

The Global Decline of Nonmarine Mollusks

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Invertebrate species represent more than 99% of animal diversity; however, they receive much less publicity and attract disproportionately minor research effort relative to vertebrates. Nonmarine mollusks (i.e., terrestrial and freshwater) are one of the most diverse and imperiled groups of animals, although not many people other than a few specialists who study the group seem to be aware of their plight. Nonmarine mollusks include a number of phylogenetically disparate lineages and species-rich assemblages that represent two molluscan classes, Bivalvia (clams and mussels) and Gastropoda (snails, slugs, and limpets). In this article we provide an overview of global nonmarine molluscan biodiversity and conservation status, including several case studies documenting the diversity and global decline of nonmarine mollusks. We conclude with a discussion of the roles that mollusks and malacologists should play in conservation, including research, conservation management strategies, and education and outreach.

Keywords: nonmarine mollusks, biodiversity, gastropods, endangered species, hotspots

The loss and decline of many charismatic vertebrate species such as mammals and birds, and even of perhaps less charming creatures such as amphibians and reptiles, has been documented and prominently featured in the popular media. However, many invertebrate species, which comprise nearly 99% of all animal diversity (Ponder and Lunney 1999) and occupy an important trophic level in the ecological pyramid of energy, are either already extinct or severely threatened. Regrettably, invertebrates receive much less publicity than vertebrates and attract a disproportionately minor research effort.

As representatives of *Unitas Malacologica* (the international umbrella organization for mollusk researchers), the Freshwater Mollusk Conservation Society, the Mollusc Specialist Group of the Species Survival Commission of

IUCN (the World Conservation Union), and several regional malacological societies, we hope to spotlight the plight of what is arguably one of the most imperiled groups of animals: nonmarine (i.e., terrestrial and freshwater) mollusks. Here, we provide a brief overview of nonmarine molluscan diversity and conservation status and illustrate our case with a few relatively well-documented examples. We conclude with our thoughts about what is needed for the future conservation of nonmarine mollusks.

Nonmarine mollusk diversity and conservation status

Nonmarine mollusks belong to the second most diverse animal phylum in terms of numbers of described species. They include phylogenetically distinct lineages and assemblages, representing two molluscan classes: Bivalvia (clams and mussels)

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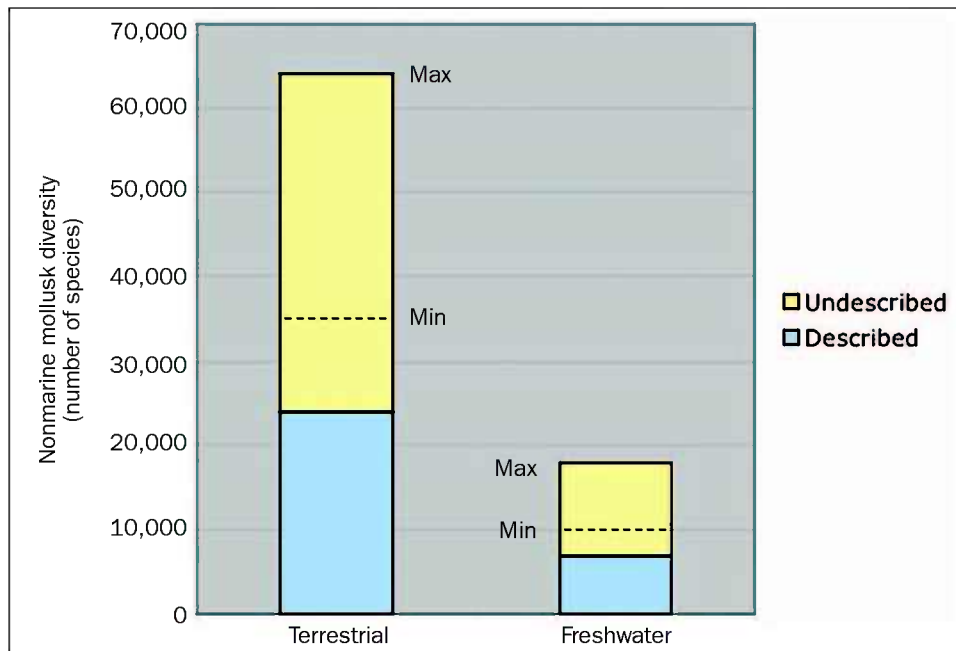


Figure 1. Estimated numbers of described and undescribed terrestrial and freshwater mollusks, assuming a total of about 200,000 molluscan species.

and Gastropoda (snails, limpets, and slugs). Global estimates of species richness for nonmarine mollusks, like estimates of total molluscan species richness, vary widely. There are three major reasons for this variation: (1) the vast array of nominal taxa whose synonymy remains uncertain (they were described by early taxonomists using shell morphology alone, and may or may not reflect real biological taxa); (2) the vast regions of the world that remain unexplored, probably harboring many undiscovered and undescribed species; and (3) the lack of an adequate cadre of molluscan taxonomists to cover the breadth of molluscan diversity. For a few taxonomic groups and geographical regions, diversity may have been overestimated because of the description of too many nominal species, but for most groups and areas, diversity is probably seriously underestimated.

Estimates of the total number of valid described and undescribed mollusk species range from 50,000 to 200,000 (van Bruggen 1995). However, most recent estimates tend to favor the higher end of the range (e.g., Stork 1999). Despite this uncertainty, and given the caveats mentioned above, we estimate that there are approximately 24,000 terrestrial and 7,000 freshwater mollusk species for which valid descriptions exist. In addition, there are probably 11,000 to 40,000 undescribed terrestrial species and 3,000 to 10,000 undescribed freshwater species (figure 1).

As of 16 May 2003, a total of 708 freshwater and 1222 terrestrial mollusk species were included in the 2002 *IUCN Red List of Threatened Species* (www.redlist.org; figure 2). This total of 1930 threatened nonmarine mollusks is nearly half the number of all known amphibian species, more than twice the number of shark and ray species, and nearly seven times the number of turtle species. In contrast, only 41 marine mollusk

species are on the *IUCN Red List*, despite their greater overall diversity (> 120,000 species). The relatively large number of nonmarine mollusks that are listed as threatened is therefore not simply a correlate of species richness.

