J. N. Am. Benthol. Soc., 2008, 27(2):471–483

DOI: 10.1899/07-059.1
Published online: 22 April 2008

# Practical applications for systematics and taxonomy in North American freshwater gastropod conservation

**Kathryn E. Perez**[1]
*University of North Carolina at Chapel Hill and Department of Biology, Duke University, Durham, North Carolina 27708 USA*

**Russell L. Minton**[2]
*Department of Biology, University of Louisiana at Monroe, Monroe, Louisiana 71209 USA*

**Abstract.** The roles of systematics in the field of conservation biology are well understood and accepted for many organisms. However, the role of systematics and taxonomy has not been reviewed in the context of species protection and management of freshwater gastropods. We provide a thorough review of the relevant theoretical literature in systematics and taxonomy and illustrate with recent examples of species delineation and taxonomy in North American freshwater gastropods that these fields play key roles in the practical designation of conservation management units. We summarize some aspects of the biology of freshwater gastropods that can confound taxonomic and management efforts. Based on our review, we recommend that effective conservation plans include the systematic research necessary to recognize unique organismal lineages as primary conservation management units. This strategy must be combined with consistent and rigorous nomenclature, taxonomy, and dissemination of research findings so that all parties have access to the highest quality information.

**Key words:** systematics, taxonomy, snail, freshwater, conservation, gastropods.

Rigorous systematic and taxonomic efforts provide the framework for scientific investigation and any conservation plan (Wheeler 2004). However, as invertebrates, freshwater gastropods belong to "the other 99%" of organisms on the planet (Ponder and Lunney 1999); consequently, basic knowledge of their taxonomy and biology are impoverished. Proper identification of conservation management units and the creation of a stable means of communicating those units that reflects evolutionary history are essential in the process of conservation; these tasks have been the focus of intense research on freshwater gastropods in recent years (e.g., Liu et al. 2003, Strong and Glaubrecht 2003, Michel 2004, Minton and Savarese 2005, Perez et al. 2005, Miller et al. 2006, Walther et al. 2006, Hershler et al. 2007a). During the course of this research, the scientific field of systematics has been in the midst of a procedural and philosophical reformation consequent to the new availability of independent data sets and testing of strategies for consilience in classifications using multiple lines of evidence (Godfray 2002, Wiens and Penkrot 2002, Wheeler 2004, Hershler et al. 2007b, Strong and Frest 2007). In this context, it is important to define clearly the working terms of taxonomy, systematics, and classification, especially given their history of intricate linkage. Herein, we define systematics as the process of constructing phylogenies, patterns of evolutionary relationship between organisms. We define classification as the process of translating phylogenies into useable systems of nested biological organization. Last, we define taxonomy as the overlaying of Linnean names onto a classification following the appropriate nomenclatural code, the description of new species, and the identification of characters that define species and higher taxa. Conservation efforts, if limited by the lack of meaningful classifications, are not maximally effective, or worse, are actively harmful to the long-term preservation of biodiversity (Daugherty et al. 1990, Lang et al. 2006).

Systematics and taxonomy currently play important roles in conservation of many organisms (e.g., Vane-Wright et al. 1991, Moritz and Faith 1998,

[1] E-mail addresses: keperez@duke.edu
[2] minton@ulm.edu

Soltis and Gitzendanner 1999), but taxonomy is frequently seen as a necessary evil in the efforts to preserve the nation's freshwater gastropod fauna (Cranston 1990). This view is partly the result of a "megafaunal bias" (Platnick 1991) against invertebrates, but it is also is caused by a laissez-faire attitude toward taxonomy in which efforts to protect a taxon are thought to outweigh by far efforts to assign names. This rationale is in stark contrast to studies of other organisms, where examples of "bad" taxonomy hindering conservation efforts are more common (e.g., Daugherty et al. 1990, Mayden and Kuhajda 1996, Bowen and Karl 1999, Karl and Bowen 1999, Berry et al. 2002, Engstrom et al. 2002, Flanagan et al. 2006, Funk and Fa 2006). Cranston (1990:269) elegantly summarized this issue: "The view that taxonomy is integrally linked to virtually all spheres of biological endeavor is so fundamental that the practitioners take it for granted that the rest of the scientific community also recognizes this. However, the continuous decline in support indicates the pivotal role of taxonomy in biological science is not widely appreciated. Thus, it is pertinent to examine the relationship between the discipline and its users, with particular reference to aquatic biology."

Sufficient data are required to affect policy and develop successful funded programs. However, the high level of imperilment of many North American freshwater gastropod taxa increases the difficulty of gathering sufficient data about species biology and interactions to implement effective conservation action (Lydeard et al. 2004). In the USA, ~60 species of freshwater gastropods are presumed extinct, 20 are on the US federal endangered or threatened species list, and another 290 species are of conservation concern (Johnson 2003). In other words, 9% of all freshwater gastropods of the USA are extinct and 48% are conservation targets. This rate of imperilment exceeds that of every other major animal group in North America—even freshwater mussels, of which 42% of all species are conservation targets. Less than 5% of US freshwater gastropods have conservation plans in place or in progress, and the conservation status of most has not been assessed.

We provide a thorough review of the relevant theoretical literature in systematics and taxonomy and illustrate applications of these fields in freshwater gastropods. We review key examples of species delineation and taxonomy in North American freshwater gastropods to highlight the importance of systematics and taxonomy to conservation actions. We summarize some aspects of the biology of freshwater gastropods that can confound taxonomic and management efforts. We also point out areas of research that have not yet seen a rigorous scientific approach and offer recommendations for incorporating systematics and taxonomic information into future gastropod conservation plans.

## Defining the Theoretical Conservation Management Unit

Identifying the appropriate conservation management unit is central to any conservation plan and potentially increases the success of the conservation measures used. Conservation management units are populations and species due protection because their adaptations, unique life-history traits, and genetic diversity allow them to succeed in their historical and present environments. A primary task of taxonomists is to draw stark lines (taxonomic names) across fuzzy boundaries (species as continua of diversity). This task has an inherent component of uncertainty. Taxonomists have the task of providing scientific names and data helpful for development of conservation guidelines for use by legislators, decision makers, agency workers, and the lay person. Taxonomists have the additional task of conveying to these end-users that taxonomic names change for good reasons; name changes indicate better understanding of an organism or group of organisms. Managers must understand this instability and be willing to accommodate the changes brought about by additional data. National agencies often conduct reviews of species and group taxonomy and natural history as part of the process of granting protection status to ensure proper recognition of management units (e.g., Nicholopoulos 1999, COSEWIC 2006). Occasionally, conservation plans are implemented before management units are appropriately defined; this event can have negative results for conservation (Greig 1979, Avise and Nelson 1989). For example, research on the freshwater gastropod *Leptoxis crassa anthonyi* (Redfield, 1854) came after the establishment of the conservation plan (Minton and Savarese 2005). This research demonstrated that conservation management units (USFWS 1997), which were established based on the assumption that genetic and geographical distance were correlated, were inconsistent with the evolutionary history of the populations (Minton and Savarese 2005; Fig. 1).

The freshwater gastropod literature also includes instances of thorough systematic work that resulted in the potential for positive conservation outcomes for freshwater gastropods. Recent work on Hydrobiidae by Hershler (Hershler 1994, Hershler and Ponder 1998, Hershler and Liu 2004, Hershler et al. 2007a, b), Ponder (Ponder et al. 1989, 1993, 1994, 1995, 2000, Ponder 1991), and others has resulted in a tremendous expansion of our knowledge of the taxonomy and systematics of

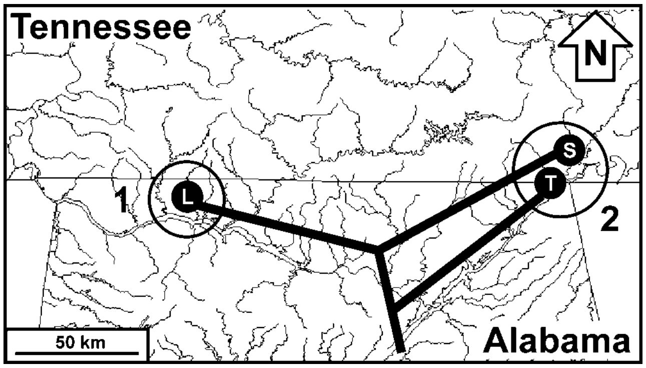


FIG. 1. Conservation management units that do not reflect phylogenetic relationships in the freshwater genus *Athearnia*. Molecular data indicated that US Fish and Wildlife Service management units (numbered) were artificial and grouped distantly related lineages together. Modified from Minton and Savarese (2005). The gray lines are streams. Heavy lines are simplified representations of lineages and their spatial relationships. L = Limestone Creek, S = Sequatchie River, T = Tennessee River.

these species. For example, the status of *Assiminea pecos* Taylor, 1987 was recently reassessed. This species was thought to be rare in the USA, but to include disjunct populations in the Cuatro Ciénegas basin, Coahuila (Mexico). New molecular data have revealed that these disjunct populations represent separate species that are indeed morphologically and conchologically distinct when examined more closely with the aid of scanning electron microscopy (Hershler et al. 2007a). Use of a rigorous systematic framework made it possible to distinguish *Assiminea cienegensis* Hershler, Liu, and Lang, 2007 from *A. pecos* (Hershler et al. 2007a), with the consequence that 2 separate management units were distinguished for conservation.

