegetation, stones, rocks, wood and other solid surfaces, or soft sediment. Some are amphibious and a few are able to tolerate periods of time out of water (e.g., some Ampullariidae); others are capable of prolonged periods of aestivation in soil during dry periods. Few groups (notably some of the rissooidean families) are found in highly saline inland habitats such as the Caspian Sea or salt lakes in Central Asia, Africa and Australia.

Most freshwater gastropods are micro-herbivorous and/or micro-omnivorous grazers feeding on bacterial films, algae and diatoms, but there are a number of exceptions: the predominantly marine Buccinidae, Marginellidae and Acochlidiida and the entirely freshwater Glacidorbidae are predators; Viviparidae and Bithyniidae are ctenidial suspension feeders at least in part; Ampullariidae are primarily macroherbivorous and are also known to feed on bryozoans and planorbid eggs. There are no pelagic/nektonic or parasitic species, with the great majority being benthic crawlers. A rare exception is the Helicostoidae—a monotypic caenogastropod family of uncertain affinity from China that lives cemented to limestone blocks (Lamy, 1926).

Taxonomic composition

New suites of anatomical, ultrastructural and molecular characters developed in the past 30 years have fuelled a revolution in our understanding of gastropod phylogenetics (Haszprunar, 1988; Ponder & Lindberg, 1997; Colgan et al., 2003; Strong, 2003). Several well supported clades are currently recognized: Caenogastropoda (containing most of the former Mesogastropoda and all the Neogastropoda); its sister group, Heterobranchia (containing the former Opisthobranchia and Pulmonata, as well as a few "mesogastropod" groups); Vetigastropoda (including many of the former Archaeogastropoda)

and Neritimorpha (previously a subgroup of "archaeogastropods").

The world's freshwater gastropod fauna is dominated by two main components: the Caenogastropoda and pulmonate heterobranchs. Several additional basal lineages of heterobranchs have also invaded freshwater (Valvatidae, Glacidorbidae, Acochlidiida) as well as some Neritimorpha (Neritiliidae, Neritidae). Only the Viviparoidea, Glacidorboidea and nearly all Hygrophila comprise superfamilial (or above) groupings with members represented exclusively in freshwater. Of the 409 families of Recent gastropods currently recognized (Bouchet & Rocroi, 2005), 26 are composed of taxa that are wholly or mostly restricted to freshwater, four have significant taxonomic representation in freshwater biotopes (Neritidae, Assimineidae, Hydrobiidae, Stenothyridae), and three are marine groups with isolated genera that have invaded freshwater [*Cremnoconchus* (Littorinidae), *Clea* (Buccinidae), *Rivomarginella* (Marginellidae)] (Table 1).

The caenogastropod component of the freshwater fauna represents numerous independent lineages and many separate colonization events. Several clades have produced spectacular endemic radiations, namely Rissooidea (Hydrobiidae s.l., Pomatiopsidae) and Cerithioidea (Pachychilidae, Paludomidae and Pleuroceridae). With the exception of a few parthenogenetic taxa [*Campeloma* (Viviparidae), *Melanoides* (Thiaridae), *Potamopyrgus antipodarum* (Hydrobiidae)], they are exclusively dioecious and reproduction is sexual. Of all the freshwater groups, only the cerithioids are aphallate and transfer sperm using spermatophores; all others use a penis. Most lay egg capsules, and development is intracapsular with embryos emerging as crawling juveniles. A free-swimming dispersal stage is present in some species, particularly those that inhabit the lower reaches of coastal streams, with a free-swimming veliger larva that may develop in the sea (Neritidae, some Thiaridae). However, many species are brooders [all Viviparidae, some Cerithioidea, Rissooidea and Heterobranchia (see below)] and retain their young in brood pouches that represent modifications of the oviduct, mantle cavity or cephalic haemocoel. While it has been suggested that there is a significant selective advantage for parental care and hence brooding among freshwater molluscs (e.g., Köhler et al., 2004), the great majority of freshwater

Table 1 Taxonomic representation and distribution of freshwater gastropods

Taxon	Representation In Freshwater	Habitat
Neritimorpha		
Superfamily Helicinoidea		
Family Neritiliidae	*	Anchialine and coastal running waters
Superfamily Neritoidea		
Family Neritidae	+	Primarily lower reaches of coastal rivers and streams, estuaries
Caenogastropoda		
Architaenioglossa		
Superfamily Ampullarioidea		
Family Ampullariidae	*	Quiet, muddy rivers, lakes, ponds, canals, rice paddies, swamps
Superfamily Viviparoidea		
Family Viviparidae	*	Rivers, lakes, ponds, swamps, canals
Sorbeoconcha		
Superfamily Cerithioidea		
Family Melanopsidae	*	Springs, streams
Family Paludomidae	*	Lakes, rivers, streams (including radiation in Lake Tanganyika)
Family Pachychilidae	*	Lakes, rivers, streams (including radiation in Sulawesi lakes)
Family Pleuroceridae	*	Rivers, streams
Family Thiaridae	*	Rivers, streams
Hypsogastropoda		
Superfamily Littorinoidea		
Family Littorinidae (*Cremnoconchus*)	−	Waterfalls
Superfamily Rissooidea		
Family Amnicolidae	*	Rivers and streams
Family Assimineidae	+, <	Estuaries, freshwater rivers and streams, springs
Family Bithyniidae	*	Quiet muddy rivers, lakes, ponds, canals, swamps
Family Cochliopidae	*	Rivers and streams, swamps, lakes
Family Helicostoidae (*Helicostoa*)	*	Cemented on limestone rocks
Family Hydrobiidae	+	Greatest diversity springs; also streams and rivers, lakes, groundwater systems, caves, estuarine marshes and mudflats
Family Lithoglyphidae	*	Streams, rivers
Family Moitessieriidae	*	Groundwater systems, caves
Family Pomatiopsidae	*/<	Rivers, permanent wetlands, stream edges, some saline springs/lakes.
Family Stenothyridae	+	Rivers, streams, estuarine
Neogastropoda		
Superfamily Buccinoidea		
Family Buccinidae (*Clea*)	−	Lower reaches of rivers
Superfamily Muricoidea		
Family Marginellidae(*Rivomarginella*)	−	Rivers, lakes and canals
Heterobranchia		
Superfamily Glacidorboidea		
Family Glacidorbidae	*	Swamps, lakes, streams