Mollusks have the dubious honor of having the highest number of documented extinctions of any major taxonomic group. A staggering 42% of the 693 recorded extinctions of animal species since the year 1500 are mollusks (260 gastropods and 31 bivalves); this is more than the total (231) of all tetrapod species that have gone extinct during the same period (figure 3). Nonmarine species constitute 99% of all molluscan extinctions. Although terrestrial vertebrate extinctions are well documented, invertebrate extinctions often go

unnoticed by the general public, by most biologists, and by many conservation agencies. Only a tiny fraction (< 2%) of known molluscan species have had their conservation status properly assessed. Thus, the level of molluscan imperilment is poorly documented and is almost certainly underestimated. This view is supported by the continuing discovery of large numbers of small, narrow-range endemics, which occur especially in the tropical regions of the world, many of which are being rapidly deforested (e.g., Madagascar [Emberton 1995] and Tanzania [Emberton et al. 1997]).

Some highlighted faunas

The following sections focus on a number of nonmarine malacofaunas that are seriously threatened. These are perhaps the best documented and most publicized examples representing the problems faced by nonmarine mollusks. They come from three distinct locations and represent three different and highly diverse molluscan groups.

Pacific island land snails. The native land snail fauna of the Pacific islands is extremely diverse and composed almost entirely of narrow-range endemics. The freshwater malacofauna is diverse on islands where permanent fresh water is found, such as New Caledonia (Haase and Bouchet 1998) and Lord Howe Island, a small island (< 15 square kilometers [km²]) off the coast of Australia (Ponder 1982). However, given that relatively little permanent freshwater habitat exists on most Pacific islands and that native bivalves are absent, our focus will be on the land snail fauna.

The family Partulidae, which is endemic to the Pacific islands, is the flagship for Pacific island invertebrate conservation (Cowie and Cook 2001, Cowie et al. 2002). Along

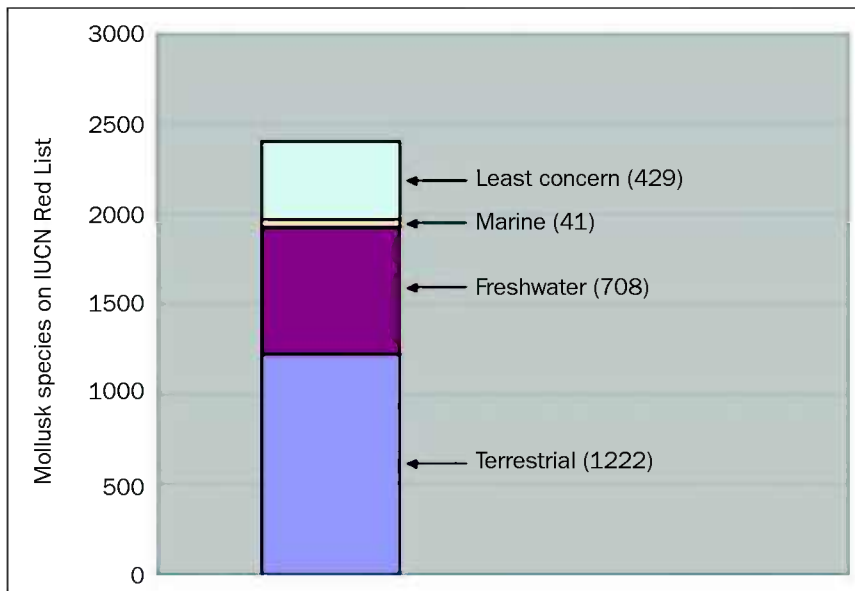


Figure 2. Total number of freshwater and terrestrial mollusks on the 2002 IUCN Red List of Threatened Species (from www.redlist.org).

with the endemic Hawaiian Achatinellinae (figure 4), a subfamily of colorful and highly variable tree snails, the Partulidae have been the subjects of a number of popular articles. However, these two groups are only a small fraction of the vast diversity of land snails on the islands of the Pacific. Although dominated by relatively few families, the land snails on these islands exhibit spectacular evolutionary radiations (Cowie 1996).

No single compilation of the overall numbers of Pacific island nonmarine snail species exists. A number of lists are available for various island groups, some recent, others more than 100 years old. All suffer from the problem that many

species remain undescribed while others have been described more than once as different species. Nevertheless, it is possible to arrive at a rough estimate of diversity. Cowie and colleagues (1995) listed 752 native Hawaiian land snail species; of these, all but 4 (and perhaps some of those 4) are endemic to the archipelago. The Samoan fauna consists of 94 native land snail species, about two-thirds of which are endemic (Cowie 1998). The Pitcairn Island group (Preece 1998) contains about 30 species of native land snails. Peake's (1981) numbers for each of the Society Islands (French Polynesia) lead to an estimate of a total fauna of about 160 species, assuming 90% single-island endemism. The small (40 km²) island of Rapa in the Austral archipelago (French Polynesia) harbors 98 native species (Solem 1983). In the Northern Mariana Islands, Bauman (1996) recorded at least 39 native species on Rota, and Kurozumi (1994) recorded at least

16 on the islands north of Saipan. Lord Howe Island has at least 85 endemic terrestrial species.

Other island groups, even those for which there are lists or compilations, remain less well known. Solem (1959) recorded about 130 species in Vanuatu, but this is a serious underestimate, because some islands in the group remain poorly investigated (Cowie 1996). Other island groups are even less well known. About 110 species have been listed from New Caledonia (Solem 1961), but Solem and colleagues (1984) considered the real number to be 300 to 400. Even the better-known archipelagoes still yield many new island records when thoroughly surveyed. For instance, new island records

of the generally well-documented partulid tree snails have been reported recently from Ofu (Cowie 2001a) and Olosega (Cowie et al. 2002) in American Samoa; and the number of known species of land snail fauna of Aunu'u, also in American Samoa, was recently increased from 2 to 22 (Cowie and Rundell 2002).