Historically, most freshwater gastropod names were based on shell morphological characters. Further work has suggested 2 basic problems with this approach to species delineation: 1) the large amount of plasticity in shell characteristics seen in many freshwater gastropods makes taxonomic unit delineation difficult; and 2) this approach has the potential to exclude valid species (e.g., morphologically cryptic species) from definition. Thus, methods in addition to shell morphology must be used to identify species accurately (Mayden 1997, Adams 2001).

Species delineation ideally reflects the systematic affinities of the group in question. For years, taxonomists relied on the biological species concept (BSC), which considers solely the presence/absence of reproductive isolation to identify separate species (de Queiroz 2005a). Some authors continue to use reproductive isolation as their criterion for defining freshwater gastropod taxa (e.g., Dillon et al. 2002). In recognition of the shortcomings of BSC (Wheeler and Meier 2000), lineage-based species concepts, such as the phylogenetic (Cracraft 1983) and unified (de Queiroz 1999, 2005b) species concepts, have gained popularity. Species delineation methods based on these lineage-based concepts are especially useful in instances where definitions based on morphological characters are problematic (e.g., Wilke and Falniowski 2000), as is often the case in freshwater gastropods (applied in: Mulvey et al. 1997, Roe and Lydeard 1998, Holznagel and Lydeard 2000, Lydeard et al. 2000, Roe et al. 2001, Minton and Lydeard 2003). These lineage-based methods treat species as independently evolving units, regardless of the criteria used for their delineation. For conservation purposes, lineage-based methods bring recognition of management units more in line with the subspecies-level approaches of the US Fish and Wildlife Service (FWS) and the International Union for Conservation of Nature and Natural Resources (IUCN 2001).

Recognition of lineages below the species level is an important conservation issue for the USA because the US Endangered Species Act (USFWS 2003) provides protection for invertebrate subspecies but not for distinct populations. In contrast, countries including Australia (Australian Government Attorney-General's Department 1999) and Canada (COSEWIC 2006) extend protection to smaller, subspecific groups. The evolutionarily significant unit (Ryder 1986) is an attractive option to apply when addressing subspecific groups because it relies less on a specific concept and more on recognizing populations that are morphologically and genetically distinct from other similar populations. The questions in all of these cases remain: How much distinction is enough, and how is the distinctness properly gauged in an evolutionary context (Pennock and Dimmick 1997)? Little agreement has been reached on these issues, but most conservation advocates recognize the need for some level of protection at and below the species level.

Regardless of the taxonomic level researchers choose, combining systematic and population genetic data appears to be the best practical approach to delineating conservation management units, with the understanding that flexibility regarding, e.g., organism-specific exceptions and changes, would have to exist. This approach might increase the number of recognized species (e.g., Ponder et al. 1994, Pfenninger and Magnin 2001) and could have consequences for regulation and policy. However, increased objectivity and accuracy in recognition of biodiversity is a benefit of modern systematics, not a drawback (Wheeler and Cracraft 1996, but see Isaac et al. 2004). A lineage-based approach to species delineation accomplishes the overall goal of

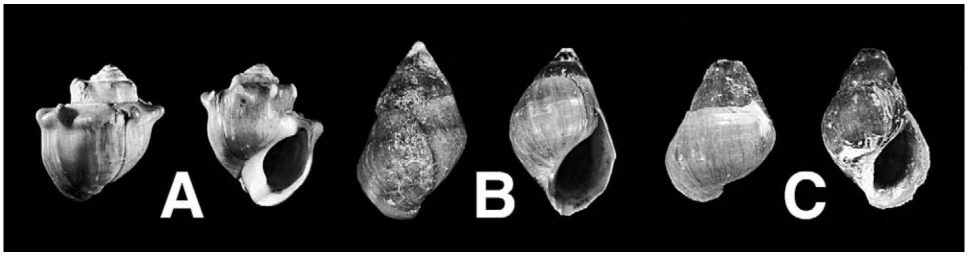


Fig. 2. Shell plasticity in *Lithasia geniculata* from the Duck River. A.—*L. g. geniculata*. B.—*L. g. fuliginosa*. C.—*L. g. pinguis*. Nuclear and mitochondrial data support recognition of a single species (Minton and Lydeard 2003).

defining species scientifically and makes best use of the precautionary principle by minimizing the potential for unintended permanent negative effects of statistical errors (McGarvey 2007). We provide a practical application of this theoretical background below.

## Defining Practical Conservation Management Units—Lessons from Freshwater Gastropods

For most of the past 2 centuries, the identification and classification of freshwater gastropods have been based on morphology, primarily on shared shell characters. Unfortunately, much of this shell-focused evidence is ambiguous when used for species delineation. Ambiguities arise from a lack of uniform data among authors, subjectivity of an author, disagreements over character utility, and explicit or implied species-concept differences (Tryon 1873, Burch 1989, Minton 2002). Different authors rarely provide comparable levels of qualitative and quantitative data in their original descriptions, and often use descriptive terms that have differing interpretations depending on the reader's prior experience (e.g., "tapering" vs "broadly conic"). Some descriptions were based on single shells, juvenile shells, or even partial shells given to the author, and the quality of description varied based on the experience of the author, their understanding of the literature, and the degree of allowable natural variation under the taxonomic philosophy of the time. Though classifications and identification keys exist for many groups (e.g., Burch 1982, Wu et al. 1997, Thompson 1999), they often are difficult for the novice user, and descriptive and diagnostic approaches can be inconsistent among them.

Complete reliance on shell morphology is potentially confounding to systematics and taxonomy because of the tendency of shells to be highly variable and phenotypically plastic. Phenotypic plasticity is well documented in freshwater gastropod shells (e.g., Adams 1900, Heller et al. 2005, Holomuzki and Biggs 2006; Fig. 2) and is seen frequently in response to environmental pressure (DeWitt 1998, Krist 2002, Prezant et al. 2006). However, the amount of shell variation ascribable to local adaptation vs true species-level characters is unknown in most cases. Burch (1982) noted that many generic groups are shell based, and that many historically used characters seem to intergrade at one point or another. Shell morphology also can converge on similar shapes and sculptures in unrelated taxa (e.g., Chambers 1980, Minton and Lydeard 2003, Minton et al. 2003). The persistence of multiple distinguishable phenotypes within species and within populations of species is common in freshwater mollusks (Dillon 1984) and provides evidence that accurate species delineation usually cannot be based on shell morphology alone. Other morphological characters can offer additional insight into correct taxonomic unit assignment. Radula morphology and soft-part anatomical characters, while potentially homoplastic (Schander and Sundberg 2001), have proven useful, when added to shell characters, in classifying some freshwater gastropod groups (Brown and Berthold 1990, Falniowski and Szarwoska 1995) but vary little in others (Dazo 1965, Minton 2002). Detailed modern anatomical treatments have expanded our knowledge regarding the taxonomic and systematic applicability of soft-part structure, function, and homology (e.g., Strong 2003, 2005, Strong and Frest 2007) and have added new informative character sets, such as protoconch and teleoconch morphology (e.g., Thompson 2000, Mihalcik and Thompson 2002). Potentially informative character sets that have not been explored thoroughly for taxonomic utility in freshwater gastropods include body color, gamete recognition, mucus composition, and genetic loci coding for traits under selection or associated with reproduction.

