Turtle Taxonomy: Methodology, Recommendations, and Guidelines

Turtle Taxonomy Working Group*

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Abstract. – Taxonomy is the logical outcome of systematic research and knowledge; together, taxonomy and systematics form the basis for virtually all research in evolution, ecology, and conservation biology. Turtle taxonomy has been a very active field in the last few decades, particularly as new research has demonstrated that many traditionally recognized higher taxa are not monophyletic and therefore in need of revision. Unfortunately, there has been little consensus on how systematic research should be translated into taxonomic change, leading to a somewhat chaotic situation, with taxonomic and nomenclatural instability and a greatly reduced ability to communicate effectively with taxonomic names. We review the importance of a stable, efficient taxonomy for turtles, both for improved scientific communication and as the legal and scientific foundation of international conservation efforts, and suggest a set of guidelines for researchers to consider when name changes are being considered. These guidelines emphasize the crucial importance of a strong, well-supported phylogeny, clear criteria for species delimitation, and classifications that avoid monotypic higher taxa and unnecessary name changes. Finally, we briefly discuss the Phylocode and DNA barcoding as examples of the new directions in which taxonomy may be moving. We illustrate our points with examples from turtles, and implore the community of turtle researchers and conservationists to work together toward a stable taxonomy that will lead to both strong science and effective conservation.

Key Words. – Reptilia; Testudines; taxonomy; nomenclature; systematics; turtles; Emydidae; *Actinemys*; *Clemmys*; *Emys*; *Emydoidea*; phylocode; DNA barcoding

Taxonomy has been defined as "the naming and assignment of organisms to taxa" (Futuyma, 1998) or "the theory and practice of classifying organisms" (Mayr and Ashlock, 1991). Taxonomy is one of the key elements of the study and protection of biodiversity. In disciplines ranging from conservation biology to biogeography to community ecology, we count, rank, classify, and study organisms and regions based on the names that we give to taxa. Taxonomic names, be they species, subspecies, or more inclusive groups like genera, families, or phyla, are both fluid (that is, they change frequently) and potentially informative. Like any set of names, taxonomies are most useful when the information that they convey is unambiguous, and when they are stable enough that we can use them to communicate that information efficiently. This dual goal, clarity of information content and stability over time, are the cornerstones of effective taxonomies, and in this paper we discuss these and other taxonomic issues with respect to turtles.

Our working group consists of individuals who approach taxonomy from a number of diverse perspectives, including conservation biology, evolutionary and population genetics, paleontology, and systematics. Some of us have proposed and implemented new names for turtles, and others have not. However, all of us have strong views on what names mean, why they are important from our individual research perspectives, and how they should be ap-

plied to turtles. If our group agrees on two things, they are that the names we use for species and higher groups are critically important, and that genetics often has a role to play in helping determine those names.

At the most fundamental level, the importance of taxonomy and nomenclature stems from the simple fact that we all need to communicate effectively if we are to conduct our more specialized research or achieve our management goals. To take one simple example, the western pond turtle ("*Clemmys*" *marmorata*) has been a candidate for listing under the US Endangered Species Act (USFWS, 1992), and the subject of at least one major recent genetic analysis (Spinks and Shaffer, 2005). For decades, the species was classified as *Clemmys marmorata* (Baird and Girard, 1852) in the widely distributed family Emydidae. However, as the genus *Clemmys* has been demonstrated to be paraphyletic (McDowell, 1964; Bickham et al., 1996; Lenk et al., 1999; Feldman and Parham, 2002), the names which have been assigned to the western pond turtle have included *Emys marmorata* (where the genus name *Emys* includes the species *blandingii*, *orbicularis*, and *marmorata*), *Actinemys marmorata* (where *Actinemys* includes only *marmorata*) and *Clemmys marmorata* (where *Clemmys* is retained in its previous usage to include *guttata*, *insculpta*, *muhlenbergii*, and *marmorata*). In this relatively simple case, the names *Actinemys, Clemmys,* and *Emys* lose their utility for communication when different researchers have different concepts of what those names mean. Also, searches of literature databases (e.g. Web of Knowledge) and DNA databases (GenBank) now yield a confusing combination of names that makes access to these important tools increasingly difficult. And perhaps most disturbing from a conservation perspective, regulatory agencies may no longer recognize the taxon as being listed on various protected species lists until the new name can be formally recognized and added to those lists. Although informatics tools are under development to efficiently untangle the confusion that stems from taxonomic instability (Patterson et al., 2006), the ideal solution is a stable taxonomy that enhances communication and information retrieval.

Our goal in this paper is to highlight some of the important issues to consider when thinking about taxonomy and classification, and in particular, when considering formal name changes. We focus on turtles, although most of our points apply equally well to any other group of organisms. One of the most difficult aspects of taxonomy is that it often includes a variety of opinions and points of view. However, for taxonomy to be most effective, a single set of names must be agreed upon and used, and that set should remain reasonably stable within the bounds of gradually expanding knowledge of the particular group of organisms. Although complete consensus among any group of users is probably impossible to achieve, we hope that reasonable agreement is possible, and emphasize its importance

throughout this paper. One clear conclusion from our collective thinking is that taxonomic changes should be considered only when the science indicates that they are absolutely necessary (Dayrat, 2005), and even then, only when some attempt at consensus has been achieved. This approach has not been followed in the recent literature on turtles, leading to a somewhat chaotic taxonomy that neither facilitates communication nor leads to nomenclatural stability.

