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DATA SET INCONGRUENCE AND THE PHYLOGENY OF CROCODILIANS

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Abstract.—Published sets of systematic data on crocodilians (18S and 28S nuclear ribosomal DNA [rDNA] restriction fragments, mitochondrial rDNA restriction fragments, 12S mitochondrial rDNA sequences, osteology, external morphology, dentition, nest type, albumin, parasites) were used to test hypotheses of data set incongruence and phylogeny. Comparing incongruence indices between molecular versus molecular data set comparisons and molecular versus morphological data set comparisons showed the morphological/molecular comparisons to be significantly more incongruent, and experiments removing taxa suggested that morphological incongruence can be localized to the separation of *Gavialis* from *Tomistoma*. Significance tests of incongruence between the five larger crocodilian data sets relative to each other and to combined data sets supported these hypotheses and demonstrated that only 1 (12S sequences vs. morphology) of the 10 pairwise comparisons of data sets show significant incongruence. Three hypotheses of crocodilian phylogeny were evaluated using combined parsimony analysis, separate parsimony analyses, and evaluation of uncombinable data. The (alligatorids(crocodylids(*Gavialis, Tomistoma*))) hypothesis of crocodilian relationships was best supported. Although this hypothesis is not supported by one of the molecular data sets and requires additional morphological homoplasy beyond that required in most-parsimonious trees based on morphology, other hypotheses require even more homoplasy, and any particular hypothesis of crocodilian evolution requires additional homoplasy in more than one data set. Alligatorid relationships were robustly supported in both combined and separate analyses. *Crocodylus* relationships were not well resolved in most-parsimonious trees from any individual data set but were completely resolved in the combined analysis. [Combined analysis; crocodilians; incongruence; phylogeny; separate analysis.]

How best to identify incongruence between data sets is a topic of current debate in systematics (e.g., Hillis, 1995). If incongruence is established, the question of how to proceed in estimating phylogeny is unclear (see Kluge, 1989; Barret et al., 1991; Bull et al., 1993; de Queiroz, 1993; Chippindale and Wiens, 1994; Miyamoto and Fitch, 1995). Swofford (1991) demonstrated an integrated approach to handling incongruence and reconstructing phylogeny that included incongruence indices, comparison of near-shortest trees, and consensus trees. Hillis (1995) and Larson (1994) suggested a shift in emphasis from comparing final conclusions to analyzing instead what trees are compatible with both combined and partitioned analyses. The arguments of these authors underscore the importance of using methods of analysis that are comparable, for which incongruence is measureable, and for which combined as well as partitioned analyses are possible.

Analysis of the extant Crocodylia is used here to demonstrate the use of incongruence measures to test hypotheses of general and localized relative data set incongruence and, following Swofford (1991), to undertake a multifaceted approach to phylogeny reconstruction. In addition to their importance as probably the only tetrapod order small enough to be manageable for detailed phylogenetic analysis, crocodilians are especially useful for studies of phylogeny and incongruence for three main reasons. First, relative to other groups, an unusually large amount of data is available for crocodilians from several potentially independent data sets. For example, none of the studies listed by Chippindale and Wiens (1994) used more potentially independent data sets than are available for crocodilians. In addition to offering independent evidence for phylogeny (Swofford, 1991; Miyamoto and Fitch, 1995), the existence of multiple data sets allows more precise identification of conflict and the testing of hypotheses of rela-

tive conflict among data sets. Second, the crocodilian data have not been analyzed with consistent methodology (Brooks and O'Grady, 1989; Norell, 1989). The importance of using comparable methods to evaluate phylogeny and data set conflict has been emphasized by many authors (e.g., Hillis, 1985; Patterson et al., 1993). Third, hypotheses of incongruence between crocodilian data sets have been suggested (e.g., Hass et al., 1992).