It is beyond the scope of this article to attempt an accurate compilation of species numbers from the widely spread taxonomic literature on land

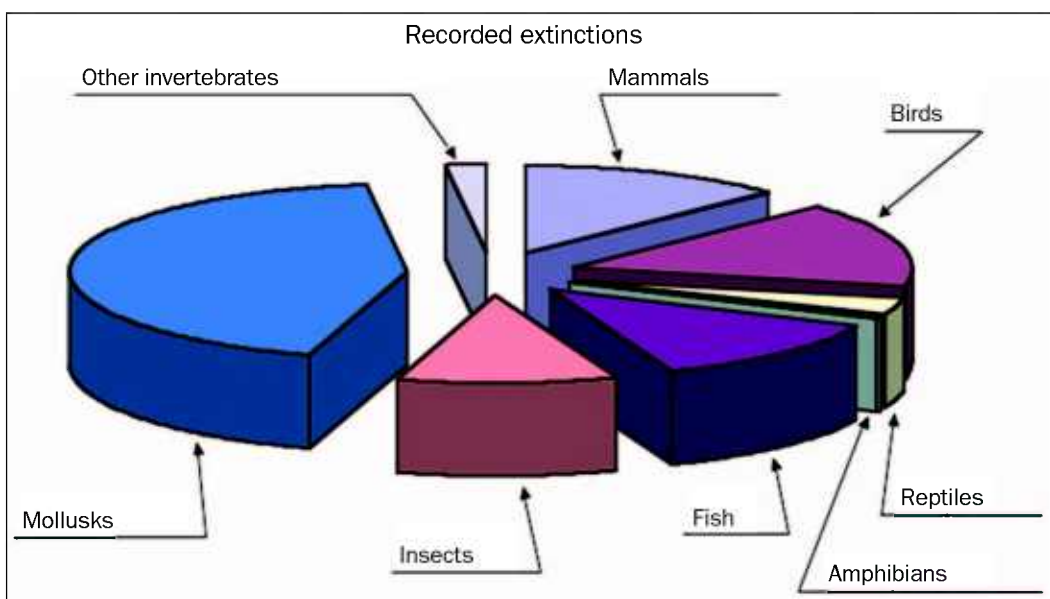


Figure 3. Proportion of recorded extinctions by major taxonomic groups of animals. Data are from the 2002 IUCN Red List of Threatened Species (www.redlist.org).



Figure 4. *Partulina mighelsiana* is endemic to the Hawaiian island of Molokai. Although not formally listed as endangered, it persists only in small, fragmented populations. Like all the Hawaiian tree snails in the subfamily Achatinellinae, it is seriously threatened. Photograph: Robert H. Cowie.

snails in the Pacific islands. However, using the numbers above as a guide, and given the extremely high levels of endemism among oceanic Pacific island land snails, an estimate of about 4000 native species seems reasonable. This number excludes the continental islands of New Zealand, which harbor an estimated 1350 native species (Barker 1999), and the island of New Guinea, which probably harbors at least 1000 (Cowie forthcoming).

These unique native snail faunas are disappearing rapidly (Bauman 1996, Cowie 2001a, Cowie and Robinson DG 2003). Many species are extinct or severely threatened, and these species are often confined to high-elevation refugia. For instance, the Amastridae, an endemic Hawaiian family of more than 300 species (Cowie et al. 1995), may now be reduced to as few as 10 or so species existing in tiny, highly localized remnant populations. The Endodontidae, probably the most diverse Pacific island family (Solem 1976), appear to be completely extinct or reduced to sparse remnant populations on every island they formerly inhabited. All the Partulidae of Moorea (French Polynesia) are extinct in the wild (Murray et al. 1988). In Hawaii, as many as 90% of the 750 recognized species of land snails are extinct. On Rota (Northern Marianas), 68% of the 43 species are extinct or declining, and in the Samoan archipelago, almost all are declining, although a smaller percentage is extinct (Cowie and Robinson DG 2003). These estimates suggest that overall perhaps 50% of the land snail fauna of the Pacific islands has disappeared in recent times.

Habitat destruction caused by agricultural and urban development (beginning with prehistoric Polynesian colonization; Hadfield 1986, Preece 1998) is an important cause of this decline, as is the modification of habitat by replacing

the native plant species suitable for native snails with alien plants on which the snails cannot survive. Alien predators (and perhaps competitors) are another major cause of decline. Rats introduced by Polynesians (*Rattus exulans*) and Europeans (*Rattus rattus*, *Rattus norvegicus*) prey on native snails (Hadfield et al. 1993). Solem (1976) suggested that introduced predatory ants have also had a serious impact, especially on ground-dwelling species such as the Endodontidae, although compelling evidence for this is lacking.

A particularly important cause of the demise of the native snails has been the deliberate introduction of predatory snails—most notably *Euglandina rosea*, the so-called cannibal snail or rosy wolfsnail—in ill-conceived attempts to control another introduced snail, the giant African snail (*Achatina fulica*). Populations of the giant African snail have not been reduced by the carnivorous snails, but native snail populations, especially of the slow-growing and slow-reproducing Partulidae and Achatinellinae, have been devastated (Murray et al. 1988, Hadfield et al. 1993, Cowie 2001b, Coote and Loève 2003). A more recent and equally serious threat is the alien predatory flatworm *Platydemus manokwari*, which was also introduced in an attempt to control the giant African snail (Hopper and Smith 1992). Reports that this flatworm can control *A. fulica* remain correlative, and the individuals who continue to promote its use as a biological control agent appear not to have considered its potential impact on native species (Muniappan 1990). In the Pacific islands, *P. manokwari* has been reported from Guam, the Northern Marianas, Palau, and Hawaii (Eldredge 1995) and more recently from Samoa (formerly Western Samoa) (Cowie and Robinson AC 2003). Much of the purported evidence that these predators can control populations of *A. fulica* is based on a poor

understanding of ecological principles. That these species prey on *A. fulica* is not evidence that they can control its populations; other factors (e.g., food) may be limiting, even to the extent that heavy predation has no effect on numbers of the extremely fecund and rapidly reproducing *A. fulica*.

These various factors, combined with the ongoing, often inadvertent introduction of alien snail species, are leading to replacement of the highly diverse and geographically structured native Pacific island snail faunas with a relatively small number (100 to 200) of mostly synanthropic, disturbance-tolerant, and now widespread snail species (Cowie 2002).

Unionoid mussels: Silence of the clams. The freshwater bivalve superfamily Unionoidea is almost cosmopolitan but reaches its greatest diversity in North America, particularly in the southeastern United States (Lydeard and Mayden 1995, Neves 1999). Unionoid mussels constitute an extraordinary evolutionary radiation, in which the life cycle involves an obligate parasitic stage on the gills or fins of a host fish (or, in one known case, an aquatic salamander); much remains to be learned about the host species of most unionoids (Watters 1994). The total number of unionoid species worldwide remains uncertain, with 860 currently recognized valid species and 4843 names available in the scientific nomenclature (Dan Graf and Kevin Cummings, the MUSSEL Project; <http://clade.acnatsci.org/mussel>).