In addition to morphological methods, biochemical and molecular methods have aided our understanding of the diversity of gastropods that exist in North American fresh waters (Raahauge and Kristensen 2000, Mangenelli et al. 2001, Minton and Lydeard 2003, Hershler and Liu 2004). However, opportunities still exist for improvement as new species are described and taxonomic reviews are conducted using traits that are plastic in many species (Cuezzo 2003, Haase 2003, Hovingh 2004) and, as such, are less useful in determining systematic relationships (Backeljau et al. 2001, Dillon et al. 2002, Wullschleger and Jokela 2002, Parmakelis et al. 2003). Immunochemical methods were popular decades ago (Andrews 1964, Burch and Lindsey 1968) and, together with chromosomal studies, are still valuable today (Natarajan et al. 1966, Choudhury and Pandit 1997, Garbar and Korniushin 2003). More recently, these methods have been augmented with data based on allozymes (Viyanant et al. 1988, Bandoni et al. 1995, Dillon and Lydeard 1998, DeVries et al. 2003) and DNA sequence fragments (Davis et al. 1999, Remigio et al. 2001). Additional data have come from the development of amplified fragment length polymorphisms and micro- and minisatellite markers (Emery et al. 2003, de Boer et al. 2004, Miller et al. 2006).

Inclusion of molecular data in taxonomic treatments has led to methods centered on molecule-only identification, such as DNA taxonomy and DNA barcoding (Hebert et al. 2003, Lipscomb et al. 2003, Scotland et al. 2003, Tautz et al. 2003, Blaxter 2004, Hebert et al. 2004, Rubinoff 2006). Discussions on these methods are ongoing, but we choose to follow the reasoning in DeSalle (2006) by endorsing a *total evidenc*e approach to taxonomy, where all available information is used to define conservation management units. New species and redescriptions of species discovered and circumscribed in this fashion are inherently testable scientific hypotheses (Goldstein et al. 2000, Dunn 2003, Hey et al. 2003, Lipscomb et al. 2003, Seberg et al. 2003, Sites and Marshall 2004). This approach probably will increase the effort necessary for identification of species and other conservation management units, but the resulting classifications will be more robust and accurate than in the absence of such effort. Similar approaches have been used with success across invertebrate taxa (Giribet and Wheeler 2002, Bond and Sierwald 2003, Williams et al. 2003, Guralnick 2005, Roe and Hartfield 2005, Hershler et al. 2006, 2007b).

Independent of the methods used for practical identification of conservation units, species delineation, particularly when dealing with narrow-range taxa or taxa of concern, should be done with both the precautionary principle and sound science (McGarvey 2007). Taxonomic oversplitting (Type I error in a hypothesis-testing framework) that results in protection of nondistinctive units has negative political, regulatory, and financial implications. For example, this direction of error could lead to a public perception of scientists as “crying wolf” and potentially wastes limited conservation dollars. However, this risk must be balanced with the fact that the direction of error protects against the permanent loss of evolutionary lineages and processes. Taxonomic undersplitting (Type II error) when a species is endangered, unrecognized, and consequently, unlisted or unprotected has long-term and potentially final consequences (Buhay et al. 2002). A rigorous scientific debate has not been conducted on the amount and direction of error in species delineation methods. For now, taxonomic unit delineation should proceed in a rigorous hypothesis- (Nixon and Wheeler 1992, Wheeler and Platnick 2000) or equivalence-testing framework (McGarvey 2007) that emphasizes precautionary action and minimizes the potential for unintended permanent negative effects of statistical errors.

A famous example of the risk of taxonomic undersplitting can be seen in ongoing discussions on the Alabama sturgeon, *Scaphirhyncus suttkusi* (Williams and Clemmer, 1991). Based on a single-gene data set, the Alabama sturgeon existed in recognition and conservation limbo until inclusive studies ultimately led to its protection (reviewed in Clark 2000). This process has cost US FWS millions of dollars over more than a decade and undoubtedly contributed to the ultimate decline of the species. Hopefully, a similar situation has been avoided in the freshwater mussel genus *Epioblasma*, where limited genetic sampling (Buhay et al. 2002) was unable to reflect evolutionary processes in the group accurately. A thorough treatment of genetic, morphological, and natural history traits (Jones et al. 2006) provided the necessary data to recognize diversity in the genus while providing the basis for future conservation. An example that used a rigorous approach to taxonomy in freshwater gastropods can be found in a recent publication on the Pecos Assiminea (Hershler et al. 2007a). Hershler et al. (2007a) used a lineage-based approach and compared the results of parsimony, neighbor-joining, and likelihood analyses of multiple data sets consisting of shell measurements and mitochondrial cytochrome oxidase subunit I (COI) sequences. Hershler et al. (2007a) roughly timed divergences with geological events and detailed biogeographic hypotheses concerning the groups they delineated. They also provided a thorough description of a new species, *Assiminea cienegensis* Hershler, Liu, and Lang, 2007, including shell and anatomical features, and published it in a peer-reviewed journal. Efforts that take this holistic approach to taxonomic unit designation will allow all workers to move past problems caused by limited data sets and sampling efforts.

## Evolutionary Processes that Complicate Designation of Conservation Management Units

One pressing problem in species delineation of gastropods is accurate recognition of the distinction between population-level processes and species-level differences (Edwards and Beerli 2000, Wiens and Penkrot 2002, Maddison and Knowles 2006). Genetic signatures of population-level processes can be present in sister taxa even several million years after speciation occurred (Thomaz et al. 1996, Arbogast et al. 2002) and have great influence on taxonomic efforts. Taxonomies of recently diverged taxa must consider population-level processes.

Freshwater pulmonate gastropods typically are excellent dispersers; however, the freshwater gastropods that tend to be of conservation concern, such as many hydrobiid and pleurocerid freshwater gastropods, have poor dispersal capabilities and consequently exist in isolated populations. Molecular data have supported this perception of isolation to some degree. Very few pleurocerid or hydrobiid lineages are found across unconnected drainages (e.g., Minton and Lydeard 2003, Perez et al. 2005, Sides 2005). The degree to which upstream and downstream populations within drainages exchange genes is not well documented. Molecular analyses of freshwater gastropod species have indicated deeply divergent intraspecific mitochondrial lineages (Dillon and Frankis 2004, Lee et al. 2007). The most widely accepted explanation for this observed pattern is the population structure and life history of freshwater gastropods. The isolated population structure of these organisms leads to geographically structured genetic variation, which increases effective population size (Wright 1943, 1951, Wakeley 2000). This increase in effective population size is proposed to lead to long-term retention of ancient mitochondrial alleles (up to 20 million y; Thomaz et al. 1996)—well beyond the coalescence times that would be expected from population size and mutation rate. Mutation rates also might be elevated in hydrobiid and pleurocerid groups by up to 8 to 14 base pairs/million y (e.g., in COI of land snails; Thacker and Hadfield 2000, Holland and Hadfield 2002, Rundell et al. 2004). In addition to stochastic elements of population history such as founder events, local extinction, and random genetic drift, adaptive genetic change also could be affecting observations of genetic diversity among closely related species (Goodacre et al. 2006). Other hypotheses that remain untested in freshwater gastropods include the possibilities that mitochondrial evolution in gastropods is exceptionally fast, or that morphs that differentiate in isolated refuges (and are then reunited) produce populations with very divergent mitochondrial lineages (Thomaz et al. 1996).

High levels of population subdivision can produce a pattern of reciprocal monophyly that could be interpreted as species-level differences. Obtaining this pattern is particularly likely when sampling within species from restricted geographic localities (Arbogast et al. 2002). Ideally, dense population-level and geographic sampling combined with use of the appropriate markers could mitigate this situation. This problem might be unavoidable in taxa whose ranges are reduced by human actions. This misleading pattern is particularly likely when data consist solely of mitochondrial DNA sequences because of the smaller effective population size of the mitochondrial genome. A final complication that must be considered is the status of populations that are in the process of speciation, before or after reproductive isolation has evolved. Historical gene flow in recently diverged species is hard to disentangle from recent contact if introgression is possible (Wakeley 1996, Rosenberg and Feldman 2002).

