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TESTS OF TURTLE PHYLOGENY: MOLECULAR, MORPHOLOGICAL, AND PALEONTOLOGICAL APPROACHES

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Abstract.—We present phylogenetic analyses of both molecular and morphological data for the 23 major lineages of living turtles and seven key fossil taxa. Nearly 1 kilobase of cytochrome *b* sequence, 325 base pairs of 12S ribosomal DNA, and 115 morphological characters contained similar phylogenetic information, although each provided unique information on different nodes of chelonian history. A character-based combinability test (implemented in PAUP*) and a nonparametric test of taxonomic congruence indicated no strong evidence for heterogeneity among data sets, and we used a combined approach to estimate a final phylogeny of the major lineages of living turtles. This approach resulted in a very well-resolved tree, with only a few of the deep branches within the Cryptodira left as an unresolved polytomy. The addition of six relatively complete fossils chosen to help resolve this basal polytomy provided little added resolution to the tree and resulted in a sharp decline in bootstrap proportions for nodes near the fossils. Branch-length analysis and independent dates from the fossil record suggest that these unresolved nodes may represent a rapid radiation of the major cryptodiran lineages 90–120 million years ago. [Combined molecular and morphological data; fossil and recent phylogeny; mitochondrial DNA; starburst phylogeny; Testudines; total evidence.]

The turtles (order Testudines) have provided key insights into tetrapod phylogenetic history at a number of phylogenetic levels. As the only living anapsid amniotes, the position of turtles relative to mammals, birds, and the remaining "reptiles" is critical in determining the basal condition and early transformations of many amniote characters (Gaffney, 1979; Gauthier et al., 1988b). Recent attempts to identify the extinct sister group of the turtles has provided new insights on the origin of the unique shell and associated shoulder girdle architecture (Reisz and Laurin, 1991; Lee, 1993, 1996; Laurin and Reisz, 1995). Within the Testudines, the quality and duration of the fossil record and morphologically based hypotheses of inter- and intrafamilial relationships have provided some of the better examples of the integration of fossil and living taxa into a single phylogenetic hypothesis of relationships (Gaffney, 1984; Gaffney and Meylan, 1988; Gaffney et al., 1991).

During the last 20 years, a certain level of stability has been achieved for hypotheses of the higher relationships among turtles (Gaffney, 1975a, 1984, 1996; Bickham and Carr, 1983; Gaffney and Meylan, 1988; Gaffney et al., 1991), with 11–13 living families currently recognized (Gaffney and Meylan, 1988; Ernst and Barbour, 1989; Iverson, 1992). Since the work of Cope (1871), these living families have typically been assigned to one of two suborders, the Pleurodira (side-necked turtles) or Cryptodira (hidden-necked turtles) (Gaffney, 1984). Although the monophyly of most chelonian families and the two suborders is reasonably secure, the relationships among the families, particularly of the relatively diverse Cryptodira, remain poorly understood and based on a handful of morphological characters (Williams, 1950; Gaffney, 1975a, 1984; Bickham and Carr, 1983; Gaffney and Meylan, 1988; Gaffney et al., 1991). Thus, the most recent hypotheses (Gaffney and Meylan, 1988; Gaffney et al., 1991; Gaffney, 1996) differ fundamentally from the traditional view of Williams (1950) (cf. Figs. 1, 2), which was widely accepted for 25 years and still has some adherents (Pritchard, 1979). Thus far, the only attempt to test these hypotheses with nonmorphological data employed a small karyological character set (Bickham

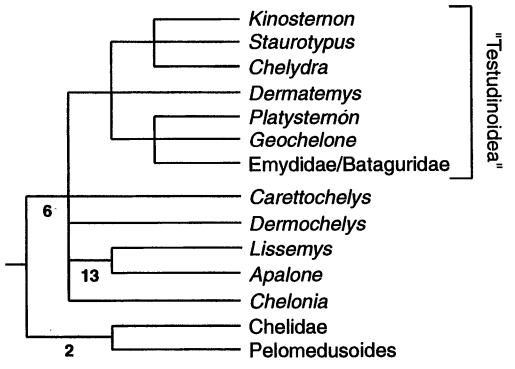

FIGURE 1. Hypothesis of chelonian relationships derived from the classification of Williams (1950). Emydidae, Bataguridae and Pelomedusoides follow the usage in this paper, but "Testudinoidea" reflects Williams's concept of this name. Numbers beneath branches refer to the numbered taxa in Table 1.

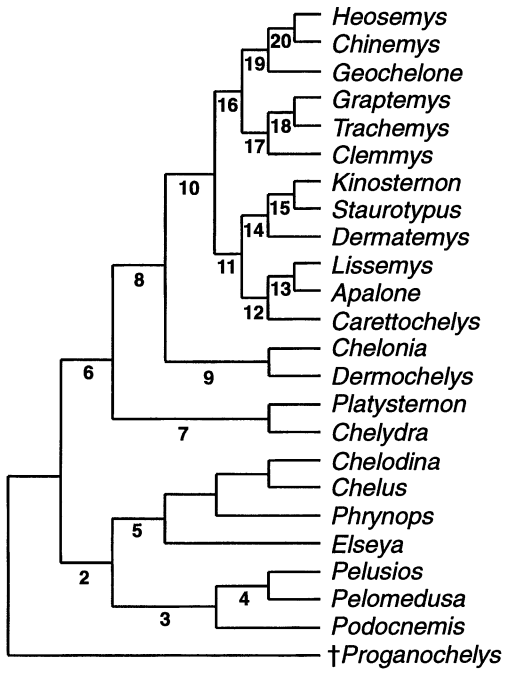

FIGURE 2. Hypothesis of chelonian relationships for the 23 living turtles used in this study based on the work of Gaffney and Meylan (1988), rooted with the fossil turtle †*Proganochelys*. Numbers refer to taxa in Table 1.

and Carr, 1983), and the results of that study differ in several key respects from the recent arrangements based on morphology.

We had two primary goals in this study. First, we compiled a greatly expanded data set for the phylogenetic analysis of 23 living turtle taxa, including representatives of all living families and subfamilies (except Pseudemydurinae, a monotypic and critically endangered Australian chelid taxon) plus all taxa of uncertain higher affinities. Our data set consisted of sequence data from two mitochondrial genes and a companion morphological data set (115 characters) for these same taxa. Our current understanding of higher turtle relationships, as outlined by Gaffney et al. (1991), is based on a subset of these morphological characters. However, this and other previous analyses have not included any statistical assessment of the robustness of the resulting phylogenetic hypothesis (e.g., Gaffney and Meylan, 1988; Gaffney et al., 1991).

Second, we used these data sets to explore the levels of concordance between molecular and morphological data in phylogenetic analysis, considered when such data sets should or should not be combined, and explored the utility of adding relatively complete fossil taxa to the analysis. Although the question of combining morphological and molecular data sets has received considerable attention in the past few years (Kluge, 1989; Shaffer et al., 1991; Bull et al., 1993; Rodrigo et al., 1993; Chippindale and Wiens, 1994; Wiens and Chippindale, 1994; Farris et al., 1995; Miyamoto and Fitch, 1995; Huelsenbeck and Bull, 1996; Huelsenbeck et al., 1996), there are few empirical examples using large data sets for taxa with an extensive fossil record.

BRIEF OVERVIEW OF RECENT HYPOTHESES OF TURTLE PHYLOGENY

Gaffney (1984) provided a complete historical overview of theories of chelonian relationships, from Linnaeus's concept of the single genus *Testudo* to the more recent views of the last several decades. The starting point for modern discussions of the phylogeny of the major groups of turtles is the work of Williams (1950). Although the emphasis of Williams's work was an anal-

ysis of adaptive variation in the structure of the cervical vertebrae, he provided a complete classification of fossil and living turtles that can be treated as a phylogenetic hypothesis (Fig. 1). During the past 20 years, Gaffney and coworkers (Gaffney, 1975a, 1984, 1996; Gaffney and Meylan, 1988; Gaffney et al., 1991; see Fig. 2) have used an extensive morphological data set to challenge much of the phylogenetic arrangement of the major groups proposed by Williams. In addition, two groups of researchers have used nonmorphological data to examine higher relationships of turtles: Chen et al. (1980) used an immunological distance approach, and Bickham and Carr (1983) analyzed variation in chromosome number and morphology among the families of the Cryptodira.

Because it is by far the most complete analysis to date, the morphological evidence of Gaffney and coworkers (Table 1, Fig. 2) is the focus of the following discussion. This work suggested that two major living groups (often recognized as suborders), the Pleurodira and Cryptodira, are each monophyletic. Within the Pleurodira, two living families have historically been recognized, the Chelidae (restricted to Australia/New Guinea and South America) and the Pelomedusidae (South America, sub-Saharan Africa, Madagascar). More recent work (Atunes and de Broin, 1988; de Broin, 1988; de Broin and de la Fuente, 1991; Meylan, 1996) has suggested restricting the family Pelomedusidae to the African genera *Pelusios* and *Pelomedusa*, using Podocnemidae for *Podocnemis*, *Peltocephalus*, and *Erymnochelys* and Pelomedusoides for the sister group of the Chelidae. In this paper, we follow this more recent view and use Pelomedusoides to include the restricted Pelomedusidae (known from the Miocene to Recent of Africa) and three additional families: the Araripemydidae (Cretaceous of South America and Africa), Bothremydidae (Cretaceous to Miocene worldwide) and Podocnemidae (Cretaceous to Recent of South America, Africa, India, and the Greater Antilles). Although this rearrangement increases the number of pleurodire families from two to five

TABLE 1. Twenty-three turtle species for which cytochrome *b* and 12S rDNA sequences were examined for the current study. Higher categories follow Gaffney and Meylan (1988) and Meylan (1996) except for the term Testudinoidae (node 19), which is used here for the first time to indicate monophyly of the Bataguridae plus Testudinidae. In this arrangement, the suffix "-oidae" is used to recognize a group that is more inclusive than the traditional family (-idae) but less inclusive than superfamily (-oidae) categories; this level has been recognized as an epifamily (Bour and Dubois, 1985). The numbers listed in parentheses for the higher taxa are used in all trees whenever these higher categories were recovered.

Testudines (1)
- Pleurodira (2)
  - Pelomedusoides (3)
    - Pelomedusidae (4)
      - *Pelusios williamsi*
      - *Pelomedusa subrufa*
    - Podocnemidae
      - *Podocnemis expansa*
  - Chelidae (5)
    - *Chelodina longicollis*
    - *Chelus fimbriata*
    - *Elseya latisternum*
    - *Phrynops gibbus*
- Cryptodira (6)
  - Chelydridae (7)
    - *Chelydra serpentina*
    - *Platysternon megacephalum*
  - Procoelocryptodira (8)
    - Chelonioidea (9)
      - Cheloniidae
        - *Chelonia mydas*
      - Dermochelyidae
        - *Dermochelys coriacea*
    - Chelomacryptodira (10)
      - Trionychoidea (11)
        - Trionychoidae (12)
          - Trionychidae (13)
            - *Apalone spinifera*
            - *Lissemys punctata*
          - Carettochelyidae
            - *Carettochelys insculpta*
        - Kinosternoidae (14)
          - Kinosternidae (15)
            - *Kinosternon odoratus*
            - *Staurotypus triporcatus*
          - Dermatemydidae
            - *Dermatemys mawii*
      - Testudinoidea (16)
        - Emydidae (17)
          - Emydinae
            - *Clemmys marmorata*
          - Deirochelyinae (18)
            - *Graptemys pseudogeographica*
            - *Trachemys scripta*
        - Testudinoidae (19)
          - Bataguridae (20)
            - *Heosemys spinosa*
            - *Chinemys reevesii*
          - Testudinidae
            - *Geochelone pardalis*

(and the number of living families from two to three), it suggests no new hypotheses for the relationships among living pleurodires.

A key feature of the current views on chelid relationships is the hypothesized nonmonophyly of either the South American or the Australian (including New Guinea) forms. In particular, the Australian genus *Chelodina* has been hypothesized as the sister group to the South American *Hydromedusa*, followed as sequential sister groups by three South American genera (*Chelus*, *Phrynops*, *Platemys*) and two Australian clades (the short-necked genera *Emydura/Elseya* and the monotypic *Pseudemydura umbrinus*; Gaffney, 1977). Assuming no transoceanic dispersal between South America and Australia, this hypothesis implies that the recognized genera of chelids should predate the split of Australia from South America (only the *Chelodina–Hydromedusa* split could be associated with the continental split) and are thus at least 55 million years old (Woodburne and Case, 1995).

Within the Cryptodira, Gaffney and coworkers considered the living families to comprise the Polycryptodira, which includes four major clades: the snapping turtles (Chelydridae), the sea turtles (Chelonioidea), the soft-shelled turtles and their allies (Trionychoidea), and the pond turtles and land tortoises (Testudinoidea) (Gaffney and Meylan, 1988), with the Chelydridae as the sister group to the remaining three clades. The various hypotheses of relationships (Williams, 1950; Bickham and Carr, 1983; Gaffney and Meylan, 1988) differ to some degree on the content and relationships of all of these groups.

Given the additional data that have become available in the last 45 years, it is fairly clear that the sea turtles are in fact a monophyletic group, although this group was left ambiguous in Williams's (1950) scheme (Fig. 1). Beyond that, there are major differences at a variety of levels. Primary among these are (1) the purported monophyly of the family Kinosternidae (possibly paraphyletic with respect to the Chelydridae [Williams, 1950] or polyphyletic based on chromosomes [Bickham and Carr, 1983]), (2) the monophyly of the Trionychoidea (viewed as polyphyletic by Williams [1950] and Bickham and Carr [1983]), (3) the placement of the Asian big-headed turtle, *Platysternon* (a snapping turtle according to Gaffney and coworkers but a testudinid [=testudinoid] according to Williams [1950] and Bickham and Carr [1983]), (4) the placement of the snapping turtles (the sister group to all other living cryptodires according to Gaffney and Meylan [1988] but a relatively derived member of the Cryptodira according to other workers), and (5) the relationships of the three components of the Testudinoidea: the primarily New World Emydidae, the primarily Old World Bataguridae, and the exclusively terrestrial Old and New World tortoises (Testudinidae).

Materials and Methods

Choice of Taxa

The 23 living taxa included in this study were selected to allow us to address several specific questions in higher systematics of turtles and to construct a hypothesis that includes all of the family level groups recognized by recent authors (Gaffney and Meylan, 1988; Ernst and Barbour, 1989; Iverson, 1992). The higher category representation (following Gaffney and Meylan, 1988) of the 23 living taxa is provided in Table 1. The four members of the Chelidae include two South American and two Australian representatives, which allowed us to test Gaffney's (1977) hypothesis that neither the Australian nor the South American chelids are monophyletic. *Platysternon* was included to examine the phylogenetic position of this problematic genus. *Staurotypus* was included to test the hypothesis that the subfamily Staurotypinae has a close relationship with the Testudinoidea (Bickham and Carr, 1983) rather than with the Kinosternidae, which is the more traditional placement. The two "batagurids" chosen include one broad-jawed (batagurine) and one narrow-jawed (geomydine) representative to test Hirayama's (1985) hypothesis that the Bataguridae is para-

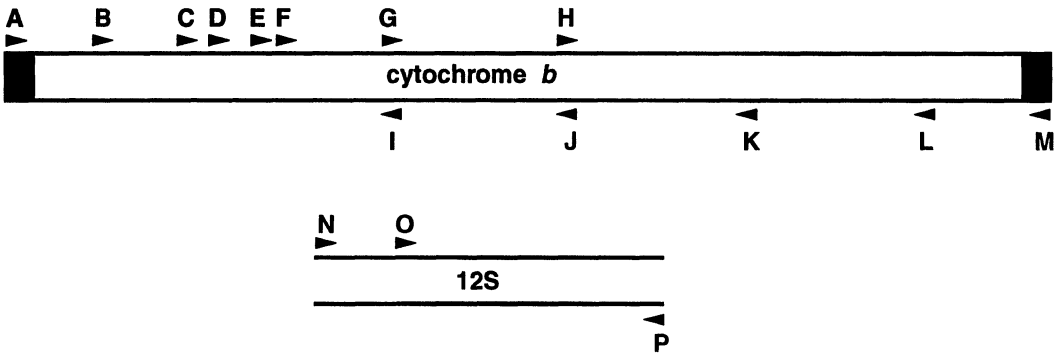

FIGURE 3. Arrangement of oligonucleotide primers for the amplification and sequencing of the mtDNA genes cytochrome *b* and 12S ribosomal DNA. For both of the regions depicted, the light strand and its associated primers is on top. The sequences of the primers are given in Table 2.

phyletic with respect to tortoises (Testudinidae) and that the narrow-jawed forms gave rise to tortoises.

Seven fossil taxa were also included in this study. †*Proganochelys* was included to root the morphological and combined data trees. The other six genera were included in an attempt to resolve relationships among the higher cryptodiran groups. Each genus exhibits a unique set of morphological characters that we hoped would help clarify higher relationships left poorly resolved by molecular data alone, morphological data for living genera alone, or those two data sets combined.

†*Proganochelys*, the Triassic sister group to all other turtles, was scored based on Gaffney's (1990) characters. †*Meiolania*, the Tertiary sister group of the living cryptodires plus the Sinemydidae, also was scored based on Gaffney's (1983, 1985, 1996) characters. †*Sinemys*, a Cretaceous representative of the Sinemydidae, was scored based on Brinkman and Peng's (1993) characters. †*Adocus* and †*Emarginachelys*, two Cretaceous trionychoids, were scored based on Meylan and Gaffney's (1989) characters. †*Lindholmemys* and †*Mongolemys* were scored based on Meylan and Gaffney's ongoing, unpublished study of material on loan to Gaffney.

Mitochondrial DNA Sequences

We obtained tissue samples from a variety of sources: wild-caught living turtles, living turtles purchased from the pet or food trade, deceased turtles salvaged from the pet trade, and zoo specimens. We extracted genomic DNA from various available tissues (blood, liver, muscle, heart, tail tips) by SDS/proteinase K digestion and phenol/chloroform extraction. Specific regions of mitochondrial DNA (mtDNA) were amplified (*Taq*-mediated polymerase chain reaction), and sequences were obtained (Sequenase 2.0, U.S. Biochemical) using the primers illustrated in Figure 3 and described in Table 2. Certain primer combinations did not result in DNA amplification for some turtles. Some of these failures probably were due to mismatches between the turtle DNA sequence and one of the primers (e.g., pelomedusids seemed to match poorly with primer M, Fig. 3), whereas other failures probably resulted from partial degradation of the turtle DNA (i.e., from salvaged pet trade animals), yielding DNA copies of insufficient length to span the longer regions between primer pairs. In these cases, we were successful in obtaining sequence from the total region of interest by amplifying overlapping short segments of DNA using combinations of internal primers. The nucleotide sequence data were recorded from the autoradiograms and inverted and aligned within individual turtles using the GeneJockey sequence processor (Biosoft, Cambridge, England). Alignments of sequences across taxa were made by eye. For cytochrome *b*,

TABLE 2. Oligonucleotide primers (5′ to 3′) used in amplification and sequencing of mitochondrial DNA of turtles. Letter identifications refer to Figure 3.