The Basics:
Species and Subspecies are the Fundamental Units of Systematic Biology

Species. — The species is probably the most important level of classification and is the only level that has been suggested to have biological "reality". An important distinction exists between the conceptualization of species and the methods by which we recognize and delimit those species (de Queiroz, 2005). The biological species concept, or BSC (Mayr, 1963), has been historically important in turtles, and most systematists likely would concur that populations that are reproductively isolated due to the evolution of intrinsic reproductive isolating barriers should be considered as distinct species. Phylogenetic, lineage-based, and genealogical species concepts have been widely applied in the last decade or so, and at least some practitioners now feel that a unified "metapopulation lineage species concept" (that of an evolutionary lineage diverging through time) is broadly applicable as a universal species concept (de Queiroz, 2005). However, a wide range of criteria are used to delimit these lineages (Sites and Crandall, 2004), and accurate species delimitation is critically important to systematics, conservation, and evolutionary studies.

Whatever species criteria are applied to turtles, it is clear that the use of molecular genetic techniques has aided, and will continue to aid, in the identification of new species and the delimitation of existing ones. In a recent review of 12 current methods for delimiting species, Sites and Crandall (2004) noted that all 12 routinely rely on molecular data and at least 7 require it. As our understanding of the number of species of turtles and their geographic distributions improves, our ability to recognize and conserve biodiversity will increase. However, it is important to remember that species recognition is a double-edged sword. While reliable systematics studies based on appropriate data and analyses improves our understanding, poorly conducted studies can set back taxonomic progress and conservation efforts. We encourage chelonian systematists to be thorough in their approach, clear about their methods, and cautious in their conclusions (see also Dayrat, 2005). Studies in which new species are described should state what species concept/criterion is being followed, and be consistent in its application. Ideally, both the concept and criterion should be established *a priori* so that all biologists can evaluate the extent to which the data support a taxonomic

decision and new data can be used to test the hypothesis of species differentiation. We have formulated a set of guidelines that summarize what we consider to be important considerations in new descriptions and renaming of turtle taxa, and present these guidelines under "Guidelines for Best Scientific Practices" (see inset box).

Subspecies. — Subspecies are, at least for metazoans, the least inclusive taxonomic category that is recognized with a formal taxonomic rank. They have been defined as "a named geographic race; a set of populations of a species that share one or more distinctive features and occupy a different geographic area from other subspecies" (Futuyma, 1998).

Subspecies are historically important components of chelonian systematics and taxonomy and as such we are obliged to deal with them. Some systematists (including some of the members of our working group) take the position that this level of classification should be discarded—either a taxon is a diagnosable lineage, in which case it should be formally recognized as a species, or it

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Guidelines for Best Scientific Practices for Revising Taxonomy

Accepting that multiple, scientifically valid philosophies exist with respect to both species and higher taxonomic categories, and that these are not likely to be reconciled any time soon, there are some recommendations that are broadly applicable to taxonomic revisions. We offer the following guidelines to workers in turtle taxonomy; think of them as caveats to keep in mind when embarking on a taxonomic revision.

1. Nomenclatural stability should be maintained as much as possible. Taxonomic changes are inevitable. However, introducing new or unfamiliar names creates a disjunction with the previous literature that leads to reduced, rather than enhanced communication about the contained taxa. For the sake of making information about turtles readily accessible, workers should try to maintain the continuity of turtle nomenclature with previously published literature unless widely supported data demands a change. The naming of new species, the accumulation of many species within a genus, or tentative data suggesting new phylogenetic relationships are not reasons to create new genera, or split up or merge existing ones.

2. Higher taxonomic names should represent monophyletic groups. We recommend that workers should only name higher level taxa that are demonstrably monophyletic, because modern systematics relies on monophyly as the primary criterion for the utility of a clade name. Anagenesis may help guide one on which monophyletic groups to name, but monophyly is the primary criterion.

3. Minimize naming new monotypic higher taxa. Monotypic higher taxa tell us nothing about shared ancestry, and therefore fail to convey interesting aspects of shared biogeography, comparative biology, and evolutionary history. Obviously, many monotypic genera and families are well established for turtles, and we feel that stability is more important than eliminating monotypic groups. In some instances monotypic taxa might be preferable due to uncertainty in their phylogenetic posi-

tions or because the rules of priority would require even more name changes if they were synonomized with their more inclusive sister-taxa. In addition, one must also remember that higher taxa containing a single living species may contain many described fossil species, in which case that taxon is not monotypic.

4. Names should not be changed unless there is *strong evidence* that the existing names do not reflect phylogenetic relationships. Although it may be tempting to name novel nodes recovered from a phylogenetic analysis, new or unfamiliar names can be deleterious to both communication and stability. This is especially true if these names are placed on poorly-supported nodes which are later refuted by additional study. Before naming a node, we recommend that workers consider the support for this node, both from a single data partition (i.e., mtDNA) and across data partitions (nDNA, morphology, behavior, etc.). To ensure stability of a name, workers should strive to seek concordance between independent data sets, with high bootstrap and Bayesian posterior support derived from each data set, before naming a new species or higher taxon.

5. Current taxonomy should be divorced from predictions about future changes in taxonomy. That is, defining a higher taxon and creating a new genus name based on the prediction that additional species will be discovered, and a genus-level name is needed to contain them, is ill advised.

6. New or redefined forms should be integrated into an existing taxonomic hierarchy unless the existing taxonomy is not adequate for the placement of the new form. For example "*Heosemys*" *leytensis* was recently placed into a phylogenetic analysis for the first time (Diesmos et al., 2005). It was found to be separate from other *Heosemys* and sister to the black marsh turtle, *Siebenrockiella crassicollis*. Rather than create a new monotypic genus, Diesmos et al. (2005) expanded *Siebenrockiella* to indicate that the two species form a clade.

is not, and should not be recognized with a name. However, other members take the view that subspecies classification can be useful and informative for delineating regional morphotypes that may fail to meet the criteria of full species under certain concepts.