### Providing Conservation Management Unit Information to Those Charged with Conserving

Once the conservation management units are discovered, identified, and studied, the final step in making this information available to those charged with conservation efforts is production of a consistent system of species description, redescription, and classification. This formal presentation of information fixes the scientific name of the organism, its type locality, essential natural history characteristics, both visible (e.g., distribution, morphology, behavior) and invisible (e.g., molecular data), and place among the rest of biodiversity (Dubois and Nemésio 2007). These names represent the management units in conservation plans, and future studies will refer back to the original and subsequent descriptions for basic knowledge of the organisms in question. The current *International Code of Zoological Nomenclature* (ICZN 1999) provides a set of universal guidelines for species description and redescription. When taxonomic workers follow the ICZN, scientists and agency workers are guaranteed to find a consistent minimum suite of information for any taxon. However, problems arise when taxonomic workers provide descriptions that are inadequate or noncompliant with the ICZN or taxonomic consumers fail to incorporate new information at all levels (new species, new name combinations, etc.).

A query for freshwater gastropods on NatureServe (2007) found that slightly >10% (84 of 835) of the nominal freshwater diversity, both native and exotic, in the USA and Canada consists of undescribed species. Most of these taxa are hydrobiids, and most have been identified in gray literature as numbered (1, 2, 3) or lettered (A, B, C) species (e.g., Frest and Johannes 2000). Froese (1999) pointed out the problems with this type of open nomenclature. The generic and species combinations frequently are not unique, and therefore, cannot be used in relational taxonomic databases nor can they be used unambiguously. Nameless species, such as these, thwart efforts to deliver useful information because no permanent label exists to which information can be attached (Froese 1999). Subsequent conservation efforts are hindered by a decreased ability to identify and reference correctly a given unit of diversity. If populations or groups of individuals are thought to warrant taxonomic recognition, researchers should publish their findings with appropriate names and descriptions in peer-reviewed outlets so that their decisions can pass scientific scrutiny. Publication of taxonomic descriptions should be a consideration when funding research because formal taxonomic work can be as beneficial as primary surveys and is rarely supported by the agencies that need this information for effective conservation.

Inconsistent use of names also affects conservation efforts by making information difficult to find. Burch (2001) identified this issue in a critical review of Dillon (2000). Turgeon et al. (1998) provided a list of names that are accepted generally in the field, and we recommend using it as the single starting point for modern nomenclature, while acknowledging that future work probably will change it. Inconsistent use of names also fails to present the most current understanding of a species. For example, recent DNA evidence identified examples where current species- (e.g., Duck River *Lithasia* [Minton and Lydeard 2003]) and genus-level (*Tritogonia* vs *Quadrula* [Serb et al. 2003, Campbell et al. 2005]) designations do not reflect systematic data. Correct species and generic assignments advance conservation goals, and when published, provide testable scientific hypotheses that should be used by the consumers of taxonomic work.

## Recommendations and Future Directions

We have 4 recommendations regarding the roles of systematics and taxonomy in freshwater gastropod conservation efforts. First, we recommend a lineage-based method for defining taxonomic units. Second, we recommend use of a variety of data sources, including morphology, gene sequences, and other natural history characteristics, when defining these units. Data sources should be analyzed in an evolutionary context to reflect evolutionary processes. These taxonomic units can then serve as the basis for in situ and ex situ conservation efforts that preserve ecological and evolutionary processes, as well as individual populations. Third, we encourage authors to follow the ICZN (1999) rules of taxonomy and nomenclature when describing or redescribing species. Any taxonomic revision must include: 1) examination of type material; 2) topotypic material (genetic, anatomical, conchological, life-history), if possible; 3) appropriate genus-level types if higher-level taxonomy is revised; 4) thorough review of museum collections to define species ranges and eliminate erroneous distribution records that could mislead species prioritization. Fourth, we recommend that data dealing with any conservation aspect of an organism be made available through peer-reviewed publications whenever possible. If peer-reviewed publication is not feasible, then we recommend making the information available through other means, such as Internet sources. However, Internet publication is not a viable option for new species descriptions, which must appear in print.

Taxonomic revisions are often a source of frustration for nontaxonomists who use taxonomic information. We recommend that taxonomists make a concerted effort to educate end-users, such as ecologists, conservationists, pest managers, and amateur naturalists, on the value of updated taxonomic information, and that they make this information readily available and useful to end-users through workshops, amateur and professional meetings, and peer-reviewed journals (Godfray 2002). As new data are gathered and new species described, we must update our database of taxonomic knowledge to enable conservation efforts.

These recommendations are generally appropriate for freshwater invertebrates, but we further encourage researchers and agencies to explore the systematics and taxonomy of those gastropod groups that have not been treated in the modern literature. Hydrobiidae (e.g., Hershler 1994, Hershler and Ponder 1998) and Pleuroceridae (e.g., Tryon 1873, Holznagel and Lydeard 2000, Graf 2001) are the 2 largest freshwater gastropod families in North America (Turgeon et al. 1998). Systematic and taxonomic reassessments of these families and smaller families, such as Physidae (Wethington and Lydeard 2007), have been initiated recently. However, many families, such as Valvatidae and Viviparidae, have not been treated comprehensively in decades, if at all. We hope that researchers, agencies, and funding agencies will focus efforts on these understudied, yet important, groups so that conservation efforts can proceed with the most complete understanding possible of natural biodiversity.

## Acknowledgements

The authors thank Ken Brown, Brian Lang, Steve Lysne, and Jeffrey Sides for their contributions to the Freshwater Mollusk Conservation Society (FMCS) gastropod work, and Alan Christian, Caryn Vaughn, David Strayer, and John Harris for organizing and editing this special issue. We also thank Paul Johnson and an anonymous referee whose input contributed greatly to this manuscript. KEP is supported by the Seeding Postdoctoral Innovators in Research and Education fellowship (SPIRE) program at University of North Carolina–Chapel Hill, funded through the Minority Opportunities in Research Division of the National Institute of General Medical Sciences (GM00678) and the laboratory of Cliff Cunningham and Duke Biology Department. RLM is partially supported by Howard Hughes Medical Institute undergraduate science education grants to ULM.

### Literature Cited

ADAMS, B. J. 2001. The species delimitation uncertainty principle. Journal of Nematology 33:153–160.

ADAMS, C. C. 1900. Variation in *Io*. Proceedings of the American Association for the Advancement of Science 49:208–225.

ANDREWS, E. B. 1964. The functional anatomy and histology of the reproductive system of some pilid gastropod molluscs. Proceedings of the Malacological Society, London 36:121–140.

ARBOGAST, B. S., S. V. EDWARDS, J. WAKELEY, P. BEERLI, AND J. B. SLOWINSKI. 2002. Estimating divergence times from molecular data on phylogenetic and population genetic timescales. Annual Review of Ecology and Systematics 33:707–740.

AUSTRALIAN GOVERNMENT ATTORNEY-GENERAL'S DEPARTMENT. 1999. Environment Protection and Biodiversity Conservation Act 1999. Attorney-General's Department, Canberra, Australia. (Available from: http://www.environment.gov.au/epbc/index.html)

AVISE, J. C., AND W. S. NELSON. 1989. Molecular genetic relationships of the extinct dusky seaside sparrow. Science 243:646–648.

BACKELJAU, T., A. BAUR, AND B. BAUR. 2001. Population and conservation genetics. Pages 383–412 *in* G. M. Barker (editor). The biology of terrestrial molluscs. CABI Publishing, Oxon, UK.

BANDONI, S. M., M. MULVEY, AND E. S. LOKER. 1995. Phylogenetic analysis of eleven species of *Biomphalaria* Preston, 1910 (Gastropoda: Planorbidae) based on comparisons of allozymes. Biological Journal of the Linnean Society 54:1–27.

BERRY, K. H., D. J. MORAFKA, AND R. W. MURPHY. 2002. Defining the desert tortoise(s): our first priority for a coherent conservation strategy. Chelonian Conservation and Biology 4:249–262.

BLAXTER, M. L. 2004. The promise of a DNA taxonomy. Philosophical Transactions of the Royal Society of London B–Biological Sciences 359:669–679.

BOND, J. E., AND P. SIERWALD. 2003. Molecular taxonomy of the *Anadenobolus excisus* (Diplopoda: Spirobolida: Rhinocricidae) species group on the Caribbean island of Jamaica. Invertebrate Systematics 17:515–528.

