Defining Turtle Diversity: Proceedings of a Workshop on Genetics, Ethics, and Taxonomy of Tortoises and Freshwater Turtles
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In Search of the Tree of Life for Turtles

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Abstract. – Based on a thorough review of the literature, we provide a bibliography of papers featuring phylogenetic hypotheses for living turtles, a composite tree of all turtle species based on those hypotheses, a compilation of the most rigorously derived trees from those papers (i.e., using contemporary methods with bootstrapping), and supertrees for selected families of turtles using input trees from those most rigorous trees. These outputs allow us to identify the branches of the tree of life for turtles that are best supported as well as those most in need of study. With the exception of the Platysternidae and Chelydridae, the phylogenetic relationships among turtle families seem to be well-resolved and well-supported. Within families, the relationships among most genera are also well-resolved; however, the reciprocal monophyly of the South American and Australian chelids, the relationships among the genera allied to the chelid genera *Batrachemys* and *Mesoclemmys*, and the monophyly of the emydid genus *Trachemys* remain problematic. The relationships among species of trionychids, geoemydids, and testudinids are best resolved (since they are based on morphology, multiple mitochondrial genes, and at least one nuclear gene), and those for the podocnemids and pelomedusids are the least understood (with no complete published tree for either). The relationships among species in the following genera are most in need of additional phylogenetic study (highest need first): *Pelusios, Podocnemis, Testudo, Kinosternon, Batrachemys* (and close relatives), *Elseya, Trachemys, Graptemys*, and *Pseudemys*. Future work should endeavor to include the broadest taxonomic and geographic sampling possible (including type specimens) in order to maximize our understanding of the evolution of modern turtle diversity. A comprehensive multilocus approach (with numerous mtDNA and nDNA genes) will clearly be the best strategy for fully resolving the tree of life for turtles.

Key Words. – Reptilia; Testudines; phylogenetics; supertree; please provide more

Although turtles have been evolving for over 200 million years, the phylogenetic relationships among them have been discussed for less than 200 years, and most of the resolution of relationships has been provided in the last 20 years. The oldest hierarchical classification of turtles appears to be that of Dumeril (1806: Fig. 1), although it enumerated only four genera and was not intended to represent an explicitly historical perspective. Many other hierarchical classifications of turtles appeared in the 1800s (reviewed by Gaffney, 1984), but the first explicit phylogenetic tree for the major groups of fossil and living turtles was published by Hay (1908; Fig. 2). However, despite the increasing acceptance of Darwin's theory of evolution by natural selection, and even the rise of the "modern synthesis" in the 1930s and 1940s, explicit phylogenetic hypotheses for turtles in the form of branching diagrams (or phylogenetic trees) were nearly absent before the 1970s (for early exceptions see Zug, 1966; Pritchard, 1967).

Fueled by the insights on phylogenetic systematics provided by Hennig (1966), and the associated emergence of cladistic methodology (reviewed by Nelson and Platnick, 1981), Gaffney (1972, 1975a,b, 1976, 1977, 1979a,b) pioneered the application of those techniques to the phylogenetics of both extant and fossil turtles. The emergence and development of DNA sequencing techniques and methods for the analysis of molecular and morphometric data (Felsenstein, 2003) has led to an exponential increase in the number of papers that have included phylogenetic trees for various turtle groups (Fig. 3; see also Fig. 2 in FitzSimmons and Hart, 2007). As a result of this activity, the phylogenetic relationships among the families of living turtles have been fairly well resolved (Fig. 4), although some controversy

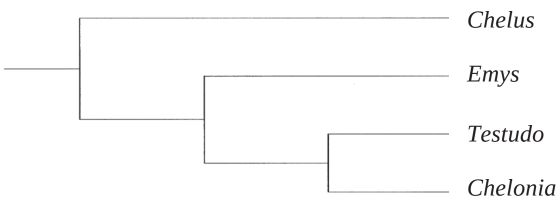

Figure 1. Phylogenetic "hypothesis" derived from Dumeril's (1806) hierarchical classification of turtles.

remains (Krenz et al., 2005; Parham et al., 2006a; see below). Progress at lower taxonomic levels has been substantial, though significant gaps still exist in coverage. For example, in Iverson's (1992) checklist of turtles, of 87 recognized genera, 26 (30%) contained more than two species, but only 18 of those (69%) had a published phylogenetic hypothesis for most of the included species. However, at the end of 2005, about 104 genera were recognized, the increase due primarily to taxonomic splitting (only two previously unknown genera, *Elusor* and *Leucocephalon*, have been described since 1992; see TTWG, 2007b). Of those, 35 (34%) included more than two species, and at least one published phylogenetic hypothesis is available for all but 4 of those 35 (89%; not *Pelochelys* [3 species], *Batrachemys* [6 species], *Pelusios* [18 species], or *Podocnemis* [6 species]).

Despite this demonstrated proliferation in phylogenetic hypotheses for most clades of turtles, an attempt to produce an all-inclusive tree of all recognized living chelonian taxa has not been forthcoming (but see Gaffney and Meylan, 1988; Cracaft and Donoghue, 2004; Moen, 2006). Such a tree for turtles is desperately needed in order to 1) provide a working hypothesis of higher and lower level relationships among turtles; 2) identify the turtle taxa most in need of additional phylogenetic attention; 3) facilitate the identification of appropriate outgroups for future phylogenátic studies of turtles (e.g., compare Honda et al., 2002a, with Spinks et al., 2004); 4) facilitate studies of character evolution in turtles (e.g., Stephens and Wiens, 2003b); 5) facilitate phylogenetic approaches to the study of zoogeography in turtles (e.g., Ronquist, 1998; Ree et al., 2005; Stephens and Wiens, 2003a); and 6) direct the appropriate setting of

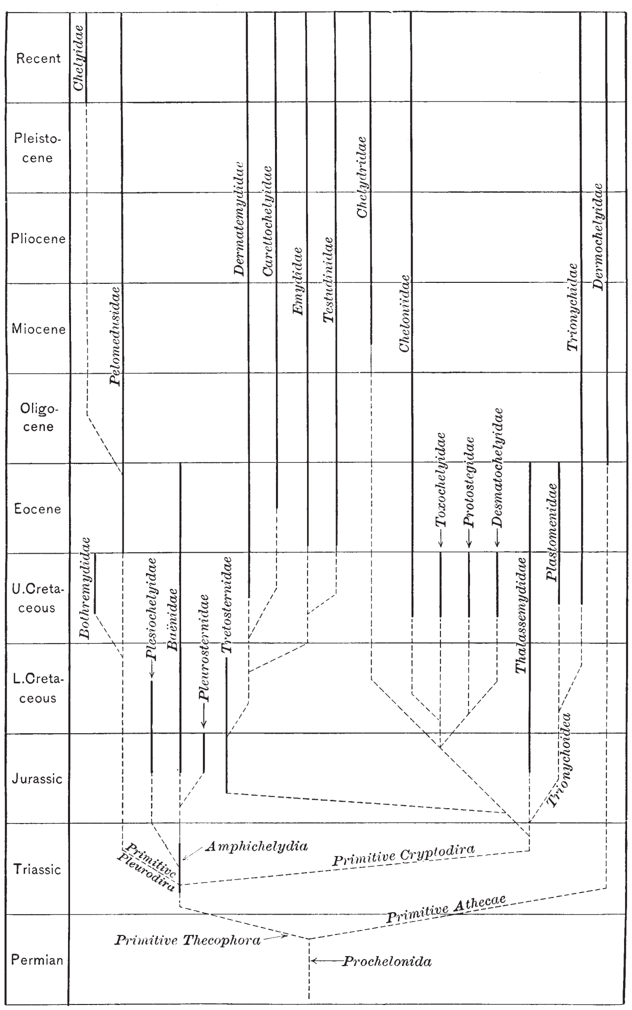

FIG. 8.—Phylogenetic chart showing supposed relationships of the families and higher groups of turtles.

Figure 2. Earliest explicit phylogeny of higher taxa of living and extinct turtles, published by Hay (1908).

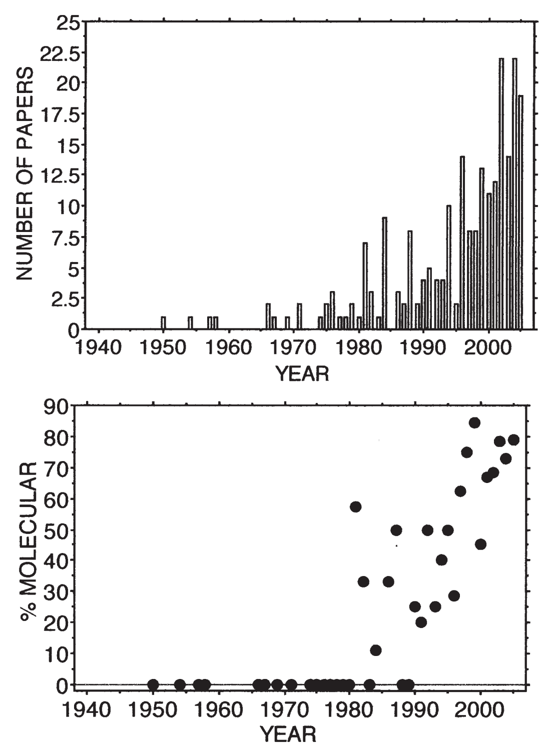

Figure 3. Publication dates of papers that included phylogenetic trees for turtle taxa at or above the species level. Dissertations and theses were excluded. **Top:** total frequency by year. **Bottom:** proportion of total papers that were primarily molecular (excluding karyotype papers). Key stimuli for increases were the synthesis of phylogenetic systematic philosophy by Hennig (1966), the first turtle cladistics paper by Gaffney (1972); the development of DNA sequencing methods (Sanger et al., 1977; Maxam and Gilbert, 1977); the pioneering of computer-based methods of phylogenetic reconstruction in the early 1980s (perhaps the biggest stimulus; reviewed by Swofford and Olsen, 1990); the development of Polymerase Chain Reaction methods (Mullis and Faloona, 1987; Saiko et al., 1988); and the development of Bayesian algorithms for phylogenetic reconstruction (Li, 1996; Mau, 1996). Only papers published through 2005 are plotted.