Identifier	Sequence[a]	Position[b]	Source
A	TGACTTGAARAACCAYCGTTG	16228	Palumbi et al., 1991
B	CCATCCAACATCTCAGCATGATGAAA	16346	Palumbi et al., 1991
C	ACTAGCATTCTCATCAGTAG	16450	Shaffer lab
D	CGAGATGTTAATAACGGCTG	16481	Shaffer lab
E	GCGCCTCATTCTTCTTTATCT	16528	Shaffer lab
F	TGCATCTACCTTCACATYGGMCG	16550	Shaffer lab
G	TGAGGACAAATATCATTCTGAGGGGCTGCAG	16677	M. Ptacek
H	TTCCTWCACGAAACAGGNTCAAACAA	16871	T. Case lab
I	CCCTCAGAATGATATTTGTCCTCA	16654	Palumbi et al., 1991
J	CCTGTTGGGTTYTTTGAKCC	16861	Shaffer lab
K	GGCAAATAGGAARTATCATTC	17062	Palumbi et al., 1991
L	TCTTCTACTGGTTGTCCTCCGATTCA	17257	M. Ptacek
M	TCATCTTCGGTTTACAAGAC	17407	Shaffer lab
N	AAACTGGGATTAGATACCCCACTAT	2509	Palumbi et al., 1991
O	CCTAGAGGAGCCTGTTC	2620	Shaffer lab
P	GAGGGTGACGGGCGGTGTGT	2897	Palumbi et al., 1991

[a] Redundancy codes: K = G and T; M = A and C; R = A and G; W = A and T; Y = C and T; N = A, C, G, and T.
[b] Positions of the 3′ nucleotides of all primers are given in reference to the complete mitochondrial genome sequence of *Xenopus* (Roe et al., 1985).

alignments were unambiguous, no insertions or deletions were detected, and all sequences were successfully translated to amino acid sequences. For 12S ribosomal DNA (rDNA), alignments were more difficult, particularly in regions with repeated nucleotide sequences (e.g., TTATT vs. TTTATT vs. TTATTT). In these areas, as well as regions with many insertions and deletions, we followed the relatively conservative approach of deleting the entire region rather than guessing at the presumed homology of individual sites.

Morphological Characters

The previous morphological analysis reported by Gaffney et al. (1991) was conducted using the (inferred) basal condition of each character for each family level taxon. In the present study, we instead used the specific characters found in each of the representative species. Thus, it was necessary to compile a new morphological data set that included specific observations for all of the 23 living species included in this study and for the fossil taxa. A total of 115 morphological characters were scored. Characters 1–39 are those used and described in detail by Gaffney et al. (1991). Characters 40–108 are those of Gaffney and Meylan (1988) (with modification of characters 40, 43, and 55 to include multiple states), and characters 109–115 are those of Gaffney (1996). Because characters 40–115 have not been described previously, we provide a brief description in Appendix 1.

Analysis

We conducted all phylogenetic analyses and character reconstructions under parsimony, using PAUP 3.1.1 (Swofford, 1993). For the combinability test only, we used PAUP* (4.0d42, PPC version; Swofford, 1996). We ran separate analyses for the cytochrome *b*, 12S, and morphological data sets and combined analyses for the two DNA sequences and for all three data sets. For each analysis, we ran 10 replicate random stepwise addition heuristic searches using the default PAUP settings, and in cases where more than one tree was found, we report the 50% majority rule consensus of multiple trees. To assess statistical reliability, we generally bootstrapped each data set 1,000 times (Felsenstein, 1985). In analyses that included the fossil taxa, bootstrap replicates sometimes led to hundreds or thousands of equally parsimonious trees, and memory/time limitations made it necessary to retain at most 500 trees at a time. The literature on interpreting boot-

strap proportions (BPs) is still in a state of uncertainty (Felsenstein and Kishino, 1993; Hillis and Bull, 1993): we consider BPs >90% as highly significant, those of 70–89% as marginally significant, and those <70% as constituting limited evidence of monophyly. For all analyses that included the morphological data set (alone or in combination), we used †*Proganochelys* as the outgroup for the living turtles (Gaffney, 1990). For the purely molecular results, we assumed that Cryptodira and Pleurodira are each monophyletic (Gaffney, 1975a; Gaffney and Meylan, 1988; Gaffney et al., 1991) and used Pleurodira as the outgroup. We also conducted analyses using mammals as an outgroup to all turtles (results not shown), although the very ancient separation of turtles and all other amniotes limited our confidence in these results.

Given the recent concern over when and how to combine data sets and trees (Kluge, 1989; Shaffer et al., 1991; Miyamoto and Fitch, 1995), we feel that the approach advocated by Bull et al. (1993) appears to make the most intuitive and statistical sense. These authors treated the problem of combining data sets in the same way that one approaches the more familiar problem of pooling subsamples in an analysis of variance. Thus, trees are computed for each data set (or partition of the total data set) separately, and then one or more tests are applied to determine whether the trees differ statistically. If they do not, then the reasonable strategy would be to pool the partitions into a single data set. However, if a strong conflict is found, then the data sets should not be combined, but rather energy should be focused on determining why the two data sets are not reflecting the common phylogenetic history of the taxa.

We used two different approaches to address this combining problem. Our primary test was that described by Farris et al. (1994; see also Swofford, 1991, for a discussion of related character incongruence indices) as implemented in the combinability test of PAUP* 4.0d42. The test computes the length of the separate trees for each of two preassigned data partitions and the length of the tree for the combined data set. The difference between the length of the sum of the two separate analyses and that of the combined data set reflects the extent to which the two partitions differ; if the two partitions strongly support very different trees, then the combined data set will have much more homoplasy than does each data set individually and the combined length will be much longer than the sum of the separate analyses. To construct a test statistic, the full data set is randomly partitioned, and the difference in tree lengths for the partition of interest is compared with the distribution of differences for the random partitions of the same size as the original data set. We used the default settings in PAUP* with 1,000 randomizations in all tests; $P < 0.05$ provided statistical evidence that the data sets should not be combined. Second, we used Templeton's (1983) test to determine whether the most-parsimonious tree generated from the molecular and morphological data partitions separately were significantly different. To carry out this test, we followed Larson's (1994) recommendations. The "Compare Trees" menu item in MacClade (Maddison and Maddison, 1992) was used to tabulate the number of morphological characters that differentially agree with (i.e., have a different number of steps on) each of the morphological and molecular most-parsimonious trees, and the Wilcoxon sign–rank test was used to determine whether the morphological data significantly support the morphology tree over the molecular tree. Based on the three-taxon case, Felsenstein (1985) found that a one-tailed test was generally accurate but occasionally was not always conservative for Templeton's test. Although this result has not been extended to cases with more than three taxa, we followed Felsenstein's (1985) and Larson's (1994) recommendation and used the more conservative two-tailed rather than the one-tailed significance test. The same analysis was conducted for the molecular data set to determine if it constitutes a significantly better fit to either tree. Again, an insignificant result for both data sets suggests that there

is no conflict between the partitions and that pooling the data sets is appropriate.

RESULTS

Molecular Analyses

Cytochrome b only.—Our complete cytochrome *b* data set consisted of 892 nucleotides sites, including most of the gene. Of these, 518 sites were variable across some taxa and were included in the analysis (Appendix 2). Ten replicate random stepwise-addition heuristic searches produced a single minimum-length tree (Fig. 4a).

Several important features emerged from this single-gene analysis. First, most of the currently recognized families of turtles were well supported, including the Emydidae (sensu stricto, Gaffney and Meylan, 1988; Seidel and Meylan, unpubl. data), Deirochelyinae, Bataguridae, Trionychidae, Kinosternidae, and Pelomedusidae (sensu stricto, Gaffney and Meylan, 1988; Seidel and Meylan, unpubl. data). These results also provided weaker support for the close relationship of the tortoises (represented here by *Geochelone*) to the batagurids and for the monophyly of the Chelidae. The hypothesized paraphyly of the Bataguridae with respect to tortoises proposed by Hirayama (1985) was not supported. At the suprafamilial level, cytochrome *b* provided marginal support (BP = 60%) for the monophyly of living marine turtles and for the monophyly of the Cryptodira (BP = 60%) and strong support for the more inclusive Pelomedusoides (i.e., the sister-group relationship of *Podocnemis* to *Pelomedusa* and *Pelusios*). Finally, the sister-group relationship of soft-shelled turtles (Trionychidae, group 13) and the monotypic Carettochelyidae emerged from this analysis, although with a BP of <50% (node 12, Fig. 4a).

Beyond these groups, cytochrome *b* alone was relatively uninformative for deeper suprafamilial relationships. In an effort to remove those characters that might be saturated and thus detract from the phylogenetic signal for the deeper nodes, we translated the sequences to amino acids and ran the analysis on this much less variable data set. This analysis produced no greater resolution (i.e., no additional nodes) but rather resulted in a severe loss of resolution for the more recent nodes of the tree. We obtained a similar result when we eliminated third codon positions, many of which represent rapidly evolving silent substitutions.

12S rDNA only.—Because of the slower rate of nucleotide substitution of 12S rDNA compared with that of cytochrome *b* (Brown et al., 1982; Brown, 1983), we included 325 base pairs from the mitochondrial 12S gene with the primary objective of acquiring information on some of the deeper nodes of the chelonian phylogeny. Ninety-nine sites were variable across some taxa (Appendix 3), resulting in two most-parsimonious trees. The 12S rDNA analysis alone contained surprisingly little strong phylogenetic information for deep or shallow nodes (Fig. 4b). Of the groups recognized in this analysis with BPs >50% (i.e., recognized with even marginal statistical support), most were also recognized in the cytochrome *b* analysis at higher BPs (nodes 3, 4, 15, 18; see Table 1, Figs. 4a, 4b). The single instance where 12S rDNA provided novel information was in strong support for the sister-group relationship of the monotypic *Dermatemys mawii* with the Kinosternidae in the Kinosternoidae (group 14, BP = 92%). The 12S rDNA data were also informative within the Chelidae and provided strong support for the monophyly of the South American chelids *Chelus* and *Phrynops* and weaker support (BP = 79%) for the paraphyly of the Australian chelid genera *Elseya* and *Chelodina*.

Combined molecular data.—Following Farris et al. (1994), we tested the two molecular data sets, and the tree lengths for the separate analyses were not significantly shorter than those for the combined molecular data sets ($P = 0.407$). We therefore combined the two data sets, and analyzed the 617 variable nucleotide sites in a single parsimony analysis. In general, the combined analysis closely followed that based on cytochrome *b*, especially when only well-supported nodes are considered (Fig. 4c). For virtually all of the nodes shared in

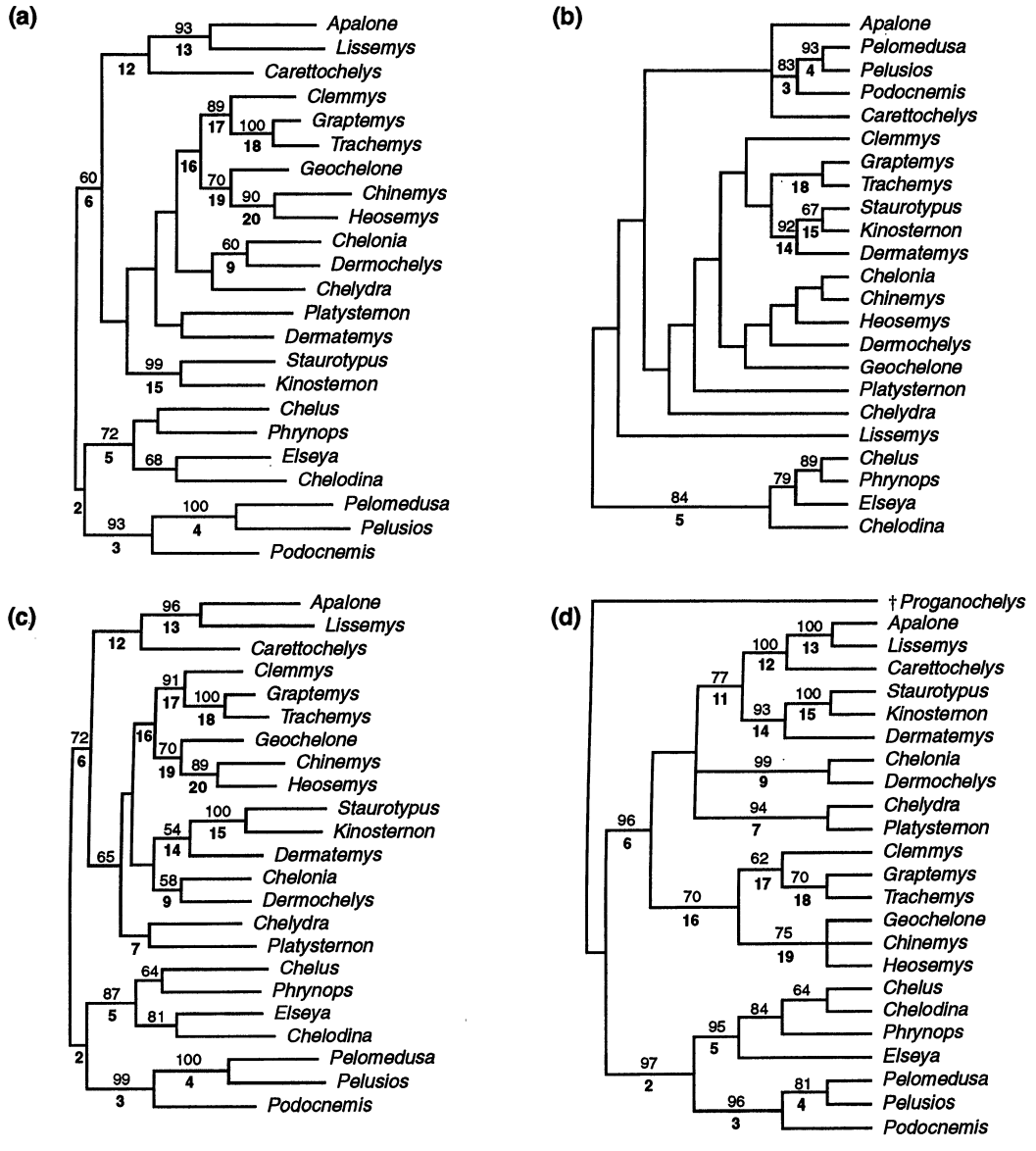

FIGURE 4. Chelonian cladograms produced by the data sets separately (plus molecular data combined). Bold numbers beneath branches refer to the numbered taxa in Table 1, and numbers above branches are bootstrap proportions (based on 1,000 bootstrap replicates) for all groups recovered in at least 50% of the bootstrap replicates. (a) The single most-parsimonious tree (shown as a phylogram with ACCTRAN optimization) based on 518 variable nucleotide sites from mitochondrial cytochrome *b*. The tree has 2,433 steps, consistency index (CI) = 0.361, CI for informative characters only = 0.328, retention index (RI) = 0.280. (b) Consensus of the two most-parsimonious trees based on 99 variable sites from mitochondrial 12S rDNA. The most-parsimonious trees from these data had 277 steps, CI = 0.484, CI based on informative characters only = 0.391, RI = 0.534. (c) The single most-parsimonious tree (shown as a phylogram with ACCTRAN optimization) based on the combined cytochrome *b* and 12S rDNA data. The tree has 2,615 steps, CI = 0.387, CI based on informative characters only = 0.347, RI = 0.350. (d) Consensus of 11 most-parsimonious trees based on 115 morphological characters. The most-parsimonious trees from these data had 174 steps, CI = 0.713, CI based on informative characters only = 0.684, RI = 0.874.

common between these two analyses, the combined data set had higher BPs, reflecting the agreement between these two genes. The combined analysis did produce several new features not seen in the analysis of either data set individually. Foremost among these is the first hint of a sister-group relationship between *Chelydra* and *Platysternon* (as suggested previously based on morphological criteria, Table 1). In addition, the monophyly of the South American chelids (*Chelus, Phrynops*) and Australian chelids(*Elseya, Chelodina*) received moderate statistical support in this analysis for the first time. Perhaps most significant is evidence against the monophyly of the Trionychoidea (Gaffney, 1975a; Gaffney and Meylan, 1988; Meylan and Gaffney, 1989).

Morphological data only.—The morphological data set consisted of 115 characters (described in Appendix 1) scored for all 23 ingroup members, a fossil outgroup †*Proganochelys quenstedti*, and six key fossil taxa (Appendix 4). For the living taxa and †*Proganochelys*, using the same search strategy as for the molecular data, we found 11 minimum-length trees, each of 174 steps. The consensus tree (Fig. 4d) is remarkably similar to the tree from the combined molecular data set (Fig. 4c), with conflicting nodes generally showing low to medium bootstrap support in both trees. Only two nodes of the morphology tree are in conflict with the combined molecular tree. The sister-group relationship of the Kinosternidae plus *Dermatemys* with Trionychidae plus *Carettochelys* (node 11, the Trionychoidea) received moderate support in the morphological analysis (BP = 77%) but was not supported in the molecular analysis. However, the alternative interpretation of the monophyly of living cryptodires exclusive of trionychids and *Carettochelys* received equally weak support (65%) in the molecular tree. A second major discrepancy is the monophyly of the South American (*Chelus, Phrynops*) and Australian (*Elseya, Chelodina*) chelids, which received weak to moderate support (BP = 64% and 81%, respectively) from the molecular data set. The morphological data provided moderate statistical support for an alternative pattern of South American and Australian chelid relationships (Fig. 4d).