Despite uncertainty regarding the number of unionoid species worldwide, in many countries where more thorough biotic surveys have been conducted, one thing is certain: The group is highly imperiled. A total of 200 unionoid species are on the *IUCN Red List*: 5 in Eurasia, 5 in Brazil, 1 in Australia, and the remaining 189 in the United States (figure 5). Within the United States and Canada, 202 of the nearly 300 unionoid species known are listed by the Natural Heritage Network as presumed extinct, possibly extinct, critically imperiled, imperiled, or vulnerable (Master et al. 2000). In the United States alone, 37 species are presumed extinct or possibly extinct (Master et al. 2000).

The most diverse unionoid mussel fauna ever known was located in the middle reaches of the Tennessee River in northern Alabama, in an area called Muscle Shoals (Garner and McGregor 2001). During the early 20th century, 69 species were reported from the area, but 32 of these species have not been recorded since the river was dramatically altered by the construction of a series of dams in the early 1900s. Although the mussel fauna of Muscle Shoals has stabilized somewhat, the species composition has been altered dramatically and now includes largely reservoir-tolerant species (Ahlstedt and McDonough 1993).

Another extraordinary radiation of unionoid mussels in the United States occurred in the Coosa watershed, which drains parts of Tennessee, Georgia, and eastern Alabama. In the upper Coosa basin, the Etowah River watershed in Georgia has lost as many as 65% of the 51 unionoid species that historically occurred in it (Burkhead et al. 1997). Extinction in the Coosa drainage is not limited to unionoid mussels: Of the



Figure 5. Native freshwater mussels (*Unionidae*) from Spring River in northern Arkansas. Photograph: Chris Barnhart.

approximately 82 freshwater snail species historically documented in the basin, 26 species and four entire genera (*Clappia*, *Gyrotoma*, *Amphigyra*, and *Neoplanorbis*) are presumed extinct (Bogan et al. 1995). Only 1 or 2 of the original 11 species of *Leptoxis* still exist (Lydeard et al. 1997). The primary cause of extinction, as at Muscle Shoals, was the construction of dams in the early to mid-1900s, although other factors, such as pollution and sediment toxicity, have contributed and continue to contribute to the demise of the malacofauna in many unimpounded headwaters of the upper Coosa basin (Paul D. Johnson, Tennessee Aquarium Research Institute, Cohutta, GA, personal communication, June 2003). The negative impacts of dams on aquatic ecosystems have been documented (Pringle et al. 2000), and a call for an international preservation network of free-flowing river systems has been made (Dynesius and Nilsson 1994). But although some dams have been removed to restore rivers (Hart and Poff 2002), numerous proposals for the construction of dams of dubious value are still being considered.

Further environmental insult to North American unionoids came with the introduction of two alien nonunionoid species, the Eurasian zebra mussel (*Dreissena polymorpha*) and the Asiatic clam (*Corbicula fluminea*). Zebra mussels settle on and smother native mussel species, thereby causing their decline; they also foul every other available surface, resulting in huge economic losses for industry (about \$4 billion each year).

In addition to impoundments and the introduction of alien species, major threats to unionoids include wetland drainage and channelization, point and nonpoint pollution,

sedimentation and siltation resulting from poor agricultural and silvicultural practices, highway and bridge construction, interbasin transfer schemes, habitat loss through dredging, and other land-use activities (Richter et al. 1997). Anecdotal evidence indicates that the decline of freshwater mollusks is probably a global phenomenon, but there are few quantitative data from most areas other than North America, Europe, and Australia.

Spring snails of the Australian outback and western North America. Until about 1980, the Australian freshwater molluscan fauna was thought to be composed of relatively few widespread, variable species. However, in the last 20 years, researchers have shown that the Australian fauna is far more diverse. The bulk of its diversity is in the family Hydrobiidae, which has more than 260 currently recognized species (Ponder and Walker 2003). Most of these species live in the relatively well-watered parts of southeastern Australia and Tasmania and occupy very narrow ranges; they are thus of considerable conservation concern (Ponder and Walker 2003). Others are found in artesian springs in some of the most arid parts of Australia.

The spring snails of the Great Artesian Basin (GAB), the largest artesian basin in the world, constitute an especially fascinating radiation of Australian hydrobiids (see Ponder and Walker 2003). Numerous freshwater springs are found across the GAB, which includes some of the driest parts of the continent. These springs are fed by continuous seepage from the artesian basin and provide a unique set of small oasis-like environments for numerous endemic fishes, crustaceans, worms, and snails (Ponder 1986). Some of the organisms found in these springs are unlike any others known in Australia or the world.

Six genera and 26 species of hydrobiids from the GAB have been described. Most of the known species are restricted to a single spring or group of springs, and almost all of them are listed as threatened species on the *IUCN Red List*. Many of the springs are located outside conservation reserves on private, pastoral leases. Remarkably, the snails have persisted in some springs where cattle have destroyed much of the aquatic and riparian vegetation. However, the populations in these tiny springs (often only a few square meters in extent) are vastly reduced compared with those in healthy springs. Unsustainable use of artesian water has caused the extinction of many springs, along with their unique aquatic fauna, and will cause more such extinctions if it continues (Ponder and Walker 2003).

An ecologically analogous situation exists in the arid habitats of the western United States and Mexico, which are home to several evolutionarily independent lineages of hydrobiids. As late as 1980, the primary reference for North American freshwater snails listed about 30 western hydrobiid species (Burch and Tottenham 1980). However, subsequent surveys combined with modern taxonomic monography have resulted in the recognition of more than 300 hydrobiid species and subspecies (Hershler 1998).

In both Australia and North America, many springs have disappeared in the recent past as a result of the unsustainable extraction of artesian water. No historical record exists for the fauna of most of these springs, but given the high levels of hydrobiid endemicity in extant springs, it is likely that many extinctions have occurred.

Other faunas

The above examples highlight the plight of a few of the more spectacular radiations of nonmarine mollusks. Other faunas that are relatively well known include the land snails of western Europe (Kerney et al. 1983), western and central Australia (Solem 1998), and parts of North America (Hubricht 1985). For the most part, these faunas are not seriously threatened, although there are many narrowly endemic species under threat (e.g., *Meridolum corneovirens* in Sydney [Clark and Richardson 2002] and *Vertigo moulinsiana* in the United Kingdom [Tattersfield 2003]). In the case of Europe, perhaps the natural ecosystems have been modified for so long that what we now see is a relatively stable, though altered, fauna. Most other faunas are much less well known, and an adequate assessment of their conservation status and needs is generally impossible. For instance, the terrestrial molluscan fauna of much of Africa remains poorly known, although recent work in East Africa is beginning to change this (e.g., Emberton et al. 1997, Tattersfield 1998). Similarly, parts of Madagascar have been subject to intense recent survey (Emberton 1995). The malacofauna of the Neotropics and Southeast Asia is not well documented but, with rampant forest destruction now taking place, may be seriously threatened (e.g., Mansur and Leme 1996).