I used combined analysis, partitioned analyses, and examination of uncombinable data (i.e., any data for which phylogenetic analysis by discrete character parsimony is impossible or uninformative, such as distance or geographic data) to estimate crocodilian phylogeny. A combined approach was used to find the globally most-parsimonious solution for the data (Kluge, 1989; Barret et al., 1991) and to exploit the special benefits of the different data sets. Taxonomic coverage and use of outgroups varies in the crocodilian studies, and by combining data the advantages of large data sets and of data informative at different levels in the tree (Hillis, 1987) can be realized. Separate analyses were used mainly for the independent assessment of hypotheses (Miyamoto and Fitch, 1995). The uncombinable data have some disadvantages relative to the discrete character data. Nevertheless, they were included in an attempt to incorporate all available evidence.

Once each data set has been analyzed with the same method, incongruence indices may be used to quantify data set conflict (Swofford, 1991). Incongruence indices have been used by some authors (e.g., Kluge, 1989; Omland, 1994; Titus and Larson, 1995), but these indices are usually used as quantitative statements of incongruence rather than as tests of specific hypotheses. Evaluation of hypotheses of incongruence requires statistical tests to assess significance, but these have rarely been applied (but see Farris et al., 1994, and citations therein). I used incongruence indices (Mickevich and Farris, 1981; Miyamoto pers. comm. to Kluge, 1989) in conjunction with significance tests (e.g., Farris et al., 1994) to examine hypotheses of data set incongruence in crocodilians.

Crocodilian Phylogeny

The eight genera and 22 extant species of the suborder Eusuchia are the surviving members of the formerly diverse Crocodylia (Clark, 1994: table 5.1 lists 24 extinct genera in addition to three modern lineages). Among these extant forms, crocodylids (*Crocodylus* + *Osteolaemus*) and alligatorids (*Alligator* + *Caiman* + *Paleosuchus* + *Melanosuchus*) (sensu Norell, 1989) are well-established monophyletic groups (Romer, 1956; Densmore, 1983; Norell, 1989). The relationships of crocodylids, alligatorids, and the monotypic (among extant forms) genera *Tomistoma* and *Gavialis* have been a contentious issue in crocodilian systematics. All morphological analyses (except Buffetaut, 1985; see Norell, 1989) have suggested that the hypothesis in Figure 1a (hypothesis A) (or minimally *Gavialis* as the sister group to the other extant crocodilians) is the true phylogeny, whereas all authors using molecular data (e.g., Densmore, 1983) have suggested that the hypothesis in Figure 1b (hypothesis B) (or minimally *Gavialis* and *Tomistoma* as sister groups) is correct. A third hypothesis, represented in Figure 1c (hypothesis C), accommodates the most strongly supported results from both the morphological analyses, which find *Gavialis* basal, and the molecular analyses, which are unrooted and group *Tomistoma* and *Gavialis* together. Obviously other trees are possible, e.g., nonmonophyly of alligatorids or crocodylids, but any support for a particular hypothesis of alligatorid or crocodylid nonmonophyly is weak and restricted to single data sets.

Diverse approaches have been used to estimate crocodilian phylogeny. Densmore and White (1991) analyzed data sets of 18S and 28S nuclear ribosomal DNA (rDNA) restriction fragments (RFLPs) and mitochondrial rDNA (mtDNA) RFLPs with UPGMA and a "compatible parsimony" method that involved performing a parsimony analysis to find those characters that showed no homoplasy and then using the