Combined molecular and morphological data (living taxa).—Again following Farris et al. (1994), we determined that the molecular and morphological data sets were combinable ($P = 0.335$). Templeton's (1983) test provided a similar result. For the morphological data set, 18 characters differed in their degree of support for the molecular or morphological most-parsimonious trees, leading to a Wilcoxon test statistic (T_s) of 42.5. This value is not statistically significant (although it is nearly so, $0.05 \leq P \leq 0.10$, $n = 18$), implying that there is not substantially better morphological support for either tree. Similarly for the molecular data, for 71 informative characters T_s = 1,204, which is well above the calculated threshold value of 936 for the $P \leq 0.05$ level. Again, the molecular data did not significantly support either of the most-parsimonious trees to the exclusion of the other. Based on both tests, we combined all of our data into a single data set of 732 variable characters, 590 of which were informative. This data set produced a single maximum parsimony tree (Fig. 5a). As might be expected, this tree reflects those nodes that received very strong support from either data set and those that received weak support from all data sets. In this fully resolved cladogram, 14 of 21 possible nodes were strongly supported statistically (BP $\geq$ 90%) and two more received moderate statistical support (70% $\leq$ BP $\leq$ 90%). For the three nodes where the morphological and molecular data sets are in conflict, the combined data produced a topology identical with the molecular analysis. Thus, the monophyletic group containing Trionychidae, Carettochelyidae, Kinosternidae, and Dermatemydidae in the Trionychoidea (node 11, Table 1) was not supported by the combined analysis. In the other conflicting region, the South American and Australian chelid genera were each reconstructed as monophyletic groups in the combined tree, although their low BP values (58% and 69%, respec-

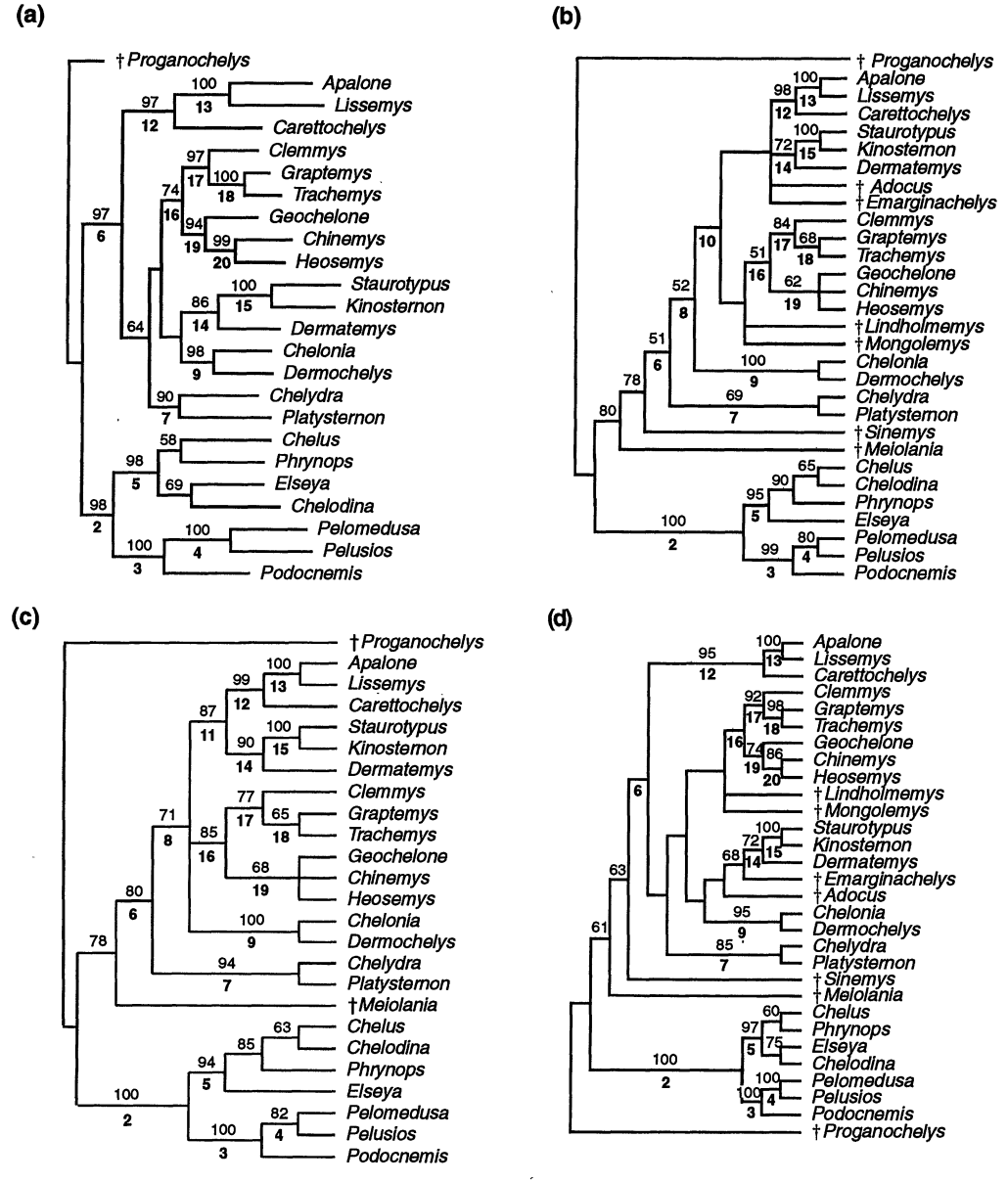

FIGURE 5. Chelonian cladograms produced by various combinations of the data sets. Bold numbers beneath branches refer to the numbered taxa in Table 1, and numbers above branches are bootstrap proportions (based on 1,000 bootstrap replicates, except as noted) for all groups recovered in at least 50% of the bootstrap replicates. (a) The single most-parsimonious tree (shown as a phylogram with ACCTRAN optimization) based on the combined molecular (cytochrome *b* and 12S rDNA) and morphological data. The most-parsimonious trees from these data had 2,793 steps, CI = 0.407, CI based on informative characters only = 0.367, RI = 0.418. (b) Consensus of nine most-parsimonious trees based on 115 morphological characters for 23 living species, the fossil outgroup †*Proganochelys*, and six additional key fossils. The most-parsimonious trees from these data had 202 steps, CI = 0.619, CI based on informative characters only = 0.593, RI = 0.834. (c) Consensus of two most-parsimonious trees based on 115 morphological characters for 23 living species, the fossil outgroup †*Proganochelys*, and the fossil †*Meiolania*. The most-parsimonious trees from these data had 178 steps, CI = 0.697, CI based on informative characters only = 0.671, RI = 0.870. (d) Consensus of three most-parsimonious trees based on the combined molecular (cytochrome *b* and 12S rDNA) and morphological data for 23 living species, the fossil outgroup †*Proganochelys*, and six additional key fossils. The most-parsimonious trees from these data had 2,819 steps, CI = 0.403, CI based on informative characters only = 0.364, RI = 0.421. BPs are based on 530 bootstrap replicates.

tively) reflect the conflict among data sets in this part of the tree.

The effect of fossils.—In an attempt to further resolve the relationships among the major groups of living cryptodires, we added six key fossils to our analysis (Appendix 4) and reanalyzed both the morphological and combined data sets. If the existing classification of these taxa is correct, we expected these fossils to provide information at three distinct levels in the cryptodiran tree. †*Meiolania* and †*Sinemys* are both considered to be sister groups to the living Cryptodira (Gaffney, 1996) and were included to help resolve basal relationships within that group. †*Adocus* and †*Emarginachelys* are considered to be the sister groups to the living Trionychoidae and the living Kinosternoidae, respectively (Meylan and Gaffney, 1989), and were included to provide further information on the purported monophyly of the Trionychoidea. †*Mongolemys* and †*Lindholmemys* are the sister groups to either the living Testudinoidea or the living Bataguridae (Meylan, unpubl.) and were included to help further resolve the position of the Testudinoidea.

The effect of these fossils on the morphological data set is illustrated in a comparison of Figure 4d (including all 23 living taxa plus †*Proganochelys*) and Figure 5b (all six fossil taxa included in addition to †*Proganochelys*). Topologically, Figure 5b differs from Figure 4d in recovering more fully the branching pattern suggested by Gaffney and Meylan (1988) and Gaffney et al. (1991) by resolving the Procoelocryptodira (node 8, BP = 52%) as the sister group to the Chelydridae and the Chelomacryptodira (node 10, BP < 50%) as the sister group of the Chelonioidea. In the absence of these fossils, the relationships among the basal groups of the living cryptodires are an unresolved polytomy in which the Testudinoidea is the sister group of an unresolved trichotomy including the Trionychoidea, Chelonioidea, and Chelydridae. However, when the fossils were included in the analysis, the living Trionychoidea (node 11) disappeared from a reasonably well-supported group (Fig. 4d, BP = 77%) into an unresolved polytomy including the Trionychoidae, Kinosternoidae, †*Adocus*, and †*Emarginachelys*. Thus, the inclusion of fossils generally allowed a more complete resolution of cryptodiran relationships, although both analyses resulted in weak bootstrap support for all of these nodes.

From a statistical perspective, an additional and striking effect of the inclusion of the fossils was seen in the reduced BP values of the nodes surrounding the fossil taxa. For example, without fossils, the Chelydridae received strong support (BP = 94%, Fig. 4d, node 7), but when fossils were included this value dropped to 69% (Fig. 5b, node 7). Other nodes that showed a striking drop in BP are the Testudinoidae (node 19, BP dropped from 75% to 62%), Kinosternoidae (node 14, BP dropped from 93% to 72%), Testudinoidea (node 16, BP dropped from 70% to 51%), and the living Cryptodira (node 6, BP dropped from 96% to 51%). Only the Emydidae (node 17) showed a marked increase in BP with the addition of fossils (from 62% to 84%).

When fossils were added either singly (†*Meiolania* only) or pairwise (two cryptodiran outgroups, two trionychoids, two testudinoids) to the analysis, the decrease in BP occurred only in the immediate vicinity of a given pair of fossils, and both topology and BP occasionally changed in other parts of the tree. To examine the impact of a single fossil to our analysis, we included †*Meiolania* as an extinct sister group to the living Cryptodira. The addition of this single taxon (Appendix 4; 91.3% complete) resulted in two general changes in the morphology-based tree (Fig. 5c). First, the BP at the base of the living Cryptodira decreased from 96% to 80%. Second, several other basal nodes within the Cryptodira emerge for the first time or BP support for those nodes increased (cf. Figs. 4d, 5c). Thus, the Testudinoidea (node 16) was more strongly supported (BP increased from 70% to 85%), as was the Trionychoidea (node 11, BP increases from 77% to 87%). There was also the emergence, with moderate support (BP = 71%), of the Procoelocryptodira (node

8), providing statistically defensible structure within the otherwise problematic higher groups of living cryptodires.

When fossils were added pairwise, the same decrease in BP in the nodes near the insertion of the fossil was found as when all six fossils were added simultaneously. For example, when only †*Adocus* and †*Emarginachelys* were added to the data matrix, the drop in BP at nodes 11 (BP = 54%) and node 14 (BP = 76%) was virtually identical to that seen with all six fossils (Fig. 5b), but all other values were within one or two percentage points of those found without fossils. We found a similar pattern in changes of bootstrap values with the other two pairs of fossil taxa. Resolution of cryptodire relationships also varied among these pairwise additions. The addition of †*Meiolania* and †*Sinemys* resulted in the topology of major groups supported by Gaffney and Meylan (1988) and Gaffney et al. (1991) (Fig. 5b). The addition of †*Adocus* and †*Emarginachelys* or †*Lindholmemys* and †*Mongolemys* resulted in the groups (((Chelydridae, Chelonioidea)Trionychoidea)Testudinoidea).

The inclusion of fossils in the combined morphological and molecular data set had a similar effect on bootstrap values (cf. Figs. 5a, 5d). With respect to living taxa, these two trees are topologically identical, and the fossils were placed essentially as expected based on previous work. (The only discrepancy was the placement of †*Adocus* as the sister group of the living Kinosternoidae rather than as the sister group of the living Trionychoidae.) Thus, the inclusion of fossils in the combined data set did not impact the tree topology. However, as in the morphological analyses, the effect on BP was striking. In all cases, BPs declined in the nodes surrounding the placement of fossil taxa. Particularly striking were the drops in BP for living Testudinoidea (node 16, BP dropped from 74% to <50%), Testudinoidae (node 19, BP dropped from 94% to 74%), and the living Cryptodira (node 6, BP dropped from 97% to <50%). Again, when the fossils were entered as pairs, each pair only affected BPs for nodes in its immediate vicinity, leaving the rest of the tree unchanged. Thus, the effect of adding fossils to the total data set appears to be one of reducing the statistical support for specific nodes rather than providing any increase in resolution. In revealing this reduced statistical support, the fossils call into question any current resolution of relationships among the major cryptodire groups. We are left with five major groups (Trionychoidae, Kinosternoidae, Chelydridae, Chelonioidea, Testudinoidea) whose relationships remain unresolved.

Discussion

Our data set allowed us to address several topics relevant to the analysis of chelonian phylogenetic relationships: the general issue of combining different classes of data; the current status of chelonian phylogeny, the areas of the tree that appear to be well understood, and those that will require additional work; the role of adding key fossils to the analysis; and what may be a general feature of this and other trees, i.e., relatively well-resolved terminal groups with extremely short internal nodes.

To Combine or Not to Combine (Data Sets)

Since Kluge's (1989) key paper, the question of how best to combine different data sets has emerged as one of the more contentious issues in phylogenetic analyses (Shaffer et al., 1991; Swofford, 1991; Bull et al., 1993; Chippindale and Wiens, 1994; Miyamoto and Fitch, 1995; Huelsenbeck et al., 1996). Most researchers agree that neither morphological nor molecular data are inherently superior in terms of homoplasy levels (Hillis, 1987; Sanderson and Donoghue, 1989) and that all data potentially contribute to phylogenetic analysis. Thus, the question is not whether to collect and use different data sets but how to combine them to estimate phylogeny.

In this study, we relied on the statistical approach advocated by Bull et al. (1993), in which data sets are compared for their inherent combinability. We primarily relied on the test statistic proposed by Farris et al. (1994), as implemented in PAUP*, be-

TABLE 3. Bootstrap percentages for the higher turtle taxa from Gaffney and Meylan (1988). The name Testudinoidae is used here for the first time to reflect the likely sister-group relationship of Testudinidae and Bataguridae within the Testudinoidea. Only groups for which two or more genera were included in the study are listed.

Higher taxon	Trees		
	Morphology	Total molecular	Total evidence
Pleurodira	97	—[a]	98
Pelomedusoides	96	99	100
Pelomedusidae	81	100	100
Chelidae	95	87	98
Chelini	84	—	—
Chelina	64	—	—
Cryptodira	96	72	97
Chelydridae	94	—	90
Procoelocryptodira	—	—	—
Chelonioidia	99	58	98
Chelomacryptodira	—	—	—
Trionychoidea	77	—	—
Trionychoidae	100	—	97
Trionychidae	100	96	100
Kinosternoidae	93	54	86
Kinosternidae	100	100	100
Testudinoidea	70	—	74
Emydidae	62	91	97
Deirochelyinae	70	100	100
Testudinoidae	75	70	94
Bataguridae	—	89	99

[a] Dashes indicate bootstrap values <50%.

cause it provides an explicit hypothesis-testing framework for determining combinability. We also used Templeton's (1983) approach as a fundamentally different (both statistically and conceptually), more tree-based approach to the combinability problem. In the present case, both the molecular and the morphological data sets were informative for the same sets of nodes and became relatively uninformative at the deeper levels of the trees. Thus, the places where they disagree were so weakly supported statistically that combining appears to be the best strategy for extracting as much information as possible from the analysis (Bull et al., 1993). Table 3 contains BPs for each data set alone and both in combination. If we were to accept only those higher groups of turtles that showed congruent strong support (nodes with BP $\geq$ 90%) for both the morphological and molecular data sets (n = 3), we would have significantly less resolution of turtle relationships than is apparent from the combined data set (14 nodes with BP $\geq$ 90%).

Although this approach is reasonable for the combination of disparate data sets, the general issue of combining data (as opposed to combining trees) is still subject to problems that are sufficiently complex that they warrant consideration on a case-by-case basis. These problems are of at least two types. First, different forms of analysis (e.g., likelihood vs. parsimony) may be most appropriate for different types of data (Shaffer et al., 1991). In such cases, taxonomic congruence may often provide insights that cannot be obtained by character congruence alone.

The second problem is more difficult to identify but may be important in the application of the bootstrap to many data sets. It centers on our perception that there may be a real difference in how morphological and molecular characters are discovered and used in systematics and on the logic behind statistical inference testing in phylogeny reconstruction (see also Sanderson, 1995). For bootstrapping, the combinability test, or any other test of which we are aware to be valid, a primary assumption is that the statistical population of characters for a given node is being randomly sampled from the universe of independent potential characters (Felsenstein, 1985; Sanderson, 1995). Under such a sampling process, the number of synapomorphies discovered for a node is an estimate of the true distribution of characters at that node, and it is reasonable to ask whether there is statistically significant character support for that node. Such a process of character discovery is well approximated by most molecular data sets, because researchers generally identify a gene, obtain sequences from a homologous piece of DNA, and use all of the scorable characters in the analysis. The choice of a specific gene based on its rate of evolution may limit the inference to genes with similar rate characteristics, but the basic logic of bootstrapping to generate probability

levels is sound. However, in at least some morphological investigations, characters are chosen by searching for those that change only once in a specific part of a tree and are invariant in the rest. If, after one or a few such characters are discovered, the researcher leaves that part of the tree and moves on to search for specific characters supporting nodes at other levels, the distribution of characters is not suitable for a statistical analysis because there is no sense in which a true distribution of character state values for a node has been sampled. This strategy may artificially reduce the confidence in a node (e.g., if after a single character is found the node is considered to be unambiguously resolved) or may inflate the apparent confidence in a node (if a particularly intensive effort is made to collect many characters for a particular node). A nonrandom sampling effort does not completely invalidate the bootstrap (although it does limit inferences to characters sampled in a similar manner; see Sanderson, 1995). However, if subsets of a data set are collected according to different sampling protocols, it is not clear how to compare them to test for combinability, let alone confidence. In our particular case, we included in the analysis all characters that have been considered across morphological studies of chelonians, so this selective form of character discovery was not a serious problem. Thus, we bootstrapped and combined our morphological and molecular characters. However, if this were not the case, testing for tree congruence among data partitions (Miyamoto and Fitch, 1995) may be a more meaningful way to assess confidence in a node than would combining characters and bootstrapping.

Phylogeny of Turtles Revisited

Given the similarity between results from our molecular and those from our morphological data sets, our combined tree (Fig. 5a) is the best current estimation of the phylogeny of living turtles. Parsimony analysis of the total data set resulted in a tree that includes most of the family-level taxa that have been traditionally recognized and reflects considerable agreement between the morphological and molecular trees. Twelve of the 18 nodes identified in the bootstrap analysis of the morphological data (Fig. 4d) are also in the molecular bootstrap tree (Fig. 4c), and the three areas of conflict received marginal statistical support in both trees. The combined tree (Fig. 5a) includes 16 of 18 nodes (Table 3) on the bootstrapped morphology tree (Fig. 4d) and 16 of 21 groups proposed by Gaffney and Meylan (1988), for full resolution of the taxa included in this study (Table 3).