Table 1 continued

Taxon	Representation In Freshwater	Habitat
Superfamily Valvatoidea		
Family Valvatidae	*	Cold, clean lakes rivers, streams
Opisthobranchia		
Acochlidiida		
Superfamily Acochlidioidea		
Family Acochlidiidae	*	Lower reaches of rivers
Superfamily Hedylopsoidea		
Family Tantulidae	*	Lakes
Superfamily Strubellioidea		
Family Strubelliidae	*	Lower reaches of rivers
Pulmonata		
Basommatophora		
Hygrophila		
Superfamily Chilinoidea		
Family Chilinidae	*	On stones and rocks in lakes and running water
Family Latiidae	*	On stones and rocks in running streams and rivers
Superfamily Acroloxoidea		
Family Acroloxidae	*	Lakes (including several Lake Baikal and Lake Ohrid endemics)
Superfamily Lymnaeoidea		
Family Lymnaeidae	*	Flowing rivers and streams, lakes to stagnant ponds, swamps
Superfamily Planorboidea		
Family Planorbidae	*	Low energy temporary and permanent ponds, streams, rivers, springs, lakes
Family Physidae	*	Ponds, wetlands, eutrophic streams, temporary aquatic habitats, springs

Classification follows Bouchet & Rocroi (2005). Note that the higher classification of the Acochlidiida is uncertain. Bouchet & Rocroi (2005) refer to it as "Group Acochlidiacea"; we tentatively use the recently proposed ordinal level name, Acochlidiida. '*' – Wholly/mostly freshwater; '+' – Partly freshwater; '−' – Isolated freshwater; '<' –Amphibious

gastropods are not brooders. Partly as a consequence of their life-history traits, many species are poor dispersers as reflected in high degrees of genetic differentiation between populations (e.g., Ponder & Colgan, 2002). In addition, they are typically habitat specialists, have restricted geographic ranges, long maturation times, low fecundity and are comparatively long lived, rendering them more susceptible to human-mediated threats (e.g., Lydeard et al., 2004; see also below).

The heterobranch component is less diverse and represents relatively few independent colonization events (see below). Heterobranchs are exclusively hermaphroditic and some pulmonates are capable of self-fertilization, although sperm exchange is typical.

As in most caenogastropods, development is intracapsular. Brooding is rare and has only been documented in a planorbid limpet (Albrecht & Glaubrecht, 2006), and some glacidorbids (Ponder, 1986; Ponder & Avern, 2000).

Freshwater pulmonates have their greatest diversity primarily in the holarctic, but are distributed worldwide, with some species widely dispersed pests. They are characterized by comparably few, relatively widespread taxa and have produced a few endemic radiations, but never approaching the scale of caenogastropods. Most pulmonates have only limited ability to exploit deeper water habitats because they lack a ctenidium (true molluscan gill) and instead use a thin, vascularized "lung" for gas exchange. However,

planorbids have a secondary gill (pseudobranch) and the efficient respiratory pigment haemoglobin so are better equipped to exploit oxygen-depleted environments. Others are associated with lentic habitats, occupying the shallows of lakes and/or temporary or ephemeral bodies of water. Many pulmonates have broad environmental tolerances, tend to be more resistant to eutrophication, anoxia, and brief exposure to air and have short generation times. Nevertheless, there are many exceptions, with some pulmonates having very short ranges including some endemic to (ancient) lakes (Boss, 1978), springs (Brown, 2001; Taylor, 2003) or a short section of a single river (Ponder & Waterhouse, 1997) while others are endangered (e.g., *Camptoceras* in Japan). These traits, together with at least some being capable of self-fertilization, enable many pulmonates to be readily passively dispersed (see below) and some are highly successful colonizers, as reflected in their ability to occupy new or ephemeral habitats (e.g., Økland, 1990) and in comparably less genetic structuring (e.g., Dillon, 2000). This renders many of them more resilient to human-mediated threats and less extinction prone than other freshwater gastropods (Boss, 1978; Davis, 1982; Michel, 1994).

Species diversity

Global patterns of freshwater gastropod species diversity are notoriously difficult to evaluate. The current taxonomy is a complex mixture of taxonomic traditions and practices of numerous generations of workers on different continents (Bouchet, 2006). Early studies of some taxa resulted in the recognition of a few conchologically variable and widespread species, or conversely in the unwarranted enormous inflation of nominal taxa, including species, subspecies and "morphs", particularly so in North America and Europe [e.g., North American Pleuroceridae with over 1,000 nominal taxa and ∼200 considered valid (Graf, 2001); Physidae with ∼460 nominal taxa, ∼80 considered valid (Taylor, 2003); European Lymnaeidae (see below)]. When applied to such complex groups, modern analytical methods incorporating molecular and newly interpreted morphological characters, combined with a new appreciation of ecological and geographical patterns, have led to a more refined understanding of genera and species.

Such studies have demonstrated that many currently recognized species are not monophyletic (Minton & Lydeard, 2003; Wethington, 2004) and/or have revealed unrecognized species complexes [e.g., European and North American lymnaeids (Remigio & Blair, 1997; Remigio, 2002); North American pleurocerids (Lydeard et al., 1998); Indonesian pachychilids (von Rintelen & Glaubrecht, 2005)]. Alternatively, some past studies have overindulged in synonymy, for example Hubendick's (1951) major review of world wide Lymnaeidae recognized only 38 valid species and two genera, while recent studies (e.g., Remigio & Blair, 1997; Kruglov, 2005) have indicated that there are several valid genera and a number of additional species, including several synonymized by Hubendick. Morphological studies on large new collections can also reveal significant previously unsuspected diversity, particularly with minute taxa, as for example among Australian glacidorbids and bithyniids (Ponder & Avern, 2000; Ponder, 2004c) and the so-called hydrobioids (see below). There is, nevertheless, a strong bias towards larger sized taxa and towards the developed world, such as North America, Europe, Japan and Australasia. A testament to our incomplete knowledge is that ∼45 new freshwater gastropod species are described on average each year, with about 87% from these better studied regions (Bouchet, unpubl. data).

Complicating efforts to evaluate their diversity, it is not feasible to accurately assess genus-level diversity for freshwater gastropods. In the absence of provincial or global revisions at the level of families or superfamilies, generic concepts are often applied locally and vary between regions—some studies employing narrow generic concepts, others very broad ones. In many areas, there are no modern treatments for much of the fauna while in others the faunas are well known and many groups have undergone recent systematic revision using molecular and/or morphological methods. In general terms, the concepts of tropical genera tend to be older and hence broader and more likely polyphyletic. In contrast, genera from many temperate biomes are often more narrowly defined. We believe that species-level data do not suffer so much from geographic differences in historical treatment and conceptual approach.