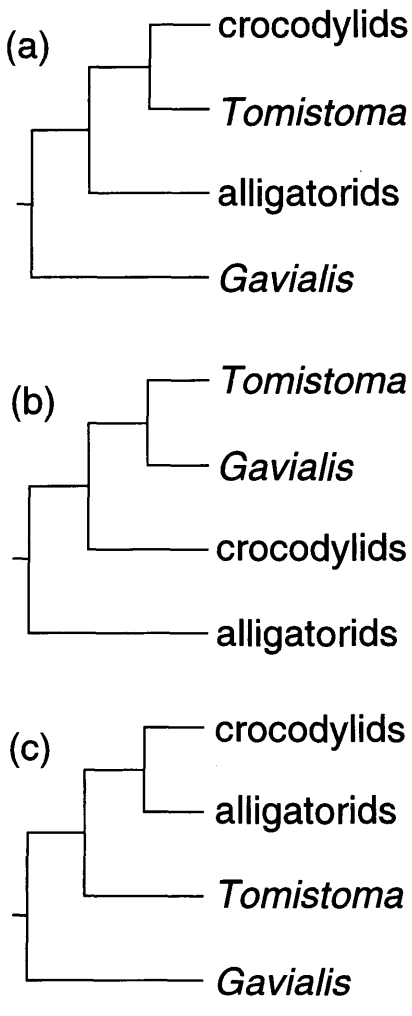

FIGURE 1. Three hypotheses of the phylogeny of major lineages of crocodilians. (a) Hypothesis from morphological studies. (b) Hypothesis from molecular studies. (c) Hypothesis that allows for basal placement of *Gavialis* and *Gavialis / Tomistoma* similarity.

nonhomoplastic characters to construct an unrooted (because no outgroups were included) compatibility tree. Densmore (1983) analyzed allozyme data with the UPGMA distance method with separate matrices for alligatorids and for crocodylids + *Gavialis* + *Tomistoma*. Norell (1988, 1989) and Clark (1994) analyzed osteological characters with parsimony and outgroups. Gatesy and Amato (1992) looked at sequence similarity of 12S mtDNA (no tree was presented). Hass et al. (1992) reanalyzed Gatesy and Amato's 12S mtDNA sequence data for five species using parsimony, the bootstrap, and outgroups. Gatesy et al. (1993) analyzed their 12S sequence data with parsimony, but because they were concerned with alligatorid relationships they included no noncrocodilians as outgroups. Distance studies using albumin antisera (Hass et al., 1992; Densmore, 1983), transferrin antisera, and hemoglobin tryptic peptides (Densmore, 1983) did not use outgroups. Chromosomal (Cohen and Gans, 1970), ecological (Greer, 1970), and external morphological (Brazaitis, 1973; Ross and Mayer, 1983) data have not been included in numerical systematic analyses. Furthermore, except for Hass et al.'s (1992) reanalysis of some of the 12S sequence data, no crocodilian systematic study to date has employed measures of support such as the bootstrap, jackknife, or decay index.

Because of the disparate methods used, degree of data conflict and strength of competing hypotheses have been difficult to assess (Brooks and O' Grady, 1989; Norell, 1989). The hypotheses of Figure 1 were evaluated relative to each other by the criteria of combined parsimony analysis, separate parsimony analyses of the larger data sets, and examination of albumin- and parasite-based phylogenies. Incongruence analyses were undertaken to address the following questions: (1) Do the individual data sets show significant incongruence with each other or with the combined set of data? (2) Is the morphological data set significantly incongruent with the molecular data sets, and if so is this incongruence predominantly due to the placement of *Gavialis* (e.g, see Hass et al., 1992)? Various tests of incongruence were used, and the results of these tests were compared.

MATERIALS AND METHODS

Estimation of Phylogeny

Data and taxa used in this study, taxonomic coverages of data sets, and character sets scored for each taxon are listed in Ta-

TABLE 1. Crocodilian and outgroup taxa analyzed and type and number of characters. See Appendix for references and discussion of characters.