We propose that subspecies classification, if used, should describe the major patterns of variation found within a species. A precise definition of "major" is elusive, but the formal subspecific description of small, isolated populations, particularly in low-vagility species, should be avoided unless there is strong reason to do otherwise. This could avoid the proliferation of named forms of small, isolated populations such as occurred with pocket gophers in western North America (Smith and Patton, 1988). However, the recognition of genetically divergent populations can have real value, and recognizing such populations as subspecies may be useful in some cases. For example, recognition of subspecies in the western USA salamander *Ensatina escholtzii* has been a key element of its interpretation as a ring-species in the midst of the speciation process (Wake, 1997, but see Highton, 1998). Among chelonians, the continued subspecific classification of Galapagos tortoises (*Geochelone nigra* ssp.) has focused attention on this insular radiation as an ongoing case study in speciation and adaptive radiation (Caccone et al., 1999, 2002; Beheregaray et al., 2004).

Genetic tools and datasets have been applied to problems at the intraspecific level, and at this point may represent the most important data for the recognition of intraspecific variation. For example, phylogeographic studies, employing mitochondrial DNA (mtDNA) and/or nuclear DNA (nDNA) sequences taken from geographically defined populations, can identify geographically restricted lineages that become candidates for subspecific recognition (Lenk et al., 1999; Engstrom et al., 2002; Starkey et al., 2003; Fritz et al., 2005; Spinks and Shaffer, 2005). Such studies can also reveal the presence of cryptic species or intraspecific groups like stocks, distinct population segments, evolutionarily significant units, or subspecies. What to call such differentiated populations will be determined by a number of factors including the level or degree of genetic differentiation (genetic distance) and the systematic philosophy of the investigator. In addition, a growing body of literature suggests that single gene analyses can often be misleading, and particular care should be taken when relying primarily on mtDNA (Funk and Omland, 2003). For this paper, suffice it to say that it may be appropriate to name subspecies of turtles where phylogeographic analyses indicate genetically differentiated populations that do not meet the requisites of species distinction, but whose recognition would aid in delineating the pattern of geographic variation within the species.

In summary, we recognize that both the "subspecies concept" and its use in systematics are controversial, and we do not seek here to resolve this controversy, even among our working group members. Rather, we emphasize that subspecies, if used, should convey real evolutionary information about lineages and geography, and must be based on field-collected specimens, adequate geographic sampling, appropriate statistical analyses of variation, and data that are reported in the primary literature and can be replicated by other researchers.

Higher Taxonomic Groups and How They Translate Into Taxonomies

Traditionally, species are grouped into genera, and genera into families; we term these collections of species "higher taxonomic groups". Generally, higher taxonomic groups are, or should be, based on phylogeny. Our understanding of turtle phylogeny is currently incomplete and changing rapidly, and future revisions of higher taxonomic groups are inevitable.

Virtually all workers agree that higher taxonomic groups should be monophyletic, and non-monophyletic groups are viewed as a problem to be fixed with taxonomic changes. However, the way in which a large, inclusive monophyletic group (like turtles, for example) should be divided into less inclusive monophyletic groups can be quite contentious. Within the turtle community, there are two distinct schools of thought guiding the creation of higher level names (we focus on genera in this discussion). The first is based on the view that genera should convey a certain level of evolutionary distinctiveness (Simpson, 1961). We call this view the 'anagenetic' perspective (anagenesis being defined as the "evolution of a feature over an arbitrary period of time"; Futuyma, 1998). The second emphasizes the utility of genera (and all other higher taxonomic names) to show hierarchical relationships only; we call this the 'phylogenetic' perspective (Hennig, 1966). The general practice in systematics has clearly moved toward the phylogenetic perspective (e.g., Cracraft and Donoghue, 2004), at least to the extent that all higher groups should be rendered monophyletic whenever possible, and we assume that most practicing turtle systematists use phylogenies as a guide in their higher-level taxonomic decisions.

However, even when all parties agree that monophyletic groups are important, there are fundamental differences between the anagenetic and purely phylogenetic viewpoints that can lead to conflicting taxonomic schemes. For example, under the anagenetic perspective, a well-accepted monophyletic genus could be split into many genera if subclades within that genus were deemed to be distinct enough. Such genera might contain one species or multiple species, but the decision on the number and content of genera would be based on their level of differentiation (genetic, morphological, or some other set of features). Under the phylogenetic perspective, the only compelling reason to split an existing genus is strong evidence that it is not monophyletic. The phylogenetic perspective claims that any measure of evolutionary distinctiveness is subjective, as indicated by the varying levels of distinctiveness that exist among animal genera (including turtles).

A few turtle examples illustrate these differences. In determining how to reclassify the apparently non-

monophyletic genus *"Clemmys,"* Holman and Fritz (2001) noted that "In all cladograms derived from molecular data, *Clemmys marmorata* is closer to the genera *Emys* and *Emydoidea* (taxa that have a plastral hinge) than to the hingeless *Clemmys guttata, C. insculpta*, and *C. muhlenbergii…* The most parsimonious nomenclatural way to resolve this situation is to put *C. marmorata* in a monotypic genus to avoid combining hinged and nonhinged species in a single clade. For this genus the name *Actinemys* Agassiz, 1857 is available" (p. 323). The reasoning behind this decision reflects the anagenetic view that the evolution of a plastral hinge (or the secondary loss of the hinge, as suggested by Holman and Fritz, 2001) is an important, genus-level character, and that hinged and non-hinged species should not be combined in the same genus. They used this reasoning as the primary justification for the recognition of *Emys, Actinemys,* and *Emydoidea* as genera, even though each contained only a single living species (*Emys trinacris* was described later, in Fritz et al., 2005). However, the plastral hinge varies within species of other turtles (Parham and Feldman, 2002; Chiari et al., 2005), leading other authors to conclude that the plastral hinge should not be viewed as a generic level character, and that a more informative taxonomy results if the clade containing the species *marmorata, orbicularis,* and *blandingii* is recognized as the genus *Emys*. Similar arguments hold for genetic data. For a given gene such as the widely used mitochondrial cytochrome *b* (cyt*b*), an anagenetic perspective might argue that there is a consistent percentage of sequence divergence among sister genera within a family, and divide existing monophyletic genera based on large levels of sequence divergence. The more purely phylogenetic view would emphasize that there is no single "genus level" of divergence for turtles, and therefore levels of divergence *per se* should not guide taxonomic decisions over the number and content of genera. For example, map turtles (*Graptemys*) and diamondback terrapins (*Malaclemys*) are sister genera that are less than 2.3% divergent for cyt*b* (Lamb and Osentoski, 1997), whereas average cyt*b* divergence among sister genera of softshell turtles (*Apalone* and *Rafetus*) is 13.4% (calculated from data in Engstrom et al., 2004).