BOWEN, B. W., AND S. A. KARL. 1999. In war, truth is the first casualty. Conservation Biology 13:1013–1016.

BROWN, D. S., AND T. BERTHOLD. 1990. *Lanistes neritoides* (Gastropoda: Ampullariidae) from west central Africa; description, comparative anatomy and phylogeny. Verhandlungen des naturwissenschaftlichen Vereins in Hamburg 31/32:119–152.

BUHAY, J. E., J. M. SERB, C. R. DEAN, Q. PARHAM, AND C. LYDEARD. 2002. Conservation genetics of two endangered unionid bivalve species, *Epioblasma florentina walkeri* and *E. capsaeformis* (Unionidae: Lampsilini). Journal of Molluscan Studies 68:385–391.

BURCH, J. B. 1982. North American freshwater snails. Identification keys, generic synonymy, supplemental notes, glossary, references, index. Walkerana 1:217–365.

BURCH, J. B. 1989. North American freshwater snails. Malacological Publications, Hamburg, Michigan.

BURCH, J. B. 2001. On the genus name *Goniobasis* (*Elimia*—Gastropoda: Pleuroceridae) and other recent nomenclatural inconsistencies. Walkerana 12:97–105.

BURCH, J. B., AND G. K. LINDSEY. 1968. An immunological approach to lymnaeid systematics. American Malacological Union Annual Reports 1968:22–23.

CAMPBELL, D. C., J. M. SERB, J. E. BUHAY, K. J. ROE, R. L. MINTON, AND C. LYDEARD. 2005. Phylogeny of North American amblemines: prodigious polyphyly proves pervasive. Invertebrate Biology 124:131–164.

CHAMBERS, S. M. 1980. Genetic divergence between populations of *Goniobasis* occupying different drainage systems. Malacologia 20:113–120.

CHOUDHURY, R. C., AND R. K. PANDIT. 1997. Chromosomes of three prosobranch gastropods from Viviparidae, Pilidae and Cyclophoridae (Order: Mesogastropoda). Caryologia 50:341–353.

CLARK, J. R. 2000. Endangered and threatened wildlife and plants; final rule to list the Alabama sturgeon as endangered. Federal Register 65:26438–26461.

COSEWIC (COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA). 2006. Guidelines for recognizing designatable units below the species level. Environment Canada, Ottawa, Ontario. (Available from: http://www.cosewic.gc.ca/pdf/assessment_process_e.pdf)

CRACRAFT, J. 1983. The significance of phylogenetic classifications for systematic and evolutionary biology. Pages 1–17 *in* J. Felsenstein (editor). Numerical taxonomy: proceedings of a NATO Advanced Study Institute. NATO Advanced Study Institute Series G (Ecological Sciences), No. 1. Springer-Verlag, Berlin, Germany.

CRANSTON, P. S. 1990. Biomonitoring and invertebrate taxonomy. Environmental Monitoring and Assessment 14:265–273.

CUEZZO, M. G. 2003. Phylogenetic analysis of the Camaenidae (Mollusca: Stylommatophora) with special emphasis on the American taxa. Zoological Journal of the Linnaean Society 138:449–476.

DAUGHERTY, C. H., A. CREE, J. M. HAY, AND M. B. THOMPSON. 1990. Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). Nature 347:177–179.

DAVIS, G. M., T. WILKE, C. SPOLSKY, C.-P. QIU, D.-C. QUI,

M.-Y. XIA, Y. ZHANG, AND G. ROSENBERG. 1999. Cytochrome oxidase 1–based phylogenetic relationships among the Pomatiopsidae, Hydrobiidae, Rissoidae, and Truncatellidae (Gastropoda: Caenogastropoda: Rissoacea). Malacologia 40:251–266.

DAZO, B. C. 1965. The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens*. Malacologia 3: 1–80.

DE BOER, M. G., M. STIFT, AND E. MICHEL. 2004. Two new highly polymorphic microsatellite loci and inadvertent minisatellite loci for *Lymnaea auricularia*. Journal of Molluscan Studies 70:95–96.

DE QUEIROZ, K. 1999. The general lineage concept of species and the defining properties of the species category. Pages 49–89 *in* R. A. Wilson (editor). Species: new interdisciplinary essays. MIT Press, Cambridge, Massachusetts.

DE QUEIROZ, K. 2005a. Ernst Mayr and the modern concept of species. Proceedings of the National Academies of Science of the United States of America 102:6600–6607.

DE QUEIROZ, K. 2005b. A unified concept of species and its consequences for the future of taxonomy. Proceedings of the California Academy of Sciences 56:196–215.

DESALLE, R. 2006. Species discovery versus species identification in DNA barcoding efforts: response to Rubinoff. Conservation Biology 20:1545–1547.

DEVRIES, D. R., D. L. ARMSTRONG, M. TOPOLSKI, W. E. PINE, J. A. JOHNSON, R. A. DUNHAM, L. ROBISON, J. DIBONA, K. NORGREN, P. HARTFIELD, AND S. COOK. 2003. Distribution, habitat use, and genetics of *Tulotoma magnifica* (Gastropoda: Viviparidae). Southeastern Naturalist 2:35–58.

DEWITT, T. J. 1998. Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. Journal of Evolutionary Biology 11: 465–480.

DILLON, R. T. 1984. What shall I measure on my snails? Allozyme data and multivariate analysis used to reduce the non-genetic component of morphological variation in *Goniobasis proxima*. Malacologia 25:503–511.

DILLON, R. T. 2000. The ecology of freshwater mollusks. Cambridge University Press, Cambridge, UK.

DILLON, R. T., AND R. C. FRANKIS. 2004. High levels of mitochondrial DNA sequence divergence in isolated populations of the freshwater snail *Goniobasis*. American Malacological Bulletin 19:69–77.

DILLON, R. T., AND C. LYDEARD. 1998. Divergence among Mobile Basin populations of the pleurocerid snail genus, *Leptoxis*, estimated by allozyme electrophoresis. Malacologia 39:113–121.

DILLON, R. T., A. R. WETHINGTON, J. M. RHETT, AND T. P. SMITH. 2002. Populations of the European freshwater pulmonate *Physa acuta* are not reproductively isolated from American *Physa heterostropha* or *Physa integra*. Invertebrate Biology 121:226–234.

DUBOIS, A., AND A. NEMÉSIO. 2007. Does nomenclatural availability of nomina of new species or subspecies require the deposition of vouchers in collections? Zootaxa 1409:1–22.

DUNN, C. P. 2003. Keeping taxonomy based in morphology. Trends in Ecology and Evolution 18:270.

EDWARDS, S. V., AND P. BEERLI. 2000. Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeography studies. Evolution 54:1839–1854.

EMERY, A. M., N. J. LOXTON, R. STOTHARD, C. S. JONES, J. SPINKS, J. LLEWELLYN-HUGHES, L. R. NOBLE, AND D. ROLLINSON. 2003. Microsatellites in the freshwater snail *Bulinus globosus* (Gastropoda: Planorbidae) from Zanzibar. Molecular Ecology Notes 3:108–110.

ENGSTROM, T. N., H. B. SHAFFER, AND W. P. MCCORD. 2002. Phylogenetic diversity of endangered and critically endangered southeast Asian softshell turtles (Trionychidae: *Chitra*). Biological Conservation 104:173–179.

FALNIOWSKI, A., AND M. SZAROWSKA. 1995. Can poorly understood new characters support a poorly understood phylogeny? Shell-structure data in Hydrobiid systematics (Mollusca: Gastropoda: Prosobranchia: Hydrobiidae). Journal of Zoological Systematics and Evolutionary Research 33:133–144.

FLANAGAN, N. S., R. PEAKALL, M. A. CLEMENTS, AND J. T. OTERO. 2006. Conservation of taxonomically difficult species: the case of the Australian orchid, *Microtis angusii*. Conservation Genetics 7:847–859.

FREST, T. J., AND E. J. JOHANNES. 2000. An annotated checklist of Idaho land and freshwater mollusks. Journal of the Idaho Academy of Science 36:1–51.

FROESE, R. 1999. The good, the bad, and the ugly: a critical look at species and their institutions from a user's perspective. Reviews in Fish Biology and Fisheries 9:375–378.