[Note that *Podocnemididae and Cheloniidae* are misspelled.]

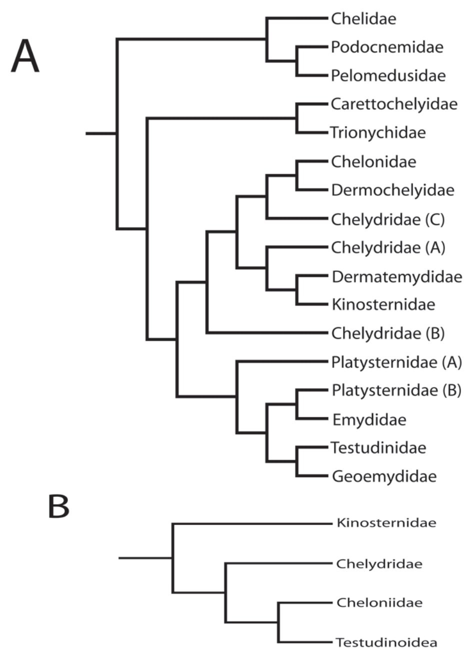

Figure 4. Current phylogenetic hypotheses of the relationships among the families of turtles. Ambiguity is illustrated by multiple placements of the families Chelydridae (in Fig. 4A, A after Cervelli et al., 2003 [ML], Near et al., 2005; B after Cervelli et al., 2003 [MP], Shaffer et al., 1997; C after Krenz et al., 2005; and in Fig. 4B, after Parham et al., 2006a) and Platysternidae (in Fig 4A, A after Krenz et al., 2005, Near et al., 2005; and B after Parham et al., 2006a).

priorities for conservation initiatives (i.e., to conserve maximum genetic diversity of turtles; e.g., Krajewski, 1994; Engstrom et al., 2002; Fritz et al., 2005; Georges and Thomson, 2006).

With the intent of addressing the first two of these deficiencies, and further stimulating the investigation of the others, we provide herein our current best synthesis of the relationships among all recognized turtle species, and identify the clades with the weakest support (and hence most in need of further study).

METHODS

We reviewed the literature and compiled a bibliography of all locatable papers containing phylogenetic trees (or networks) that included turtles as terminal taxa (Appendix A). Based on the phylogenetic hypotheses generated in those papers, we identified the most recent and strongly supported trees for each family clade, giving preference to those with the most extensive character and taxon sampling (Appendix B). We then generated a compiled tree for all extant turtle species by concatenating this phylogenetic information (e.g., see Beck and Beck, 2005, and Jonsson and Fjeldsa, 2006, for justifications of this method).

For comparison with the compiled tree, we undertook a supertree analysis (Bininda-Emonds, 2004b) based on the "best" (see below) available trees. First, we compiled a list of candidate trees by higher taxon and tallied the character of the input data set and the methods of analysis (Appendix C). From that subset of potential input trees, in an attempt to maximize independence of our selected trees (Bininda-Emonds, 2004b:363), we first discarded redundant trees (e.g., trees in the same or different papers based on data partitions when a combined analysis was also available), as well as those based strictly on morphological characters. We next gave preference to trees with extensive character and taxon sampling and that used maximum parsimony analysis that included bootstrap values for nodes (or where those values could be calculated by our reanalysis of the reported data). We also discarded as redundant trees from separate papers that exhibited extensive overlap in genetic markers. Our purpose in doing so was to prevent disproportionate representation of any one kind of genetic data that might bias a supertree analysis if the majority of input trees were derived from the same class of DNA sequence data (see Bininda-Emonds, 2004c, for a discussion of issues relevant to data quality in supertree construction). An unfortunate consequence of this necessary approach was that an adequate sample of input trees (only 22 total) was available for only five families (Cheloniidae, Kinosternidae, Geoemydidae, Emydidae, and Testudinidae). For simplicity, we have included only extant taxa in this first supertree analysis for turtles.

Although there is considerable discussion about the most robust method for supertree construction (Wilkinson et al., 2005), we used matrix representation with parsimony (MRP), because it is generally accepted as one of the best current

Figure 5. Current phylogenetic hypothesis of the relationships within the turtle family Chelidae.

[Note that *pallidipectoris* is misspelled and will be changed in final draft.]

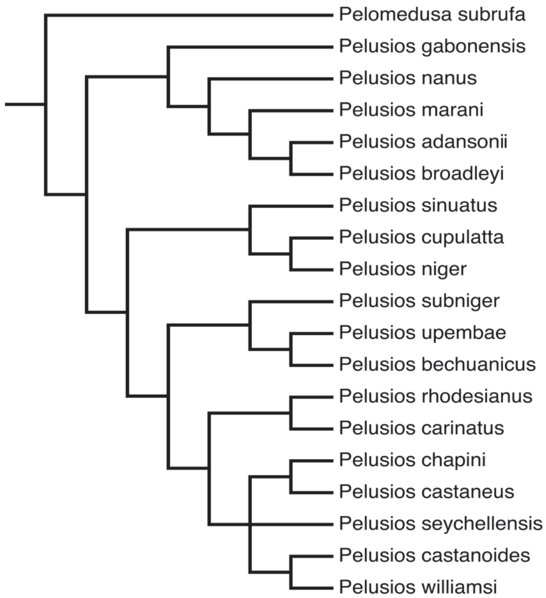

Figure 6. Current phylogenetic hypothesis of the relationships within the turtle family Pelomedusidae.

[Note that A & B after E. madagascariensis are missing]

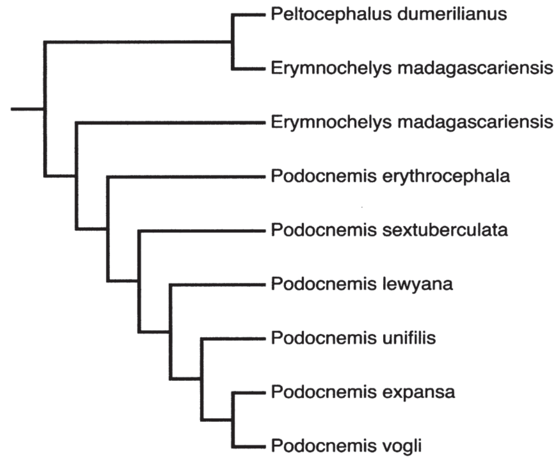

Figure 7. Current phylogenetic hypotheses of the relationships within the turtle family Podocnemididae. Ambiguity is illustrated by the double placement of *Erymnochelys* (A after Meylan, 1996, and Starkey et al. unpublished; and B after Georges et al.. 1998, Noonan, 2000, and Noonan and Chippindale, 2006).

methods (Sanderson et al., 1998; Bininda-Emonds, 2004a,b; Burleigh et al., 2004), and because it has been applied productively in a number of recent studies (Salamin et al., 2002; Ruta et al., 2003; Davies et al., 2004; Kerr, 2005).

Exploratory MRP matrices for this study were initially constructed using SuperTree 0.85b (Salamin et al., 2002; http://www.tcd.ie/Botany/NS/SuperTree.html), and the Baum/Ragan coding scheme was used with nodes weighted by bootstrap support values (Davies et al., 2004). Final MRP matrices were constructed using r8s (Sanderson, 2004). For trees published without bootstrap support, we reanalyzed the original dataset to obtain those values with 1000 MP replicates using PAUP 4.0B (Swofford, 2001). Weights were calculated following Farris (in Salamin et al., 2002) and manually input into PAUP files using TreeEdit (evolve.zoo.ox.ac.uk/software/TreeEdit/main.html).