One natural outcome of the phylogenetic view is that monotypic genera (and families) are largely uninformative, since they tell us little about phylogenetic relationships—in that sense, they are redundant with the fact that the contained single taxon is a species (Parham and Feldman, 2002; Spinks et al., 2004). Alternatively, the anagenetic view claims that monotypic genera and families are sufficiently distinct that they should be named, and that avoiding them obscures important evolutionary distinctiveness of some lineages. Extinct lineages add yet another dimension to this issue, because the fossil record indicates that many living monotypic groups are the lone survivors of more-diversified clades from the past (Carettochelyidae, Dermochelyidae, Dermatemydidae, and Platysternidae are all family-level examples, and *Emydoidea, Trionyx,* and *Erymnochelys* are examples at the genus-level). In such cases, these higher taxa are not monotypic, although their living representatives consist of a single species.

Guidelines for Taxonomic Changes

Like it or not, taxonomic change is an inevitable part of phylogenetic research; this is true for turtles as well as any other group. Taxonomic and associated nomenclatural changes are the logical result of advances in systematic biology. However, new insights into phylogenetic relationships can lead to a variety of taxonomic changes, including no change at all. In this section, we provide some guidelines on when, and how, to bring about taxonomic changes in turtles. We break the discussion into two related parts: a brief discussion of the more formal 'rules' governing nomenclatural changes, and what we consider to be 'best scientific practices' on how to proceed when one must propose a taxonomic change, given the systematic conclusions (see also Dayrat, 2005). In all cases, we hope that all researchers proposing changes will value the balance of communicating the newest taxonomic and/or phylogenetic results with the need to try to maintain stability of names.

The Rules of Nomenclatural Changes

In principle, taxonomic changes are based on an objective review of all available evidence and a solid theoretical foundation. In practice, however, there is no universal agreement on systematic theory, and little consensus on how phylogenies translate into names. In general, the informal rule in taxonomy is that the latest published revision is valid until refuted. Unfortunately, this rule is not always realistic or followed—some published revisions may be known to be incorrect, but rigorous refutation often requires as much or more time and effort than the original study did, rendering correction a slow process. An important consideration for all taxonomists is that taxonomy has acquired importance beyond the biological sciences; conservation actions, legislation, and public awareness do not have the understanding, interest, tolerance, or time required to stay updated on taxonomic developments, but instead risk being confused or hindered by scientific name changes and unclear taxon definitions. It is also important to recognize that some taxonomic revisions are published based on inadequate data and/or incomplete descriptions, and we tend to view them as hypotheses to be tested, rather than changes to be accepted. It is to recognize and perhaps define such cases that we emphasize the following rules:

1. Proposed nomenclatural changes must be in accordance with the regulations set forth in the most recent edition of the International Code of Zoological Nomenclature (ICZN) (http://www.iczn.org/iczn/index.jsp).

2. Taxonomic and associated nomenclatural changes should be published in widely-available, peer-reviewed scientific publications that are indexed in the Zoological Record. Peer-reviewed publications are defined as publications that regularly publish the names of their editorial review board and external reviewers. A widely available publication is defined as a publication that is open to public subscription and purchase of individual issues, and which makes reprints of its contained articles available in paper and/or electronic format for authors to distribute person-to-person upon request. Obviously, "widely-available, peer-reviewed scientific publications" are somewhat subjective terms, and the ICZN is not strict on these issues. We strongly recommend that only peer-reviewed scientific journals that are available at libraries and other institutions be considered appropriate outlets for taxonomic changes. We also recommend that these journals be accessible through the major scientific on-line search engines whenever possible.

3. The taxonomic and/or species concept and criteria used to identify taxa should be clearly indicated in the publication, and the methodology used should be clearly and fully described. The methodology should be appropriate to the taxonomic group under investigation, and should ideally include a wide range of approaches (e.g., morphological, genetic, behavioral). Methods and results should be fully presented, and taxonomic conclusions must be solidly based on these results.

Proposed taxonomic changes that meet the three criteria above are more likely to be accepted into wide usage. Proposed taxonomic changes that do not fully meet all three criteria should probably not be adopted without additional independent research and debate. Until such time, the previous, 'traditional' taxonomic arrangement should probably be retained for practical purposes.

There are no simple formulas or rules for making taxonomic revisions. However, we hope that workers will take these guidelines into consideration before proposing changes. Ideally, workers would explicitly address all of these issues as part of their justification for proposed taxonomic changes.

Why it Matters:
The Relationship Between Taxonomic Decisions and Conservation Effects

Taxonomy is the logical outcome of systematic research, and conservation must be based on and guided by the best-available taxonomy. In this sense, taxonomy (and systematic biology) assumes a critical role in guiding the management of species at risk, and 'getting the taxonomy right' is essential (Lovich and Gibbons, 1997). This is particularly critical at the species level, since it is a major focus of conservation actions. It is just as harmful to not recognize distinct species that exist in nature as it is to incorrectly recognize taxa that do not exist in nature—the former can lead to extinction due to neglect, whereas

the latter can lead to the squandering of conservation resources on invalid taxa. We discuss these and other issues below.