Within the Cryptodira, the Testudinoidea (sensu Gaffney, 1984; Gaffney and Meylan, 1988) was only supported at a BP of 74% (node 16, Fig. 5a), a surprisingly low value given the virtually universal acceptance of this group (Williams, 1950; Bickham and Carr, 1983; see Gaffney, 1984). However, the independent support for the Testudinoidea by both the morphological (BP = 70%) and molecular (BP < 50%, but present in the most-parsimonious tree in Fig. 4c) data sets strengthens the interpretation of the monophyly of this group (e.g., Miyamoto and Fitch, 1995). The Testudinoidea contains two well-supported groups: a restricted Emydidae (sensu Gaffney, 1975a) and the currently unnamed group that includes the Bataguridae and the Testudinidae (node 19, Table 1). For this group, defined here as the most recent common ancestor of *Chinemys reevesii* (a batagurid) and *Geochelone pardalis* (a testudinid) and all of its descendants, we propose the name Testudinoidae. Within the Testudinoidae, strong support for the monophyly of the Bataguridae rests entirely on the molecular data set (Fig. 4c). Hirayama (1985) suggested that the Bataguridae may be paraphyletic with respect to the monophyletic Testudinidae, whereas Lamb and Lydeard (1994) found weak support for a paraphyletic Testudinidae with respect to batagurids. The resolution of this problem clearly awaits additional data from more complete sampling of both groups rather than the sparse sampling available at present, and

we are currently investigating this problem.

Other cryptodiran groups for which strong and unambiguous support is now in hand include the Kinosternidae (monophyly questioned on the basis of karyological data by Bickham and Carr, 1983), the Kinosternoidae (Kinosternidae + Dermatemydidae), the Trionychidae, the Trionychoidae (Trionychidae + Carettochelyidae), the two marine turtle families (Dermochelyidae + Cheloniidae) as the Chelonioidea, and the previously questioned grouping of the snapping turtles (represented by *Chelydra* in our data set) with the Asian big-headed turtle (*Platysternon*) in a monophyletic Chelydridae (Gaffney, 1975b; Gaffney and Meylan, 1988; Iverson, 1992). All of these groups received strong bootstrap support (90–100%) and were supported to some extent by both molecular and morphological data sets.

Within the Pleurodira, the monophyly of the restricted Pelomedusidae and that of Pelomedusoides are strongly supported (both BP = 100%), as is the family Chelidae. (Our unpublished work suggests that the restricted Podocnemidae is also well supported.)

In two areas, results from the analysis of the combined data set are in conflict with current hypotheses of turtle phylogeny. Additionally, all data sets failed to corroborate the existence of certain higher groups within the Cryptodira. The two areas of conflict are alternatives to the superfamily Trionychoidea (Trionychidae, Carettochelyidae, Kinosternidae, Dermatemydidae) and to the proposed relationships within the Chelidae that are found in both the molecular and total evidence trees. The Trionychoidea is a particularly interesting example because its discovery has been considered one of the more innovative and important advances in chelonian higher level relationships (Gaffney, 1975a, 1984; Meylan and Gaffney, 1989). However, the Trionychoidea is polyphyletic in our combined analysis, and even the morphological data set (on which the group was originally proposed) provided only moderate statistical support (BP = 77%) for this grouping. Although no analysis provided strong support for the placement of the two subgroups (Trionychoidae and Kinosternoidae), there was modest support (BP = 64%) for the placement of the Trionychoidae as the sister group to the remaining cryptodires, as suggested by Bickham and Carr (1983) based on chromosomes.

The novel arrangement suggested for the Chelidae by the molecular and combined analyses includes the monophyly of both the South American and the Australian chelids rather than paraphyly of the Australian chelids with respect to South American forms as proposed by Gaffney (1977) and Gaffney and Meylan (1988). The molecular arrangement was also supported in an analysis of all 16 recognized genera and subgenera of chelids for 370 base pairs of 12S rRNA (Seddon et al., 1997), although BPs were relatively low in that analysis (BP = 64% for the Australian taxa, 84% for the South American genera exclusive of *Hydromedusa*, <50% for the South American taxa including *Hydromedusa*). If the most recent divergence between a South American and Australian lineage resulted from the separation of these two continents, the hypothesis of relationships based on morphology requires that most of the living genera existed before the time of separation of Australia from South America (as recently as 55 million years ago [MYA]), for which there is some evidence (Wood and Moody, 1976, for the South American chelid *Hydromedusa*). The alternative of the monophyly of each continent is consistent with (but does not require) a much younger age for the chelid genera, and we are currently testing these alternatives using a molecular clock approach. At this point, we tentatively accept the monophyly of the South American and Australian chelids, although this area remains important for future research.

The Effect of Fossils: Good, Bad, or Indifferent?

Since the publication of two very influential articles nearly a decade ago (Doyle and Donoghue, 1987; Gauthier et al.,

1988a), the general consensus among systematists appears to be that the addition of fossils to a data set is useful both for resolving phylogenetic relationships among the living forms (Gauthier et al., 1988a; Meylan and Gaffney, 1989; Gaffney et al., 1991; Novacek, 1992; Wilson, 1992) and for more accurately reconstructing the pattern of character state changes during phylogeny (Doyle and Donoghue, 1987). Although we agree that there are advantages to including fossils, there is also apparently a cost in terms of lowered statistical support for individual nodes. The impact of including fossils has been noted empirically (Novacek, 1992), and the effects of completeness and age of the added fossils has been studied via simulation (Huelsenbeck, 1991). Our analysis is the first empirical examination of the effect on BPs of adding fossils.

Part of the effect of fossils on BPs is simply the result of including additional taxa rather than a function of the completeness or age of the specimen. Adding any taxon to a tree without adding new characters will dilute support for the tree simply because the tree becomes a more complex statement with more possible solutions. If the new specimen is relatively incomplete, the problem is exacerbated because it leads to many equally parsimonious solutions and thus decreased certainty about any particular tree. Even if the relationships of the added taxon and its sister group are both resolved, the two nodes are likely to have lower BPs than those previously observed for the sister group because two nodes must now share the evidence that previously served for one.

Huelsenbeck (1991) explored the specific problems in the resolving power of fossils compared with living taxa by simulating the effects of incompleteness, age, and rate of character evolution on tree stability. His primary conclusions were that very incomplete fossils will lead to multiple most-parsimonious trees and therefore greater uncertainty about particular nodes. He suggested that a fossil's ability to improve the resolution of a tree increases with completeness of the fossil and temporal proximity to its ancestral node and decreases when the rate of character evolution is slow (Huelsenbeck, 1991: fig. 4). These results make intuitive sense because incomplete specimens lack key synapomorphies and thus lead to multiple equally parsimonious trees, and more recently derived members of extinct lineages are more likely to have lost or transformed the informative original synapomorphy for a group than are taxa that are preserved earlier in the history of a clade.

In our study, the effect of the inclusion of fossils was a decrease in resolution as reflected in decreased BP support for several nodes (Figs. 4d–5d). This reduced resolution took the form of sharply reduced BPs in the vicinity of fossils even though we specifically chose the most complete and earliest known fossils for three specific parts of the chelonian phylogeny. We tried to separate the impact on BP caused by incompleteness from that caused by the inclusion of additional taxa by adding single taxa that differ in completeness. Another potentially important factor is the branch length between an inserted taxon and its sister group.

To examine the completeness issue, we reanalyzed the morphological data set with single fossils (in addition to †*Proganochelys*) that differ in completeness. †*Adocus* and †*Emarginachelys* are two late Cretaceous trionychoids that influenced the same general area of the tree. †*Adocus* is 93% complete, and †*Emarginachelys* is only 79% complete. After adding †*Adocus* to the morphological data set, a heuristic search produced four equally parsimonious trees. As expected from Huelsenbeck's (1991) simulations, the addition of †*Emarginachelys* resulted in 27 equal-length trees. Adding †*Adocus* to the data set did not reduce the BP of the next higher node, *Carettochelys* + Trionychidae (node 12), apparently because of the long length of that branch. It did reduce the BP for the next lower node, the Trionychoidea (node 11), from 77% to 60%. In contrast, the less complete †*Emarginachelys* affected the next higher node (*Dermatemys* + Kinosternidae, node 14), reducing the BP from 93% to 69%.

However, addition of this taxon did not seriously reduce the BP for the Trionychoidea (node 11; 77% without and 75% with †*Emarginachelys*). Thus, for these data the effect on BP is a function of where the fossil falls and the strength of the immediately surrounding nodes, in addition to completeness per se.

Are we better off having the fossils in this analysis or not? For a partial data set (morphology only), the addition of a single key fossil can allow for greater resolution and a shift in BP. This was particularly evident for †*Meiolania* (Fig. 5c), where the addition of a single, relatively complete fossil allowed for much greater resolution of the basal cryptodiran relationships. However, the most robust tree was derived from the combined data set, and here the effect of fossils on branching order was minimal. Well-resolved nodes for the combined data set remained intact with or without the fossils, and only poorly supported nodes based solely on morphological characters switched their relative branching order. In terms of BP, and thus statistical support for the phylogenetic hypothesis of living taxa, it appears at first glance that "more is worse," because BPs invariably decrease with the addition of fossils. However, this interpretation misses an important point in the interpretation of BPs. The value of a BP for any group is relative and is based in part on the presence or absence of other taxa in the neighborhood of a node. For the living turtles, many monophyletic groups are well defined by many characters and so have high BPs. However, if we specifically choose a fossil to be very near the base of a group (as we have done here), then the new, lower BP reflects the uncertainty concerning exactly where the fossil falls relative to the living taxa. Of course, if a new taxon (fossil or living) is very incomplete, then it really cannot add much to the analysis, and it probably should not be included. In our case, there were no fossils that were so obviously incomplete (as noted by Wiens and Reeder [1995], the decrease in accuracy incurred for most reasonable levels of missing characters is small). Instead, the addition of the fossils pointed out that although we have strong support for the proposed phylogeny of living turtles, some of that support reflects the gaps left by the absence of fossil forms. When the fossils are added back in to the analysis, we have relatively little confidence in their precise placement on the tree. Thus, as Huelsenbeck (1991) pointed out from simulation studies, fossil specimens do not produce a misleading hypothesis, but they often lead to so many equally parsimonious trees that they obscure the true phylogeny. By conducting the analysis with and without the fossils, we were able to pinpoint the source of the uncertainty as the placement of the fossil itself, rather than a reshuffling of the branching order of the living taxa.

Short Branches, Rapid Radiations, and Chelonian Phylogeny

The most critical shortcoming in our understanding of the relationships among turtles is the lack of resolution among the major groups of living cryptodires. The pattern of deep phylogenetic history uncovered for the living Cryptodira, several well-defined clades whose relationships are represented by an unresolved (starburst) tree, is a frequent observation in other groups and may have at least three causes (for further discussion, see Kraus and Miyamoto, 1991; Shaffer et al., 1991; Philippe et al., 1994; Shaffer and McKnight, 1996): (1) the wrong characters have been sampled, and many of the characters have become saturated with multiple substitutions during the deep splits of the early Cryptodira; (2) an insufficient number of the slowly evolving characters needed to resolve the deep internal nodes of the chelonian phylogeny have been examined; and (3) the diversification of these clades was sufficiently rapid that the true history approximates a starburst pattern, and the polytomy in Figure 5a is a reasonable approximation of the phylogenetic history. Differentiating the first two interpretations from the third is important both because of the different views of phylogenetic history that they portray and because of the different predictions that can be made con-

cerning the outcome of future efforts to resolve the relationships among these groups (Philippe et al., 1994).

For cryptodiran relationships, the issue revolves around the actual branch lengths (and associated times of divergence) for the four internal branches linking the five unresolved higher groups, Trionychoidae, Kinosternoidae, Chelonioidae, Chelydridae, and Testudinoidea. Because our molecular data set consisted of only cytochrome *b* and partial 12S sequences, our conclusions are tentative pending the collection of additional sequence information from more slowly evolving genes. However, several lines of evidence point toward a rapid starburst phylogeny at the base of the Cryptodira.

First, the fossil record suggests that the major groups of cryptodires appeared over a relatively brief period of 30 million years or less (comprising no more than about 14% of the total history of turtles). Assuming that the Wealdan (ca. 120 MYA) trionychoid †*Peltochelys* nests within the Trionychoidea as the sister group of the Trionychidae + Carettochelyidae (Meylan, 1988), it dates this early cryptodiran split. The oldest chelonioid, an as yet unnamed protostegid from the Santana Formation of Brazil (Hirayama, 1994), is about 110 million years old, the oldest testudinoid, †*Lindholmemys* (Riabinin, 1935), is about 95 million years old, and the oldest chelydrid, an unnamed form from the Turonian of North America (Hutchison, pers. comm.), is about 90 million years old. Divergence among the major groups may have occurred far more rapidly than the fossil record indicates. Although these dates only establish the minimum age of first occurrence for each lineage, their relatively tight clustering in time is suggestive of a major radiation of these cryptodiran lineages between 120 and 90 MYA.

Second, the internal branches linking these five groups of cryptodires are short for both data sets and extremely short for the molecular data. For the morphological characters, under DELTRAN reconstruction, 88 steps were required within the cryptodires, of which 10 (11%) occurred on the branches under consideration. Under the ACCTRAN reconstruction, 13 of 84 (15%) of the changes occurred along these branches. For the molecular data, these values are much smaller (DELTRAN, 46 of 1,666 [2.8%] of the total DNA substitutions within the cryptodires, ACCTRAN, 65 of 1,649 [3.9%]). Although branch lengths per se are difficult to reconstruct and interpret, the observation of very short internal branches, particularly on the molecular tree, is at least consistent with a starburst radiation.

Third, as emphasized by Kraus and Miyamoto (1991), a prediction of a true starburst phylogeny is that the genetic distances among the members of each clade should be approximately equal, which is roughly the case with our data. Using *Apalone*, *Trachemys*, *Staurotypus*, *Chelonia*, and *Chelydra* as representatives of each of the five major cryptodiran lineages, mean genetic distances (adjusted for missing data for our total DNA data set, computed with PAUP) ranged from 0.267 (*Chelonia–Trachemys*) to 0.387 (*Staurotypus–Apalone*), with most values clustered around 0.35 (mean of 10 pairwise distances = 0.329, SD = 0.040). Although these values are not identical, their low variance is again suggestive of a starburst at the base of the Cryptodira.

Taken together, these lines of evidence suggest that there may have been a rapid series of cladogenic events about 100 MYA that established the five living clades of cryptodires. Although our data are not conclusive on this point, a starburst tree is a valid alternative to "not enough data," and we anxiously await the collection of additional information that may help resolve this point. The most productive source of such new data will probably be the relatively conservative exons from nuclear genes. If sequence data from a few such genes continue to produce an unresolved polytomy at the base of the Cryptodira, then it will constitute strong support for the interpretation of a rapid starburst phylogeny that shaped the following 100 million years of chelonian evolution.

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APPENDIX 1
CHARACTER DESCRIPTIONS

Characters 1–39 are from Gaffney et al. (1991), who provided complete descriptions.

40. *Splenial bone (present = 0; absent without enlarged prearticular bone = 1; absent with enlarged prearticular bone = 2).*—A splenial is present on the medial surface of the jaw in most amniotes. It is present in †*Proganochelys* (Gaffney, 1990) and some cryptodires and pleurodires (Gaffney, 1979). When it is absent, as in most living turtles, both the prearticular and angular enter Meckel's groove. The most highly derived condition is that in which the prearticular is enlarged and excludes the angular from contact with Meckel's groove (McDowell, 1964). This character was ordered and unpolarized.
41. *Cervical scute (present = 0; absent = 1).*—A small, unpaired scale appears on the midline on the anterior edge of the nuchal bone in most turtles, including †*Proganochelys*, all chelids, and most cryptodires. It is alternatively termed the nuchal or cervical scale, and its absence can be considered derived.
42. *Cervical vertebra 2 biconvex (absent = 0; present = 1).*—The cervical vertebrae of turtles are primitively amphicoelous. Formed (concavoconvex) cervical centra appear within the phylogeny of turtles at least three times (within the Baenidae, in the common ancestor of the Centrocryptodira, and in the common ancestor of the Eupleurodira). (See character 33 for the presence/absence of the concavoconvex condition.) Only in the Pelomedusoides is the second cervical biconvex, which is considered the derived condition.
43. *Diploid number of chromosomes (28 = 1; 34 = 2; 36 = 3; 50 = 4; 52 = 5; 54 = 6; 56 = 7; 66 = 8; 68 = 9).*—Reviews of the karyology of cryptodires (Bickham and Carr, 1983) and pleurodires (Bull and Legler, 1980) have provided the diploid chromosome number for all recent genera used in this study. This character was ordered and unpolarized.
44. *Occipital condyle (includes basioccipital = 0; excludes basioccipital = 1).*—The basioccipital forms a major component of the occipital condyle in most vertebrates, including most turtles (Gaffney, 1979). When it is not included, the condyle is formed by the two exoccipitals in turtles, and this condition is considered derived.
45. *Precolumellar fossa (not large and deep = 0; large and deep = 1).*—The precolumellar fossa is a variably developed pit in the quadrate just anterior to the incisura columellae auris in some pleurodires (Williams, 1954). A large deep precolumellar fossa is considered derived.
46. *Cheek emargination (does not reach parietal = 0; reaches parietal = 1).*—Primitively the skull roof of turtles is quite complete both dorsally and laterally (Gaffney, 1979). Emargination of this roof is an important feature in the evolution of the turtle skull. Various groups may show temporal emargination and/or cheek emargination. Exten-

sive cheek emargination that reaches the parietal is considered derived.