The binary matrices were analyzed with PAUP 4.0B using weighted parsimony. We performed heuristic searches with 250 replicates of random taxon addition, subtree pruning-regrafting and branch swapping, holding 10 trees at each replicate. These saved trees served as starting trees in a second search using tree bisection-reconnection with a tree

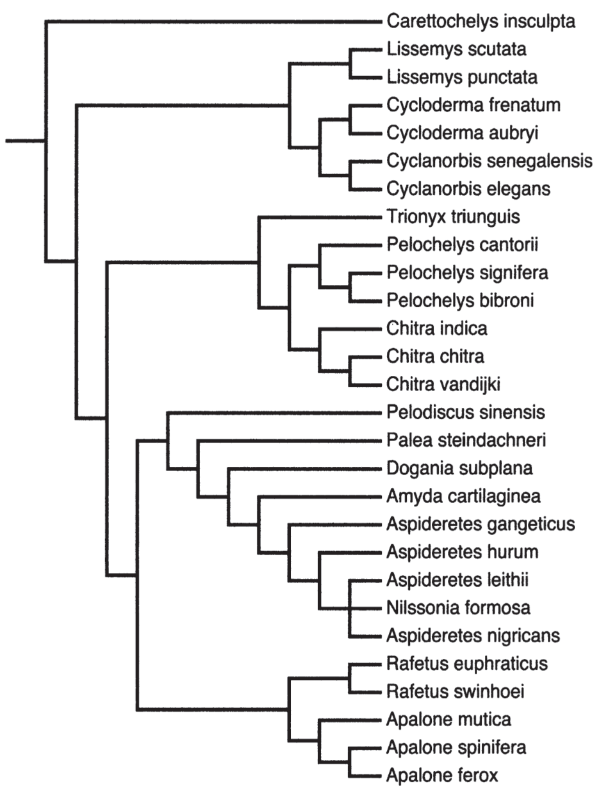

Figure 8. Current phylogenetic hypothesis of the relationships within the turtle family Trionychidae. The monotypic genus *Carettochelys* is included as the only representative of the family Carettochelyidae.

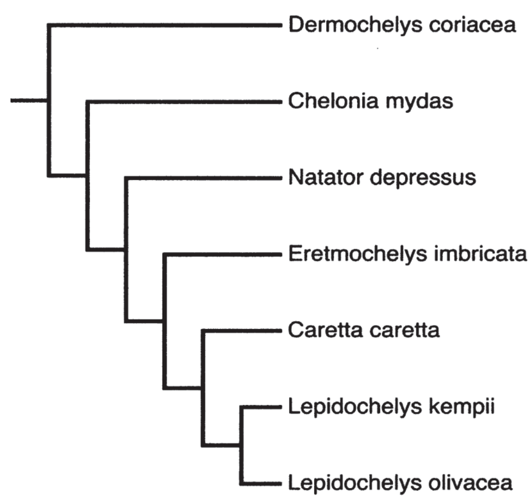

Figure 9. Current phylogenetic hypothesis of the relationships within the turtle family Cheloniidae. The monotypic genus *Dermochelys* is included as the only representative of the family Dermochelyidae. The topology of the single perfect supertree was identical to that illustrated here.

limit of 10,000 equally most parsimonious trees (Davies et al., 2004). Majority rule (50%) and strict consensuses (both constrained so that previously recognized families were monophyletic) were used to explore agreement between saved tree populations.

Finally, we have attempted to match names at the tips of our trees to those recognized through late 2006 by the Turtle Taxonomy Working Group (TTWG, 2007b). However, undescribed taxa are included in some trees (e.g., Chelidae, Testudinidae), because the additional forms have been identified in the literature, and more recent taxonomic changes have been included in the published list by the TTWG (2007b) since we performed our supertree analysis.

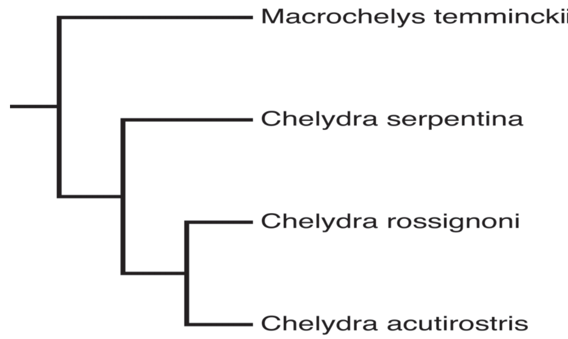

Figure 10. Current phylogenetic hypothesis of the relationships within the turtle family Chelydridae.

RESULTS AND DISCUSSION

Although phylogenetic trees including living turtle taxa have appeared in at least 142 publications (Appendix A), relatively few have included more than a few species, applied rigorous methods of phylogenetic reconstruction, provided support values for nodes using multiple reconstruction algorithms, and made objective comparisons of trees based on individual data partitions (e.g., cytb vs. ND4 vs. 12S/16S rRNA vs. Rag1 vs. morphology; see Table 1). In addition, there has been an obvious increase in the number of studies based primarily on molecular work, whereas the numbers of primarily morphology-based papers has remained fairly constant (Fig. 3). Nevertheless, we were able to compile at least preliminary trees for all living turtle families and species (Figs. 4-14) However, because of incomplete taxon sampling, the paucity of trees for several families, and discordance among trees within several families, our attempt to generate a single supertree for all turtle taxa was not successful (in that most families were not resolved as monophyletic). Appropriate input trees (in number and taxonomic diversity) were available for supertree analysis within only five families: the Cheloniidae (Fig. 9), Kinosternidae (Fig. 11B), Geoemydidae (Fig. 13B), Emydidae, and Testudinidae (Fig. 14B).

Compiled Trees

Inter-Familial Relationships. — The monophyly of each of the two living subclasses of turtles (Cryptodira and Pleurodira) is well-supported in nearly all recent phylogenetic

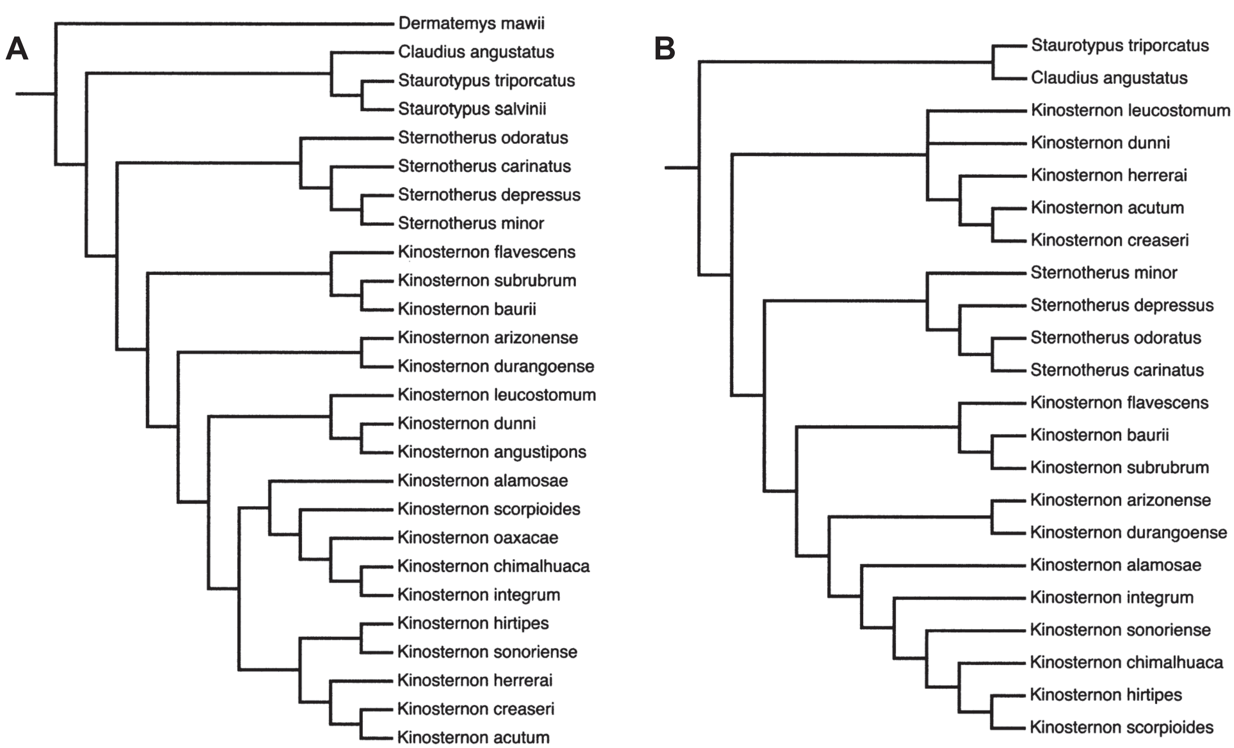

Figure 11. Current phylogenetic hypotheses (A = compiled tree; B = single perfect supertree) of the relationships within the turtle family Kinosternidae. The monotypic genus *Dermatemys* is included as the only representative of the family Dermatemydidae.