Nonmarine mollusk conservation strategies

Molluscan conservation strategies (e.g., Killeen et al. 1998), including regional strategies that focus on the nonmarine mollusks of Australia (Ponder 1997), South Africa (Herbert 1998), and the Pacific islands (Cowie forthcoming), have been promulgated in several specialized journals or symposium volumes. Many of the issues addressed in these publications are applicable worldwide. What follow are our perceptions of the primary needs for nonmarine mollusk conservation. These needs fall into four major areas: molluscan biodiversity hotspots, research, management, and education and outreach.

Molluscan biodiversity hotspots. Given the limited resources for species-by-species approaches to conservation, it has been suggested that conservation biologists identify biodiversity hotspots, or areas where endemic species are found in exceptional concentrations and where they may be undergoing rapid extinction or decline resulting from the loss or degradation of their habitat, the impact of invasive species, and other human-caused phenomena. Recently, 25 locations were identified as hotspots for conservation prioritization, and it was suggested that the limited conservation resources available should be put into these areas first (Myers 2003). The 25

hotspots were identified using areas with high levels of species endemism in plants, mammals, birds, reptiles and amphibians, and it was suggested that a significant portion (approximately 25%) of the world's biota could be protected by focusing on these areas, which cover 1.4% of Earth's surface. However, invertebrate diversity is not specifically mentioned in any of these vertebrate- and plant-oriented estimates, which rely on the assumption that invertebrates will track the pattern of diversity exhibited by the usual indicator species. Although invertebrate species represent about 99% of animal diversity (Ponder and Lunney 1999), they have rarely served as indicator species (Ponder 1994) and are highly underrepresented in conservation research (Clark and May 2002). The reason for this failure to use invertebrate indicator species has been the lack of basic biological knowledge about most invertebrate faunas around the world, which is in part a result of the grossly disproportionate distribution of taxonomic effort toward vertebrates and higher plants (Gaston and May 1992). Certainly many invertebrate species would be protected by focusing on vertebrate- and vascular plant-based hotspots, but equally certainly, because of the restricted range of many invertebrate species, many others would be omitted (Lawler et al. 2003). A study of the tropical rain forest biota of eastern Australia has shown that snails and insects were strong predictors of conservation priorities for vertebrates, but not vice versa (Moritz et al. 2001).

Research. Biotic surveys and taxonomic studies remain critically important, particularly in poorly inventoried areas, if biologists are to have an accurate picture of the true levels of species richness and extinction and if managers are to determine appropriate locations for conservation efforts. Non-marine molluscan hotspots need to be identified in order to improve or modify management practices to accommodate mollusks' needs and, if necessary, to guide the establishment of new areas specifically related to mollusks. A recent example in which mollusks were used in combination with data from other groups (including corals, lobsters, and reef fish) helped to delineate global hotspots for marine biodiversity (Roberts et al. 2002). Similar efforts need to be applied to non-marine mollusks.

To identify nonmarine molluscan hotspots, researchers need to conduct extensive field surveys. Combined with modern surveys, data on the historical distribution of non-marine mollusks should be collected whenever possible to ascertain species trajectories (declines and increases). This information can guide not only the geographic focus of conservation efforts but also appropriate management efforts dealing with, for instance, the replacement of native species by aliens. Historical information can be gleaned to some extent from the literature, but far more information resides in the vast collections of the world's natural history museums and other biological research collections (Mikkelsen and Bieler 2000, Ponder et al. 2001). Making this information available is arguably the most important function of a modern natural history museum, although care must be taken in

interpreting the data to ensure that historical collection efforts accurately reflect regional and local species diversity (Bouchet et al. 2002).

Surveys must be followed by taxonomic work to describe and inventory the surveyed fauna. Even supposedly better-known regions warrant further investigation. For example, using data derived in part from recent taxonomic studies, Thompson (2000) and Mihalcik and Thompson (2002) estimated that about 50% of the hydrobiid species and 30% to 50% of the species of the freshwater snail genus *Elimia* in the southeastern United States remain undescribed. The necessary taxonomic work will, of course, require the proper training of more taxonomists, and this must be done quickly, before the few remaining molluscan taxonomic experts retire. The US National Science Foundation offers the Biodiversity Surveys and Inventories Program and a special program, created more recently, called Partnerships for Enhancing Expertise in Taxonomy (Rodman and Cody 2003). Together, these programs serve as a model for overcoming the molluscan taxonomic and conservation impediment. Regrettably, however, there are few similar programs outside the United States and few or no funding opportunities for workers located in most of the megadiverse areas of the world.

In addition to surveys and taxonomic studies, molecular phylogenetic and phylogeographic research is necessary to understand how genetic variation is partitioned spatially and temporally (Clark and Richardson 2002, Lydeard and Lindberg 2003). For instance, extraordinarily high levels of apparently intraspecific mitochondrial genetic variation have been documented within several nominal pulmonate species (Thomaz et al. 1996). However, it is quite possible that this high level of genetic variation can be explained, in part, by the presence of currently unrecognized, cryptic species. Much has been written arguing that scientists and managers can conserve biodiversity only if they know what it is they are conserving. This necessitates the development of technologies and methods to accumulate molecular and morphological data for phylogenetic studies inexpensively and rapidly. Furthermore, biologists need to cooperate more, and build more effective national and international networks, to maximize the information obtained from each funded study.

Scientists remain woefully ignorant of the ecology of most individual mollusk species and the ecological role these species play in ecosystem processes. For instance, differences in life-history strategy, such as food choices, may be fundamental in determining the vulnerability of snail populations to unnaturally high levels of predation by introduced predators (Hadfield et al. 1993, Rundell and Cowie 2003). Biologists know nothing, except in very general terms, of the food preferences of the vast majority of land snails.

Finally, scientists need to broaden their research horizons to encompass the interrelationships between living things at all levels and integrate environmental research across disciplines. In addition to documenting species richness, it is important to understand and eventually predict the ecological

impact that the process of species colonization and extinction may play on communities and ecosystem function (Tilman et al. 1994). Indeed, current conservation approaches argue for the need to focus at multiple scales that sustain the full complement of biota and the supporting natural systems (Poiani et al. 2000).