FUNK, S. M., AND J. E. FA. 2006. Phylogeography of the endemic St. Lucia whiptail lizard *Cnemidophorus vanzoi*: conservation genetics at the species boundary. Conservation Genetics 7:651–663.

GARBAR, A. V., AND A. V. KORNIUSHIN. 2003. Karyotypes of European species of *Radix* (Gastropoda: Pulmonata: Lymnaeidae) and their relevance to species distinction in the genus. Malacologia 45:141–148.

GIRIBET, G., AND W. C. WHEELER. 2002. On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. Invertebrate Biology 121:271–324.

GODFRAY, C. J. 2002. Challenges for taxonomy—the discipline will have to reinvent itself if it is to survive and flourish. Nature 417:17–19.

GOLDSTEIN, P. Z., R. DESALLE, G. AMATO, AND A. P. VOGLER. 2000. Conservation genetics at the species boundary. Conservation Biology 14:120–131.

GOODACRE, S. L., D. THOMAZ, AND E. K. DAVIES. 2006. Mitochondrial gene diversity in *Cepaea*: population structure, history and positive selection. Biological Journal of the Linnean Society 87:167–184.

GRAF, D. L. 2001. The cleansing of the Augean Stables, or a lexicon of the nominal species of the Pleuroceridae (Gastropoda: Prosobranchia) of recent North America, North of Mexico. Walkerana 12:1–124.

GREIG, J. C. 1979. Principles of genetic conservation in relation to wildlife management in southern Africa. South African Journal of Wildlife 9:57–78.

GURALNICK, R. P. 2005. Combined molecular and morphological approaches to documenting regional biodiversity and ecological patterns in problematic taxa: a case study in the bivalve group *Cyclocalyx* (Sphaeriidae, Bivalvia) from western North America. Zoologica Scripta 34:469–482.

HAASE, M. 2003. A new spring snail of the genus *Graziana* (Caenogastropoda: Hydrobiidae) from Switzerland. Journal of Molluscan Studies 69:107–112.

HEBERT, P. D. N., A. CYWINSKA, S. L. BALL, AND J. R. DEWAARD. 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society of London B–Biological Sciences 270:313–321.

HEBERT, P. D. N., M. Y. STOECKLE, T. S. ZEMLAK, AND C. M. FRANCIS. 2004. Identification of birds through DNA barcoding. PLoS Biology 2:1657–1663.

HELLER, J., P. MORDAN, F. BEN-AMI, AND N. SIVAN. 2005. Conchometrics, systematics and distribution of *Melanopsis* (Mollusca: Gastropoda) in the Levant. Zoological Journal of the Linnean Society 144:229–260.

HERSHLER, R. 1994. A review of the North American freshwater snail genus *Pyrgulopsis* (Hydrobiidae). Smithsonian Contributions to Zoology 554:1–115.

HERSHLER, R., AND H.-P. LIU. 2004. Taxonomic reappraisal of species assigned to the North American freshwater gastropod subgenus *Natricola* (Rissooidea: Hydrobiidae). Veliger 47:66–81.

HERSHLER, R., H.-P. LIU, T. J. FREST, E. J. JOHANNES, AND W. H. CLARK. 2006. Genetic structure of the western North American aquatic gastropod genus *Taylorconcha* and description of a second species. Journal of Molluscan Studies 72:167–177.

HERSHLER, R., H.-P. LIU, AND B. K. LANG. 2007a. Genetic and morphologic variation of the Pecos Assiminea, an endangered mollusk of the Rio Grande region, United States and Mexico (Caenogastropoda: Rissooidea: Assimineidae). Hydrobiologia 579:317–335.

HERSHLER, R., H.-P. LIU, AND D. W. SADA. 2007b. Origin and diversification of the soldier meadow springsnails (Hydrobiidae: *Pyrgulopsis*), a species flock in the northwest Great Basin, United States. Journal of Molluscan Studies 73:167–183.

HERSHLER, R., AND W. F. PONDER. 1998. A review of morphological characters of hydrobioid snails. Smithsonian Contributions to Zoology 600:1–55.

HEY, J., R. S. WAPLES, M. L. ARNOLD, R. K. BUTLIN, AND R. G. HARRISON. 2003. Understanding and confronting species uncertainty in biology and conservation. Trends in Ecology and Evolution 18:597–603.

HOLLAND, B. S., AND M. G. HADFIELD. 2002. Islands within an island: phylogeography and conservation genetics of the endangered Hawaiian tree snail *Achatinella mustelina*. Molecular Ecology 11:365–375.

HOLOMUZKI, J. R., AND B. J. F. BIGGS. 2006. Habitat-specific variation and performance trade-offs in shell armature of New Zealand mudsnails. Ecology 87:1038–1047.

HOLZNAGEL, W. E., AND C. LYDEARD. 2000. A molecular phylogeny of North American Pleuroceridae (Gastropoda: Cerithioidea) based on mitochondrial 16S rDNA sequences. Journal of Molluscan Studies 66:233–257.

HOVINGH, P. 2004. Intermountain freshwater mollusks, USA (*Margaritifera, Anodonta, Gonidea, Valvata, Ferrissia*): geography, conservation, and fish management implications. Monographs of the Western North American Naturalist 2:109–135.

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE). 1999. International code of zoological nomenclature. 4th edition. International Trust for Zoological Nomenclature, London, UK.

ISAAC, N. J. B., J. MALLET, AND G. M. MACE. 2004. Taxonomic inflation: its influence on macroecology and conservation. Trends in Ecology and Evolution 19:464–469.

IUCN (INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES). 2001. IUCN Red List categories and criteria. Version 3.1. Species Survival Commission, International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

JOHNSON, P. J. 2003. Sustaining America's aquatic biodiversity. Freshwater snail biodiversity and conservation. Publication 420–530. Virginia Cooperative Extension, Blacksburg, Virginia. (Available from: http://www.ext.vt.edu/pubs/fisheries/420–530/420–530.html)

JONES, J. W., R. J. NEVES, S. A. AHLSTEDT, AND E. M. HALLERMAN. 2006. A holistic approach to taxonomic evaluation of two closely related endangered freshwater mussel species, the oyster mussel *Epioblasma capsaeformis* and the tan riffleshell *Epioblasma florentina walkeri* (Bivalvia: Unionidae). Journal of Molluscan Studies 72:267–283.

KARL, S. A., AND B. W. BOWEN. 1999. Evolutionary significant units versus geopolitical taxonomy: molecular systematics of an endangered sea turtle (genus *Chelonia*). Conservation Biology 13:990–999.

KRIST, A. C. 2002. Crayfish induce a defensive shell shape in a freshwater snail. Invertebrate Biology 12:235–242.

LANG, B., D. KELT, AND S. SHUSTER. 2006. The role of controlled propagation on an endangered species: demographic effects of habitat heterogeneity among captive and native populations of the Socorro isopod (Crustacea: Flabellifera). Biodiversity and Conservation 15:3909–3935.

LEE, T., H. C. HONG, J. J. KIM, AND D. Ó FOIGHIL. Phylogenetic and taxonomic incongruence involving nuclear and mitochondrial markers in Korean populations of the freshwater snail genus *Semisulcospira* (Cerithioidea: Pleuroceridae). Molecular Phylogenetics and Evolution 43:386–397.

LIPSCOMB, D., N. PLATNICK, AND Q. WHEELER. 2003. The intellectual content of taxonomy: a comment on DNA taxonomy. Trends in Ecology and Evolution 18:65–66.

LIU, H., R. HERSHLER, AND K. CLIFT. 2003. Mitochondrial DNA sequences reveal extensive cryptic diversity within a western American springsnail. Molecular Ecology 12: 2771–2782.

LYDEARD, C., A. BOGAN, P. BOUCHET, S. A. CLARK, R. H. COWIE, K. S. CUMMINGS, T. J. FREST, D. HERBERT, R. HERSHLER, K. E. PEREZ, W. F. PONDER, B. ROTH, M. SEDDON, E. STRONG, AND F. G. THOMPSON. 2004. The global decline of nonmarine mollusks. BioScience 54:321–330.

LYDEARD, C., R. L. MINTON, AND J. D. WILLIAMS. 2000. Prodigious polyphyly in imperiled freshwater pearlymussels: a phylogenetic test of species and generic designations. Pages 145–158 *in* E. M. Harper, J. D. Taylor, and J. A. Crame (editors). The evolutionary biology of the Bivalvia. Geological Society Special Publications 177. Geological Society of London, London, UK.