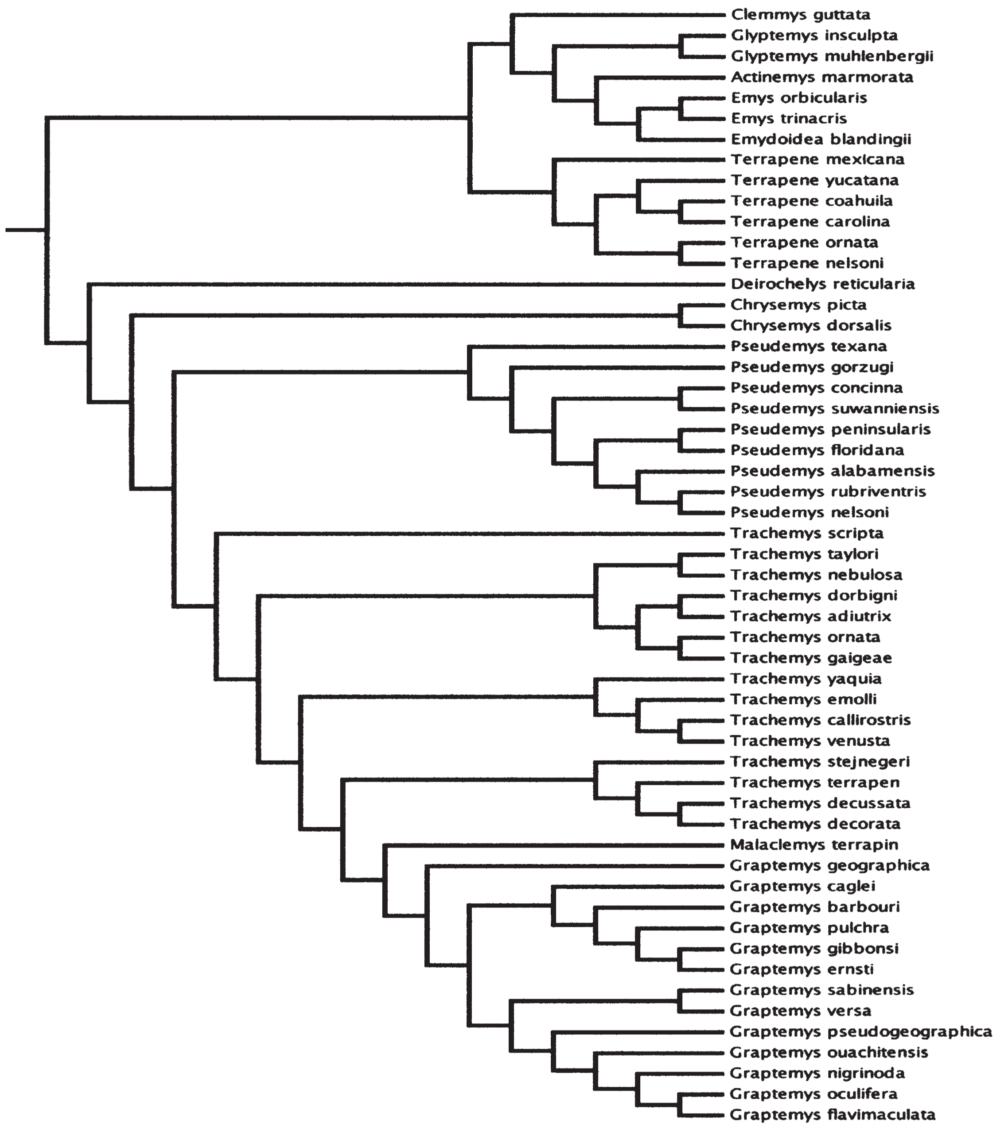

Figure 12. Current phylogenetic hypothesis of the relationships within the turtle family Emydidae.

reconstructions, whether based on morphologic or molecular data (Gaffney and Meylan, 1988; Shaffer et al., 1997; Cervelli et al., 2003; Fujita et al., 2004; Krenz et al., 2005:**Fig. 5B**; Near et al., 2005; Parham et al., 2006a; but see Wu et al., 1999; and Krenz et al. 2005:**Fig. 5B [?]**). Furthermore, with the exception of the placement of the Chelydridae and the Platysternidae, the phylogenetic relationships among most of the rest of the families is also well-resolved (Fig. 4).

Once considered to be closely related to the Chelydridae (e.g., Gaffney and Meylan, 1988; Shaffer et al., 1997), the monotypic family Platysternidae has recently (Krenz et al., 2005; Near et al., 2005) been considered to be sister to the Testudinoidea (= Emydidae + Geoemydidae + Testudinidae) based on combined nuclear (RAG-2) and mitochondrial (cytochrome *b* and 12S) DNA sequence data. However, based on the entire mitochondrial genome, Parham et al. (2006a) found support for the Platysternidae as sister to the Emydidae (Fig. 4). In addition, that study also revealed a novel placement for the sea turtles (Cheloniidae) and the snapping turtles (Chelydridae) (Fig. 4, inset). As is evident from the various positions (A-C) of the Chelydridae in Fig. 4, its phylogenetic position among the Cryptodira is the least resolved of all turtle families. Final resolution of the phylogenetic position of these two families will require broader taxon and character sampling (i.e., from both the nuclear and mitochondrial genomes, as well as from morphology). A reconsideration of the shared morphology of chelydrids and platysternids in light of recent paleontological data may also prove useful.

Although there is no recent disagreement that the testudinids and geoemydids are closely related (i.e., belong to the monophyletic Testuguria; e.g., Parham et al., 2006a), recent analysis by Spinks et al. (2004:Fig. 3) reconstructed the Geoemydidae as paraphyletic with respect to the testudinids (though with low support), suggesting that the genus *Rhinoclemmys* might deserve familial status in order to preserve a monophyletic taxonomy. However, Le and

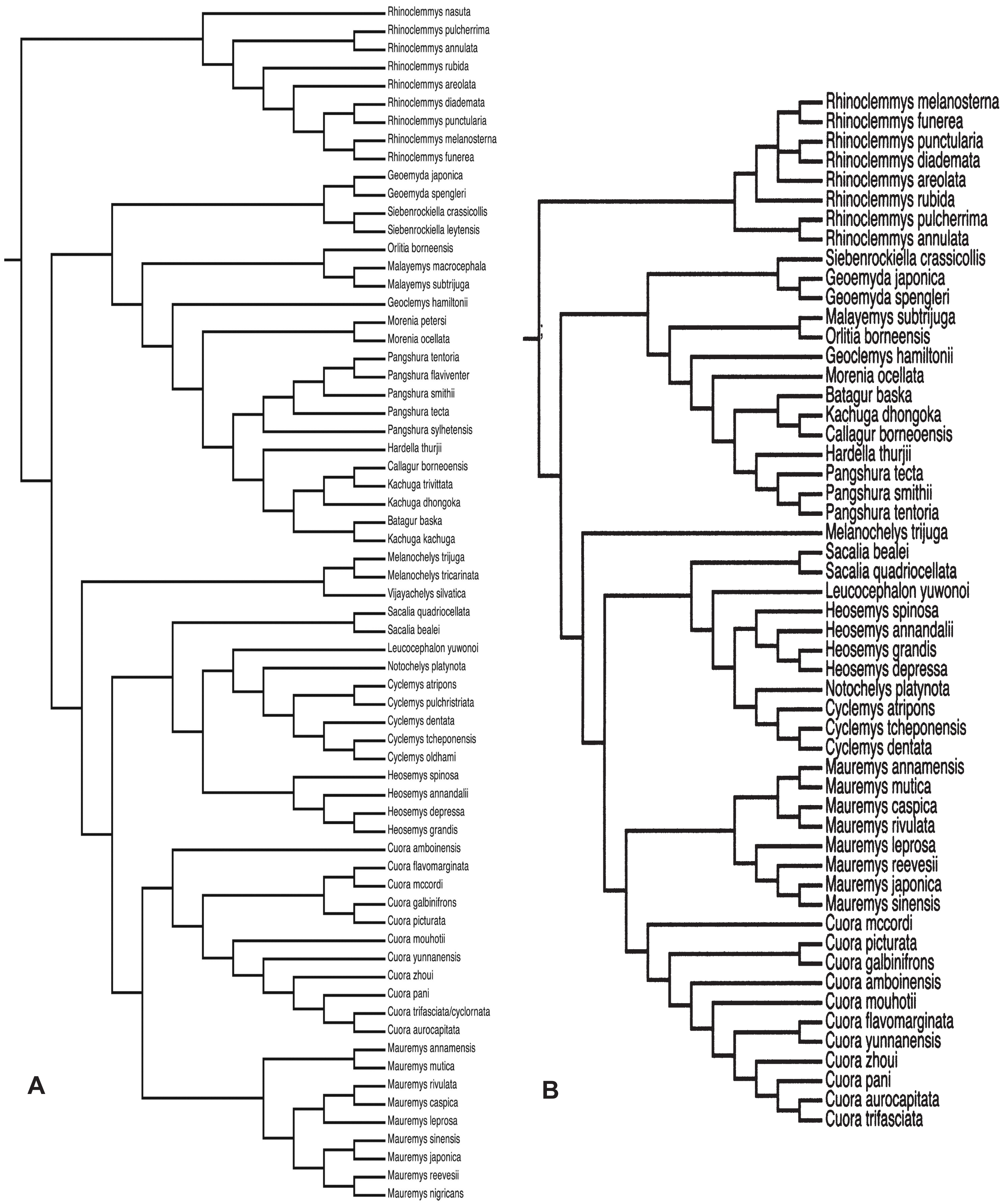

Figure 13. Current phylogenetic hypotheses (A = compiled tree; B = 50% majority rule supertree based of 3186 equally parsimonius trees in second search; 461 trees revealed by initial search) of the relationships within the turtle family Geoemydidae.

McCord (in review) resolved *Rhinoclemmys* as sister to the rest of the geoemydids, and recommended its recognition as a subfamily of the Geoemydidae.