47. *Quadratojugal (present = 0; absent = 1).*—A quadratojugal bone is present on the lateral surface of the skull in most amniotes, including most turtles (Gaffney, 1979). Its absence is considered derived.
48. *Cervical vertebrae 5 and 8 biconvex (absent = 0; present = 1).*—The cervical vertebrae of turtles are primitively amphicoelous. As discussed for character 42, a number of conditions deviate from this. Biconvex fifth and eighth cervicals are found only in chelids, and this condition is considered derived. Because both vertebrae define the same group and may be functionally related, we consider this a single character rather than two independent characters for cervicals 5 and 8.
49. *Frontals separate nasals (no = 0; partly or completely = 1).*—The primitive conditions for tetrapods is to have paired nasal bones that meet for all of their midline length as seen in †*Proganochelys* (Gaffney, 1990). Separation of the nasals by anterior processes of the frontals is considered derived.
50. *Suture at symphysis (absent = 0; present = 1).*—Although most tetrapods have the lower jaws joined by a suture, †*Proganochelys* and nearly all other turtles have a fused symphysis. Thus, a sutured symphysis is considered derived in the few turtles in which it occurs.
51. *Exoccipitals meet dorsal to foramen magnum (absent = 0; present = 1).*—The primitive condition for turtles is to have the supraoccipital form the dorsal limit of the foramen magnum with the exoccipitals and basioccipital contributing the remainder of the margin (Gaffney, 1979). Exclusion of the supraoccipital from the foramen magnum by a midline meeting of the exoccipitals is considered derived.
52. *Parietals very small (no = 0; yes = 1).*—Most turtles, like most tetrapods, have large parietals that make up a large part of the skull roof. The presence of very small parietals is considered the derived condition in turtles.
53. *Cervical vertebrae (shorter than thoracics = 0; longer than thoracics = 1).*—Typically, turtles have a short neck, much shorter than the length of the shell. A cervical series longer than the thoracic series is considered derived.
54. *Medial part of jugal and postorbital (face posteriorly = 0; face laterally = 1).*—In most turtles, the medial process of the jugal and ventral part of the postorbital form the posterior margin of the orbit and face posteriorly. In pleurodires, these parts are expanded into a broad wall that usually faces posteriorly. A wall that faces laterally is considered derived.
55. *Plastral buttresses (not reaching costals = 0; reaching costals 5 and 6 = 1; reaching costal 5 only = 2).*—In the shell of †*Proganochelys*, the axillary and inguinal buttresses of the plastron do not extend dorsally to contact the carapace (Gaffney, 1990). Dorsal expansion of both pairs of plastral buttresses has occurred at least three times, in pleurodires, baenids, and testudinoids. In most forms contact is with costals 5 and 6. The condition in which only costal 5 is contacted is considered derived.
56. *Elongate costiform processes of the nuchal (absent = 0; present = 1).*—Elongate costiform processes of the nuchal do not occur in †*Proganochelys*, pleurodires, or primitive cryptodires. Their presence is considered derived.
57. *Caudal vertebral series with an anterior biconcave centrum (absent = 0; present = 1).*—The caudal vertebrae are amphicoelous in †*Proganochelys*, primitive pleurodires, and primitive cryptodires. Formed caudal centra occur in most turtles, including all living forms, but few possess an anterior biconcave centrum in the tail, which is considered derived.
58. *Plastron attachment to carapace (firmly sutured = 0; ligamentously attached = 1).*—†*Proganochelys*, all pleurodires, and primitive cryptodires have the plastron firmly sutured to the carapace. A ligamentous attachment of the type seen in chelydrids and chelonioids is considered derived.
59. *Incisura columellae auris (open = 0; closed = 1).*—The incisura is open primitively in tetrapods and in turtles. The derived condition is that where the quadrate encloses the stapes completely.
60. *Origin of ilio-tibialis muscle on distoanterior corner of ilium (absent = 0; present = 1).*—When Zug (1971) examined the pelvic musculature of a large series of cryptodiran turtles, he found only three genera in which the ilio-tibialis originated on the distoanterior corner of the ilium. This condition is considered derived.
61. *Forelimb digits (not elongate = 0; elongate = 1).*—The digits of turtles are typically short with highly mobile joints between the phalanges. Elongate phalanges that lack joints and, along with flattened carpal and tarsal elements, form flippers are considered derived.
62. *Nuchal with facet(s) (absent = 0; single facet = 1; double facet = 2).*—The cervical vertebrae of most turtles do not articulate with the nuchal bone. A knob or facet on the ventral surface of the nuchal that articulates with the eighth cervical is considered derived. In *Carettochelys* and †*Peltochelys*, these facets are double (Meylan, 1988).
63. *Trabeculae of basisphenoid close together or fused (absent = 0; present = 1).*—In the primitive condition of the basisphenoid, the trabeculae are widely spaced and the sella turcica is well developed (Gaffney, 1979, 1990). When the trabeculae lie close together or are fused for most of their length into a rodlike rostrum basisphenoidale that reduces or obliterates the sella turcica, the condition is considered derived.
64. *Paired foramina anterius canalis corotici interni (separated = 0; close together = 1).*—These foramina open within the sella turcica and in most turtles are separated by a wall of bone many times their diameter. Separation of these foramina by a space two or three times their diameter or less is considered derived (Gaffney, 1976, 1979).
65. *Sella turcica (partly concealed by dorsum sellae = 0;*

not concealed by dorsum sellae = 1).—Primitively the dorsum sellae in turtles overhangs the posterior part of the sella turcica (Gaffney, 1976, 1979). A reduced dorsum sellae that does not overhang the sella turcica is considered derived.

66. *Foramen palatinum posterious (present = 0; absent = 1).*—The foramen palatinum posterious is the expression of the sauropsid suborbital fenestra in turtles. Its absence is clearly derived (Gaffney, 1979).
67. *Stapedial artery (larger than palatine artery = 0; smaller than palatine artery = 1).*—Primitively much of the blood flow to the head of turtles occurs via the stapedial artery (McDowell, 1961; Albrecht, 1967, 1976; Gaffney, 1975a, 1979). A reduced stapedial artery and enlarged palatine artery are considered derived. The size of the stapedial artery can be estimated by the size of the foramen stapedio-temporalis, and that of the palatine artery can be estimated by the size of the canalis caroticus lateralis. However, in trionychids the stapedial artery is quite reduced, although the foramen stapedio-temporalis may not be (Albrecht, 1967, 1976).
68. *Palatine contribution to braincase (small or absent = 0; large = 1).*—In most turtles, the palatine is restricted to the palate between the maxilla and the pterygoid (Gaffney, 1979). A large dorsal process of the palatine that makes a significant contribution to the side wall of the braincase is considered derived.
69. *Tenth thoracic rib in contact with adjacent costal (present = 0; absent = 1).*—All 10 thoracic vertebrae of most turtles, like those of †*Proganochelys* (Gaffney, 1990), are in contact with the adjacent costal bones via the rib heads. Abscence of this contact for the 10th thoracic is considered derived.
70. *Thelial process (absent = 0; present = 1).*—The anterior margin of the ilium of †*Proganochelys* (Gaffney, 1990) and most other turtles (Zug, 1971) is without any major protuberance. The presence of such a protuberance, or thelial process, is considered derived.
71. *Caudifibularis muscle (absent = 0; present = 1).*—The caudifibularis muscle was present in only a few of the cryptodiran turtles examined by Zug (1971). Its presence is considered derived.
72. *Opisthocoelous cervical vertebrae (few or none = 0; at least six = 1).*—The cervical vertebrae of turtles are primitively amphicoelous (Gaffney and Meylan, 1988; Gaffney, 1990). Among those species with formed cervical centra, it is common for two or three anterior vertebrae to be opisthocoelous. The occurrence of a long series of opisthocoelous cervicals (numbers 2–7 or more) is considered derived.
73. *Maxillary "tooth" on upper triturating surface (absent = 0; present = 1).*—The upper jaw of †*Proganochelys* (Gaffney, 1990) and most other turtles (Gaffney, 1979) is flat. Long ridges occur in some forms but differ from a short maxillary tooth (Meylan and Gaffney, 1989), which is considered derived.
74. *Parietal makes up one third or more of processus trochlearis oticum (absent = 0; present = 1).*—The processus trochlearis oticum is a feature diagnostic of cryptodires. It is typically formed by the quadrate and prootic, but in some forms the quadratojugal and/or the parietal contribute. A significant contribution to this structure from the parietal is considered derived.
75. *Vomer–pterygoid contact (present = 0; absent = 1).*—The vomer is a single (paired in †*Proganochelys*) midline element that extends from the premaxillae, between the palatines, to the pterygoids in most turtles (Gaffney, 1979), including †*Proganochelys* (Gaffney, 1990). When the palatines meet on the midline preventing contact between the vomer and the pterygoids, this condition is considered derived.
76. *Palatines truncated anteriorly (absent = 0; present = 1).*—In most turtles, the palatines extend anteriorly such that they separate most of the fossa nasalis from the internal nares. In those forms in which these elements are truncated anteriorly there is a large area of communication between the internal nares and the fossa nasalis in the bony skull, which is considered a derived condition.
77. *Processus externus of pterygoid (present = 0; absent = 1).*—Nearly all turtles have a distinct external process of the pterygoid. In pleurodires, it forms the processus trochlearis pterygoideus. In most cryptodires, it forms a vertical plate that limits lateral motion of the lower jaw. Absence of this process is considered derived.
78. *Shell scutes (present = 0; absent = 1).*—The shells of †*Proganochelys* (Gaffney, 1990) and most other turtles are covered with epidermal scutes that leave obvious scute sulci on the bone surface. The lack of scutes (and scute sulci) is considered derived.
79. *Basisphenoid divides pterygoids (absent = 0; present = 1).*—In †*Proganochelys* (Gaffney, 1990) and in most turtles, the pterygoids meet on the midline anterior to the basisphenoid, preventing the basisphenoid from contacting bones of the anterior portion of the palate (the palatines and/or vomer). When the basisphenoid divides the pterygoids to contact those more anterior elements, this condition is considered derived.
80. *Proboscis (absent = 0; present = 1).*—Among living turtles, a proboscis is absent in all pleurodires and in 10 of 12 families of cryptodires. It is not yet possible to determine with any degree of certainty that extinct forms possessed a proboscis. It seems most parsimonious to assume that presence of a proboscis is a derived condition.
81. *Premaxillae (paired = 0; fused = 1).*—The premaxillae of vertebrates are typically paired (Gaffney, 1979). A single premaxilla is considered derived.
82. *Midline sulcus of plastron (relatively straight = 0; extremely sinuous = 1).*—The sulcus along the midline of the plastron usually follows the midline sutures fairly closely. A sulcus that follows a sinuous path, crossing back and forth across the midline suture (Meylan, 1988: fig. 4) is considered derived.
83. *Peripheral bones (surround costals = 0; reduced or absent*

= 1).—In most turtles, including †*Proganochelys*, peripheral elements form a complete ring of bone between the nuchal and pygal. When this ring is reduced or absent, such that costals reach the shell margin, this condition is considered derived.

84. *Pygal and suprapygal (present = 0; absent = 1).*—Most turtles, including †*Proganochelys* (Gaffney, 1990), have a pygal and one or more suprapygal elements along the midline, posterior to the neurals. Absence of these elements is considered derived.
85. *V-shaped entoplastron (absent = 0; present = 1).*—The entoplastron of most turtles is a round or lozenge-shaped element in the anterior lobe of the plastron. When this element is a broad V-shaped structure, with or without a superficial dermal callosity, this condition is considered derived.
86. *Cervical and thoracic vertebrae (meet at centrum and zygapophyses = 0; meet at zygapophyses only = 1).*—The typical condition of vertebrae in tetrapods is to articulate via the centrum and zygapophyses. This is generally true for the articulation between the neck and body vertebrae of turtles. However, in some forms this contact is via the zygapophyses alone, which is considered a derived condition.
87. *Premaxillae in apertura narium externum (present = 0; absent = 1).*—The premaxillae of most vertebrates, including most turtles, extend from the mouth to the external nares. In some turtles, the maxillae meet on the midline dorsal to the premaxillae, excluding them from the external nares. This condition is considered derived.
88. *Lips (absent = 0; present = 1).*—Fleshy lips are not known to occur in any pleurodire and occur in only 1 of 12 families of cryptodires. Their presence is interpreted as a derived condition.
89. *Plastral scale set 2 (present = 0; absent = 1).*—Primitively, turtles have seven pairs of scales that cover the plastron (Hutchison and Bramble, 1981); this is true for †*Proganochelys*, †*Proterochersis*, †*Kayentachelys*, †*Glyptops*, †*Pleurosternon*, and a number of other cryptodires. Absence of scale set 2 is considered derived.
90. *Plastral scale set 3 contacts inframarginals (absent = 0; present = 1).*—In the primitive turtle plastron, contact between plastral scale set 3 (humerals) and the inframarginals is prevented by the presence of large pectorals (scale set 4) (Gaffney, 1990: fig. 92). Contact of the humerals and the inframarginals is considered derived.
91. *Foramen caroticum laterale (smaller than or equal to foramen anterius canalis caroticus interni = 0; larger than foramen anterius canalis caroticus internus = 1).*—The internal carotid artery of turtles gives rise to the stapedial artery in the otic region and the cerebral carotid and palatine arteries adjacent to the braincase. The size of these carotid and palatine arteries usually dictates the diameters of the foramen anterius canalis carotici interni (F.A.C.C.I.) and the foramen caroticum lateralis (F.C.L.), respectively (Gaffney, 1975a, 1979). In †*Proganochelys*, the palatine artery is not enclosed in bone so it is not possible to compare these structures (Gaffney, 1990). In most pleurodires and primitive cryptodires, these two foramina are approximately equal in diameter (Gaffney, 1979; Gaffney and Meylan, 1988). When the F.C.L. is greater in diameter than the F.A.C.C.I., this condition is considered derived.
92. *Foramen stapedio-temporalis (large = 0; small or absent = 1).*—†*Proganochelys* has an opening between the prootic, quadrate, and opisthotic that appears to be homologous to the clearly defined foramen stapedio-temporalis of casichelydians (Gaffney, 1990). In casichelydians, this structure is generally large (Gaffney, 1979). Its reduction or absence is considered derived.
93. *Tricarinate carapace (absent = 0; present = 1).*—The carapace of †*Proganochelys* and most turtles is relatively smooth. The presence of three well-developed, long, continuous keels is considered derived.
94. *Plastral scale set 5 (abdominals) (present = 0; absent = 1).*—Primitively, turtles have seven pairs of scales that cover the plastron; this is true for †*Proganochelys*, †*Proterochesis*, †*Kayentachelys*, †*Glyptops*, *Pleurosternon*, and a number of other cryptodires. The absence of scale set 5, the abdominals, is considered derived.
95. *Peripheral bones (not in 10 pairs = 0; in 10 pairs = 1).*—Peripheral bones in turtles usually occur in 11 or more (†*Proganochelys* character state based on number of marginals; Gaffney, 1990) pairs when present (Meylan and Gaffney, 1989). The presence of only 10 pairs is considered derived.
96. *Ninth and 10th thoracic ribs contact adjacent costals (present = 0; absent = 1).*—All 10 thoracic vertebrae of most turtles, like those of †*Proganochelys* (Gaffney, 1990), are in contact with the adjacent costal bones via the rib heads. When the 9th and 10th thoracics lack this contact, this condition is considered derived. This character may be a further derived condition for character 69.
97. *Frontal enters orbit (absent = 0; present = 1).*—In †*Proganochelys*, the frontals are excluded from the orbits (Gaffney, 1990). However, in all pleurodires and all basal cryptodires they enter the orbits, suggesting that frontal contribution to the orbit margin is the primitive condition for the Casichelydia. Thus, exclusion of the frontal from the orbit within the Casichelydia is a further derived condition.
98. *Maxilla contacts quadratojugal (absent = 0; present = 1).*—In †*Proganochelys* (Gaffney, 1990) and most other turtles (Gaffney, 1979), the quadratojugal is excluded from contact with the maxilla by the jugal. Contact between the quadratojugal and maxilla is considered derived.
99. *Ilial notch in pelvis (absent = 0; present = 1).*—The ilium of †*Proganochelys* and most other turtles is without a notch just posterior to the acetabulum. Meylan (1987) pointed out that such a notch was present in kinosternid turtles and could be considered a derived condition.
100. *Musk duct incised in anterior peripherals (absent = 0; present = 1).*—Numerous turtle species have

musk glands and musk ducts. Normally, the musk ducts exit from the bridge peripherals. In some forms, the musk ducts exit from the anterior part of the carapace via grooves in the anterior peripherals (Hutchison, 1991). The presence of musk duct grooves in the anterior peripherals is considered derived.

101. *Inframarginal scutes separate carapacial and plastral scutes (present = 0; absent = 1).*—The inframarginals of †*Proganochelys* remain unknown (Gaffney, 1990). However, a complete series of inframarginals is present in †*Proterochesis* and basal cryptodires, suggesting that the presence of inframarginals is the primitive condition for turtles. Reduction of the inframarginal series, such that the marginal scales contact the plastral scales, is considered derived.
102. *Cervical vertebra 8 biconvex (absent = 0; present = 1).*—The cervical vertebrae of turtles are primitively amphicoelous. Formed (concavoconvex) cervical centra appear within the phylogeny of turtles at least three times (see characters 42, 48, 72). A biconvex eighth cervical does not occur in basal centrocryptodirans (i.e., †*Meiolania*; Gaffney, 1985), and its restricted distribution suggests that its occurrence is a derived condition.
103. *"Batagurine" process (absent = 0; present = 1).*—The structure that McDowell (1964) identified as the batagurine process allowed the separation of batagurines from emydines in what was then considered to constitute the Emydidae. This process is not present in †*Proganochelys* (Gaffney, 1990) or pleurodires (Gaffney, 1979). However, this posterior extention of the pterygoid that contacts the basioccipital is present in nearly all cryptodires. It is secondarily absent in what McDowell considered emydines (Emydidae sensu stricto), and this further derived condition allowed the distinction that McDowell recognized.
104. *Plastral scale set 4 (present = 0; absent = 1).*—Primitively, turtles have seven pairs of scales that cover the plastron (Hutchison and Bramble, 1981); this is true for †*Proganochelys*, †*Proterochersis*, †*Kayentachelys*, †*Glyptops*, *Pleurosternon*, and a number of other cryptodires. Absence of scale set 4 is considered derived.
105. *Foreclaws elongate (absent = 0; present = 1).*—In †*Proganochelys* (Gaffney, 1990), as in most turtles, the claws of the front and hind feet are about equal in length. Significantly elongated foreclaws (in males only) are considered derived.
106. *Epipterygoid contacts jugal (absent = 0; present = 1).*—Although the epipterygoid is not well preserved in †*Proganochelys*, it seems unlikely that it extended anteriolaterally to reach the jugal. The jugal is located well lateral to the foramen palatinum posterius, and that region of the skull is well preserved in SMNS 16980 (Gaffney, 1990). In most turtles that have an epipterygoid, it is limited to the side wall of the braincase. When this element extends anteriorly and laterally to meet the jugal, this condition is considered derived.
107. *Transverse processes of cervical vertebrae reduced and restricted to the anterior part of the centrum (absent = 0; present = 1).*—The transverse processes of the cervicals of †*Proganochelys* (Gaffney, 1990), pleurodires, and basal cryptodires (including †*Meiolania*; Gaffney, 1985) are robust and located near the center of the centrum. Reduced and anteriorly located processes are considered derived (see Williams, 1950; Meylan and Gaffney, 1989).
108. *Cervical vertebrae with ventral processes on posterior centra (absent = 0; present = 1).*—The centra in the posterior part of the cervical series of †*Proganochelys* (Gaffney, 1990), pleurodires, and basal cryptodires (including †*Meiolania*; Gaffney, 1985) lack ventral processes. Presence of such processes is considered derived (see Williams, 1950; Meylan, 1987; Meylan and Gaffney, 1989).
109. *Foramen palatinum posterius behind orbit (absent = 0; present = 1).*—In †*Proganochelys* and cryptodires, the foramen palatinum posterius is located in the floor of the orbit (Gaffney, 1979, 1990). In pleurodires, this structure is located posterior to a bony wall that marks the posterior margin of the orbit, which is considered a derived condition.
110. *Articulation between cervicals 7 and 8 double (absent = 0; present = 1).*—The cervical vertebrae of turtles are primitively amphicoelous (see character 42). In all living pleurodires and basal centrocryptodires (those cryptodires with formed cervical centra), the articulation between cervicals 7 and 8 is single. A double articulation at this location is considered derived (see Williams, 1950).
111. *Postorbital exposed posteriorly by temporal emargination (absent = 0; present = 1).*—Primitively, the postorbital of turtles does not reach the posterior margin of the skull because of broad parietal–squamosal contact (Gaffney, 1979, 1990). Temporal emargination sufficient to expose this element is considered derived.
112. *Dorsal process of epiplastron (present = 0; absent = 1).*—†*Proganochelys*, †*Proterochesis*, and basal cryptodires have a well-developed dorsal process of the epiplastron (Gaffney, 1990). The absence of this structure is considered derived.
113. *Entoplastron divides epiplastra (present = 0; absent = 1).*—†*Proganochelys*, †*Proterochesis*, and basal cryptodires have epiplastra separated by an entoplastron that reaches the anterior margin of the plastron (Gaffney, 1990). Exclusion of the entoplastron from the plastron margin is considered derived.
114. *Thyroid fenestra divided by midline contact of pubis and ischium (present = 0; absent = 1).*—The pelvis of †*Proganochelys* has a clearly divided thyroid fenestra (Gaffney, 1990); this is also a common condition among living turtles (Meylan, 1987). Failure of the pubis and ischium to divide the thyroid fenestra is considered derived.
115. *Glenoid neck present on scapula (absent = 0; present = 1).*—The scapula of certain turtles has a short but significant process between the point where the acromion process joins the scapular body and the glenoid fossa (i.e., chelonioids). We have adopted the name glenoid neck for this structure. It is absent in †*Proganochelys* (Gaffney, 1990) and most other turtles, and its presence is considered derived.