With the above caveats, the global freshwater gastropod fauna is estimated as approximately 4,000

Table 2 Total number of valid described species of freshwater gastropods arranged by main zoogeographical region; number of introduced species is indicated in parentheses

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Neritimorpha									
Neritiliidae	4	0	0	2	4	2	3	0	5
Neritidae	45–55	2	~10	14	20–45	~40	42	0	~110
Caenogastropoda									
Ampullariidae	(1)	1 (1)	50–113	28	25 (4)	(1)	0 (4)	0	105–170
Viviparidae	20–25	27	1	19	40–60	19 (1)	0 (2)	0	125–150
Sorbeoconcha									
Melanopsidae	20–50	0	0	0	0	1	2	0	~25–50
Paludomidae	0	0	0	66	28	?	0	0	~100
Pachychilidae	0	0	30–60	22	70–100	43	0	0	165–225
Pleuroceridae	35	156	0	0	4	0	0	0	~200
Thiaridae	20	0	30	34	20–40	20–40	20–35	0	135
Hypsogastropoda									
Littorinidae	0	0	0	0	2	0	0	0	2
Amnicolidae	150–200	19	0	0	0	0	0	0	~200
Assimineidae	0	2	?	11	4	2	0	0	~20
Bithyniidae	45	0	0	34	~25	24	0 (1)	0	~130
Cochliopidae	17	50	176	3	0	0	0	0	246
Helicostoidae	0	0	0	0	1	0	0	0	1
Hydrobiidae	700–750	105	21	13	7	252 (1)	75 (1)	0	~1250
Lithoglyphidae	30	61	?	0			0	0	~100
Moitessieriidae	55	0	0	0	0	0	0	0	55
Pomatiopsidae	17	6	1	10	~130	9	0	0	~170
Stenothyridae	6	0	0	0	~50	~5	0	0	~60
Neogastropoda									
Buccinidae	0	0	0	0	8–10	0	0	0	8–10
Marginellidae	0	0	0	0	2	0	0	0	2
Heterobranchia									
Glacidorbidae	0	0	1	0	0	19	0	0	20
Valvatidae	60	10	0	1	0	0	0	0	71
Acochlidiida									
Acochlidiidae	0	0	0	0	0	2	2	0	4
Tantulidae	0	0	1	0	0	0	0	0	1
Strubelliidae	0	0	0	0	0	1	1	0	1
Pulmonata									
Chilinidae	0	0	~15	0	0	0	0	0	~15
Latiidae	0	0	0	0	0	1	0	0	1
Acroloxidae	40	1	0	0	0	0	0	0	~40
Lymnaeidae	40–120	56	7	2	19	7	5 (2)	0	~100
Planorbidae	100–200	57	59	116	49	43	8 (2)	0	~250
Physidae	15	31	38	(1)	1	(1)	0 (4)	0	~80
Total	1,408–1,711	585	440–533	366	509–606	490–514	154–169	0	3,795–3,972
All red list categories (Excluding LC)	94	215	10	100	2	92	11	0	

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

valid described species (Table 2). In some cases, the number of species is certainly overestimated, but these are vastly overshadowed by areas of the world yet to be even superficially inventoried with most likely thousands waiting to be discovered (Lydeard et al., 2004), either as entirely new entities or through the recognition of cryptic taxa. The most speciose assemblage by far is the hydrobioids (Rissooidea)—a diversity long masked by their tiny, rather featureless shells and often very restricted ranges. While most families are probably known within 70–90% of actual diversity, the estimated 1,000 species of hydrobioids may represent as little as 25% of their actual diversity as evidenced by the fact that they comprise about 80% of current new species descriptions (compiled 1997–2003; Bouchet, unpubl. data). This suggests that the total number of freshwater gastropods is probably on the order of ~8,000 species.

Phylogeny and historical processes

The phylogenetic framework

In addition to our changing concepts of higher classification and species diversity, the phylogenetic framework for a few freshwater clades has been considerably refined, especially with the use of molecular techniques (see below). However, few comprehensive phylogenies for individual families or the higher taxonomic groupings that contain freshwater taxa have been published to date. For those that have been published, variable taxon sampling, incongruence between morphological and molecular data, compounded by weak support of basal nodes, has often resulted in conflicting interpretations concerning the monophyly and/or affinity of freshwater clades and the number of freshwater invasions [e.g., Neritimorpha (Holthuis, 1995; Kano et al., 2002); Architaenioglossa (Colgan et al., 2003; Simone, 2004); Hygrophila (Barker, 2001; Dayrat et al. 2001); Cerithioidea (e.g., Lydeard et al., 2002); Rissooidea (see below)].

The large assemblage of marine, brackish and freshwater lineages currently placed in the Rissooidea arguably are in the most urgent need of revision. This putative superfamily encompasses the largest and most threatened radiations of freshwater taxa and yet their systematics are just beginning to be clarified. The only phylogenetic analysis encompassing the whole group (Ponder, 1988) requires rigorous testing using molecular data and a substantial sampling of outgroup taxa; results with a small subset of taxa indicate that the rissooideans as presently recognized, are at least diphyletic (Colgan et al., 2007). In the past, all brackish and freshwater members of the group were united in the heterogeneous "Hydrobiidae" (=hydrobioid, or Hydrobiidae s.l.) by some authors, while others recognized different families and even superfamilies. Based on molecular and refined anatomical data, the composition of several monophyletic lineages from within this assemblage has begun to be elucidated (e.g., Amnicolidae, Cochliopidae, Moitessieriidae and Lithoglyphidae) (e.g., Wilke et al., 2001; Hausdorf et al., 2003). Nevertheless, the affinities and composition of many families remain to be more thoroughly evaluated; indeed monophyly of the Hydrobiidae as currently defined is unlikely (Haase, 2005). Additionally, establishing a robust phylogenetic framework for this group will clarify our understanding of their conquest of freshwater. For example, it was estimated that New Zealand "hydrobiids" (=Tateinae, possibly a distinct family; Ponder, unpubl. data) independently conquered freshwater three times (Haase, 2005); it appears that this has happened separately in a number of other hydrobioid groups.