At this time five family pairs appear to be firmly supported as sister taxa: Podocnemididae–Pelomedusidae, Carettochelyidae–Trionychidae; Cheloniidae–Dermochelyidae; Dermatemydidae–Kinosternidae; and Testudinidae–Geoemydidae. The Chelidae is strongly supported as the sister group of the Podocnemididae–Pelomedusidae (= Pelomedusoides) as

[Note that *Leucocephalon* and *Notochelys* should be sister taxa in Fig. 13A, and this will be corrected in final draft]

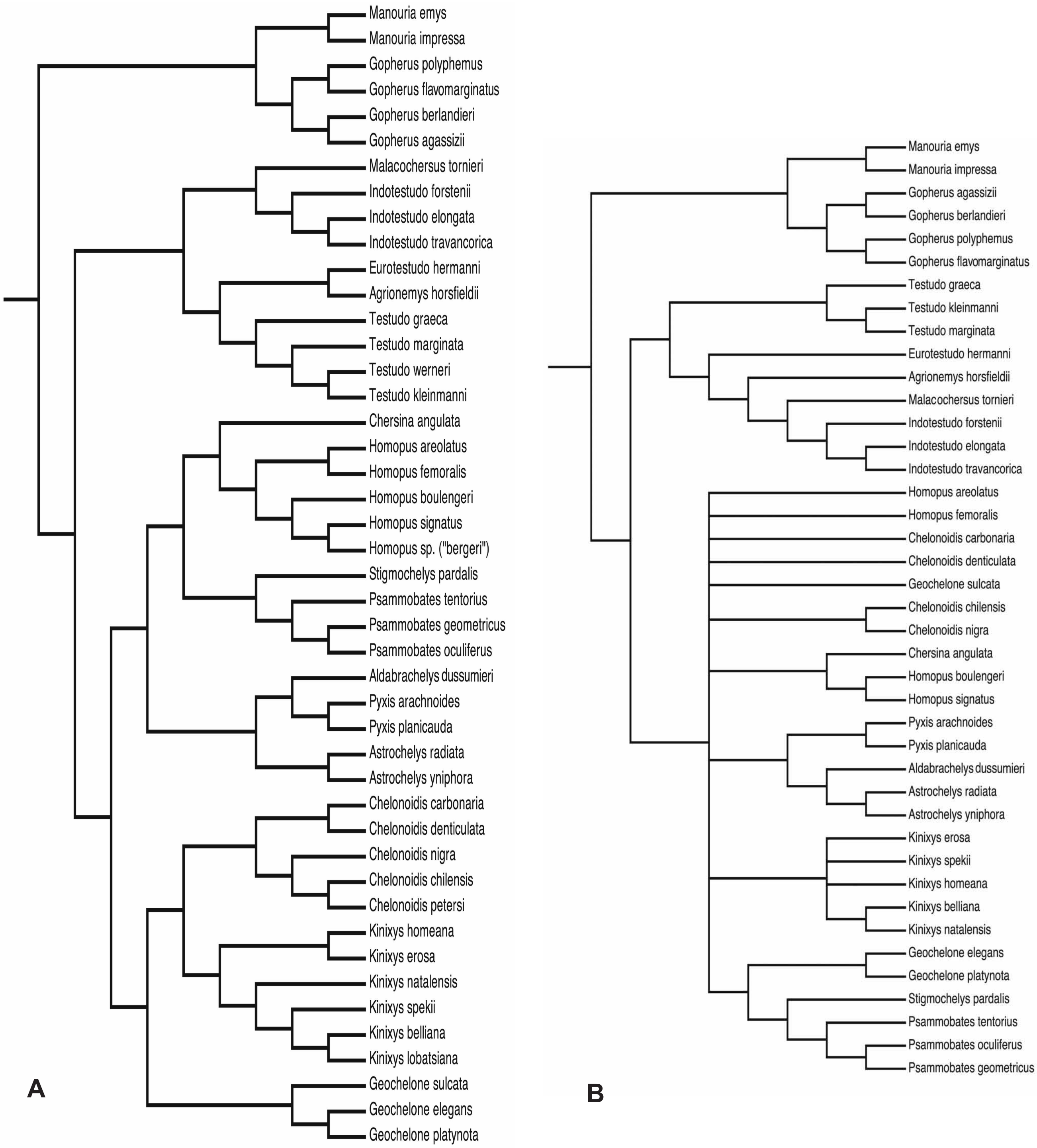

Figure 14. Current phylogenetic hypotheses (A = compiled tree; B = 50% majority rule supertree based on 10,000 equally parsimonious trees; 325 trees revealed by initial search) of the relationships within the turtle family Testudinidae.

a monophyletic Pleurodira, and the Trionychidae–Carettochelyidae (= Trionychia) is strongly supported as the sister group of the other living Cryptodira. The major remaining higher level questions for turtles are the phylogenetic relationships among the three other cryptodire family pairs and the Emydidae, Chelydridae, and Platysternidae.

Chelidae. — Resolution of the relationships among most of the chelids in Fig. 5 should be considered tentative, because of incomplete taxon sampling (Georges et al., 1998), reduced character sets (Seddon et al., 1997; McCord et al., 2002; Bour and Zaher, 2005), disagreements over character scoring (compare McCord et al., 2002; and Bour and Zaher, 2005), unreported bootstrap support for resolved nodes (Georges et al., 1998), and considerable undescribed (Georges and Thomson, 2006) and recently described (Bour and Zaher, 2005; Thomson et al., 2006) diversity. Particularly problematic are the relationships within the polyphyletic genus *Elseya* (Georges and Thomson, 2006) and the clade including the older genera *Batrachemys* and *Mesoclemmys* and the recently described or resurrected monotypic genera *Rhinemys*, *Ranacephala*, and *Bufocephala* (McCord et al., 2002). Despite this uncertainty, a consensus does appear to be emerging that the family includes three monophyletic groups, the Australasian long-necked turtles (*Chelodina* and *Macrochelodina*), the Australasian short-necked turtles (*Elseya* and relatives), and the South American species (with *Hydromedusa* as sister to the other South American forms; compare Gaffney and Meylan, 1988). However, the reciprocal monophyly of the Australian and South American taxa is still not resolved. Work currently underway should soon resolve the relationships among at least the Australian species (A. Georges, N. FitzSimmons, *pers. comm.*).

Pelomedusidae. — The genus *Pelomedusa* has been considered to be sister to the genus *Pelusios* by all recent authors (Fig. 6); however, no rigorous phylogenetic study to date has included *Pelomedusa* along with reasonable sampling within the speciose genus *Pelusios* (with at least 18 species; TTWG, 2007b). In fact, no phylogenetic hypothesis has previously been published for the species of the genus *Pelusios*. The tree provided in Fig. 6 is based entirely on morphology, as hypothesized by Roger Bour (unpubl. data). In addition, the description of two new cryptic species of *Pelusios* in the last six years (Appendix B) suggests that undescribed diversity remains in this genus [only the genus *Testudo* potentially includes more diversity; but see below]. Even a preliminary molecular phylogeny within this genus is sorely needed.

Podocnemididae. — Recognition of this clade as a separate family is a relatively recent concept (following de Broin, 1988), but well-supported phylogenetically (see references above under inter-family relationships). However, resolution among the genera and species is still unclear (Fig. 7). The position of *Erymnochelys* as sister to *Peltocephalus* is supported by Meylan (1996) and Starkey et al. (unpubl. data), but placement of *Erymnochelys* as sister to *Podocnemis* is supported by Georges et al. (1998), Noonan (2000), and Noonan and Chippindale (2006). A well-supported tree for the members of the genus *Podocnemis* is needed, and is currently underway (Starkey et al., unpubl. data).

Trionychidae and Carettochelyidae. — Following the work of Meylan (1987; based on morphology) and Engstrom (Engstrom et al., 2002, 2004; based on nuclear and mitochondrial DNA sequences and morphology), resolution of the relationships among the softshell turtles and their sister relationship to the monotypic family Carettochelyidae are quite well supported (Fig. 8). However, despite these comprehensive analyses, one clade remains poorly resolved, that including the genera *Aspideretes* and *Nilssonia*. Broader genomic sampling might clarify that last problematic softshell clade.

Cheloniidae and Dermochelyidae. — The position of *Dermochelys* as sister to the rest of the living marine turtles has long been supported (e.g., Gaffney and Meylan, 1988). In addition, the three most recent phylogenetic analyses of sea turtle species all supported the tree illustrated in Fig. 9 (Bowen and Karl, 1997; Dutton et al., 1996; Parham and Fastovsky, 1997). Nevertheless, additional genomic sampling (since only mtDNA data are currently available), analyzed by algorithms developed after those studies were published, should provide the definitive test of this hypothesis.

Chelydridae. — The relationships among the taxa in this family (Fig. 10) are well-resolved (Phillips et al., 1996; Shaffer et al., 2007), and additional cryptic diversity seems unlikely to emerge (Shaffer et al., 2007).

Kinosternidae and Dermatemydidae. — No recent disagreement exists concerning the relationships among the genera in these two families (Fig. 11A), whether based on morphology (Hutchison, 1991; Iverson, 1991, 1998) or molecules (Iverson, 1998; Krenz et al., 2005; Fujita et al., 2004). However, published phylogenetic studies to date either had reasonably comprehensive taxon sampling but minimal character sampling (Iverson, 1998) or minimal taxon sampling and only slightly better character sampling (Serb et al., 2001; Walker et al., 1998). In addition, to date only mitochondrial DNA has been sampled. As a result, there is considerable uncertainty in the relationships within even the two best-studied clades, *Sternotherus* (compare Iverson, 1998 and Walker et al., 1998) and the *Kinosternon flavescens* species complex (compare Iverson, 1998, Walker et al., 1998, and Serb et al., 2001). Because of this poor resolution, a more comprehensive study of nuclear and mitochondrial genes and morphology is underway (Iverson and Le, unpubl. data).