The Focus of Conservation on Species. — In the realm of conservation, including conservation-related legislation in many countries, the basic unit is usually the species. Most regulatory agencies focus on the species-level unit, with subspecies or other less inclusive but diagnosable lineages (Evolutionarily Significant Units, Distinct Population Segments, etc.) considered to be of lesser or no importance. The level of concern directed at sub-specific taxa or lineages varies greatly across the world, with most nations and inter-governmental organizations (e.g., CITES, IUCN, FAO, CBD, CMS) paying little or no attention to any taxonomic units below the level of species. In the USA and some other countries, mechanisms exist to recognize and address conservation needs of lower taxonomic units. However, rightly or wrongly, sub-specific classification units garner proportionally less emphasis than do species. Similarly, supra-species classification units such as genera, families, and orders, are rarely taken into account by regulatory processes, although some conservation value is placed on species contained in monotypic higher taxa compared to species in polytypic genera and families (which further emphasizes that monotypic taxa should not be created arbitrarily).

Recognizing that conservation and legislative priorities focus on the species level, it is particularly important that thorough evaluations of potentially distinctive forms below the species level are carried out to ascertain whether they may warrant recognition as species. Parallel efforts should also be made to encourage the conservation and regulatory communities to encompass intra-specific units within their scope of activities. For example, IUCN is moving towards regional evaluations of taxa to facilitate regional conservation efforts, but remains focused on the species level.

Taxonomy Driven by Politics and Opportunism. — Recognizing species diversity is a fundamental requirement for conservation actions. The importance of conservation and management as a motivation for taxonomic revision at the species level is often recognized in the scientific literature, and has been taken to extremes by some taxonomists. As global biodiversity loss rose to the top of the global environmental agenda during a period of economic constraints, declining scientific and conservation funding was re-focused onto biodiversity conservation at the expense of traditional museum-based taxonomy. Predictably, taxonomy redefined itself to some extent as "biodiversity research". During the same period, theoretical developments in systematics led many taxonomists to abandon the traditional biological species concept, and adopt phylogenetic/evolutionary species concepts (Frost and Hillis, 1990). An ideological dislike for the concept of subspecies developed, with the logical result that if a taxon was recognizably different and perceived to be on an independent evolutionary path, some authorities 'automatically' regarded it as a distinct species (Collins, 1991; Grismer, 1999).

In cases that can be interpreted and justified either way (lumping or splitting at the species or subspecies ranking), some conservation-oriented biologists may find it tempting to err on the side of splitting or elevating a taxon, presumably because a higher-ranked or more diverse taxon could garner additional scientific and conservation attention. Finely-split taxa also are more likely to be endemic to a single political jurisdiction, rendering them easier to protect and manage.

There are dangers inherent to proposing, supporting, or retaining exaggerated taxonomy. Taxonomy is a public science, and subject to more intense peer scrutiny than many other branches of the biological sciences. On the one hand, fellow taxonomists understand and sympathize with taxonomic decisions made in good faith based on best available information and a solid theoretical framework, even when subsequent data and/or improved theoretical understanding later demonstrate these decisions to have been inappropriate. Recent cases include the recognition, based on subsequent genetic data, that a number of recently-described Asian geoemydid turtles were actually human-created hybrids rather than valid species (Parham et al., 2001; Spinks et al., 2004; Stuart and Parham, 2007). On the other hand, taxonomists who knowingly employ doubtful taxonomic practices or incomplete datasets degrade taxonomy and run the risk of being seen as less than objectively scientific by their colleagues, the general public, and legislative and regulatory authorities. We cannot emphasize enough the importance to conservation of bringing the strongest, most objective science possible to the table when taxonomic decisions are being made. In addition, it is critically important that when doubt exists over the validity of taxa that are receiving conservation attention, the best available taxonomic tools, which are likely to be genetic, should be brought to bear to help resolve these issues. Examples of such taxa might include the Plymouth red-bellied turtle (*Pseudemys rubriventris "bangsi"*; Iverson and Graham, 1990) and the Cat Island slider (*Trachemys terrapen "felis"*; Seidel and Adkins, 1987). Other entire clades that receive high conservation priorities remain in need of further work on species boundaries; the Asian box turtles (*Cuora*) are a case in point (Parham et al., 2001; Spinks and Shaffer, 2007).

Taxonomy and Legislation. — Regulatory authorities (and non-systematist conservationists) abhor changes to the names of taxa. Taxa of conservation and regulatory interest are usually managed from codified lists; altering the names on such a list is often a slow, laborious, and convoluted process, sometimes requiring parliamentary approval and lengthy delays. In some legislative processes, a taxonomic definition is given when including a taxon in a list. When systematic progress changes the taxon name or scope, the original intent and definition of the taxon remain subject to the regulation. For example, the genus *Podocnemis* was listed under CITES Appendix II in 1975 (http://www.cites.org/eng/app/appendices.shtml). When subsequent taxonomic revision split *Podocnemis* into *Podocnemis* plus *Peltocephalus* plus *Erymnochelys*, these names were 'automatically' included in the same list (Inskipp and Gillett,

2005). Alternatively, if genus A is listed in CITES, but genus B is not, and taxonomic research shows that genus B is a member of genus A, then the species originally included in genus B are not automatically included in CITES. For example, the keeled box turtle was long known as *Pyxidea mouhotii* but recently shifted to *Cuora* (Honda et al., 2002). The entire genus *Cuora* was listed in CITES in 2000, when nine species were recognized and before *mouhotii* was transferred out of *Pyxidea*. If *Pyxidea mouhotii* had not been listed independently in 2002, then *Cuora mouhotii* would not have been included in the CITES listing.