APPENDIX 2. Aligned sequence data for 892 base pairs of cytochrome *b* for 23 taxa of turtles. GenBank accession numbers (in the same order as the sequences listed below) are U81342–U81364.

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Apalone          ATCTCCATCT GATGAAATTT TGGATCCCTA TTAGGCGCTT GCCTAGCCAT CCAAATCATC ACAGGGTTAT TCCTAGCCAT ACATTACTCA CCAAACATCT
Chelus           ..T..A.C.A T......... ...C..A... C....AA.A. ........C. A...C.A.CT .....CA.C. .......... ......T... T..G....T.
Clemmys          ..T...GCT. .......C.. .......... C.......... ..T..ATTC. A....C...T ..C..AA.C. .......... ...C.....C ...G......
Graptemys        .....AGCA. .......C.. .......... ......A... .....ATTC. A....C...T ..T..AA.T. .......T.. ...C.....C ...G......
Pelomedusa       .....AGCA. .......C.. ...C..A... C....AATA. ....GAT.T. A.......C. .....TA.T. ..T....T.. ...C...A.. .........A
Pelusios         .....AGCA. .......C.. ...C...... C..A.GATA. ..G..AT.C. A.....TTC. .....CA.C. .TT....A.. ...C...CAG .ACC.A.CA.
Phrynops         .....AGCA. .......C.. C..C.....T C....A..A. ....T.TAC. A...C.AGC. ..C..AA.C. .......... ...C...... ..C.......
Staurotypus      .....AGC.. ....G..... ......A..T C.T...ATC. ..T..AT.C. A.....TGC. ..C..CA.C. ..T....T.. ...C...... T.CG....A.
Kinosternon      ..T..AGC.. .......C.. C.....AT.. C.C...ATC. ..T..AT.C. G.......CT ..C..TA.C. .......A.. ...C..T... T.TG....A.
Trachemys        .....TGCT. ....G..C.. .......T.. .....TA... .....AT.C. A......C.T ..C..AA.T. ....G..T.. ...C.....C ...G....T.
Chelonia         .....TGCA. .......C.. C.....A... C...C.A.C. .......AC. A.....T... ..C..AA.C. .T.....A.. ...C...... ...G......
Geochelone       .....TGC.. .......C.. C.....A... ......ATC. ..T..ATTC. A....CT..T ..C..AA.C. .T.....A.. ...C...... ...G......
Elseya           ......GCT. T......C.. C.....AT.. C....A..A. ....CATTC. A...T.AGC. .....AA.C. ..T....T.. ...C...... T.TG......
Carettochelys    ..T..TGCT. .......C.. C..C..A..C C....A..C. .....AT.C. T........C. .....CC.C. ....C..A.. ......A... T..G....T.
Chelodina        ..T..GTATC TT.....C.. C..G..AT.. C....AATA. .....ATTG. ....C.AGCT .....CC... .TT..T.T.. ...C...... ..CG......
Chelydra         .....TGCT. .......... C.....AT.. .........C. ..T..ATTG. A......G.. ..C..AA.C. ....G..A.. ...C..T... ...G.T.CT.
Chinemys         .....TGCT. T......C.. C.....A... C.....A.C. .....AT.G. A.......CT ..C..AA.C. .......A.. ...C...... ...G......
Lissemys         .....AG.A. .......CA. A......... C....A..C. .....TTAC. A......G.. .....A.... .......... ...C...... .........TA
Podocnemis       ......GC.. .......C.. C..C..T... C.G..A..C. .T..C.TAC. A..G.....A .....CA.C. .......A.. ...C..T... .........C
Platysternon     ....TGCT. .......C.. C.....A... C....TATC. .....ATTT. A.......... ..T..AA.C. .T.....A.. ...C.....G ...G..G...
Heosemys         ......GCT. .......C.. C..C..A... C.......C. ..T..ATTC. A.....T... ..C..AA.C. ..T....A.. ...C...... ...G.T....
Dermochelys      .....TGCA. .......C.. ...C..A... C....T..C. .T....TAC. A........T ..C..AA.C. ..T....A.. ...C..T... ...G....T.
Dermatemys       ..T..TGCT. .......C.. C.....A... ........C. .....ATAC. A.......... ..T..AA.C. .T........ .......... ...G.T....

Apalone          TAACAGCATT CTCATCAGTC TCCCACATCA CCCGAGACGT ACAATACGGC TGATTAATCC GAAATATACA CGCCAATGGG GCCTCACTAT TCTTCATGTG
Chelus           CCCT..... .......A.. ........TC AA........ G........A ........T. .......G.. ...A..C..A ..A..... .T.....C..
Clemmys          C.CT..... .........A G....T.... .......T.. .......... ...C.C.... .T..C..... T.....C..C ..C..... .......A..
Graptemys        C.CT..... .........G G.......T. .......... .........A ...C.T.... .C.....T.. T..T..C..C .....C..C. .......A..
Pelomedusa       CC..C..C.. .......... G.T..... .T..T..... C.......... ...C.CC... ..GGCT.... .......... .....CA.C. .T.....C..
Pelusios         C.CAT..C.. .........T A....T..TG .T........ C.......... ...C.CC... .....T.... ...T..C..A .....T..C. .......C..
Phrynops         CCCTG..... .......A.. G........C AA.....T.. G.......... ...C...... ....C..... T..A..C... .......... .......C..
Staurotypus      CCCT..... ....A....A G......CT. .T........ .......... ...C.T.... .C..CC..... ......C..C ..T...A... .......C..
Kinosternon      C.CT..... .........T A....T.CA. TT........ .......... ...C.C..T. ....CC.C.. T.....C..C ..T..T.... ....T..A..
Trachemys        C.CT..... .........A G......... .......... .........A ...C.T..T. .T........ T..T..C..C .....C..C. .......A..
Chelonia         CC.T...T.. T......A.T G.T..... .......T.. .......... ...C.T.... .T..C..... T..T..C..C .....C.... .......A..
Geochelone       C.CT..... T........A G....T.... .......... ...G.....A ...C.T.... .......... T..T..C..A ..T..CA.C. .......A..
Elseya           CC........ .......A.. .........C AA........ T.....T... ...C.G..T. ....C..... ......C... C.T..... ....T..A..
Carettochelys    C.TT...C.. T..C.....A G......... .T.A..... .......A.A ...C.G..T. .C..C..... .....C.A.. ......T... .......C..
Chelodina        CCCT..... .......AAT CT..CAC.TC A......T.. T.....T..A .......... ....CG.... T.....C..A .......... .......A..
Chelydra         CCCTG..... .......A.. A.T.....T. .......... .........A ...C...... .C..C..... ......C..C ........C. .......C..
Chinemys         C.CT..... .........A G....T.... .......... .........A ...C.T.... .C........ T.....C... .....CA.C. .......A..
Lissemys         .......... ...T...A.. .....T..T. .A..T..T.. ......T..G ...C..... A......G.. ...T..C..A ..A..... .......C..
Podocnemis       ACTT..... .......... G....T.... .A.....T.. .......... ...C...... .C..C..... .T.A..C..C ..T..CA.R. .......C..
Platysternon     CCCTG..... T......A.T A.A.....T .T.....T.. .........A ...C.T..T. .C..C..... ...T..C..T .....CT... .........A
Heosemys         C.TT..... .........A G....T..T. .......T.. .........A ...C.T.... .C..C..... T........A .....CA.C. ....T..A..
Dermochelys      CCCTC..C.. .........T G.T..... .......... .........A ...C...... ....C..... .........C .....CT... ....T..A..
Dermatemys       C.T..... .......A.. A.A..... .......... C........A ...C.C..T. ....CC.... ......C..C .....C.... .......A..
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APPENDIX 2. Continued.

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Apalone         TATTTACCTA CATATTGGAC GAGGAATATA TTATGGCTCA TACCTATACA AACAAACTTG AAACACAGGC GTAATCCTAC TACTATTAAC CATGGCAACA
Chelus          ...A.....G ..C..C.... ....C..C.. C........T .......... .GA....C.. ...T.....A .......... .CT..C..GT ...A..T..T
Clemmys         ...C.....C ..C..C.... .....C.C.. ...C...... ..TT...... ..G.G..C.. .........A ACC.C...TT ....T..... A..A..C..T
Graptemys       C..C.....T .......... .....C.T.. ...C...... .......... ..G....C.. .........A A.T....... ....CC.... A..A..C..T
Pelomedusa      .C.C..TT.T .......... .C.....T.. C..C..A..T .T...CA.T. ..A....C.. .T....G... A.C..A..C. ..T.C..... A..A..C...
Pelusios        CC.C.....C ..C....... ....T..C.. C..C..G..G .....TA.T. ..A....... .T....G..T ..C.....C. ....CC.... A..A..C...
Phrynops        C..A.....C ..C....... .......C.. C......... .....G.... ..A....C.. .........A .....A.... .C..CC..GT A..A..C..C
Staurotypus     C.....TA.G ..C..C.... ....C..T.. C..C...... .....C..T. ..G....... .........A A.TC.T.... .......... T..AAT...T
Kinosternon     ...C...A.G ..C....... .......C.. C..C...... .....G.... ..G....... ......T..A A.T..A...T .....C.... ...A..C..C
Trachemys       C..C.....T .......... .....C.T.. ...C...... ..TT...... ..G....C.. .........A A.T....... ....CC.... A..A..C..T
Chelonia        ...C.....C .......... .......T.. C..C..T..C ........T. ..G....C.. ......T..A A.C.....T. ........G. A..A..T..C
Geochelone      C........C ..C..C..C. .....C.T.. C.CC.....T .......... ..G....C.. .........A A.T..T.... ....CC..GT ...A..T..T
Elseya          C..C...T.C .......... .......C.. C......... .....C.... .CA....C.. ...TT.T..A .....GT.... ....TC..GT ...A..C..C
Carettochelys   C..C...... ..CG.C.... .....G.C.. C..C...... .......T.. ..G....A.. .....TC..A A.T..A.... .TT.CAC.G. A..A.....T
Chelodina       C..C...... ..C....... .......T.. ......T..C .....C.... ..A....... ...T.....A ...G....C. .....C..GT T..A..C..T
Chelydra        .........C .....C..C. .....C.T.. C..C..A... ...T....T. ..G....C.. ...T..C..A ........T. .CT....... T..A..C..T
Chinemys        C........C ........C. .....C.C.. C......... ...T...... ..G....C.. .........A A.C....... ..T.CC.... T..A..C..T
Lissemys        .......... ..C..C.... ....T..G.. .......... ..T..C.... ..G....C.. ...T.TC..A A.T..T.... ..T..C.... A..A..C...
Podocnemis      .C.A..TT.. ..C....... ....CT.C.. C..C.....C .T.T.TA... C.A....A.. G.....G..T A.TG.....T ..T.CC.... ...A..C..T
Platysternon    C..C..TA.C ..C..C.... .....C.... C..C...... ...T.G.... ..G.G..A.. ...T.....G A.C..T..T. .....C.... T..A..C..C
Heosemys        C........T ..C.....C. .....C.C.. C..C...... ...T...... ..G....C.. .........A A.C.....CA ..T.CC.... T..A..C..C
Dermochelys     .........C ..C..C.... .....C.T.. C..C..A... .....T.... ..G....C.. .....T..A A.T....... .C...C..GT ...A..C..C
Dermatemys      C..C...... ..C..C.... .GAACC.G.. C.....T..T ...T..A... ..A....C.. .T.......A A.T..T.... .....C..CT ...A..C..T

Apalone         GCATTCATAG GATATGTTCT ACCATGAGGA CAAATATCCT TCTGAGGAGC TACAGTCATC ACTAATCTAC TCTCAGCCAT TCCCTATATT GGCACCACAA
Chelus          ........G. .C..C..C.. .........C ........A. .T.....C.. A..T..A... ..C....... .T......C. A..A....C. ..ACA...T.
Clemmys         ......G... .C..C..C.. .........C .......... .....A.C.. C.....T..T ..C..C..C. .T......G. ...A...... ....A....C
Graptemys       .G....G... .C.....C.. .........C .......... .T.....T.. A..C..T..T .C..C..... .......... ...A..C... ..G.A....C
Pelomedusa      ..C..T.... ....CA.C.. .......... ........T. .......C.. C..G..A... .....C..C. .A..T..... C........A ..A....ACT
Pelusios        ..C..T.... .G..CA..T. ...C.....C .......... .T.....T.. C.....A... ..C.....C. .A..T....C C......G.A ..AC....CC
Phrynops        ......G... .C.....G.. .........C ........A. .......... C.....A... .....C.... ....T..... C.....C..C ..ACA.....
Staurotypus     .......... .G..C..C.. .........C ........A. .......G.. C..C..A... ........C. .......... C..T...... ..TGT.T..C
Kinosternon     .......... .......... .......... ........A. .T........ ...C..A..T ..C..C..C. .A.....T.. C......... ......T..C
Trachemys       ......G... .C.....C.. .........C .......... .......T.. A..C..T..T ......T... ....G..... ...A..C... ..T.A....T
Chelonia        ......G... .C..C..C.. .......... ........A. .T.....G.. C..C...... ..A..C.... .......... C..A..C..C ....A....C
Geochelone      .......... .C.....C.. .........C ........A. .......T.. ...T.....T ..C..C.... .........C C..T.....C ....G...CC
Elseya          ......G... .C..C..A.. .........C ........A. .......G.. ......A... ..C..C..C. .A........ C..A..CG.A ...C.T...C
Carettochelys   .......... .......C.. ........AC ........A. .......G.. ...C..A... ..A..C...T .A.....A.. A..A..C..C ....A...CC
Chelodina       ......G.G. .T.....A.. .......... ........A. .......G.. ......A..T ..C.....T. .T.....T.. C..A...GC. ..AC.A...C
Chelydra        .....TG... .T..C..C.. .........C ........A. .......T.. ......T... .C..C..G. .......... A..T..C..A ..T.AT...T
Chinemys        ......G... .T.....C.. .........T ........A. ....G..C.. ...T...... ..C..C.... .A..G....C C..T..C... ....AT..CC
Lissemys        .......... .C..C..A.. .......... ........G. .......G.. ...T..A..T ..A..C..T. .A..T..... C..AC.C... ....AT....
Podocnemis      ........G. .C...A.C.. .........G ..G....... .......T.. ...T.....T ..C..C..C. .A........ C.....C... ..A.AT..CC
Platysternon    ......G... .T........ C.....G..C ........A. .......C.. ...T..A... ..C..C.... .......T.. ...A.....G ....G....T
Heosemys        .....TG... .C.....CT. .........C ........A. .......C.. C..C...... ..C..C.... .T.....T.C C..G..C... ..T.AT..TT
Dermochelys     ......G... .......A.. T.......... ........A. .......... C..C.....T .....C.... .......... C..A..C... ....AT..GC
Dermatemys      .....TG... .C..C..AT. ..T......C ........AA. .......... ...T..A..T ..C..C.... .......... C..A..C..A ..T.AT....
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APPENDIX 2. Continued.

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Apalone       TAGTACAATG AGTATGAGGG GGATTTTCTG TAGACAATGC TACCCTAACA CGATTCTTTA CCCTACACTT TTTACTTCCG TTCATAATCC TAGGACTTGC
Chelus        .....AC... .A.C.....A .....C..A. .......... C..T.....C ........C. .A........ CA..A.A..C .....C.... ....GA.GAT
Clemmys       ....G..... .A.C.....A ........A. .......C.. A........C ........CG ..T.C..T.. C.....A..A ..T.CC..TA ....C..GA.
Graptemys     .......... .A.C.....T .....C..A. .......C.. A........C .......... ..T.C..... CC.C..A..A ..T.CC..TA ....T..AA.
Pelomedusa    ....C..G.. .A.C.....A ........A. .......... A........C ........C. .......... C...ACC..A .....C...T C.A.T...A.
Pelusios      ....C..... .A.C.....A .....C..A. .G.....C.. ..........T ..C....... .T........ CC.GACC..T ..T..C..TG CCA.CT.CT.
Phrynops      ....C..... .A.C..G..T .....C..C. .......C.. ....T....C ........C. .GT.C..... CC.CA.C..A ..T..C...A C...CA.A.T
Staurotypus   .T........ .A.C.....A ..G..C..A. ....T...C. A........C ........C. .A..C..T.. CC.C..C..C ..T......G C...TT.A..
Kinosternon   .......... .A.T.....T .....C..A. .......... A..TT....T .......... .A..C..... C.....A..T ..T.C...TG C...C..C..
Trachemys     .......... .A.C.....C .....C..A. .....G.C.. A.....G..C .......... ..T.C..... .A.C..A..A ..TGCC..TA ....T..AA.
Chelonia      .......... .A.C.....A ..G.....A. .......... A........C ........C. ..T.C..... CC..T.A..A ..TGCC..TA CC..C...A.
Geochelone    .......... .A.T...... ..C.....A. ....T..C.. ..........T ........C. ..T.C..... CC....A..A ....CC..TA .....A.A..
Elseya        .T...G.G.. .A.C...... .....C..C. .......C.. C.....G..C ........C. .AT.C..... .C..A.C..A ...GCT..T. .....A.AA.
Carettochelys ....T..... .........A .....C..AA .T........ A.........  ........C. .TT..... CC.CT.A..A ...TCT...A ....C..AA.
Chelodina     .C.....G.. .A.C.....T ........A. .......... C........T ..C.....C. .AT.T..... AC....A..A .........A .....A.GA.
Chelydra      .......... .A.T.....A .....C..A. .......C.. A........C .......... ..T.C..... .C....A..A ....CC..TA .T..C.....
Chinemys      .T........ .A.T...... ..G..C..A. .......... C........C ........C. ..T.T..... .C....C..C ..TGCT..TG CC..TT.A..
Lissemys      .......... .........A ..T..C..A. ....T..... A..AT...AC ........C. .A..T..... CC.C..A..A ..TT...... .T..CACAA.
Podocnemis    .C........ ...G...... .....C..A. .......C.. ...A..T..T .......... .AT.C..... CC..ACC..A .....C.... ....TA.AA.
Platysternon  .......G.. GA.T.....T ..G.....A. .G.....C.. A...T....C .......... ..T.C..... .C.TT.A..A .....T.CTT C...CG.C..
Heosemys      .......... .A.T...... ........A. ....T..C.. C.....G..C .......... ..T.C..... CC....A..T ....CT...G CT..C.....
Dermochelys   .......... .A.C...... .....C..A. .......... A..T.....C .......... .AT.C..... CC....C..A ..T.CC...A .C..T.....
Dermatemys    .......... .A.C.....A ..T..C..A. ........C. A..T..C..T ........C. .AT.C..... .C.CT.A..A .........TA C...C..AA.