Emydidae. — Except for the genus *Trachemys*, the monophyly of and the relationships among the other genera in this family appear well resolved (Fig. 12), despite the fact that no data are yet available from the nuclear genome. As is evident from the compiled tree, *Trachemys* as currently constituted appears to be paraphyletic, and the relationships among the included species are tentative at best (compare Seidel, 2002 versus Stephens and Wiens, 2003b). Resolution among species in the genera *Pseudemys* and *Graptemys* is also unclear and will require extensive intraspecific (i.e., geographic) and interspecific sampling. For example, the tree generated by Stephens and Wiens (2003b) did not include all recognized taxa in the genus *Pseudemys*, and *Graptemys o. ouachitensis* and *G. o. sabinensis* were resolved in separate clades in that paper. Finally, although there is some agreement (Minx, 1996; Feldman and Parham, 2002; among others) that the genus *Terrapene* includes two monophyletic clades (*ornata/nelsoni* and *carolina/coahuila/mexicana/yucatana*), the relationships among the taxa in the latter clade are poorly resolved (Stephens and Wiens, 2003) and will also require extensive geographic sampling to clarify.

Geoemydidae. — Several taxa of geoemydid turtles were described in the 1990s based on turtles supplied by animal dealers. Despite their being morphologically distinguishable and purportedly field-collected (with some of them being shipped in large numbers and capable of producing fertile, identical F1 offspring), six have been shown to be of hybrid origin (see Parham et al., 2001; Spinks et al., 2004, and Stuart and Parham, 2006; and papers cited therein). Whether those hybridizations were the result of human husbandry or natural events (or both) remains to be determined definitively. Three other new taxa appear to be valid species based on genetic and morphological analysis, but have not yet been field collected (Stuart and Parham, 2006). Further study of the propensity of turtles in this family to hybridize, even between members of distant clades (e.g., *Sacalia* and *Cuora*), will be essential for a full understanding of the evolution of the turtles in this family.

Despite the confusion caused by the hybrid descriptions, the relationships among most of the genera and species of geoemydid turtles have been well resolved (Fig. 13A; Spinks et al., 2004; Le, 2006; and other references in Appendix B). Nevertheless, several problematic clades do remain (e.g., the genera *Cyclemys*, *Cuora*, and *Mauremys*, each *sensu lato*). Recent morphological and molecular work (e.g., Guicking et al., 2002; and references therein) has suggested that instead of including only two species (Iverson, 1992), the genus *Cyclemys* may include as many as nine species (note that only five of these are included in Fig. 13A, because the species boundaries are so unclear). Only thorough geographic and genetic sampling can clarify the actual number of species in this genus. However, their historic transport in the food and pet trades, and hence opportunity for genetic contamination through escape and hybridization, may complicate those efforts.

Within the genus *Cuora*, molecular sampling within *C. amboinensis* will no doubt reveal that it is a species complex (C. Ernst, *pers. comm.*), and more complete taxon and geographic sampling will be necessary to sort out relationships within the *C. trifasciata*/*C. cyclornata* complex (compare Blanck et al., 2006, and Spinks and Shaffer, 2006). The fact that *C. trifasciata* hybridizes easily with at least six other species (Vetter and van Dijk, 2006) complicates this work, as does the very recent evidence for mitochondrial introgression and nuclear-mitochondrial pseudogenes in that species (Spinks and Shaffer, 2006).

Finally, within the genus *Mauremys*, the relationships among the European species have been the only significant area of recent contention (Spinks et al., 2004; Feldman and Parham, 2004; Fritz et al., 2006; Le, 2006). Thorough geographic and molecular sampling will be necessary to test the most parsimonious biogeographic hypothesis of monophyly of the European taxa (e.g., see Le, 2006). Resolution of this problem has significant taxonomic implications (e.g., compare Spinks et al., 2004, and Vetter and van Dijk, 2006).

Testudinidae. — As a result of the recent work by Le et al. (2006), Parham et al. (2006b) and other sources cited in Appendix B, the phylogenetic relationships among the genera of tortoises are quite well resolved in the compiled tree (Fig. 14A), even if the generic nomenclature is not (see TTWG, 2007b). However, rigorous phylogenetic hypotheses for species in several problematic genera (e.g., *Homopus*, *Kinixys*, *Psammobates*, *Aldabrachelys/Dipsochelys*, and especially *Testudo*) are still lacking. Because of the tremendous uncertainty surrounding species boundaries in the genus *Testudo* (five species recognized in Iverson, 1992; 22 recognized in Guyot Jackson, 2004), and concern for conservation in that genus (e.g., Ballasina, 1995), a thorough molecular phylogenetic study of that genus is desperately needed.

Supertree Analyses

Our attempt to produce a single informative supertree for all turtles was unsuccessful. This was in large part due to the necessary restriction of input trees to those produced by maximum parsimony analysis, with reported bootstraps, and to those with minimal redundancy in character sets, but also to the dearth of published trees for several families and the fact that most molecular phylogenies are based on only a few mitochondrial genes (Table 1). Hence, well-resolved supertrees could not be generated for all families. However, for the cheloniids the supertree and compiled trees were identical (Fig. 9), reflecting the concordance of all three input trees. Unfortunately, as mentioned previously, the nuclear genome has not been sampled for marine turtles.

For the kinosternids, the single perfect supertree (Fig. 11B) differed from the compiled tree in suggesting a paraphyletic genus *Kinosternon*, the placement of the *K.*

Table 1. Summary of primary data partitions on which published trees for turtle families have been based. See Appendix C for full source material. Available but yet unpublished data are indicated with an x.

		Mitochondrial genes					Nuclear genes			
Family	Morphology	cytb	ND4	12/16S rRNA	Control	CO1	cmos	R35	Rag1	Rag2
Chelidae	+	-	-	+	-	+	+	-	-	-
Pelomedusidae	-	-	-	-	-	-	-	-	-	-
Podocnemididae	-	x	x	-	-	-	-	-	-	-
Trionychidae	+	+	+	-	-	-	-	+	-	-
Kinosternidae	+	+	+	-	+	-	-	-	-	-
Cheloniidae	+	+	+	-	+	-	-	-	-	-
Emydidae	+	+	+	+	+	-	-	-	-	-
Geoemydidae	+	+	+	+	-	+	x	+	x	-
Testudinidae	+	+	+	+	+	+	+	-	-	+

herrerai clade with the *K. leucostomum* clade, alternative relationships among the species of *Sternotherus*, the incorporation of the *K. hirtipes* group within the *K. scorpioides* group, and alternative relationships among the members of the latter two groups. These disparities apparently reflect the differences between the cytb (Iverson, 1998), ND4 (Starkey, 1997), and control region (Walker et al., 1998; Serb et al., 2001) gene trees included in the supertree analysis. The inclusion of additional genetic data (especially from nuclear genes) will most likely be necessary to resolve these conflicts.

The majority rule supertree for the geoemydids (Fig. 13B) is generally very similar to the compiled tree, with the primary differences being the placement of *R. areolata* within the genus *Rhinoclemmys*; the placement of the monotypic genera *Hardella*, *Notochelys*, and *Leucocephalon*; the basal relationships within the genus *Mauremys*; and the positions within the genus *Cuora* of *C. mccordi*, *C. amboinensis*, and *C. flavomarginata*. Most of the discrepancy between the compiled and supertree was a result of basing the former primarily on published and unpublished multi-locus studies with extensive taxon and character sampling (Spinks et al, 2004; Diesmos et al., 2005; Le, 2006; Le and McCord, in review), whereas the latter was based entirely on three published studies with minimal overlap in gene sampling (Honda et al., 2002a; Spinks et al., 2004; Parham et al., 2004), only one of which (Spinks et al., 2004) included a nuclear gene. Publication of the work by Le (2006) and Le and McCord (in review) may provide nearly complete resolution of the relationship within this family.

Both the consensus and 50% majority rule supertrees produced for the family Emydidae were nearly completely unresolved. For example, neither was able to resolve even the genus *Graptemys* as monophyletic. Hence, those trees are not illustrated nor discussed further.

The input trees for the supertree analysis of the Testudinidae were based primarily on 12S and 16S rRNA and cyt b mtDNA (only Le et al., 2006 included nuclear data), and the resulting majority rule tree was quite different from the compiled tree (Fig. 14A vs. 14B). In addition to not being fully resolved, the majority rule did not recognize the genera *Homopus*, *Geochelone*, or *Chelonoidis* as monophyletic. It also differed from the compiled tree in the placement of *Agrionemys*, *Eurotestudo*, and *Aldabrachelys*; the relationships within *Kinixys*; and the poor resolution among the more derived genera. Additional taxon sampling to supplement that of Le et al. (2006) should clarify these uncertainties.