In most jurisdictions, a listed species is not defined; rather, the taxonomic name is a placeholder for the biological entity that is being listed. If that listed species name is changed by scientific revision, existing legislation may no longer protect the biological entity that was originally intended. This is certainly a problem for nomenclatural name changes, as when a listed species changes genus (e.g., the shift of *Trionyx swinhoei* to *Rafetus swinhoei*, Meylan, 1987), and this may require changes in legislation to clarify the transfer of legal protection. An even greater problem exists for cases where an existing species is split into two or more sibling species. For example, recent taxonomic analysis of *Malayemys subtrijuga* identified two distinct taxa, *M. subtrijuga* and *M. macrocephala* (Brophy, 2004). *Malayemys subtrijuga* was already listed as protected in Thailand, however, *M. macrocephala* will not be protected there until the Thai Wild Animals Reservations and Protection Act is amended to include that name. Other countries address taxonomic/nomenclatural change by including additional new names for existing taxa, in effect making the law a list of synonyms. Indian legislation would, for example, name *Cyclemys mouhotii*, *Pyxidea mouhotii*, and *Cuora mouhotii* in its list of protected species.

In summary, we recognize that taxonomic changes are necessary as our understanding of the evolutionary history and diversity of turtles matures, and some changes are both necessary and desirable. However, taxonomic changes also lead to confusion, a lack of ability to communicate effectively, and unanticipated changes in conservation status and international protection. There is value to increased taxonomic understanding, and with it comes the necessity for nomenclatural change, and we provide some guidelines on when to implement such changes. However, in today's world, where a species' name has implications far beyond the traditional biological scientific community, it is imperative that systematists also remember the wider implications of their taxonomic and nomenclatural decisions.

The Future of Taxonomy?
Rank-Free Classification, the Phylocode, and DNA Barcoding

We end our discussion with a description of two new directions in taxonomy that purport to solve many of the problems inherent with our current way of conducting taxonomic research. Each has strong advocates and equally

strong detractors. In presenting them, the TTWG takes no position on them, since we have members who span the range of opinions on these topics. However, in the spirit of keeping abreast of new developments in the field, we present them as important future directions in taxonomy.

Rank-Free Classification and Phylocode. — Within the general systematics community, there is now broad consensus that classifications above the species level should be based on monophyletic groups (defined as an ancestor and all of its descendant taxa). In this sense, the majority of current systematists, including most turtle systematists, embrace the idea that classifications should be phylogenetic.

Although the monophyly criterion represents one of the most broadly agreed-upon concepts in current systematics, the concept of a stable, monophyly-based classification is often at odds with Linnaean, or rank-based classification methods. As pointed out by de Queiroz and Gauthier (1990, 1992, 1994), rank-based methods of classification are typological—a type specimen is assigned to define a species, and a higher taxon is defined with reference to a type species. Although this approach to naming genera, families, and other rank-based higher taxa has been in effect for over 200 years, it leads to a number of undesirable features as systematists attempt to create phylogenetic classifications (de Queiroz and Gauthier, 1990, 1992, 1994). Primary among these features are: 1) instability of names, 2) either poorly defined higher taxa or changes in the definition of a named taxon over time, and 3) a tendency for taxa to become monotypic with revision. Several of these problems have become quite severe in turtle classification. For example, using the checklist compiled for this volume of the world's turtles (Turtle Taxonomy Working Group, this volume), the number of species per genus overall now stands at between 3.05 and 3.48 (depending on how certain contentious genera are resolved); within the Pleurodira, that number is 3.74-5.0, while the Cryptodira have 2.86–3.16 species per genus on average. Perhaps more telling, the number of monotypic genera (that is, genera that contain only a single species) now stands at about 45% (range is 40–46% depending on taxonomy), or nearly half of the ca. 100 recognized turtle genera.

The reason for this largely stems from the consequences of applying the Linnaean rank-based system to phylogenetic classifications. For example, when a genus is found to have another genus nested within it, then either the nested genus must be synonymized into the more inclusive one, or the more inclusive genus must be split into several smaller genera.

Recent work on the old genus "*Clemmys*" demonstrates this point. Phylogenetic analyses (Bickham et al., 1996; Lenk et al., 1999; Feldman and Parham, 2002) have demonstrated that the four species that previously comprised the genus "*Clemmys*" (*guttata, muhlenbergii, insculpta,* and *marmorata*) are paraphyletic with respect to *Emydoidea*, *Emys*, and *Terrapene* (Fig. 1A). Given that these latter three genera cannot be contained within the genus "*Clemmys*" under the Linnaean rank-based system, some taxonomic change is required. One suggested solution (Fig. 1B) has been to resurrect two old genera (*Actinemys* and *Glyptemys*) to accommodate three species (*Actinemys marmorata, Glyptemys insculpta, G. muhlenbergii*), and leave *guttata* in the now-monotypic genus *Clemmys* (Holman and Fritz, 2001). Although all genera under this solution are monophyletic, it results in five genera to contain a total of seven living (and two fossil) species. If one of the goals of higher-level taxonomy is to convey phylogenetic information about how species are related (the phylogenetic view of taxonomy discussed above), this solution is at odds with that stated goal. Interestingly, it appears to also be at odds with the anagenetic goal; if *marmorata* and *guttata* are sufficiently distinct to be placed in different genera, why were they originally placed in the same genus? Another, recently proposed alternative by Feldman and Parham (2002), would recognize the monophyly of *blandingii, marmorata,* and *orbicularis* in the more inclusive genus *Emys* by relegating the old genus *Emydoidea* to the synonymy of *Emys* and shifting *marmorata* from *Clemmys* to *Emys* (Fig. 1C, Fig. 2). The final alternative, to include all species previously assigned to *Emys, Emydoidea, Clemmys*, and *Terrapene* to a single genus has not been seriously proposed because of the number of name changes it would entail. While each of the first two solutions is justifiable and has its proponents (e.g., Stephens and Wiens, 2003; Spinks and Shaffer, 2005), the primary point is that both require a substantial set of nomenclatural changes purely as a consequence of Linnaean ranks. If the names *Emys, Emydoidea,* and *Clemmys* were not of equal rank, then no name changes would necessarily be required as phylogenetic resolution continues to improve.