MADDISON, W. P., AND L. L. KNOWLES. 2006. Inferring phylogeny despite incomplete lineage sorting. Systematic Biology 55:21–30.

MANGANELLI, G., M. OLIVERIO, I. SPARACIO, AND F. GIUSTI. 2001. Morphological and molecular analysis of the status and relationships of the land snail *'Cernuella' usticensis* (Calcara, 1842) (Stylommatophora: Helicoidea). Journal of Molluscan Studies 67:447–462.

MAYDEN, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pages 381–424 *in* M. F. Claridge, H. A. Dawah, and M. R. Wilson (editors). Species: the units of biodiversity. Chapman and Hall, London, UK.

MAYDEN, R. L., AND B. R. KUHAJDA. 1996. Systematics, taxonomy and conservation status of the endangered Alabama sturgeon, *Scaphirhynchus suttkusi* Williams and Clemmer (Actinopterygii: Acipenseridae). Copeia 1996: 241–273.

MCGARVEY, D. J. 2007. Merging precaution with sound science under the Endangered Species Act. BioScience 57:65–70.

MICHEL, E. 2004. *Vinundu*: a new genus of gastropod (Cerithioidea: 'Thiaridae') with two species from Lake Tanganyika, East Africa, and its molecular phylogenetic relationships. Journal of Molluscan Studies 70:1–19.

MIHALCIK, E. L., AND F. G. THOMPSON. 2002. A taxonomic review of the freshwater snails referred to as *Elimia curvicostata*, and related species. Walkerana 13:1–108.

MILLER, M. P., D. WEIGEL, AND K. E. MOCK. 2006. Patterns of genetic structure in the endangered aquatic gastropod *Valvata utahensis* (Mollusca: Valvatidae) at small and large spatial scales. Freshwater Biology 51:2362–2375.

MINTON, R. L. 2002. A cladistic analysis of the genus *Lithasia* (Caenogastropoda: Pleuroceridae) using morphological characters. Nautilus 116:39–49.

MINTON, R. L., J. GARNER, AND C. LYDEARD. 2003. Rediscovery, systematics, and re-description of *Leptoxis melanoides* (Conrad, 1834) (Gastropoda: Pleuroceridae) from the Black Warrior River drainage, Alabama, U.S.A. Proceedings of the Biological Society of Washington 116:531–541.

MINTON, R. L., AND C. LYDEARD. 2003. Phylogeny, taxonomy, genetics and global heritage ranks of an imperiled, freshwater snail genus *Lithasia* (Pleuroceridae). Molecular Ecology 12:75–87.

MINTON, R. L., AND S. P. SAVARESE. 2005. Consideration of genetic relationships in management decisions for the endangered Anthony's riversnail, *Leptoxis crassa anthonyi* (Redfield, 1854). Nautilus 119:11–14.

MORITZ, C., AND D. P. FAITH. 1998. Comparative phylogeography and the identification of genetically divergent areas in conservation. Molecular Ecology 7:419–429.

MULVEY, M., C. LYDEARD, D. L. PYER, K. M. HICKS, J. BRIM-BOX, J. D. WILLIAMS, AND R. S. BUTLER. 1997. Conservation genetics of North American freshwater mussels: lessons from the genera *Amblema* and *Megalonaias*. Conservation Biology 11:868–878.

NATARAJAN, R., L. HUBRICHT, AND J. B. BURCH. 1966. Chromosomes of eight species of Succineidae (Gastropoda, Stylommatophora) from the southern United States. Acta Biologica Academiae Scientarium Hungaricae 17: 105–120.

NATURESERVE. 2007. NatureServe explorer: an online encyclopedia of life [web application]. Version 6.1. NatureServe, Arlington, Virginia. (Available from: http://www.natureserve.org/explorer)

NICHOLOPOULOS, J. 1999. The endangered species listing program. Endangered Species Bulletin 24:6–9.

NIXON, K. C., AND Q. D. WHEELER. 1992. Extinction and the origin of species. Pages 119–143 *in* M. J. Novacek and Q. D. Wheeler (editors). Extinction and phylogeny. Columbia University Press, New York.

PARMAKELIS, A., E. SPANOS, G. PAPAGIANNAKIS, C. LOUIS, AND M. MYLONAS. 2003. Mitochondrial DNA phylogeny and morphological diversity in the genus *Mastus* (Beck, 1837): a study in a recent (Holocene) island group (Koufonisi, south-east Crete). Biological Journal of the Linnean Society 78:383–399.

PENNOCK, D. S., AND W. W. DIMMICK. 1997. Critique of the evolutionarily significant unit as a definition for "distinct population segments" under the U.S. Endangered Species Act. Conservation Biology 11:611–619.

PEREZ, K. E., W. F. PONDER, D. J. COLGAN, S. A. CLARK, AND C. LYDEARD. 2005. Molecular phylogeny and biogeography of spring-associated hydrobiid snails of the Great Artesian Basin, Australia. Molecular Phylogenetics and Evolution 34:545–556.

PFENNIGER, M., AND F. MAGNIN. 2001. Phenotypic evolution and hidden speciation in *Candidula unifasciata* spp. (Helicellinae, Gastropoda) inferred by 16S variation and quantitative shell traits. Molecular Ecology 10: 2541–2554.

PLATNICK, N. I. 1991. Patterns of biodiversity: tropical vs. temperate. Journal of Natural History 25:1083–1088.

PONDER, W. F. 1991. The eastern seaboard species of *Jardinella* (Mollusca, Gastropoda, Hydrobiidae), Queensland rainforest-inhabiting freshwater snails derived from the west. Records of the Australian Museum 43:275–289.

PONDER, W. F., G. A. CLARK, A. C. MILLER, AND A. TOLUZZI. 1993. On a major radiation of freshwater snails in Tasmania and eastern Victoria: a preliminary overview of the *Beddomeia* group (Mollusca: Gastropoda: Hydrobiidae). Invertebrate Taxonomy 7:501–750.

PONDER, W. F., S. A. CLARK, AND A. C. MILLER. 2000. A new genus and two new species of Hydrobiidae (Mollusca: Gastropoda: Caenogastropoda) from Western Australia. Journal of the Royal Society of Western Australia 82:109–120.

PONDER, W. F., D. J. COLGAN, G. A. CLARK, A. C. MILLER, AND T. TERZIS. 1994. Microgeographic genetic and morphological differentiation of freshwater snails—the Hydrobiidae of Wilsons Promontory, Victoria, south-eastern Australia. Australian Journal of Zoology 42:557–678.

PONDER, W. F., P. EGGLER, AND D. J. COLGAN. 1995. Genetic differentiation of aquatic snails (Gastropoda: Hydrobiidae) from artesian springs in arid Australia. Biological Journal of the Linnean Society 56:553–596.

Ponder, W. F., R. Hershler, and B. Jenkins. 1989. An endemic radiation of hydrobiid snails from artesian springs in northern South Australia: their taxonomy, physiology, distribution and anatomy. Malacologia 31:1–140.

Ponder, W. F., and D. Lunney. 1999. The other 99%. The conservation and diversity of invertebrates. Transactions of the Royal Zoological Society of New South Wales, Mosman, Australia.

Prezant, R. S., E. J. Chapman, and A. McDougall. 2006. *In utero* predator-induced responses in the viviparid snail *Bellamya chinensis*. Canadian Journal of Zoology 84:600–608.

Raahauge, P., and T. K. Kristensen. 2000. A comparison of *Bulinus africanus* group species (Planorbidae; Gastropoda) by use of the internal transcribed spacer 1 region combined by morphological and anatomical characters. Acta Tropica 75:85–94.

Remigio, E. A., D. A. W. Lepitzki, J. S. Lee, and P. D. N. Hebert. 2001. Molecular systematic relationships and evidence for a recent origin of the thermal spring endemic snails *Physella johnsoni* and *Physella wrighti* (Pulmonata: Physidae). Canadian Journal of Zoology 79:1941–1950.

Roe, K. J., and P. D. Hartfield. 2005. *Hamiota*, a new genus of freshwater mussel (Bivalvia: Unionidae) from the Gulf of Mexico drainages of the southeastern United States. Nautilus 119:1–10.