These preliminary supertree analyses for turtles generally corroborated the results of the compiled tree approach. Discrepancies apparently reflected the incongruence among input trees which were based on variable gene partitions (sometimes overlapping and sometimes not). Our complied tree approach had the possible advantage of relying more heavily on the most recent, most inclusive phylogenetic analyses, whereas by default the supertree analyses often included trees based on a single gene alongside trees based on multiple genes (sometimes both mitochondrial and nuclear). In any case, the exercise did demonstrate that most recent phylogenetic studies of turtles have focused on but a few mitochondrial genes (Table 1; Appendix C). This has produced some disparity in the resulting trees, particularly among poorly supported nodes. The more recent inclusion of multiple gene datasets (both mt and nDNA; e.g., Engstrom et al., 2004; Spinks et al., 2004; Deismos et al., 2005; Le et. al., 2006) has produced better resolution in trees, although evaluation of individual gene trees is needed in order to determine which genes contributed most strongly to that resolution. Once both taxon and gene sampling are more complete for turtles, comparisons among single gene trees, trees based on total evidence, and supertrees based on individual gene trees as input should be very informative.

Conclusions

The last decade has seen amazing progress in the search for the "tree of life" for turtles, and this progress has had many ancillary benefits to turtle taxonomy and conservation. However, for this progress to continue, the next decade must see greater attention paid to comprehensive sampling of both markers and taxa in molecular studies (including subsampling within species). The value of many otherwise excellent studies over the past decade has been diminished because closely related taxa were not adequately sampled, because outgroups were inappropriately chosen, or because analysis relied too heavily on small regions of the genome. Emerging genetic resources show promise in overcoming the marker limitation issue. Engstrom et al. (this volume) compiled all known primer pairs for turtles and found that many mtDNA primer pairs are known to be useful across turtles, but that nuclear sequence markers are in short supply. A bacterial artificial chromosome (BAC) library was recently constructed for *Chrysemys picta bellii* and has been employed to develop a set of 96 new nuclear markers, many of which appear to be useful across turtles (Shaffer and Thomson, in review; R.C. Thomson et al., unpubl. data). These resources, coupled with increasing cooperation in assembling tissue banks within the academic and herpetocultural communities, make an attempt at recovering the tree of life for all turtle species using a comprehensive multi-marker approach a reasonable goal in the near future. We hope that this summary of current phylogenetic hypotheses for turtles will guide future investigators appropriately.

We also conclude by offering two comments concerning the impact of phylogenetics on turtle taxonomy. First, we understand the temptation of authors to propose taxonomic changes (sometime extensive) whenever a new well-resolved tree is at variance with current taxonomy (e.g., see the discussion regarding the genus name *Emys* by the Turtle Taxonomy Working Group, 2007a). However, for the sake of nomenclatural stability, we recommend restraint in proposing taxonomic changes until taxon and character sampling are adequate to provide robust support for such changes. To do otherwise will add confusion to an already complex literature (see Frazier, 2006, and Bour, 2006, for one example), and may even hamper conservation efforts for this unique and imperiled clade of vertebrates (TTWG, 2007a).

Second, because zoological taxonomy is still operating under the rules of ICZN (but see TTWG, 2007a), binomial nomenclature is ultimately based on type specimens. It is therefore essential that future workers take seriously the goal of including type specimens in their analyses, if for no other reasons than to be sure that taxonomic names are being applied appropriately (e.g., see Guicking et al., 2002; Parham et al., 2004; Blanck et al., 2006 and Lehn et al., this volume) and that we are not overlooking cryptic diversity in turtles.

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Appendix A

Literature that includes phylogenetic trees for Recent taxa of turtles. Paleontological papers with minimal focus on living taxa are excluded (including a number by Auffenberg and Gaffney). Papers reporting networks of relationships are also included.

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Zug, G.R. 1971. Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtle. Miscellaneous Publications, Museum of Zoology, University of Michigan 142:1-98.

Appendix B

Literature sources on which the complied trees for turtles were based. Most full citations appear in Appendix A; those listed here lacked phylogenetic trees.

Family level (based primarily on Near et al., 2005; Fujita et al., 2004; Shaffer et al., 1997; and Noonan, 2000; but see Krenz et al., 2005, and Parham et al., 2006a, for the positions of the Chelydridae and Platysternidae, respectively).

Chelidae (based primarily on Georges and Thomson, 2006, McCord et al., 2002, and a 50% majority rule tree based on a parsimony analysis of the data matrix in Bour and Zaher, 2005). Additional sources included Derr et al. (1987), Georges et al. (1998), and the following:

Thomson, S., Georges, A., and Limpus, C.J. 2006. A new species of freshwater turtle in the genus *Elseya* (Testudines: Chelidae) from central coastal Queensland, Australia. Chelonian Conservation and Biology 5:74-86.

Pelomedusidae (based primarily on a preliminary interpretation of morphology from Bour, 1983 and unpublished). Additional sources included Noonan (2000), and the following:

Bour, R. 1983. Trois populations endémiques de genre *Pelusios* (Reptilia, Chelonii, Pelomedusidae) aux îles Seychelles; relations avec les especes africaines et malgaches. Bull. Mus. Natl. Hist. Natur. Paris 4(5):343-382.
Bour, R. 1986. Notes sur *Pelusios adansonii* (Schweigger, 1812) et sure une nouvelle espèce affine du Kenya (Chelonii, Pelomedusidae). Studia Geologica Salmanticencsia. Studia Palaeocheloniologica 2(2):23-54.
Bour, R. 2000. Une nouvelle espèce de *Pelusios* du Gabon (Reptilia, Chelonii, Pelomedusidae). Manouria 3(8):1-32.
Bour, R., and Maran, J. 2003. Une nouvelle espèce de *Pelusios* de Côte d'Ivoire (Reptilia, Chelonii, Pelomedusidae). Manouria 6(21):24-43.

Podocnemididae (based mainly on Starkey et al., unpublished MS; Noonan, 2000; and Noonan and Chippindale, 2006).

Trionychidae (based on Engstrom et al., 2002 and 2004).

Cheloniidae (based primarily on Bowen and Karl, 1997); additional sources included Dutton et al. (1996), and Parham and Fastovsky (1997).

Chelydridae (based on Phillips et al., 1996; and Shaffer et al., 2007).

Kinosternidae (based primarily on Iverson, 1998); additional sources included Hutchison (1991); Serb et al. (2001); and Walker et al. (1998).

Emydidae (based primarily on Stephens and Wiens, 2003b); additional sources included Fritz et al. (2005); Seidel (2002); Starkey (1997); and Starkey et al. (2003).

Geoemydidae (based primarily on Spinks et al., 2004; Le, 2006; Le and McCord, in review); additional sources included Barth et al., (2004); Diesmos et al. (2005); Feldman and Parham (2004); Guicking et al. (2002); Parham et al. (2004); Praschag et al. (2006); Stuart and Parham (2004), and the following:

Moll, E.O. 1986. Survey of the freshwater turtles of India. Part I: The genus *Kachuga*. Journal of the Bombay Natural History Society 83:538-552. [*Kachuga*]

MOLL, E.O. 1987. Survey of the freshwater turtles of India. Part II: The genus *Kachuga* . Journal of the Bombay Natural History Society 84:7-25. [*Kachuga*]

Testudinidae (based primarily on Le et al., 2006); additional sources included Baard (1990); Cunningham (2002); Fritz, et al. (2005); Iverson et al. (2001); Loveridge and Williams (1957); Parham et al. (2006b); Reynoso and Montellano-Ballesteros (2004); and the following:

BROADLEY, D.G. 1993. A review of the southern African species of *Kinixys* Bell (Reptilia: Testudinidae). Annals of the Transvaal Museum 36(6):41-52.

PERÄLÄ, J. 2001. A new species of *Testudo* (Testudines: Testudinidae) from the Middle East, with implications for conservation. Journal of Herpetology 35:567-582.

APPENDIX C

Compilation of candidate trees for supertree analysis. These studies each involved extensive character and taxon sampling, and either reported bootstraps or included raw data that allowed us to calculate bootstraps by resubmitting the data to maximum parsimony analysis (“reran”). For each entry, citation is followed by the text figure depicting the tree, a summary of the data set on which the tree was based, and the method of phylogenetic anlysis used (MP = maximum parsimony; ML = maximum likelihood; NJ = neighbor joining; and MB = MrBayes). Figure numbers in **bold** are those chosen as input trees for the supertree analyses. Some trees were collapsed to species level (so indicated).