Apalone       AATAATCCAC CTACTCTTCC TCCACGAAAC CGGATCAAAT AACCCAACAG GACTTAACTC AAACACCGAC AAAATCCCAT TCCACCCCTA CTTCTCATAT
Chelus        .T..G.A... .....A.... .A..T..... A..T.....C ..T..... ..T.A..... C...TG.... .....T..CC .T.....A.. T..T..T..C
Clemmys       ....G.A... ..G......T .A........ .........C .......... ....A..... ....G....T ........T. .......... .........C
Graptemys     .T..G.A... .....T..T. .A..T..... T........C ..T..... .GT.A..... ....G....T .......... .......T.. T.........C
Pelomedusa    C.C......T ...T.AC... .........A A.....T..C ..T..... .......... C...C.T... .......... .T........ .........C
Pelusios      TC....T... ..CT.A.... .......... A..C..T..C .....C.... ....C..... C...TA.... .......... .T........ .........C
Phrynops      GGC.G..... ..C..A.... ....T..... A..T..... .....C.... ....A..... C...TG.... ........G. .......A.. ......C..C
Staurotypus   .....CA... ..C..T..TT .A........ T..C..... .......... .GT.A..T.. ......T..T .......... .......A.. T..T.....C
Kinosternon   .....CA... .....T.... .T........ T..C..... .......... ....C..T.. ...T..T..T .......... .......A.. ...T.....C
Trachemys     .T..G.A... .....T.... .A..T..... T........C .......... ..T.A..... ....GT...T .......... .......T.. .........C
Chelonia      .GC.G.A..T ...T.A.... .G........ A........C .......... ..T.A..T.. ...T..... ........C. .......... ......C..C
Geochelone    ...TG.A..T .....A.... .A........ T........C .......... ....A..T.. .........T .......... .T.....A.. T.....T..C
Elseya        C...C.A... ..C..AC.A. .A........ A........ .......... ....A..... ....TGT... .......... .......A.. ......T..C
Carettochelys ...CG..... ..C..A.... .AT..... A........C ..T..... .C..A..... ...T.TA... .......... .T........ ...T..C...
Chelodina     .G..G.A... .....A..T. .A..T..... A..G.....C ...T....G. .TA.A..... C..TTG...T ......T... .......A.. ......T..C
Chelydra      ....G.A..T T....T.... .T..Y..... ...C..... .......... .C..A..... .GC.T.T..T .....T..Y. .......A.. T.....T..C
Chinemys      .GCTG.A..T T......... .........T .........C ..T..... ..T.A..... ....G..... ........T. .......... .........C
Lissemys      ....G.A... ..T..A...T .A........ T........ .......TC. .......... ...T..A... ...G...... .......... ...T.....C
Podocnemis    .......... ..T..A.... .......... A..C.....C ..T....C. ....A..... .......... .......... .......A.. ....A....C
Platysternon  ....G.A..T ..T..A..T. .AY.T..G.. A........C ...T..... .GT.A..... ......T..T .......TC. .......G.. ...T.....C
Heosemys      ...CG.A..T T....T.... ....T..... .........C ..T..... ..T.A..... ....G....T .....T.... .......... T.........
Dermochelys   .GC.G..... ..C..A.... .A..T..... T........ .......... ....A..... ....G.T..T ........T. .......A.. ......T..C
Dermatemys    ....G.A..T .....A..T. .A........ T........ .......... .CT.A..... ...T..... .....TA... .......A.. T.........
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APPENDIX 2. Continued.

Apalone	AAAGACCTAT	TAGGATTTGT	AGCAATACTT	ACCGTACTCC	TATCAATCGC	CATATTCTAC	CCAAACCTAC	TAGGAGACCC	AGACAACTTC	ACACCCGCTA
Chelus	.....TA	....TA...C	T.T.G..A.A	..TTGC..A.	..A.CC.AA.	AT..C.A.T.	...TT.T...	.TACT.....	...T.....	..C..A..C.
Clemmys	C	.....C..A.	CTT.....A	G..C....G.	..A.CC.AA.	AC.....C.	..C.....TT	.....	...T.....T	.....A....
Graptemys	.....TC	....CA.CA.	CTT.....A	G..C.C..A.	..A.CC.AA.	AT.....CT	.....T..TT	.....	...T.....	.....A..C.
Pelomedusa	.....T.	.....G.AAA	TCT.C.TA.A	.T..G...AT	..A.CC.AA.	.T.....CTA	..T.....G.	..AC.....	...G..T...	..C..A....
Pelusios	.....TC	....CA.AAA	TTT.C.CA.G	.TT.G...AA	CTATCC.AA.	.C.CC..CT.	..T.....TT	.TAC.....	T..A.....	.....T..C.
Phrynops	CC	....C..AT.	.T.....A	...TGC..A.	..A.CC.A..	.C.....CA	.....	C.	...C.....	.....	..C..A..C.
Staurotypus	.....T..C	....CA..A.	CCT.C.....	.TTA.T..A.	..A...C.AA.	AT.....CA	..CT....G.	.....	.....	.....	..C..A....
Kinosternon	..G.....CC	....CA.AA.	CCT.....C	...T....A.	...T.C.A..	AC.....CA	..C.....CT	.....	.....	.....	.TT..A..C.
Trachemys	CC	....CA.CA.	TTT.....A	...C.C..A.	..A.TC.AA.	AT.....CT	.....T..CT	.....	...T.....	.....	.....A..C.
Chelonia	.....T..C	.....C.CA.	TTT.....A	...C.C....	..A.CT.AA.	AC.T....C.	..CT..T...	.....	.....	.....	.....A..C.
Geochelone	.....	.....C.AA.	CCT.....	...A.T..A.	..A.CC.A..	AC....T.C.	.....	CT	.....	.....	.T...A....
Elseya	C	....CC.CA.	CCT....A.C	..ATGC..A.	.CA.TC.T..	.C....T...	.....	.....	.....	T	.....A..Y.
Carettochelys	.....G.C.	.T.....GA.	CCT.....A	G..A.C....	.CAATC.AA.	AC.....TT	...T....CT	.....	...A.....T	.....	.....A..C.
Chelodina	CC	....C..CAC	CCT....GCA	CTAC.C..A.	..A.CC.A..	TT.....C..	...T....C.	.....	.....	T	.....T....
Chelydra	.....	....CC..A.	TTT....ACA	...C.CT.AT	..A.TT.A..	AC.....	.....T.	.T..T..T..	.....	..G..A..C.
Chinemys	.....T..C	....CC.CA.	CTT.....	..T..CT.A.	.TATCC.A..	AT.G....T.	.....C.	....T.....	G.....	.....	.....A....
Lissemys	.....TA.TC	.....C.CC.	.AT.GC...G	..TA.TT.A.	.TA....TA.	TT.....C.	.....T...	.CA.T.....	CA.T..T..T	T.....	.....
Podocnemis	.....A.CC	....CA...C	.ATCC..A.A	G.ATAC....	..A.TC.AT.	.....CTA	..C.....C.	..TCG.....	T..A.....	.....	.....A.
Platysternon	.....T..C	.....A..A.	CCT..C...A	...T....A.	..A.CC....	AC.....C.	.....T..TT	.....	G.....	T	.....A..C.
Heosemys	.....T...	....CC.CA.	CCT.....C	...C.C..A.	.TA.CC.A..	AT.....C.	.....	T	.....	T	.....A....
Dermochelys	.....T..C	....CC.GA.	CCT....T.A	...C.C....	.TA.CC.AA.	AC....T.C.	..T...T...	.....	.....	.TC..A....
Dermatemys	.....T..C	....GA.AA.	CCT..C...A	..AT.C..A.	..A.CC.AA.	AC.C....CA	..T.....G.	.T.....	.....	..C..A..A.

Apalone	ACCCACTATC	TACACCCCCA	CATATCAAAC	CAGAGTGATA	CTTCTTATTC	GCCTACGCCA	TCCTACGATC	TATTCCTAAT	AAACTAGGAG	GCGTACTCGC
Chelus	....G...GT	C.....T...	.....T....	....A.....	....C....T	........T.	.....	A..C.....C	.....	.T.....A..
Clemmys	.....	C..C..A...	.....T..G.	....A.....	...TC.T..T	........A.	.....	A..C..A...	...T....C.	.....
Graptemys	....CT....	C..C..T...	.....	....A..G..	...TC.T...	........A.	.T.....	...C..A..C	..GT....T.	.A.....T..
Pelomedusa	.T..C.....	......TAA.	..C.....	.....	....C.C..T	........T.	..T....C..	C..C..C...	...T....C.	.A...T.A..
Pelusios	....C...AT	C..C..T.T.	.....	.T..A..G..	....C....T	..T.....A.	.......C..	C..C..A..C	.....G....	.G..GT.A..
Phrynops	....C..CAG	C..C.....	.....G.	.....G..	T...C....T	......A.T.	.....	A..C..A..C	.....G.	.A..C..G..
Staurotypus	....TT..A.	C..T.....T	..C..T....	....A.....	....C.T...	.....T..A.	.T.....	A..C..A..C	...T.....	.A.....
Kinosternon	.T..T..TAT	...T.....	.....T....	....A.....	....C.C..T	.....T..A.	.....	A.....A...	...T.....	.T.....T..
Trachemys	....C..TAT	C..T...T..	.....T....	....A.....	...TC.T...	........A.	.T.....	.....A..C	..G.....T.	.A.....T..
Chelonia	....T.....	C..T..T..C	..C.....	....A.....	....C....T	........A.	.....	A..C..A..C	.....C.	.A.....A..
Geochelone	....C.....	A..C..T..C	.....T....	....A..G..	....C....T	.....T..A.	....C.....	.....A...	.....G....	.....T..
Elseya	.....A.	C..T..A..C	..C..T....	.G..A.....	.C..C.....	........A.	.....	A.....C..C	.....	.T..G..A..
Carettochelys	.....C..	A..C..T..C	..C.....	....A.....	...TG.G...	..T.....	.....	A..C..A..C	.....T..C.	.A..G..T..
Chelodina	.T.....GT	A..C..A..C	..C..T....	.....	....C.....	.....T....	..T.....	A..C.....	.....	.A..T..A..
Chelydra	....C..GGT	A..C..A...	..C.....	....A.....	....C....T	........A.	.....	A..C..A..C	.....	.T...T.A..
Chinemys	.T...T....	C..T.....C	..C..T....	....A.....	....C.C...	........A.	....C.....	...C..A..C	.....	.....T..
Lissemys	.....	A.....TA..	.....	....A.....	....C....T	..T..T..T.	.....	AG....A..C	.....T.	.A.....T..
Podocnemis	....CT..GT	C..T..A...	.....	....A.....	.....	........A.	....G.....	C..C..A...	.....C....	.T..TT.A..
Platysternon	....T.....	C..T..T..C	.....T....	.T..A.....	....C.C...	..T..T..A.	.....	A.....C	.....C.	.....T..
Heosemys	....T.....	C..C..T...	.....G.	....A.....	...TC.....	..T.....A.	....C.....	...C..A...	.....	.....T..
Dermochelys	....CT....	C..C..A...	.....	....A.....	....C.....	........A.	.....	A..C..C...	.....C.	.A.....A..
Dermatemys	....C...A.	C..C..T..C	.....T....	....A.....	....C....T	.....T..A.	..T.....	C..C..A..C	.....T.	.....

APPENDIX 2. Continued.

Apalone	CCTACTCATA	TCTATTCTAG	TACTATTCAT	CCTACCCATA	CTTCACACAT	CAAAACAACG	AACACTGACA	TTCCGCCCTA	TCACCCAAAC	AC
Chelus	......AC.C	..A..C...A	.CT.....C.	.A......CC	..A...CT..	....	...CTCC.T.	.....A..A.	.A........	CA
Clemmys	....A.AC.C	.....C....	.GT.....C.	AA.......C	T.A.......	....	T...ACCCA.	.....A..CC	.A..A....T	C.
Graptemys	......AT.C	.....C..T.	..T.....C.	AA.G....CC	..A.......	....	....ACCCA.	.....A..AC	.T..A.....	C.
Pelomedusa	......ATCC	..AG.AACTA	.C..C.....	.A.......G	..A.....C.	.C.......C	.T..GCA..C	.....A...T	....A....T	C.
Pelusios	...C..AGCC	..GG.AACCA	.C..T..TC.	.A......CC	T.A.....C.	.C........	CT..ACC..C	.....A..CT	.A.......T	T.
Phrynops	...TT.AT.C	..A..C...A	.C..CC..C.	AA.G....CC	....	....G.....	...CGCT.T.	.....A..C.	.G......G.	.A
Staurotypus	......AGCT	..C..C..TA	.C..C...T.	A..C..A...	ACA.......	.C........	....ACT.T.	.....A..AC	.T.......T	C.
Kinosternon	......ATCC	..A..C..CA	.C..C..T..	AT.G..A..C	T.A.......	.C........	....GCC.TG	.....A..AT	....	C.
Trachemys	......AC.C	.....C..T.	....G..TC.	AA......CT	..A.......	....	....ACCCA.	.....A..AC	.T..A.....	C.
Chelonia	......AT.C	..C..C...A	.TT.....C.	AA......CC	T.A.....G.	....	....GCCT..	.....A..AC	.........T	C.
Geochelone	....T.TT.C	....	..T.....C.	AA....A..C	..A.......	....	.T..ACC.T.	.....A..CT	.A.......T	C.
Elseya	A...T.....	..A..A....	.....C.AC.	.A....AG.C	..C...CT..	....	....ACC...	.....A..A.	.A..-----	--
Carettochelys	T......T.T	..C......A	.CTC....C.	A..C..A..T	..A.......	....	C...A.A.T.	.....A..A.	..T.......	C.
Chelodina	AT....AC.G	..A..CT..A	.C...C..C.	AA....A..T	..A..TCT..	....	....GCT...	.....A..C.	....	.A
Chelydra	...T..AT.C	..C..C..CA	.C...C.TT.	AA.......C	..C.......	....	....A.CCA.	..T..A..AT	GA..T....T	CT
Chinemys	...CA.AGC.	.....C..T.	.......T..	AA.G..GG.C	T.A..T....	.......G..	T...GCTT..	..T..A..AC	.A..A....T	C.
Lissemys	......AC..	..A..CT...	..T.......	G.....T...	..C.......	....	...CA.....	.....A..A.	.A..T.....	.T
Podocnemis	...TT..T..	..A..CGC.A	.C..CG..C.	TA.C......	..A.....C.	.C........	...C..C...	.A......C.	.TT.A.....	C.
Platysternon	...C..AT..	G.......TA	.....C..C.	AA.G..T..C	..A..T....	....	...CACAT..	.....A..AC	.A.......T	C.
Heosemys	...CT.AT.C	..C..C..C.	..T.......	AA....AGCC	..A.......	.......G..	C...TCTT..	.....A..A.	CA.......T	TT
Dermochelys	....T.ATC.	..C..C....	.G.....TC.	AA....T...	T.A..T....	....	....GCCT..	.....A..AC	....	C.
Dermatemys	T.....AT.C	.....C..TA	.C..C...G.	AA....AGCC	T.A......G	....	....GCCCT.	.....A..CC	.A.......T	C.

APPENDIX 3. Aligned sequence data for approximately 350 base pairs of 12S rDNA for 23 taxa of turtles. Regions of questionable allignment are in lowercase and were not used for phylogenetic analyses in this study. GenBank accession numbers (in the same order as the sequences listed below) are U81319–U81341.