As a radical solution to this and other problems stemming from the Linnaean rank-based system, an alternative scheme has evolved over the last 10 years known as the Phylocode (http://www.ohiou.edu/phylocode/). Although the details of Phylocode are still being worked out, the system has reached a relatively mature state, with a codified set of standards for naming taxa at all levels in the hierarchy of life. Essentially, Phylocode proposes that taxa be defined with reference to a phylogenetic tree, rather than with respect to type specimens. It also proposes that ranks (but not named groups) be abandoned, since they are a primary source of instability in the Linnaean system. Thus, a named taxon might be defined as "the monophyletic group defined by the most recent common ancestor of an eastern box turtle (*Terrapene carolina*) and a painted turtle (*Chrysemys picta*), and all species derived from that ancestor", and it might be called Emydidae. Using such a definition, Emydidae will always be monophyletic—it has to be, since its very definition is based on monophyly. As a consequence, two important aspects of a named taxon—definition and monophyly—remain stable under Phylocode. However, the content of a group may change as phylogenetic hypotheses change. In the above example, based on the current state of knowledge,

Emydidae would contain 48 species (as noted in our other chapter in this volume, Turtle Taxonomy Working Group, 2007). If subsequent research demonstrated unequivocally that the eastern box turtle and the painted turtle were sister species (an unlikely result, obviously), then Emydidae as defined would consist solely of those two species. The definition would remain unchanged, and Emydidae would still be monophyletic, but its content would be quite different.

One of the natural (but not absolutely essential) consequences of the phylogenetic method of naming taxa embodied in the Phylocode is to abandon ranks. It is important to be clear on exactly what this means, and the costs and benefits of Linnaean ranks in a phylogenetic context. The greatest downfall of ranks is clearly demonstrated in the "*Clemmys*" example (Fig. 1). Because *Emydoidea* and *Clemmys* are both genera, the discovery that the former is nested within the latter (Fig. 1A) means that a nomenclatural change must follow—either *Emydoidea* must be synonymized (Fig. 1C), or *Clemmys* must be divided into additional genera (Fig. 1B). Whatever solution one chooses demands multiple name

changes and taxonomic destabilization; the sole reason for those changes is the identical rank of *Emydoidea* and *Clemmys*.

Under a rank-free system, different nodes can be named (or not), and authors can use the full list of names associated with a terminal species (or not). Thus, if *Clemmys* were defined as "the group containing the most recent common ancestor of the terminals *guttata* and *orbicularis* and all of its descendants", and *Emys* were defined as "the group containing the most recent common ancestor of the terminals *orbicularis* and *marmorata* and all of its descendants", this would imply (given our current phylogenetic understanding) that *marmorata* is a member of both *Emys* and *Clemmys* at different phylogenetic levels. Because these are rank-free names, there is no conflict in one being nested within the other, and there are no necessary name changes if future phylogenetic research implies a different set of relationships. The same principle holds for all taxonomic levels.

Rank free classifications following the Phylocode have been proposed several times for turtles in the literature to date. The first was by Joyce et al. (2004) who used 25
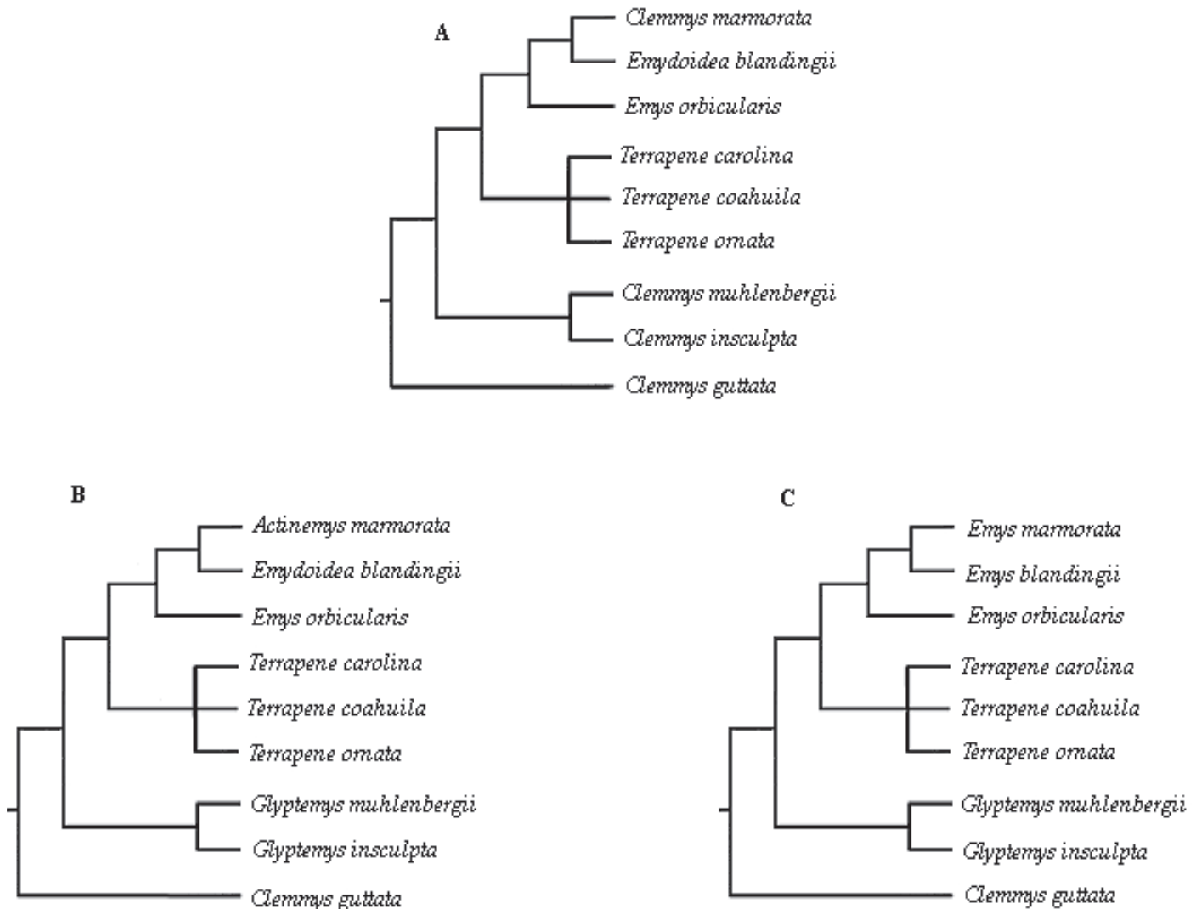