The affinities of valvatids and their allies were long unstable and they were often placed in the wrong higher taxa, in part due to their combination of plesiomorphic and autapomorphic features and small body size (Fig. 1). Detailed anatomical work and refinement of morphological homologies clarified the basal position of valvatoideans in the Heterobranchia and the assemblage of other allied lineages (Haszprunar, 1988; Ponder, 1991; Barker, 2001) with confirmation from molecular studies (Colgan et al., 2003). However, the position of the probably paedomorphic glacidorbids within the Heterobranchia is still disputed (see Ponder & Avern, 2000).

Surprisingly little has been done regarding the phylogenetic relationships of the freshwater pulmonates (Hygrophila), although some families, notably Planorbidae (Morgan et al., 2002; Albrecht et al., 2004), Physidae (Wethington, 2004) and Lymnaeidae (see above) have recently been investigated using mainly molecular data. However, some old

Fig. 1 *Valvata studeri.* Boeters & Falkner, 1998. Size 3 mm. Photo courtesy G. Falkner

classifications remain firmly entrenched. For example, the major group of freshwater limpets, the Ancylidae, was shown by Hubendick (1978) to be almost indistinguishable from Planorbidae, a finding ignored by many subsequent workers outside Europe. Recent molecular analyses have shown that the limpet form has arisen several times within the planorbids (Albrecht et al., 2004), with the typical ancylids nested within that family.

But for many taxa, no modern cladistic and/or taxonomic treatment is available (Chilinoidea, Acochlidiida). In contrast, some freshwater representatives have not been sampled in existing cladistic studies, leaving their systematic affinities unresolved (e.g., *Clea* in the Buccinidae); rarely the taxonomic placement of taxon is unknown (Helicostoidae).

Despite our often limited grasp of phylogenetic relationships, it is clear that gastropods have invaded freshwater biotopes many times. Published estimates, although not comparable as classifications have changed and fossil lineages have been variably included or excluded, range from 6 to 7 (Hutchinson, 1967), or 10 (Taylor in Gray, 1988), to as many as 15 Recent freshwater gastropod colonizations (Vermeij & Dudley, 2000). Based on the current classification (Bouchet & Rocroi, 2005) and our present understanding of gastropod phylogenetic relationships, we estimate that there are a minimum of 33–38 independent freshwater lineages represented among Recent gastropods: in the Rissooidea, there are at least 2 each in Assimineidae and Cochliopidae, 1–2 in Pomatiopsidae, at least 1 each in Stenothyridae,

Lithoglyphidae, Moitessieriidae, 1 in Bithyniidae, possibly 1 in Helicostoidae, possibly 6–8 in the Hydrobiidae; 5–6 in the Neritimorpha (Holthuis, 1995); 2–3 in the Cerithioidea (Lydeard et al., 2002); probably 2 each in the "Architaenioglossa" (e.g., Simone, 2004) and the Acochlidiida; and 1 in each of the Litttorinidae, Buccinidae, Marginellidae, Glacidorbidae, Valvatidae and Hygrophila (see Table 1).

The fossil record

While shelled marine molluscs have an excellent fossil record that of freshwater taxa is relatively poor. Fossilization in freshwater habitats is biased towards lowland and lake deposits, with many other habitats that are significant for gastropod diversity represented poorly or not at all (e.g., springs, streams, groundwater). This incomplete record is compounded by the poor preservation potential of the often light, thin shells of many freshwater taxa and acidic environments. Thus, the fossil record for freshwater gastropods is patchy at best and likely to significantly underestimate the age and diversity of freshwater lineages. Moreover, assignments of Palaeozoic fossils to modern freshwater lineages, often based on fragmentary shells, are problematic. Despite these difficulties, most modern groups appear to make their first appearance during the Jurassic or Cretaceous (Tracey et al., 1993), with most families in place by the end of the Mesozoic (Taylor in Gray, 1988; Taylor, 1988). Other elements of apparently more recent marine origin first appear during the Tertiary: chilinids first appear in the Late Paleocene or early Eocene, neritiliids during the Middle Eocene and freshwater buccinids are first known from the Miocene. There is no fossil record for freshwater littorinids or marginellids.

Regardless of their earliest documented occurrence, the cosmopolitan distribution pattern of many lineages indicates their widespread presence in Pangaea long before the break-up of this supercontinent (e.g., Viviparidae). Others are widely distributed on several major continents and have continental biogeographic patterns consistent with a Gondwanan origin (e.g., Pachychilidae—S. America, Africa, Madagascar, Asia; Thiaridae *s.s.*—S. America, Africa, Asia, India, Australia; Ampullariidae—S. America, Africa, S. Asia). Glacidorbidae are found in southern

Australia and Chile (Ponder & Avern, 2000), also suggesting a Gondwanan origin. Those of more recent marine origin occupy more isolated habitats and have not penetrated far inland (*Clea*, *Rivomarginella*, Acochlidiida).

Distribution and main areas of endemicity

Like other freshwater and marine invertebrates, freshwater gastropods present an overall pattern of high diversity in the tropics, with decreasing species richness as well as decreasing endemicity at higher latitudes. There are, however, always exceptions; for example, Tasmania has the most diverse freshwater fauna in Australia, and some groups have low tropical diversity (hydrobioid families, Glacidorbidae). Unlike for land snails, small oceanic islands are noteworthy for generally low levels of freshwater gastropod species richness and endemism (e.g., Starmühlner, 1979), although there are again some exceptions where the number of endemics is surprisingly high [e.g., Lord Howe Island (Ponder, 1982); Viti Levu, Fiji (Haase et al., 2006)].

Of course, both vicariance and dispersal have shaped modern distribution patterns; while vicariance arguably has been dominant in historical contexts, dispersal has certainly played an important role, including via such mechanisms as by animal transport (birds, insects), rafting on aquatic vegetation, marine/brackish larval dispersal phase, stream capture and even by air (e.g., cyclonic storms) (Purchon, 1977). Obviously, the significance and impact of each mechanism is more a function of the individual characteristics of each lineage: life habit (e.g. living on aquatic vegetation vs. attached beneath stones), ecological and physiological tolerances of individuals, mode of respiration, vagility, tolerance to saline water, sexual, reproductive and developmental strategies and ability to withstand desiccation. Such variables differ significantly among species and lineages and, hence, determine local patchiness and geographic range (Purchon, 1977; Davis, 1982; Taylor, 1988; Ponder & Colgan, 2002).