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Apalone          AGAAAACTAC GAGCaaaa-- CGCTTAAAAC TCCAAGGACT TGGCGGTACT TCAAATCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGCTAAAC
Chelus           AGAGAACTAC CAACccta-- TATTAGAAAC TCAAAGGACT TGACGGTGTC TCAAACCCAA CTAGAGGAGC CTGTCCCAAA ACCGATAATC CACGATACAC
Clemmys          AGAGAACTAC GAGCacaaa- CGCTTAAAAC TCTAGGGACT TGGCGGTACC TCAAACCCAC CTAGAGGAGC CTGTTCTATA ACCGATAATC CACGATTTAC
Graptemys        AGAGAATTAC GAGCaaaa-- AGCTTAAAAC TCTAAGGACT TGGCGGTGCC TCAAACCCAC CTAGAGGAGC CTGTTCTATA ATCGATGATC CACGATCCAC
Pelomedusa       CGAGAACTAC GAGCctac-- AGCTTAAAAC TTAAAGGACT TGGCGGTGTC CCATACCCAA CTAGAGGAGC CTGTTCTATA AGCGATTATC CACGATCAAC
Pelusios         AGAGAACTAC TAGCttgt-- AGCTTAAAAC TCAAAGGACT TGGCGGTGTC -CACACCCTA CTAGAGGAGC CTGTTCTATA AGCGATAATC CACGATAAAC
Phrynops         AGAGTACTAC TAACcaca-- CATTTGAAAC TCAAAGGACT TGACGGTGCC TCAAACCCAA CTAGAGGAGC CTGTTCTATA ATCGATTATC CACGATTTAC
Staurotypus      AGAGAATTAC GAGCtatata TGCTTAAAAC TCTAAGGACT TGGCGGTACC TCAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATTCAC
Kinosternon      AGAGAATTAC GAGCtaaaca TGCTTAAAAC TCTAAGGACT TGGCGGTACC TCAAACCCAC CTAGAGGAGC CTGTTCTATA ATCGACAATC CACGATTCAC
Trachemys        AGAGAATTAC GAGCaaaa-- CGCTTAAAAC TCTAAGGACT TGGCGGTGCC TCAAACCCAC CTAGAGGAGC CTGTTCTATA ATCGATAACC CACGATCTAC
Chelonia         AGAGAACTAC GAGCataa-- CGCTTAAAAC TCTAAGGACT TGGCGGTACC TCAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATCTAC
Geochelone       AGAGAACTAC GAGCaaaa-- CGCTTAAAAC TCTAAGGACT TGGCGGTGCT TYAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATTTAC
Elseya           AGAGAACTAC AAACcaaa-- CGTTTAAAAC TCAAAGGACT TGGCGGTGTC CCAAACCCAC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATTCAC
Carettochelys    AGAGAATTAC GAGCaaaa-- AGCTTAAAAC TCTAAGGACT TGGCGGTACC TCAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATTCAC
Chelodina        AGAGAACTAC AAACcaaa-- CGTTTAAAAC TCAAAGGACT TGGCGGTGCT TCAAACCCAC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATACAC
Chelydra         AGAGAACTAC GAGCaata-- CGCTTAAAAC TCTAAGGACT TGGCGGTACC TCAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAACC CACGATCTAC
Chinemys         AGAGAACTAC GAGCaaaa-- CGCTTAAAAC TCTAAGGACT TGGCGGTACC TCAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATCCAC
Lissemys         AGAATACTAC GAGCaaaa-- TGCTTAAAAC TCTAAGGACT TGGCGGTACC TCACACCCAC CTAGAGGAGC CTGTTCTATA ATCGATACTC CACGCTAAAC
Podocnemis       AGAGAACTAC AAGCcaaa-- TGCTTAAAAC TCAAAGGACT TGACGGTGCC TCAAACCCAC CTAGAGGAGC CTGTTCTATA AGCGATAATC CACGATAAAC
Platysternon     AGAGAACTAC GAGCccaaa- CGCTTAAAAC TCTAAGGACT TGGCGGTACC TCAARCCTCC -TAGAGGAGC CTGTTCTATA ATCGATAATC CACGATCTAC
Heosemys         AGAGAACTAC GAGCaaaa-- TGCTTAAAAC TCTAAGGACT TGGCGGTACT YCAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATTTAC
Dermochelys      AGAGAACTAC GAGCaaaa-- CGCTTGAAAC TCTAAGGACT TGGCGGTACC TCAAACCCCC CTAGAGGAGC CTGTTCTATA ATCGATAATC CACGATTCAC
Dermatemys       AGAGGATTAC AAGCcaaa-- TGCTTGAAAC TCTAAGGACT TGGCGGTATC TCAAACCCAC CTAGAGGAGC CTGTCCTATA ATCGATAATC CACGATTCAC

Apalone          CTCACCATCT TTTGCCaacc -CAGCCTATA TACCACCGTc a-cAGCTTAC CTTGTGAAA- gaaa-aaaaG TAAGCTAAAC AGT-taaaac aaCTAGAAAG
Chelus           CTAACCACTT CTAGCCca-- -CAGCCTATA TACCTCCGTc tccAGCCTAC CTTATGAAA- g-tacaaaaG TAGGCACAAC AGT-taac-c aaCTAACAAG
Clemmys          CTCACCATCT CTCGCCaac- -CAGCCTATA TACCACCGTc accAGCTTAC CCTATGAAG- gatacaaaaG TAAGCAAAAC AATataa-at caTTAACAAG
Graptemys        CTCACCATCT CTTGCCaat- -CAGCCTATA TACCACCGTc tccAGCTTAC CTTGTGAAG- gatataaaaG CAGGCAAAAC AATataa-ac caTTAACAAG
Pelomedusa       CTTACCACCC TTTGCCat-c -CAGCCTATA TACCGCCGTc taaAGCTCAC CTTATGAAA- gctaaaaa-G TAAGCAAAAT AGC-tactac agCTAGAAAG
Pelusios         CTTACCACCC TTTGCCatat -CAGCCTATA TACCGCCGTc tccAGCTTAC CTTATGAGA- gcta-aaaaG TAAGCAAAAT AGCcctctac agCTAGAAAG
Phrynops         CTCACCACCC TTAGCCca-- -CAGCCTATA TACCTCCGTc ttcAGCCTAC CCTGTGAAA- g-tataaaaG TAGGCACAAT AGT-caaca- agCTACTAAC
Staurotypus      CTCACCATCT CTTGCTaact -CCGCCTATA TACCGCCGT- a-aAGCTTAC CTTATGAAA- gacg-aaaaG TAGGCAAAAT AATctaa-ac a-TTAATAAA
Kinosternon      CTCACCATCT CTTGCCaact -CCGCCTATA TACCGCCGTc a-tAGCTTAC CTTATGAAA- gata-aaaaG TAAGCAAAAT AATctaa-ac aaTTAACAAA
Trachemys        CTCACCATCT CTTGCCaac- -CAGCCTATA TACCACCGTc gccAGCTTAC CCCGTGAGG- -atacaaaaG TAAGCAAGAT AATataa-ac caTTAACAAG
Chelonia         CTCACCATCT CTTGCCaaac -CAGCTTATA TACCACCGTc accAGCCTAC CCCATGAGG- cccacaaagG TAAGCTAAAT AACCtaa-ac aaTTAATAAG
Geochelone       CCTACCATCT CTTGCCaata -CCGCCTATA TACCACCGTc attAGCCTAC CCTATGAAG- gatataagaG TAAGCAAAAT AGCtaacaac agCTAACAAG
Elseya           CTCACCACCT CTCGCCca-- -CAGCCTATA TACCTCCGTc a-cAGCTTAC CCTACCAAG- gaga-aaaaG TAAGCACAAT AGTct-acac aaCTAACAAG
Carettochelys    CTCACCATCC TTTGCCtaat aCAGCCTATA TACCGCCGTc a-cAGCTTAC CCTATGAAG- -acataaaaG TAAGCCGAAC AGCtacatcc agCTAAAAAG
Chelodina        CTCACCATCT CTAGCCca-- -CAGCCTATA TACCTCCGTc tacAGCTTAC CCTGTGAAG- gaattaaaaG TAAGCATAAC AGTtaacac- agCTAACAAG
Chelydra         CTCACCATCC CTTGCCaatt -CCGCCTATA TACCACCGTc accAGCTTAC CCTATGAAGg gacacaaaaG TAAGCAAAAC AGCctaaac- aaCTAACAAG
Chinemys         CTCACCATCT CTTGCCaatc -CCGCCTATA TACCACCGTc accAGCTTAC CCCATGAGG- --cattaaaG TAAGCAAAAT AACtaaaag- --TTAACAAG
Lissemys         CTCACCACTC CTTGCCacc- -CAGCTTATA TACCACCGTc t-tAGCTTAC CCCATGAGG- g-caa-aaaG TTAGCACAAC AGTttaaac- agCTAATAAG
Podocnemis       CTTACCATCT TTTGCCccc- -CAGCCTATA TACCGCCGTc tccAGCCTAC CTTGTGAGA- gg-aaagaaG TAAGCACAAT AGTccatac- aaCTAGAACG
Platysternon     CTCACCATCC CTTGTCaatt -CAGCCTATA TACCACCGTc atcAGCTTGA CCCTGTGAA- ggtacca-aG TAAGCAAAAT AATctaaat- aaCTAGCAAG
Heosemys         CTCACCATCC CTTGCCaatt -CCGCCTATA TACCACCGTc accAGCTTAC CCTATGAGG- -gtataaaaG TAGGCAAAAT AACt-aatt- agTTAACAAG
Dermochelys      CTCACCATCT CTTGCCaatc -CCGCCTATA TACCACCGTc accAGCTTAC CCCGTGAGG- --taaaaaaG TAAGCAAAAT AACccac--- aaCTAGCAAT
Dermatemys       CTCACCATCT CTTGCCaata -CCGCCTATA TACCGCCGTc accAGCTGAC CTTATGAAA- -ggaaaaaaG TAAGCAAAAT AATctaaaca -aTTAATAAG
```

APPENDIX 3. Continued.

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Apalone        TCAGGTCAAG GTGTAGCCAA ttaa--gatg -gaagaaaTGG GCTACATTT T-ctAAAATA GAAATaacc -------ac- GAAACAGAAC CATGAAACac
Chelus         TCAGGTCAAG GTGTAGCCAA tgaaatggtg -ga-ga--TGG GCTACATTT T-ctACAATA GAAACatat tacattgac- AGAACGGA-T TTTGAAACta
Clemmys        TCAGGTCAAG GTGTAGCTAA ctga--gatg -gaagaagTGG GCTACATTT T-ctATATTA GAAATaaac tc-----ac- GGAAAGGAAC TATGAAACag
Graptemys      TCAGGTCAAG GTGTAGCTAA ttga--gatg -gaagaaaTGG GCTACATTT T-ctATACTA GAAATaaca ctc----ac- GGAAAGGAAC CATGAAACag
Pelomedusa     TCAGGTCCAG GTGTAGCCAA tag---ggtg -gatgtaaTGG GCTACATTT T-ctAAAATA GAAATattc -------ac- GGACAGAC-C CTTGAAACag
Pelusios       TCAGGTCCAG GTGTAGCCAA taga---gtg -gatgtaaTGG GCTACATTT T-ctAAAATA GAAATattc -------ac- GAACAGAC-C CTTGAAACag
Phrynops       TCAGTTCCAG GTGTAGCTAC tcctatggtg -gacgtaaTGG GCTACATTT T-ctAAGCTA GAAACaact attct--ac- GGAAGGGCAC TTTGAAACag
Staurotypus    TCAGGTCAAG GTGTAGCTTA ttga--gatg -gaagaaaTGG GCTACATTT T-ctATATTA GAAATtaac c------ac- GGAAAGACAC CTTGAAACag
Kinosternon    TCAGGTCAAG GTGTAGCTTA ctga--gatg -gaagaaaTGG GCTACATTT T-ctATATTA GAAATaact -------ac- GGAAAGATAC CTTGAAATag
Trachemys      TCAGGTCAAG GTGTAGCTAA ctga--gatg -gaagaaaTGG GCTACATTT T-ctATACTA GAAATaaca actc---ac- GGAAAGGAAA CATGAAACta
Chelonia       TCAGGTCAAG GTGTAGCTAA ctga--gatg -gaacaaaTGG GCTACATTT T-ctATTCTA GAAATaacc -------ac- GGAAGGAGAC CATGAAATag
Geochelone     TCAGGTCAAG GTGTAGCTAA ttga--gatg -gaagaaaTGG GCTACATTT T-ctAAATTA GAAATaatc tc-----ac- GGAAAGAA-C TATGAAACaa
Elseya         TCAGGTCAAG GTGTAGCCAA ctga--ggtg -gaagaaaTGG GCTACATTT T-ctACACTA GAAATattc -------ac- GGAAAGAG-C TCTGAAATat
Carettochelys  TCAGGTCAAG GTGTAGCTTA ctag--gatg -gaagaaaTGG GCTACATTT TcttACCAAA GAAATacca -------ac- GGATATGAAC TTTGAAACaa
Chelodina      TCAGGTCAAG GTGTAGCCAA ctga--gatg -gaagaaaTGG GCTACATTT T-ctATACTA GAATTattt ta-----ac- GGAAAGAG-C CTTGAAAAca
Chelydra       TCAGGTCAAG GTGTAGCTAA ttga--gatg -gaagaaaTGG GCTACATTT T-ctACATTA GAAATaatt c------ac- GGAAGGAA-C CATGAAATgg
Chinemys       TCAGGTCAAG GTGTAGCTTA ttga--gatg ggaagaaaTGG GCTACATTT T-ctATACTA GAAATaaat tt-----ac- GGAAAGGAAC TATGAAATaa
Lissemys       TCAGGTCAAG GTGTAGCCAA -tgg--agtg -gaagaaaTGG GCTACATTT T-ctATAATA GATATtacc -------ac- GGAATTGCGC CATGAAATac
Podocnemis     TCAGGTCCAG -CGTAGCCAA -tga--gatg -gaagaaaTGG GCTACATTT T-ctAATATA GAAATagtc -------ac- GGAGAGAG-C CCTGAAAAaa
Platysternon   TCAGGTCAAG GTGTAGCTAA ctga--gatg -gaagaaaTGG GCTACATTT T-ctTTATTA GGAATcact ta-----ac- AGAAAGGA-C CATGAAATaa
Heosemys       TCAGGTCAAG GTGTAGCTAA ctga--gatg -gaagaaaTGG GCTACATTT T-ctACACTA GAAATtaat tt-----ac- GGAAAGGAAC TATGAAATaa
Dermochelys    TCAGGTCAAG GTGTAGCTAA ttga--gatg -gaagaaaTGG GCTACATTT T-ctATATTA GAAATcagt ac-----aca GGAAGGAGAC TATGAAACaa
Dermatemys     TCAGGTCAAG GTGTAGCTTA ctga--gatg -gaagaaaTGG GCTACATTT T-ctATAATA GAAATaacc -------ac- GGAAGGAAAC CATGAAACag

Apalone        gg--tctaaa caaGAAGGAT TTAGTAGTAA actgagaaca gagggc
Chelus         aa-cccgaaa aaaGAAGGAT TTAGCAGTAA tgtaagaata gagagc
Clemmys        -----tccta aaaGTCGGAT TTAGCAGTAA actgtgaaca gagagcccag
Graptemys      -----tccag caaGTAGGAT TTAGCAGTAA actgagaaca gaga
Pelomedusa     gga---ctaa taaGTTGGAT TTAGCAGTAA tctaagaata gaaagcctat atta
Pelusios       gga---ctaa gaaGCAGGAT TT
Phrynops       ggacccgaag caaGCAGGAT TTAGCAGTAA tgta
Staurotypus    ggcttctaag caaGTAGGAT TTAGCAGTAA actg
Kinosternon    ga-ttctacg cagGATGGAT TT
Trachemys      g----tccag caaGTAGGAT TTAGCAGTAA actg
Chelonia       g----tccca caaGCAGGAT TTAGCAGAAA ctggaaa
Geochelone     g----tccta taaGCAGGAT TTGGCAGTAG acatacat
Elseya         aga--tccta aaaGCAGGAT TTAGCAGTAA tgtgaaagca gagag
Carettochelys  g--tcttaac aaaGCCGGAT TTAGCAGTAA attgaaagca gagagttcaa ttt
Chelodina      ttg--ctcta aaaGCAGGAT TTAGCAGTAA tatgagaaca g
Chelydra       g----tccca caaGTAGGAT TTAGCAGTAA actggggata gag
Chinemys       g----tccca caaGTAGGAT TTAGCAGTAA accgggatca tgaatacccg atttaa
Lissemys       gg--ccaaaa caaGCAGGAT TTAGAAGTAA attgagaaca gagagcctaa ttaaaa
Podocnemis     gg---cctca aaaGCAGAAT TTAGCAGTAA ttttggaata gtgagccaaa atta
Platysternon   g----tccca taaGTAGGAT TTAGCAGTAA actgggaaca gagagcccaa tt
Heosemys       g----tccaa caaGTAGGAT TTAGCAGTAA accgggatca aaatgcccaa ttt
Dermochelys    g----tccca caaGTAGGAT TTAGCAGTAA actggg
Dermatemys     g----ttcca caaGTAGGAT TTAGCAGTAA actggaacag agagcccaat ttaag
```

APPENDIX 4. Morphological data for 115 characters for 23 living and 7 fossil taxa of turtles. For character descriptions, see Appendix 1.

	Character No.
	1111111111111111
	1111111111222222222233333333334444444444555555555566666666677777777778888888889999999990000000000111111
Taxon	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345
Proganochelys	000000000000000000000000000000000000000000000?000000000000000?000000000?000000000000000?000000000000000?000000000
Elseya	111110000110010010011111011111111011111000400111100000100007?000000000?000001000000000000000000010001100000010011?1
Phrynops	111110000110010010011111011111111011111000400111111100100017?000000000?000001000000000000000000010001100000010011?1
Chelus	111110000110010011011111011111111011111000400111111111110001?000000000?000001000000000000000000010001100000010011?1
Chelodina	111110000110011010011111011111111011111000600111111111110000?000000000?000001000000000000000000010001100000010111?1
Podocnemis	11?110000110011011111111011110110111111111000000000010001?000000000?000001000000000000000000010001000000001001101
Pelusios	11?110000110011011111111011110011011111111211000000000100017?000000000?000001000000000000000000010001000000001011101
Pelomedusa	11?110000110011011111111011111011011111111311000000000100017?000000000?000001000000000000000000010001000000001011101
Platysternon	111111111111101101100001100111101110010100600000000000011111000000000000000010000000000000000000010001100011001101
Chelydra	111111111111101101100001100111101110010100500000000000011111000000001000000010000000000000000000010001100011001101
Chelonia	111111111111100101100001100111101111110100700000000000000010?111111000?000000000000000000000000010000010001101111100
Dermochelys	111111111111100101100001100111101111110100?000000000000000010?111111000?000000000?000000??000??0000?001000110111100
Dermatemys	111111111111101101100001101111101111110100700000000000000000000000000011111010000000000000000011110000100000110011101
Kinosternon	111111111111101101100001101111101111110100700000000000000000000000000011111000000000000000001111111101110011001101101
Staurotypus	111111111111101101100001101111101111110100600000000000001000000000011111000000000000000000111111110111001100110111101
Carettochelys	111111111111101101100001101111101111110110900000000000000011?020000111?101111111?000000??000?101100?11?001101111101
Lissemys	111111111111101101100001101111101111110110800000000000000110000000111011011111111?111111??000?001000?01?001101111101
Apalone	111111111111101101100001101111101111110110800000000010000110000000111011011111111?111111??000?001000?01?001101111101
Clemmys	111111111111101101100001101111101111110100400000000000200000000000000000000000000000000000010000001000011000110111111
Graptemys	111111111111101101100001101111101111110100400000000000200007?000000000?000000000000000000010000001000111011110111111
Trachemys	111111111111101101100001101111101111110100400000000000200000000000000000000000000000000000010000001000110011110111111
Heosemys	111111111111101101100001101111101111110200500000000000010000?000000000?000000000000000000010000001000111000110111111
Chinemys	111111111111101101100001101111101111110200500000000000010000?000000000?000000000000000000010000001000111000110111111
Geochelone	111111111111101101100001101111101111110200500000000000010001000000000000000000000000000000010000001000111000110111111
Adocus	111111111111101101100001101111101111?1101007000000000000000?000000?101?11100000?010000000000000000000000100?110111111
Emarginachelys	1111111?11111011?1100?01??11111011???1???0?000000?00000??00?000000?111?010000007000000?10?00000100?00110?110?11111
Meiolania	111111111111100100000101000111101000000007000000000007000?0?000000?0?00000100?0000000?0?000000000?0100000000111?
Sinemys	11?111111111010?0000?01??111110110000??1??010??0100000?111?????000????100??00???00000????00000?10??0110??100011??
Lindholmemys	1111111?11111011?1100?01???11110?????????0??0????0??0?01??00??????0??????0000000?00000?0?10?0000?1???0?10????0?111??
Mongolemys	1111111?11111011111100?01???111101??????00????00?00?00010?00?00??7000????0000000?00000?0?10?0000??0?00?10?0??0?111??