Figure 1. A current phylogeny of ten species of emydine turtles, and three alternative taxonomic schemes (after Feldman and Parham, 2002). The recently-named *Emys trinacris* (Fritz et al., 2005) is not shown, since it was not described at the time that this tree was developed; it would presumably be the sister species to *orbicularis*. Panel A shows the previously-used names, and the paraphyly of the old name "*Clemmys*" as applied to the four species *guttata, insculpta, marmorata,* and *muhlenbergii;* virtually all systematists recognize that this non-monophyly requires taxonomic changes. Panel B solves this problem by proposing two new generic names, leading to a total of three name changes and three monotypic genera, whereas Panel C solves the same problem by proposing a total of four name changes and one monotypic genus. See text for details.

relatively inclusive clades (down to the Linnaean rank level of family) of turtles as a test case to explore the challenges of converting well-established rank-based names into a rank-free taxonomic system. As an example from the other end of the phylogenetic spectrum, Engstrom et al. (2004) proposed a rank-free classification for the 26 species of softshell turtles (the traditional family Trionychidae) based on their molecular and morphological phylogenetic analysis. These two examples span a broad range of taxonomic levels, and deal with the challenges inherent in switching to a rank-free classification.

Figure 2. The three species that comprise the "*Emys* complex". **Top:** *Emys orbicularis* from Iran (photo by James Parham). **Middle:** *Emys* or *Actinemys marmorata* from California (photo by Jerome Maran). **Bottom:** *Emys* or *Emydoidea blandingii* from Michigan (photo by Michael Benard).

Like most of the systematics community, our Turtle Taxonomy Working Group includes a range of opinions on the costs and benefits of ranked vs. rank-free classifications, and whether or not the principles embodied in the Phylocode represent a net benefit or not to solving taxonomic issues with turtles. The literature similarly includes a full range of opinions from well respected taxonomists working across the tree of life. We make no explicit recommendations, other than the obvious one— that the community of turtle systematists should make every effort to track the new advances that are taking place in the larger systematics community and be open to meeting the challenges of refining and stabilizing the taxonomy of turtles.

DNA Barcoding. — DNA barcoding refers to the idea that species identification for an individual can potentially be determined by a small fragment of DNA sequence from that individual. The Consortium for the Barcode of Life (http://barcoding.si.edu/DNABarCoding.htm) has recommended that the cytochrome c oxidase subunit 1 mitochondrial region (COI) be used as the standard barcode region for all "higher" animals. This recommended region is short (about 650 base pairs in length), well characterized, and easy to use.

DNA barcoding can potentially contribute to two important empirical problems in taxonomic research and its applications. The less controversial is the rapid, inexpensive identification of organisms and their products when more traditional characters are either unreliable or inapplicable. For turtles, this might include pieces of meat, shell, or medicinal powders, hatchlings or eggs, and melanistic or otherwise unrecognizable specimens, to name a few examples (e.g., Roman and Bowen, 2000). Situations ranging from forensic analysis in criminal cases such as illegal trade, to the repatriation of captive specimens to the wild, all require rapid, accurate identification, and DNA barcoding could provide critical identifications for these and other important activities. Much more controversial is the idea that new, cryptic species might also be identified from DNA barcode data. This application is closely linked to the idea that species differ by a constant, minimal threshold level of COI sequence divergence. If, for example, species were generally 2% sequence divergent for COI, and a genetic survey from across a species range found populations that were more than 2% divergent from the rest of the species, those populations would be targeted as possibly new, cryptic species. This strategy has been explicitly advocated for poorly-known, hyperdiverse taxa like insects (Smith et al., 2006) and crustaceans (Lefebure et al., 2006), although serious issues have also been raised with the strategy (Rubinoff, 2006).

The Turtle Taxonomy Working Group recognizes that the application of DNA barcoding is a potentially useful management and forensics tool for many species. However, we also recognize that relying on a single mitochondrial gene is fraught with problems (Funk and Omland, 2003; Rubinoff, 2006), and that progress will rely on adequate characterization of known-locality specimens from across the range of each species as a precursor

to reliable DNA barcoding efforts. We do not recommend DNA barcoding as a mechanism for discovering new species, given the range of sequence divergence currently known for turtle species (compare Lamb and Osentoski, 1997, and Engstrom et al., 2004). We further recognize that some closely-related species may not be amenable to barcoding identification, and that the unusual situation imposed by hybridization in turtles (Parham et al., 2001; Spinks et al., 2004; Stuart and Parham, 2007) will further challenge the utility of the approach.

Concluding Thoughts

Taxonomy is clearly an active field with a variety of opinions and scientific strategies. Our working group includes many diverse opinions that cover this broad spectrum of science. However, we are absolutely united in our view that taxonomy and nomenclature are critical to the future of both science and conservation involving turtles. This leads us to the unified position that taxonomic revisions and usage must reflect the strongest available science, based on clear and unambiguous interpretations of that science, and published in the appropriate, widely-available, and peer-reviewed scientific literature. We feel that when the guidelines of our "Best Scientific Practices" are followed, and when reasonable consensus of the turtle community is sought, that the taxonomy of turtles will become the essential tool for communication and conservation action that it should be. We hope that all practitioners of turtle taxonomy, whether working at the intraspecific level or the deepest phylogeny of the group, will work together to achieve a stable classification of turtles that is maximally informative, based on the best available science, and reflective of the broadest possible consensus within the turtle community.

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