Thus, many apparently ancient freshwater taxa have broad geographic ranges primarily as a result of vicariance modified by dispersal. These lineages mostly belong to higher taxa comprising exclusively freshwater members (Viviparidae, Bithyniidae, Hydrobiidae s.l., Planorbidae and Lymnaeidae); other presumably old lineages are more restricted in geographic range (Glacidorbidae, Chilinidae, Latiidae, Acroloxidae). All are highly modified reflecting the special challenges presented by life in this biotope. Other groups are freshwater remnants of previously euryhaline groups (e.g., Melanopsidae), have euryhaline and/or marine members (e.g., Neritidae, Littorinidae, Stenothyridae, Assimineidae) and/or are amphidromous (some Thiaridae, Neritidae and probably at least some Stenothyridae) with greater opportunities for dispersal and colonization. The presumed most recent colonizers (e.g., Littorinidae, Buccinidae, Marginellidae, some Assimineidae) are characterized by being less highly modified, less speciose and have a more restricted distribution with more or less clear kinship to marine and/or brackish water relatives (e.g., Purchon, 1977). For a summary of continental distribution patterns of freshwater gastropod families and genera, see Bănărescu (1990), although the classification differs from the one adopted here.

At the level of continents, the Palearctic region has the most speciose freshwater gastropod fauna ($\sim$1,408–1,711 valid, described species), with the remaining continental regions of comparable diversity ($\sim$350–600 species). Apart from Africa, most regions have seen marked increases in recent years through the description of the highly endemic hydrobioid faunas (see *Phylogenetic Framework*, above). Surprisingly species-poor are the rivers and streams of South America, particularly of the Amazon basin, which contain, among other things an extraordinary diversity of freshwater fishes; it is not yet clear if this is a sampling/study artefact or an actual pattern. In contrast, groups important from an economic, human health or veterinary perspective (see below) have received considerable attention, even in developing countries.

While a thorough species-level inventory is far from complete, some continental areas stand out for their exceptional diversity and disproportionately high numbers of endemics. Gargominy & Bouchet (1998) identified 27 areas of special importance for freshwater mollusc diversity as key hotspots of diversity with high rates of endemism among freshwater gastropods. Regrettably, most areas important for molluscan diversity have not been recognized by inclusion in the Ramsar List of Wetlands of

International Importance (www.ramsar.org/key_sitel-ist.htm). Although a number of resolutions have greatly expanded the classification of wetlands currently recognized under the Ramsar typology (Ramsar Convention Secretariat, 2004), few government parties have used these additional criteria to designate sites.

Global hotspots of freshwater gastropod diversity can be broadly classified according to 4 main categories (see Table 3):

1. *Springs and groundwater.* Springs, and sometimes the small headwater streams fed by them, are inhabited by taxa that are typically not found in larger streams or rivers. Single sites usually have low species richness (1–6 species) with populations consisting of 100's, and often 1,000's or even (rarely) millions of individuals. However, as a consequence of spatial isolating mechanisms, spring and headwater habitats regionally support rich assemblages of gastropods dominated primarily by hydrobioids. Similarly, underground aquifers, including underground rivers, are also dominated by hydrobioids with over 300 stygobiont species documented worldwide. As such habitats extend over very small areas, and as most species occur in only a very limited number of sites with single-site endemics commonplace, spring-dwelling gastropods are extremely vulnerable to loss of habitat. Remarkable examples include the artesian springs of the Great Artesian Basin of Australia (Ponder, 2004a); springs and small streams in SE Australia and Tasmania (Ponder & Colgan, 2002) and New Caledonia (Haase & Bouchet 1998); springs and caves in the Dinaric Alps of the Balkans (Radoman, 1983), and other karst regions of France and Spain (Bank, 2004); aquifer-fed springs in Florida, the arid south western United States and Mexico (Hershler, 1998, 1999) (Fig. 2).

2. *Large rivers and their first and second order tributaries.* The Congo (Africa), Mekong (Asia), Mobile Bay basin (North America), Uruguay and Rio de la Plata (South America) are noteworthy for their mollusc faunas that are sometimes extremely speciose, and often do not occur in other types of freshwater habitats (Fig. 2); the Zrmanja in eastern Europe and the coastal rivers of the Guinean region in Africa are also locally important hotspots. The most speciose representatives are usually microhabitat specialists, with highly patchy distributions scattered among the mosaic of microhabitats (flow regimes, sediment type, vegetation) offered by rivers and streams. Habitats of special importance are rapids which are inhabited by species adapted to highly oxygenated water. The gastropods are dominated by the Viviparidae (North America, Eurasia, Oriental region, Australia), Pachychilidae, Pleuroceridae (North America, Japan), Thiaridae (tropical regions), Pomatiopsidae and Stenothyridae (Oriental region); pulmonates are usually only poorly represented (Fig. 3).

3. *Ancient oligotrophic lakes.* Ancient lakes with the most speciose faunas include Lakes Baikal, Ohrid, Tanganyika and the Sulawesi lakes (Fig. 2), with the Viviparidae, Pachychilidae, Paludomidae, Thiaridae and hydrobioid families among the Caenogastropoda and the heterobranch families Planorbidae, Acroloxidae, Ancylidae and Valvatidae best represented. Rissooid and cerithioid lineages predominate among the groups prone to radiate in ancient lakes (Boss, 1978), typically with one clade or the other being dominant, often to the almost complete exclusion of members of the other lineage (e.g., Michel, 1994); Lake Poso (Haase & Bouchet, 2006) and the Malili lakes in Sulawesi are exceptions (Bouchet, 1995). As elsewhere, pulmonates are typically less speciose and have lower rates of endemicity. Planorbids are the most speciose of the pulmonate groups, but tend to be better represented in temperate rather than tropical lakes. Fossil gastropod faunas of long-lived lakes such as the well-known Miocene Lake Steinheim (Janz, 1999) and Plio-Pleistocene Lake Turkana (Williamson, 1981) have been important and influential (but not uncontroversial) models in evolutionary biology for rates and patterns of speciation.