Management. The resources that are currently available to manage global nonmarine molluscan biodiversity are insufficient. Scientific knowledge is scanty and scattered. Often there are too few staff to manage the existing protected areas, which typically focus on vertebrate species. Because of the lack of resources, mollusks and other less charismatic groups are usually ignored. Nevertheless, regional and species-specific conservation action plans must be developed on the basis of appropriately designed scientific studies, such as that undertaken in the United Kingdom for conservation of the land snail *V. moulinsiana* (Tattersfield 2003). To develop such plans, greater integration, coordination, and networking among conservation management agencies, research institutions, and other stakeholders is essential. This approach will ensure that conservation is scientifically based and will help to avoid potentially disastrous ecological, economic, or legal consequences. Furthermore, local and national governments and their agencies, and nongovernmental organizations of all kinds (from international organizations to local conservation societies), must forge relationships to ensure that their goals are not competitive or contradictory and that their actions are in concert. Mollusks must not be ignored when new conservation areas are created. Both new and existing reserves must be adequately managed, with attention paid to mollusks, and in some instances reserves should be established explicitly for mollusks.

A major management concern is the impact of alien species, which may prey on, or perhaps outcompete, native mollusk species. Management priorities must include the reduction or halt of the spread of aliens. The control of alien species depends on integrating scientific knowledge of their pathways of introduction and potential impacts (Cowie forthcoming, Cowie and Robinson DG 2003). Eradication of populations of alien snails has proved possible in a small number of cases, but, of course, it is better to prevent their introduction in the first place. Many species of plants and animals may affect native molluscan biodiversity, and preventing their initial introduction should be a fundamental management goal. Prevention involves preentry screening, port-of-entry quarantine inspection, and immediate postentry eradication if new propagules are detected.

Finally, conservation practitioners should take heed of the emerging concept of ecosystem health (Rapport et al. 1998, Horwitz et al. 2001), which integrates physical, biological, and sociological knowledge and needs into a holistic paradigm for ecosystem management. However, this should not be taken to suggest that if a region is managed for conservation of the charismatic megafauna, mollusks will automatically be preserved. Often mollusks and other invertebrates have specific needs that must be addressed explicitly, needs that can only

be determined by appropriate management-oriented scientific research.

Education and outreach. Education about the importance of nonmarine mollusks as a major component of global biodiversity is a high priority if an extinction crisis is to be averted. It is imperative that scientists participate in educating policymakers and the general public about the integral role nonmarine mollusks play in the natural ecosystems that provide clean air, water, food, and overall quality of life. Environmental issues, including the significance of mollusks and other invertebrates, must be integrated in the general curriculum from kindergarten through college. Real support will be achieved only through trust in scientists as experts, and this trust can be obtained only if scientists are prepared to foster it by sharing their knowledge.

The current wave of excitement generated by the sequencing of the human genome and the development of functional genomics and proteonomics has led to the impression that virtually every gene that is linked to a human disease will be discovered soon and a cure developed shortly thereafter. However, it is important to realize that many diseases may be environmentally linked to the production of hazardous wastes (e.g., endocrine-disruption contaminants and PCBs [polychlorinated biphenyls]) and to the disruption of natural ecosystem processes. Eliminating the cause of such diseases by maintaining a healthy ecosystem should be a significant public health concern (Horwitz et al. 2001). As an integral component of healthy ecosystems, molluscan diversity is valuable both for its own sake and as an indicator of conditions that may affect other species, including our own.

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References cited

- Ahlstedt SA, McDonough TA. 1993. Quantitative evaluation of commercial mussel populations in the Tennessee River portion of Wheeler Reservoir, Alabama. Pages 38–49 in Cummings KS, Buchanan AC, Koch LM, eds. Conservation and Management of Freshwater Mussels: Proceedings of a UMRCC Symposium, 12–14 October 1992, St. Louis, Missouri. Rock Island (IL): Upper Mississippi River Conservation Committee.
- Barker GM. 1999. Naturalised Terrestrial Stylommatophora (Mollusca: Gastropoda). Lincoln (New Zealand): Manaaki Whenua Press. FNZ 38.
- Bauman S. 1996. Diversity and decline of land snails on Rota, Mariana Islands. American Malacological Bulletin 12: 13–27.
- Bogan AE, Pierson JM, Hartfield P. 1995. Decline in the freshwater gastropod fauna in the Mobile Bay basin. Pages 249–252 in LaRoe ET, Farris GS, Puckett CE, Doran PD, Mac MJ, eds. Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. Washington (DC): US Department of the Interior, National Biological Service.
- Bouchet P, Lozouet P, Maestrati P, Heros V. 2002. Assessing the magnitude of species richness in tropical marine environments: Exceptionally