Family level			
Shaffer et al. (1997)	Fig. 4a	892 cytb	MP
	Fig. 4b	325 12S rDNA	MP
	Fig. 4c	892 cyt b and 325 12S rDNA	MP
	Fig. 4d	115 morphology	MP
	Fig. 5a	892 cytb, 325 12S rDNA, 115 morphology	MP
	Fig. 5b	115 morphology with fossils	MP
	Fig. 5c	115 morphology with fossils	MP
	Fig. 5d	892 cytb, 325 12S rDNA, 115 morphology with fossils	MP
Cervelli et al. (2003)	Fig. 7 right	270 U17 snoRNA	MP (bootstraps w and w/o indels)
Fujita et al. (2004)	Fig. 4	1093 R35 nuclear intron	ML/ML/MP/MP
Krenz et al. (2005)	Fig. 4A	2793 RAG-1	MP
	Fig. 4B	2793 RAG-1	MB
	Fig. 5A	2793 RAG-1, 892 cyt b, 325 12S rDNA	MP
	Fig. 5B	2793 RAG-1, 892 cyt b, 325 12S rDNA	MB (Note: Fig 1 is Shaffer et al., 1997 with bootstraps)
Near et al. (2005)	Fig A1	892 cytb, 2790 RAG-1, 1009 R35	MB (bootstraps only >95%)
Parham et al. (2006a)	Fig. 3	7.2-16.2kb mtDNA	MP
Chelidae			
Seddon et al. (1997)	Fig. 3	411 12S rRNA	MP
Georges et al. (1998)	Fig. 1	394 12S rRNA, 474 16S rRNA, 345 CO1, 365 c-mos	MP weight/MP not/ML (only >70% bootstraps)
	Fig. 2	12S rRNA, 474 16S rRNA	MP weight/MP not/ML (only >70% bootstraps reported)
	Fig. 3	394 12S rRNA, 474 16S rRNA, 345 CO1	MP weight/MP not/ML (only >70%)
	Fig. 4	consensus of Figs 1-3	MP weight/MP not/ML (no bootstraps)
McCord et al. (2001)	Fig. 2	18 morphological	MP (no bootstraps; JBI reran)
Bour and Zaher (2005)	Fig. 7	19 morphological	MP (no bootstraps; JBI reran)
Pelomedusidae/Podocnemididae			
Noonan (2000)	Fig. 1	921 12S and16S rRNA	MP (and ML)
Starkey et al. (unpubl.)	Fig.	cytb and ND4	MB
Trionychidae			
Meylan (1987)	Figs. 31-34	no bootstraps, but see Engstrom et al 2004	
Weisrock and Janzen (2000)	Fig. 1	806-811 cytb	MP (collapsed)
	Fig. 2	806-811 cytb	NJ
Engstrom and McCord (2002)	Fig. 1	731 ND4/Hist	ML/MP
Engstrom et al. (2004)	Fig. 1	reanalysis of Meylan 1987 with bootstraps	MP
	Fig. 4	735 ND4/His, 1144 cyt b, 1063 R35 separate & combined	MB
	Fig. 5a	3 genes plus morphology	MP
	Fig. 5b	DNA data only	ML
	Fig. 5c	DNA data only	MB
	Fig. 5d	DNA plus morphology	MB
Kinosternidae			
Starkey (1997)	Fig. 19	992 ND4-Leu	NJ (“*leucostomum*” sample is bad)
	Fig. 20	992 ND4-Leu	MP (“*leucostomum*” sample is bad)
Walker et al. (1998)	**Fig. 2**	402 control region	Min evol method (but MP bootstraps)
Iverson (1998)	**Fig. 2**	290 cytb, 34 protein, 27 morphological	MP
Serb et al. (2001)	**Fig. 2**	1158 control region	MP
	Fig. 3	1158 control region	NJ
Cheloniidae/Dermochelyidae			
Bowen et al. (1993)	**Fig. 1 right**	503 cytb	MP bootstraps (but only > 85%) (collapsed)
Dutton et al. (1996)	Fig. 3a.	907 ND4-LEU	MP
	Fig. 3b	526 control region	MP
	Fig. 4b	ND4-LEU, cytb (from Bowen et al. 1993)	MP
	Fig. 4a	ND4-LEU, cytb, control	MP
Bowen and Karl (1997)	Fig. 2.1 top	repeat of Dutton et al 1996	MP
	Fig. 2.1 low	“anonymous mtDNA” (Karl et al. unpublished)	MP
Parham and Fastovsky (1997)	**Fig. 4**	24 morphological	MP no bootstraps (JBI reran)

Emydidae			
Lamb et al. (1994)	**Fig. 6**	74 restriction sites, 380 cytb, 344 control region	MP
Bickham et al. (1996)	**Fig. 3**	556 16S rRNA	MP
	Fig. 4 top	556 16S rRNA	MP
	Fig. 4 bottom	556 16S rRNA	MP
Starkey (1997)	**Fig. 15**	992 ND4-Leu	MP
	Fig. 16	992 ND4-Leu	NJ
	Fig. 17	992 ND4-Leu	MP (positions weighted)
Lamb and Osentoski (1997)	Fig. 3	386-440 cytb, 216-246 control region	MP
Feldman and Parham (2001) (and 2002)	**Fig. 2 (left)**	1200 cytb/threonine, 900 ND4/His/Ser/Leu	MP
Seidel (2002)	Fig. 2	23 morphological	MP (collapsed)
Stephens and Wiens (2003b)	Fig. 7	225 morphological, 345 control region, 1181 cytb	MP
[Note: this paper includes 12 other trees with bootstraps for small partitions of overall data set, e.g. a gene at a time]			
Geoemydidae			
Yasukawa et al. (2001)	Fig. 3	35 morphological	MP (no bootstraps; JBI reran)
	Fig. 4	35 morphological	NJ (no bootstraps)
Parham et al. (2001)	Fig. 3 top	700 CO1, 900 ND4/His/Ser/Leu	MP (lower: ML w/o bootstraps)
Honda et al. (2002a)	Fig. 2a	410 12S, 472 16S rRNA	NJ (all with bootstraps > 50%)
	Fig. 2b	410 12S, 472 16S rRNA	ML (all with bootstraps > 50%)
	Fig. 2c	410 12S, 472 16S rRNA	MP (all with bootstraps > 50%)
Guicking et al. (2002)	Fig. 2	982 cytb	MP (collapsed)
Spinks et al. (2004)	Fig. 2	1140 cytb	ML (but MP bootstraps)
	Fig. 3	1140 cytb, 400 12S rDNA, 1000 R35	ML (but MP bootstraps / MB >95%)
Parham et al. (2004)	**Fig. 1**	831 CO1, 892 ND4/His/Ser/Leu (mtDNA)	MP
Feldman and Parham (2004)	Fig. 1A	831 CO1, 892 ND4/His/Ser/Leu (mtDNA)	MP (collapse)
	Fig. 1B	831 CO1, 892 ND4/His/Ser/Leu (mtDNA)	MB
Stuart and Parham (2004)	Fig. 1	831 CO1, 892 ND4/His/Ser/Leu (mtDNA)	MP
	Fig. 2	831 CO1, 892 ND4/His/Ser/Leu (mtDNA)	ML
Barth et al (2004)	Fig. 2	1080 cytb/threonine	MP/ML/NJ
	Fig. 3A	1080 cytb/threonine	MP/ML (different taxa)
	Fig. 3B	1080 cytb/threonine	ML/MB/NJ
Diesmos et al. (2005)	Fig. 2	cytb, 12S, R35 from Spinks et al (2004) with *leytensis*	MP
Le and McCord (in review)	Fig. 5	1140 cytb, 409 12S, 580 16S, 602 cmos, 642 Rag1	MP
Testudinidae			
Lamb and Lydeard (1994)	Fig. 3A	352 cytb	MP (unweighted)
	Fig. 3B	352 cytb	MP (transversions weighted)
Caccone et al. (1999)	Fig. 2 top left	401 12S rRNA	MP
	Fig. 2 top rt	568 16S rRNA	MP
	Fig. 2 low left	386 cytb	MP
	Fig. 2 low rt	combined	MP (bootstraps in Table 3)
Meylan and Sterrer (2000)	Fig. 8	28 morphology	MP (no bootstraps; ML reran)
Gerlach (2001)	Fig. 5	66 morphological	MP (bootstraps "92-100%"; JBI reran)
Iverson et al. (2001)	**Fig. 1**	1094 cytb	MP/NJ
van der Kuyl (2002)	**Fig. 2A**	404 12S rRNA	MP (collapsed)
	Fig. 2B4	404 12S rRNA	ML (no bootstraps)
	Fig. 2C	404 12S rRNA	NJ
Palkovacs et al. (2002)	Fig. 2A	386 cytb, 403 12S rRNA, 568 16S rRNA	MB
	Fig. 2B	386 cytb, 403 12S rRNA, 568 16S rRNA	ML
	Fig. 3A	386 cytb, 403 12S rRNA, 568 16S rRNA	MP
	Fig. 3B	386 cytb, 403 12S rRNA, 568 16S rRNA	NJ
Caccone et al. (2002)	Fig. 4	430 12S, 553 16S, 416 cytb, 934 control, 1790 ND5, 520 ND6	ML/MP/NJ/MB
Cunningham (2002)	**Fig. 5.8**	1167 cytb+ND4	MP
Perälä (2002)	Fig. 3	61 morphological	MP
	Fig. 4	61 morphological	MP (only outgroup differs from Fig. 3)
Semyenova et al. (2004)	Fig. 5	213 RAPD fragments	UPGMA
Fritz et al. (2005)	Fig. 2	1124 cytb	NJ
	Fig. 3	1124 cytb	MP (collapsed)
	Fig. 5	84 ISSR fingerprints	NJ
Le et al. (2006)	**Fig. 2**	1140 cytb, 408 12S, 583 16S, 602 cmos, 654 Rag2	MP
	Fig. 3	1140 cytb, 408 12S, 583 16S, 602 cmos, 654 Rag2	ML/MB
Parham et al. (2006b)	**Fig. 3**	14858 complete mtDNA	MP/ML/MB