4. *Monsoonal wetlands* and their associated rivers and streams can harbour significant faunas, as for example, in many parts of Asia and northern Australia, which are dominated by Viviparidae, Thiaridae, Bithyniidae, Lymnaeidae and

Table 3 Gastropod species hotspot diversity categorized by primary habitat

Region/Drainage/Basin	Species (endemic)	Dominant taxa
Springs and groundwater		
South western U.S.	~100 (≥ 58)	Hydrobioid families
Cuatro Cienegas basin, Mexico	12 (9)	Hydrobioid families
Florida, U.S.	84 (43)	Hydrobioid families
Mountainous regions in Southern France and Spain	150 (140)	Hydrobioid families
Southern Alps and Balkans region	220 (200)	Hydrobioid families
Great Artesian basin, Australia*	59 (42)	Hydrobiidae
Western Tasmania, Australia*	206 (191)	Hydrobiidae
New Caledonia	81 (65)	Hydrobiidae
Ancient oligotrophic lakes		
Titicaca	24 (15)	Hydrobioid families, Planorbidae
Ohrid and Ohrid basin	72 (55)	Hydrobioid families, Lymnaeidae, Planorbidae
Victoria	28 (13)	Viviparidae, Planorbidae
Tanganyika*	83 (65)	Paludomidae; 18 endemic genera with important radiation in *Lavigeria*
Malawi	28 (16)	Ampullariidae, Thiaridae
Baikal	147 (114)	Amnicolidae, Lithoglyphidae, Valvatidae, Planorbidae, Acroloxidae
Biwa	38 (19)	endemic subgenus *Biwamelania* (Pleuroceridae), Planorbidae
Inle and Inle watershed	44 (30)	Viviparidae, Pachychilidae, Bithyniidae
Sulawesi lakes	~50 (~40)	Pachychilidae, Hydrobiidae, Planorbidae; 3 endemic genera
Large rivers and their first and second order tributaries		
Tombigbee-Alabama rivers of the Mobile Bay basin	~118 (110)	Pleuroceridae (76 species); 6 endemic genera
Lower Uruguay River and Rio de la Plata, Argentina-Uruguay-Brazil	54 (26)	Pachychilidae
Western lowland forest of Guinea and Ivory Coast	~28 (~19 + 9 near endemic)	*Saulea*(Ampullariidae), *Sierraia* (Bithyniidae), *Soapitia* (Hydrobiidae), *Pseudocleopatra* (Paludomidae)
Lower Zaire Basin	96 (24)	Pachychilidae, Paludomidae, Thiaridae, Bithyniidae, Assimineidae, hydrobioid families; 5 endemic 'rheophilous' genera
Zrmanja	16 (5)	Hydrobioid families
Northwestern Ghats, India	~60 (~10)	2 endemic genera: *Turbinicola* (Ampullariidae), *Cremnoconchus* (Littorinidae)
Lower Mekong River in Thailand, Laos, Cambodia	~140 (111)	Triculinae (Pomatiopsidae) (92 endemic species); Stenothyridae (19 endemic species); Buccinidae; Marginellidae
Monsoonal wetlands		
Northern Australia	56 (13)	Viviparidae, Thiaridae, Bithyniidae, Lymnaeidae, Planorbidae

Data on monsoonal wetlands are included only for Northern Australia; reliable figures for other areas are unavailable. Main source: Gargominy & Bouchet 1998, unpubl. data. Number of endemic species is indicated in parentheses. "*" – Estimate includes undescribed species when such information is available. Note that the hydrobiid fauna of Tasmania is primarily from small groundwater-fed streams, some rivers, caves and a few springs

Planorbidae. For example, according to a recent analysis, the monsoonal rivers and associated wetlands flowing into the Gulf of Carpentaria in northern Australia have 56 species, 13 of which are endemic (Ponder, unpubl. data). Reliable comparative data is not available for other likely similarly diverse areas in e.g., S.E. Asia.
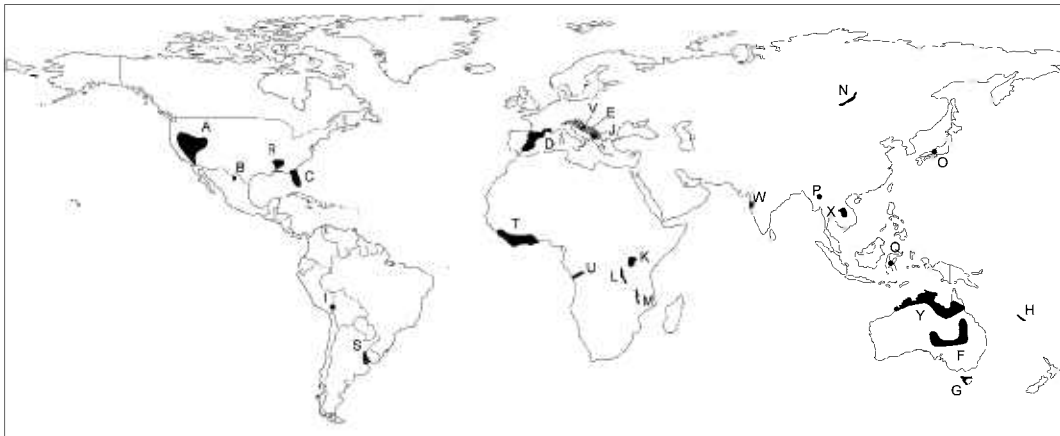
Fig. 2 Hotspots of gastropod diversity. A–H. Springs and groundwater. I–Q. Lakes. R–X. Rivers. Y. Monsoonal wetlands. A: South western U.S.; B: Cuatro Cienegas basin, Mexico; C: Florida, U.S.; D: Mountainous regions in Southern France and Spain; E: Southern Alps and Balkans region; Northern Italy, Austria, former Yugoslavia, Bulgaria, Greece; F: Great Artesian basin, Australia; G: Western Tasmania, Australia; H: New Caledonia. I: Titicaca, Peru-Bolivia; J: Ohrid and Ohrid basin, former Yugoslavia; K: Victoria; Kenya, Sudan, Uganda; L: Tanganyika; Burundi, Tanzania, D.R. Congo; M: Malawi; Malawi, Mozambique; N: Baikal, Russia; O: Biwa, Japan; P: Inle, Burma; Q: Sulawesi lakes, Indonesia. R: Tombigbee-Alabama rivers of the Mobile Bay basin; S: Lower Uruguay River and Rio de la Plata; Argentina, Uruguay, Brazil; T: Western lowland forest of Guinea and Ivory Coast; U: Lower Zaire Basin; V: Zrmanja; W: Northwestern Ghats, India; X: Lower Mekong River; Thailand, Laos, Cambodia. Y: Northern Australia
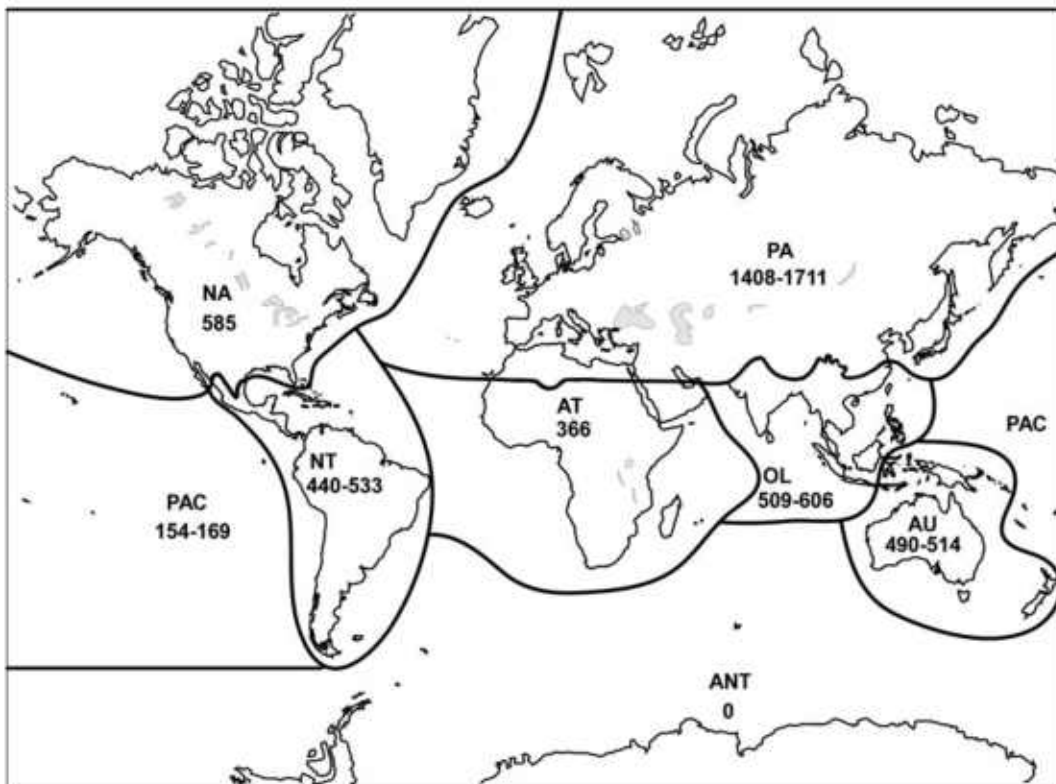
Fig. 3 Distribution of freshwater gastropod species per zoogeographic region. PA—Palaearctic, NA—Nearctic, NT—Neotropical, AT—Afrotropical, OL—Oriental, AU—Australasian, PAC—Pacific Oceanic Islands, ANT—Antarctic