- high numbers of mollusks at a New Caledonia site. *Biological Journal of the Linnean Society* 75: 421–436.
- Burch JB, Tottenham JL. 1980. North American freshwater snails: Species list, ranges and illustrations. *Walkerana* 1: 81–215.
- Burkhead NM, Walsh SJ, Freeman BJ, Williams JD. 1997. Status and restoration of the Etowah River, an imperiled southern Appalachian ecosystem. Pages 375–444 in Benz GW, Collins DE, eds. *Aquatic Fauna in Peril: The Southeastern Perspective*. Decatur (GA): Southeast Aquatic Research Institute.
- Clark JA, May RM. 2002. Taxonomic bias in conservation research. *Science* 297: 191–192.
- Clark SA, Richardson BJ. 2002. Spatial analysis of genetic variation as a rapid assessment tool in the management of narrow-range endemics. *Invertebrate Systematics* 16: 583–587.
- Coote T, Loève É. 2003. From 61 species to five: Endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. *Oryx* 37: 91–96.
- Cowie RH. 1996. Pacific island land snails: Relationships, origins, and determinants of diversity. Pages 347–372 in Keast A, Miller SE, eds. *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. Amsterdam: SPB Academic.
- . 1998. *Catalog of the Nonmarine Snails and Slugs of the Samoan Islands*. Honolulu: Bishop Museum Press.
- . 2001a. Decline and homogenization of Pacific faunas: The land snails of American Samoa. *Biological Conservation* 99: 207–222.
- . 2001b. Can snails ever be effective and safe biocontrol agents? *International Journal of Pest Management* 47: 23–40.
- . 2002. Invertebrate invasions on Pacific islands and the replacement of unique native faunas: A synthesis of the land and freshwater snails. *Biological Invasions* 3: 119–136.
- . Disappearing snails and alien invasions: The biodiversity/conservation interface in the Pacific. *Journal of Conchology Special Publication* 3. Forthcoming.
- Cowie RH, Cook RP. 2001. Extinction or survival: Partulid tree snails in American Samoa. *Biodiversity and Conservation* 10: 143–159.
- Cowie RH, Robinson AC. 2003. The decline of native Pacific island faunas: Changes in status of the land snails of Samoa through the 20th century. *Biological Conservation* 110: 55–65.
- Cowie RH, Robinson DG. 2003. Pathways of introduction of nonindigenous land and freshwater snails and slugs. Pages 93–123 in Ruiz G, Carlton JT, eds. *Invasive Species: Vectors and Management Strategies*. Washington (DC): Island Press.
- Cowie RH, Rundell RJ. 2002. The land snails of a small tropical Pacific island, Aunu'u, American Samoa. *Pacific Science* 56: 143–147.
- Cowie RH, Evenhuis NL, Christensen CC. 1995. *Catalog of the Native Land and Freshwater Molluscs of the Hawaiian Islands*. Oegstgeest-Leiden (The Netherlands): Backhuys.
- Cowie RH, Rundell RJ, Milka F, Setu P. 2002. The endangered partulid tree snail *Samoana thurstoni* on Olosega and the land snail diversity of the Manu'a Islands, American Samoa. *American Malacological Bulletin* 17: 37–43.
- Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266: 753–762.
- Eldredge LG. 1995. Triclad flatworm tours the Pacific. *Aliens* 2: 11.
- Emberton KC. 1995. On the endangered biodiversity of Madagascan land snails. Pages 69–89 in van Bruggen AC, Wells SM, Kemperman TCM, eds. *Biodiversity and Conservation of the Mollusca*. Oegstgeest-Leiden (The Netherlands): Backhuys.
- Emberton KC, Pearce TA, Kasigwa PE, Tattersfield P, Habibu Z. 1997. High diversity and regional endemism in land snails of eastern Tanzania. *Biodiversity and Conservation* 6: 1123–1136.
- Garner JT, McGregor SW. 2001. Current status of freshwater mussels (Unionidae, Margaritiferidae) in the Muscle Shoals area of Tennessee River in Alabama (Muscle Shoals revisited again). *American Malacological Bulletin* 16: 155–170.
- Gaston KJ, May RM. 1992. The taxonomy of taxonomists. *Nature* 356: 281–282.
- Haase M, Bouchet P. 1998. Radiation of crenobiontic gastropods on an ancient continental island: The Hemisomia-clade in New Caledonia (Gastropoda: Hydrobiidae). *Hydrobiologia* 367: 43–129.
- Hadfield MG. 1986. Extinction in Hawaiian achatinelline snails. *Malacologia* 27: 67–81.
- Hadfield MG, Miller SE, Carwile AH. 1993. The decimation of endemic Hawaiian tree snails by alien predators. *American Zoologist* 33: 610–622.
- Hart DD, Poff NL. 2002. A special section on dam removal and river restoration. *BioScience* 52: 653–655.
- Herbert DG. 1998. Molluscan conservation in South Africa: Diversity, issues and priorities. Pages 61–76 in Killeen IJ, Seddon MB, Holmes AM, eds. *Molluscan Conservation: A Strategy for the 21st Century*. *Journal of Conchology Special Publication* 2. Dorchester (United Kingdom): Conchological Society of Great Britain and Ireland, Dorset Press.
- Hershler R. 1998. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States, pt. 1: Genus *Pyrgulopsis*. *Veliger* 41: 1–132.
- Hopper DR, Smith BD. 1992. Status of tree snails (Gastropoda: Partulidae) on Guam, with a resurvey of sites studied by H. E. Crampton in 1920. *Pacific Science* 46: 77–85.
- Horwitz P, Lindsay M, O'Connor M. 2001. Biodiversity, endemism, sense of place, and public health: Inter-relationships for Australian inland aquatic systems. *Ecosystem Health* 7: 253–265.
- Hubricht L. 1985. *The Distributions of the Native Land Mollusks of the Eastern United States*. Chicago: Field Museum of Natural History. *Fieldiana: Zoology*, no. 24.
- Kerney MP, Cameron RAD, Jungbluth JH. 1983. *Die Landschnecken Nord- und Mitteleuropas*. Hamburg (Germany): Verlag Paul Parey.
- Killeen IJ, Seddon MB, Holmes AM. 1998. *Molluscan Conservation: A Strategy for the 21st Century*. *Journal of Conchology Special Publication* 2. Dorchester (United Kingdom): Conchological Society of Great Britain and Ireland, Dorset Press.
- Kurozumi T. 1994. Land molluscs from the Northern Mariana Islands, Micronesia. *Natural History Research* 1 (special issue): 113–119.
- Lawler JJ, White D, Sifneos JC, Master LL. 2003. Rare species and the use of indicator groups for conservation planning. *Conservation Biology* 17: 875–882.
- Lydeard C, Lindberg DR. 2003. *Molecular Systematics and Phylogeography of Mollusks*. Washington (DC): Smithsonian Books.
- Lydeard C, Mayden RL. 1995. A diverse and endangered aquatic ecosystem of the southeast United States. *Conservation Biology* 9: 800–805.
- Lydeard C, Holznagel WE, Garner J, Hartfield P, Pierson JM. 1997. A molecular phylogeny of Mobile River drainage basin pleurocerid snails (Caenogastropoda: Cerithioidea). *Molecular Phylogenetics and Evolution* 7: 117–128.
- Mansur MCD, Leme JLM. 1996. The endangered giant *Megalobulimus* from the Atlantic forest of Brasil. *Tentacle* 6: 14–15.
- Master LL, Stein BA, Kutner LS, Hammerson GA. 2000. Vanishing assets: Conservation status of U.S. species. Pages 93–118 in Stein BA, Kutner LS, Adams JS, eds. *Precious Heritage: The Status of Biodiversity in the United States*. New York: Oxford University Press.
- Mihalcik EL, Thompson FG. 2002. A taxonomic revision of the freshwater snails referred to as *Elimia curvicastrata*, and related species. *Walkerana* 13 (29/30): 1–108.
- Mikkelsen PM, Bieler R. 2000. Marine bivalves of the Florida Keys: Discovered biodiversity. Pages 367–387 in Harper EM, Taylor JD, Crame JA, eds. *The Evolutionary Biology of the Bivalvia*. London: Geological Society. *Special publication* no. 177.
- Moritz C, Richardson KS, Ferrier S, Monteith GB, Stanicic J, Williams SE, Whiffin T. 2001. Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London*, B 268: 1875–1881.
- Muniappan R. 1990. Use of the planarian, *Platydemus manokwari*, and other natural enemies to control the giant African snail. Pages 179–183 in Bay-Petersen J, ed. *The Use of Natural Enemies to Control Agricultural Pests*. Taipei (Taiwan): Food and Fertilizer Technology Center for the Asian and Pacific Region.