Roe, K. J., P. Hartfield, and C. Lydeard. 2001. Molecular systematics of the threatened and endangered superconglutinate producing mussels of the genus *Lampsilis*. Molecular Ecology 10:2225–2234.

Roe, K. J., and C. Lydeard. 1998. Molecular systematics of the freshwater genus *Potamilus*. Malacologia 39:195–205.

Rosenberg, N. A., and M. W. Feldman. 2002. The relationship between coalescence times and population divergence times. Pages 130–164 *in* M. Slatkin and M. Veuille (editors). Modern developments in theoretical population genetics. Oxford University Press, Oxford, UK.

Rubinoff, D. 2006. DNA barcoding evolves into the familiar. Conservation Biology 20:1548–1549.

Rundell, R. J., B. S. Holland, and R. H. Cowie. 2004. Molecular phylogeny and biogeography of the endemic Hawaiian Succineidae (Gastropoda: Pulmonata). Molecular Phylogenetics and Evolution 31:246–255.

Ryder, O. A. 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecology and Evolution 1:9–10.

Schander, C., and P. Sundberg. 2001. Useful characters in gastropod phylogeny: soft information or hard facts? Systematic Biology 50:136–141.

Scotland, R., C. Hughes, D. Bailey, and A. Wortley. 2003. The Big Machine and the much-maligned taxonomist. Systematics and Biodiversity 1:139–143.

Seberg, O., C. J. Humphries, S. Knapp, D. W. Stevenson, G. Petersen, N. Scharff, and N. M. Andersen. 2003. Shortcuts in systematics? A commentary on DNA-based taxonomy. Trends in Ecology and Evolution 18:63–65.

Serb, J. M., J. E. Buhay, and C. Lydeard. 2003. Molecular systematics of the North American freshwater bivalve genus *Quadrula* (Unionidae: Ambleminae) based on mitochondrial ND1 sequences. Molecular Phylogenetics and Evolution 28:1–11.

Sides, J. D. 2005. The systematics of freshwater snails of the genus *Pleurocera* (Gastropoda: Pleuroceridae) from the Mobile River Basin. PhD Dissertation, University of Alabama, Tuscaloosa, Alabama.

Sites, J. W., and J. C. Marshall. 2004. Empirical criteria for delimiting species. Annual Review of Ecology and Systematics 35:199–229.

Soltis, P. S., and M. A. Gitzendanner. 1999. Molecular systematics and the conservation of rare species. Conservation Biology 13:471–483.

Strong, E. E. 2003. Refining molluscan characters: morphology, character coding and the phylogeny of the Caenogastropoda (Gastropoda). Zoological Journal of the Linnean Society 137:447–554.

Strong, E. E. 2005. A morphological reanalysis of *Pleurocera acuta* and *Elimia livescens* (Gastropoda: Cerithioidea: Pleuroceridae). Nautilus 119:119–132.

Strong, E. E., and T. J. Frest. 2007. On the anatomy and systematics of *Juga* from western North America (Gastropoda: Cerithioidea: Pleuroceridae). Nautilus 121: 43–65.

Strong, E. E., and M. Glaubrecht. 2003. Anatomy and systematic affinity of *Stanleya neritinoides* (Smith, 1880), an enigmatic member of the thalassoid gastropod fauna from Lake Tanganyika, East Africa (Cerithioidea, Paludomidae). Acta Zoologica 84:249–265.

Tautz, D., P. Arctander, A. Minelli, R. H. Thomas, and A. P. Vogler. 2003. A plea for DNA taxonomy. Trends in Ecology and Evolution 18:70–74.

Thacker, R. W., and M. G. Hadfield. 2000. Mitochondrial phylogeny of extant Hawaiian tree snails. Molecular Phylogenetics and Evolution 16:263–270.

Thomaz, D., A. Guiller, and B. Clarke. 1996. Extreme divergence of mitochondrial DNA within species of pulmonate land snails. Proceedings of the Royal Society of London B–Biological Sciences 263:363–368.

Thompson, F. G. 1999. An identification manual for the freshwater snails of Florida. Walkerana 10:1–96.

Thompson, F. G. 2000. Freshwater snails of the genus *Elimia* from the Coosa River system, Alabama. Walkerana 11:1–54.

Tryon, G. W. 1873. Land and fresh-water shells of North America. Part IV. Strepomatidae. Smithsonian Miscellaneous Collections 16:1–435.

Turgeon, D. D., J. F. Quinn, A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. 2nd edition. Special Publication 26. American Fisheries Society, Bethesda, Maryland.

USFWS (US Fish and Wildlife Service). 1997. Recovery plan for Anthony's riversnail. US Fish and Wildlife Service, Atlanta, Georgia. (Available from: http://www.fws.gov/policy/library/01fr32250.pdf)

USFWS (US FISH AND WILDLIFE SERVICE). 2003. Endangered Species Act of 1973, as amended through the 108th Congress. US Fish and Wildlife Service, Washington, DC. (Available from: http://www.fws.gov/endangered/pdfs/ESAall.pdf)

VANE-WRIGHT, R. I., C. J. HUMPHRIES, AND P. H. WILLIAMS. 1991. What to protect? Systematics and the agony of choice. Biological Conservation 55:235–254.

VIYANANT, V., E. S. UPATHAM, B. L. BLAS, AND H. C. YUAN. 1988. Analysis of allozymes by electrofocusing in shistosome snail hosts (*Oncomelania hupensis*) from China and the Philippines. Malacological Review 20:91–104.

WAKELEY, J. 1996. Pairwise differences under a general model of population subdivision. Journal of Genetics 75:81–89.

WAKELEY, J. 2000. The effects of subdivision on the genetic divergence of populations and species. Evolution 54: 1092–1101.

WALTHER, A. C., T. LEE, J. B. BURCH, AND D. Ó FOIGHIL. *E Pluribus Unum*: a phylogenetic and phylogeographic reassessment of *Laevapex* (Pulmonata: Ancylidae), a North American genus of freshwater limpets. Molecular Phylogenetics and Evolution 40:501–516.

WETHINGTON, A. R., AND C. LYDEARD. 2007. A molecular phylogeny of Physidae (Gastropoda: Basommatophora) based on mitochondrial DNA sequences. Journal of Molluscan Studies 73:241–257.

WHEELER, Q. D. 2004. Taxonomic triage and the poverty of phylogeny. Philosophical Transactions of the Royal Society of London B–Biological Sciences 359:571–583.

WHEELER, Q. D., AND J. CRACRAFT. 1996. Taxonomic preparedness: are we ready to meet the biodiversity challenge? Pages 435–446 *in* E. O. Wilson, M. Kudla-Reaka, and D. Wilson (editors). Biodiversity II: understanding and protecting our biological resource. National Academy of Sciences Press, Washington, DC.

WHEELER, Q. D., AND R. MEIER. 2000. Species concepts and phylogenetic theory. Columbia University Press, New York.

WHEELER, Q. D., AND N. PLATNICK. 2000. The phylogenetic species concept (sensu Wheeler and Platnick). Pages 55–69 *in* Q. D. Wheeler and R. Meier (editors). Species concepts and phylogenetic theory: a debate. Columbia University Press, New York.

WIENS, J. J., AND T. A. PENKROT. 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). Systematic Biology 51:69–91.

WILKE, T., AND A. FALNIOWSKI. 2000. The genus *Adriohydrobia*: polytypic species or polymorphic populations? Journal of Zoological Systematics and Evolutionary Research 39: 227–234.

WILLIAMS, S. T., D. G. REID, AND D. T. J. LITTLEWOOD. 2003. A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. Molecular Phylogenetics and Evolution 28:60–86.

WRIGHT, S. 1943. Isolation by distance. Genetics 28:114–138.

WRIGHT, S. 1951. The genetical structure of populations. Annnals of Eugenics 15:323–354.

WU, S.-K., R. D. OESCH, AND M. E. GORDON. 1997. Missouri aquatic snails. Missouri Department of Conservation, Jefferson City, Missouri. (Available from: http://www.lwatrous.com/missouri_mollusks/)

WULLSCHLEGER, E. B., AND J. JOKELA. 2002. Morphological plasticity and divergence in life history traits between two closely related freshwater snails, *Lymnaea ovata* and *Lymnaea peregra*. Journal of Molluscan Studies 68:1–5.

*Received: 20 June 2007*
*Accepted: 25 January 2008*