Human related issues

Utility of freshwater gastropods

The potential of freshwater molluscs as indicators is largely unrealized but could be a powerful tool in raising awareness and improving their public image (Ponder, 1994; Seddon, 1998). Their low vagility, adequate size, often large population numbers and the ease of collection and identification of many species render them a useful and practical tool in biomonitoring programs (Chirombe et al. 1997; Langston et al., 1998; Lee et al., 2002). For example, freshwater gastropods are promising tools as pollution indicators through assessments of molluscan community composition and/or biological monitoring programs that rate water quality and status of aquatic biotopes based on invertebrate assemblages. They also have utility in monitoring and assessing the effects of endocrine-disrupting compounds and as monitors of heavy metal contamination (e.g., Salanki et al., 2003; El-Gamal & Sharshar, 2004). Owing to practical considerations (simple anatomy, low cost, fewer ethical issues), freshwater molluscs are also being used in neurotoxicological testing to evaluate the effects of environmental pollutants on neuronal processes and to clarify the mechanisms of action of these substances at the cellular level (Salanki, 2000).

Freshwater gastropods and human health

Some freshwater snails are vectors of disease, serving as the intermediate hosts for a number of infections for which humans or their livestock are definitive hosts. The most significant are snail-transmitted helminthiases caused by trematodes (flukes). At least 40 million people are infected with liver (*Opisthorchis*) and lung flukes (*Paragonimus*) and over 200 million people with schistosomiasis (Peters & Pasvol, 2001) primarily in Africa, Southeast Asia and South America—often with devastating socio-economic consequences. The principal vectors are pomatiopsids and planorbids (schistosomiasis), as well as pachychilids, pleurocerids, thiarids, bithyniids and lymnaeids (liver and lung flukes) (Malek & Cheng, 1974; Davis, 1980; Davis et al., 1994; Ponder et al., 2006). Dam construction has had the adverse effect of enlarging suitable habitat for snail vectors and increasing the prevalence of schistosomiasis (McAllister et al., 2000). Humans are also affected by a number of other infections for which they are accidental hosts, such as angiostrongyliases (nematode infections of rodents and other mammals) which pass through ampullariid intermediate hosts. Ampullariids and pachychilids are often locally harvested as a food resource in Southeast Asia, Philippines and Indonesia furthering the spread of angiostrongyliasis and paragonimiasis, respectively (e.g. Liat et al., 1978).

Exotic freshwater gastropod species

Freshwater snails are routinely inadvertently introduced mainly through the aquarium trade in association with aquatic plants and freshwater fish. Accidental introductions also occur with aquaculture, as fouling organisms on ships and boats and through canals or other modifications of existing waterways (Pointier, 1999; Cowie & Robinson, 2003). The most successful colonizers have been pulmonates (Physidae, Lymnaeidae, Planorbidae) and parthenogenetic species (*Melanoides tuberculata*, *Potamopyrgus antipodarum*), as a single individual is often sufficient to establish a viable population. Introduced taxa tend to flourish in modified environments where they often outnumber native species or are the only ones present.

Although inadvertent introductions are far more common, deliberate introductions have been the most successful and typically the most harmful to native faunas, as a concerted effort is made to ensure their success (Cowie & Robinson, 2003). As with accidental introductions, deliberate introductions have occurred most commonly through the aquarium trade. But freshwater snails have also been introduced intentionally for use as food (Ampullariidae) and as biocontrol agents for invasive aquatic macrophytes (Ampullariidae) and for vectors of disease (see above) (Pointier, 1999; Cowie & Robinson, 2003). Deliberate introductions have been carried out with little or no thought of the impact on native species, rarely with pre-release testing or post-release monitoring of non-target impacts (Cowie, 2001). Consequently, some exotic species (notably *Pomacea canaliculata*) have become serious pests, adversely impacting agriculture (rice, taro production) and/or native faunas and floras through predation and competition (Purchon, 1977; Cowie, 2001).