- Murray J, Murray E, Johnson MS, Clarke B. 1988. The extinction of *Partula* on Moorea. *Pacific Science* 42: 150–153.
- Myers N. 2003. Biodiversity hotspots revisited. *BioScience* 53: 916–917.
- Neves RJ. 1999. Conservation and commerce: Management of freshwater mussel (*Bivalvia: Unionoidea*) resources in the United States. *Malacologia* 41: 461–474.
- Peake JE. 1981. The land snails of islands—a dispersalist's viewpoint. Pages 247–263 in Forey PL, ed. *The Evolving Biosphere: Chance, Change and Challenge*. New York: Cambridge University Press.
- Poiani KA, Richter BD, Anderson MG, Richter HE. 2000. Biodiversity conservation at multiple scales: Functional sites, landscapes, and networks. *BioScience* 50: 133–146.
- Ponder WF. 1982. Hydrobiidae of Lord Howe Island (Mollusca: Gastropoda: Prosobranchia). *Australian Journal of Marine and Freshwater Research* 33: 89–159.
- . 1986. Mound springs of the Great Artesian Basin. Pages 403–420 in De Deckker P, Williams WD, eds. *Limnology in Australia*. Melbourne (Australia): CSIRO.
- . 1994. Australian freshwater Mollusca: Conservation priorities and indicator species. *Records of the Queensland Museum* 36: 191–196.
- . 1997. Conservation status, threats and habitat requirements of Australian terrestrial and freshwater Mollusca. *Memoirs of the Museum of Victoria* 56: 421–430.
- Ponder WF, Lunney D, eds. 1999. *The Other 99%: The Conservation and Biodiversity of Invertebrates*. Mosman (Australia): Royal Zoological Society of New South Wales.
- Ponder WF, Walker KE. 2003. From mound springs to mighty rivers: The conservation status of freshwater molluscs in Australia. *Aquatic Ecosystem Health and Management* 6: 19–28.
- Ponder WF, Carter GA, Flemons P, Chapman RR. 2001. The evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology* 15: 648–657.
- Preece RC. 1998. Impact of early Polynesian occupation on the land snail fauna of Henderson Island, Pitcairn group (South Pacific). *Philosophical Transactions of the Royal Society of London, B* 353: 347–368.
- Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical–temperate comparisons. *BioScience* 50: 807–823.
- Rapport D, Costanza R, Epstein PR, Gaudet C, Levins R. 1998. *Ecosystem Health*. Oxford (United Kingdom): Blackwell Science.
- Richter BD, Braun DP, Mendelson MA, Master LL. 1997. Threats to imperiled freshwater fauna. *Conservation Biology* 11: 1081–1093.
- Roberts CM, et al. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295: 1280–1284.
- Rodman JE, Cody JH. 2003. The taxonomic impediment overcome: NSF's Partnerships for Enhancing Expertise in Taxonomy (PEET) as a model. *Systematic Biology* 52: 428–435.
- Rundell RJ, Cowie RH. 2003. Growth and reproduction in Hawaiian succineid land snails. *Journal of Molluscan Studies* 69: 288–289.
- Solem A. 1959. *Systematics and Zoogeography of the Land and Freshwater Mollusca of the New Hebrides*. Chicago: Chicago Natural History Museum. *Fieldiana: Zoology*, vol. 43, no. 1. (1 March 2004; www.fortsasbooks.com/zoology/zoology11.htm)
- . 1961. *New Caledonian Land and Fresh-water Snails: An Annotated Check List*. Chicago: Chicago Natural History Museum. *Fieldiana: Zoology*, vol. 41, no. 3. (1 March 2004; www.fortsasbooks.com/zoology/zoology11.htm)
- . 1976. Endodontoid Land Snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra), pt. 1: Family Endodontidae. Chicago: Field Museum of Natural History.
- . 1983. Endodontoid Land Snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra), pt. 2: Families Punctidae and Charopidae, Zoogeography. Chicago: Field Museum of Natural History.
- . 1998. Family Camaenidae. Pages 1112–1113 in Beesley PL, Ross GJB, Wells A, eds. *Mollusca: The Southern Synthesis*, vol. 5, part B. Melbourne (Australia): CSIRO.
- Solem A, Tillier S, Mordan P. 1984. Pseudo-operculate pulmonate land snails from New Caledonia. *Veliger* 27: 193–199.
- Stork NE. 1999. Estimating the number of species on Earth. Pages 1–7 in Ponder WF, Lunney D, eds. *The Other 99%: The Conservation and Biodiversity of Invertebrates*. Mosman (Australia): Royal Zoological Society of New South Wales.
- Tattersfield P. 1998. Patterns of diversity and endemism in East African land snails and the implications for conservation. Pages 77–86 in Killeen IJ, Seddon MB, Holmes AM. 1998. *Molluscan Conservation: A Strategy for the 21st Century*. *Journal of Conchology Special Publication* 2. Dorchester (United Kingdom): Conchological Society of Great Britain and Ireland, Dorset Press.
- . 2003. New major study on the hydrological requirements of the protected wetland snail *Vertigo moulinsiana* in the UK. *Tentacle* 11: 12–13.
- Thomaz D, Guiller A, Clarke B. 1996. Extreme divergence of mitochondrial DNA within species of pulmonate land snails. *Proceedings of the Royal Society of London, B* 263: 363–368.
- Thompson FG. 2000. Freshwater snails of the genus *Elimia* from the Coosa River System, Alabama. *Walkerana* 11 (25): 1–54.
- Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65–66.
- van Bruggen AC. 1995. Biodiversity of Mollusca: Time for a new approach. Pages 1–19 in van Bruggen AC, Wells SM, Kemperman TCM, eds. *Biodiversity and Conservation of the Mollusca*. Oegstgeest-Leiden (The Netherlands): Backhuys.
- Watters GT. 1994. *An Annotated Bibliography of the Reproduction and Propagation of the Unionoidea (Primarily of North America)*. Columbus: Ohio Biological Survey, College of Biological Sciences, Ohio State University.