Threats

Regrettably, only 2% of all mollusc species have had their conservation status rigorously assessed, so current estimates of threat are a severe underestimate (Seddon, 1998; Lydeard et al., 2004). Nevertheless, it is clear that terrestrial and freshwater molluscs arguably represent the most threatened group of animals (Lydeard et al., 2004). Freshwater gastropods, which comprise ∼5% of the world's gastropod fauna, face a disproportionately high degree of threat; of the 289 species of molluscs listed as extinct in the 2006 IUCN Red List of Threatened Species (www.redlist.org), 57 (∼20%) are gastropod species from continental waters. Terrestrial gastropods, representing ∼30% of the world's gastropod fauna, are also facing a major crisis with 197 species listed as extinct (Table 4).

The decline of the world's freshwater gastropod fauna, indeed of freshwater molluscs in general, can be attributed to two main drivers: life-history traits and anthropogenic effects. As described above, in addition to low vagility, the most sensitive species are habitat specialists, have restricted geographic ranges, long maturation times, low fecundity and are comparatively long lived. These traits render them unable to adapt to conspicuous changes in flow regimes, siltation and pollution and unable to effectively compete with introduced species. In many areas, the most significant cause of declines in native snail populations has been dam construction for flood control, hydroelectric power generation, recreation and water storage, which has converted species-rich riffle and shoal habitats into low-energy rivers and pools, greatly reducing and fragmenting suitable habitats and resulting in a cascade of effects both up and downstream (Bogan, 1998; McAllister et al., 2000). This does not always lead to increased numbers of lentic taxa, as changes in flooding regimes can also have adverse impacts on species adapted to such habitats (McAllister et al., 2000). Similarly, the regulation of flow regimes in previously relatively stable habitats may adversely affect species unable to adapt to dramatic changes in water levels and/or velocities. More subtle changes induced as a result of these disturbances also contribute to species declines. For example, a change in the nature of biofilms as a result of altered flow regimes in the Murray – Darling system in Australia has caused the near extinction of riverine viviparids (Sheldon & Walker, 1997).

Threats to spring snails are of a different nature. They are mostly narrow range endemics that can go from unthreatened or vulnerable to extinct without any transitional level of threat, as it may take only one intervention to destroy the only known population of a species. For instance, depletion of ground water for a number of urban and rural uses including water capture for stock, irrigation or mining, spring or landscape modification and trampling by cattle have already destroyed many springs in rural/pastoral areas of Europe, United States and Australia (Sada & Vinyard, 2002; Ponder & Walker, 2003).

Additional sources of habitat degradation, fragmentation and/or loss include gravel mining and other sources of mine waste pollution, dredging, channelization, siltation from agriculture and logging, pesticide and heavy metal loading, organic pollution, acidification, salination, waterborne disease control, urban and agricultural development, unsustainable water extraction for irrigation, stock and urban use,

Table 4 Comparison of rates of threat for groups of molluscs

	∼Described valid species diversity	Extinct	Critically endangered	Endangered	Vulnerable	All red list categories (Excluding LC)	Rate of threat
Mollusca		289	265	222	488	2,085	
Gastropoda	∼78,000	258	213	194	473	1,882	0.024
Freshwater	∼4,000	57	45	62	204	520	0.130
Terrestrial	∼24,000	197	166	130	265	1,281	0.053
Marine	∼50,000	4	2	3	6	84	0.00168

Source: 2006 IUCN Red List of Threatened Species (www.redlist.org). Rate of threat is estimated from number of Red Listed species (excludes Least Concern) as a percent of estimated currently valid species diversity; does not take into account proportion of species assessed and thus may not accurately reflect relative rate of threat across categories. LC: Least Concern

competition and/or smothering from introduced species (Thomas, 1997; Bogan, 1998; Seddon, 1998; McAllister et al., 2000; Ponder & Walker, 2003). As with damming, it is often not just localized damage, but the cascade of effects both up and downstream that impact a wide range of communities.

Conservation priorities

Despite significant roles in human cultural history, molluscs, as with many invertebrates, have a poor public image (Kay, 1995a). This attitude further impedes allocation of meagre conservation resources in competition with the demands from larger charismatic animals and plants (Ponder, 1995; Wells, 1995; Bouchet & Gargominy, 1998; Seddon, 1998; Lydeard et al., 2004). The often drab-coloured and uncharismatic freshwater species, arguably facing the most serious risks and most deservedly meriting public concern and action, are desperately in need of champions.

Effective management of these threatened resources is often complicated by habitat fragmentation or political obstacles, as large rivers and lakes are often transnational. Although often not feasible, narrow range endemics inhabiting a single stream or spring are best preserved within large protected areas (Ponder, 1995), as many critical sites outside reserves can be so small that they attract little interest from conservation agencies and can suffer from edge effects. Moreover, as noted above, currently recognized species do not necessarily reflect natural evolutionary entities, with clear implications for devising accurate and effective management strategies based on species-targeted approaches. In contrast, habitat-based conservation strategies circumvent many of these problems and may be the preferred option in many circumstances (e.g., Ponder, 2004b).

Major museum collections are a key component of understanding the spatial distribution of species, both past and present (Wells, 1995; Ponder, 1999, 2004b), but much of this information is not yet accessible to the global community via computerized databases. This lack of access hampers or prevents assessment of conservation status by contributors to the Red List—a vital communication tool between scientists and conservation strategists and managers, as well as local or national conservation agencies. Currently,

Mollusc Action Plans, as called for by the IUCN Species Survival Commission (SSC), are limited in the extent to which they can offer explicit recommendations in comparison with well-known taxa (e.g., tetrapods) (Bouchet & Gargominy, 1998). With the limitations discussed above, the magnitude of the threat of extinction as indicated by the IUCN Red List of Threatened Species, is certainly a grave underestimate.

Conserving our molluscan resources will effectively require a multiplicity of approaches, including research (systematics, ecology, life history, physiology, morphology, genetics), inventories (distribution, population size, biogeography), enhanced database infrastructure including digitization of significant museum collections, mitigation of human impacts, active intervention to promote recovery (including removal of invasive species, captive breeding programs, re-introduction, restoration of habitat), training in taxonomic expertise and enhanced communication and outreach (Kay, 1995b; Ponder, 1995; Seddon, 1998; McAllister et al., 2000; Lydeard et al., 2004). But considering the already-documented severity of the plight of freshwater gastropods, these strategies cannot proceed in a step-wise linear fashion—by then it will be too late (e.g., Wells, 1995; Lydeard et al., 2004; Ponder, 2004b).

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