	Character sets										
						Morphology					
Taxon (OTU)	No. chars.	18S RFLP	28S RFLP	mt RFLP	12S sequences	External[a]	Dentition	Osteology	Chromosomes[a]	Nest[a]
Crocodylus acutus	159	x	x	x		x	x	x	x	x
C. cataphractus	159	x	x	x		x	x	x	x	x
C. intermedius	121	x	x			x	x	x	x	x
C. johnsoni	159	x	x	x		x	x	x	x	x
C. moreletii	158	x	x	x		x	x	x	x	
C. niloticus	159	x	x	x		x	x	x	x	x
C. mindorensis	159	x	x	x		x	x	x	x	x
C. novaeguineae	159	x	x	x		x	x	x	x	x
C. palustris	159	x	x	x		x	x	x	x	x
C. porosus	159	x	x	x		x	x	x	x	x
C. rhombifer	240	x	x	x	x	x	x	x	x	x
C. siamensis	159	x	x	x		x	x	x	x	x
Osteolaemus tetraspis	121	x	x			x	x	x	x	x
Tomistoma schlegelii	240	x	x	x	x	x	x	x	x	x
Gavialis gangeticus	240	x	x	x	x	x	x	x	x	x
Alligator mississippiensis	240	x	x	x	x	x	x	x	x	x
A. sinensis	140				x	x	x	x	x	
Caiman crocodilus	202	x	x		x	x	x	x	x	x
C. latirostris	141				x	x	x	x	x	x
Melanosuchus niger	141				x	x	x	x	x	x
Paleosuchus trigonatus	141				x	x	x	x	x	x
P. palpebrosus	141				x	x	x	x	x	x
Bernissartia fagesii[b]	52							x		
Goniopholis sp.[b]	52							x		
Apteryx australis[b]	79				x					
Sphenodon punctatus[b]	79				x					
No. characters/data set		26	33	38	79	5	1	54	3	1

[a] Character set not used previously in numerical systematic analysis.
[b] Outgroup.

ble 1. Character sources and descriptions are listed in the Appendix. The matrix of character states is available on request. Data sets of 18S nuclear rDNA RFLPs, 28S rDNA RFLPs, mtDNA RFLPs, morphology (=osteology, dentition, external), and 12S mtDNA sequences were analyzed separately using parsimony and with bootstrap parsimony analyses. Each of these data sets has at least 26 characters, whereas the remaining data sets include 1 (nest) and 3 (chromosome) characters. Data sets from 18S, 28S, and mitochondrial RFLPs and from morphology were analyzed with all characters equally weighted. The 12S sequence data were analyzed under a variety of assumptions, including equal weighting, differential weighting of transitions and transversions (a 3:1 ratio was determined empirically), inclusion or exclusion of ambiguously aligned regions, and treating gaps as single insertion/deletion events or as unknown states. Sequences were aligned with CLUSTAL V (Higgins et al., 1992) and by eye. The alignment used and the details of the assumptions (e.g., which regions were considered ambiguously aligned) are available on request. Tree length distributions were analyzed for each of these data sets using the g_1 statistic to test for hierarchical signal (Hillis and Huelsenbeck, 1992).

The fossil crocodilians *Bernissartia* and *Goniopholis* were used as outgroups for the morphological data because Clark (1994) found that they form either a monophyletic sister group or sequential outgroups to all extant species and because data are avail-

able for these fossils (Norell, 1988, 1989; Clark, 1994). It has been suggested that any molecule evolving fast enough to be phylogenetically informative within Crocodylia will be useless for rooting purposes because extant outgroups are so distant that their sequences would be essentially randomized relative to those of crocodilians (Norell, 1989). However, this contention has not been tested. Hass et al. (1992) reanalyzed the 12S sequence data of Gatesy and Amato (1992) for four species using outgroups and obtained high bootstrap values, but they presented no alignment or test to determine whether the root they found joined randomly to their cladogram. Furthermore, they used a lizard, a mammal, and a turtle as outgroups. These groups are more distantly related to crocodilians than the more appropriate outgroup Aves (Gauthier et al., 1988) but were used because of "an apparently large deletion in all the bird 12S sequences that we examined" (Hass et al., 1992:198). I rooted the 12S sequence data of Gatesy et al. (1993) and Gatesy and Amato (1992) with bird (brown kiwi, *Apteryx australis*) and lepidosaur (tuatara, *Sphenodon punctatus*) sequences obtained from GenBank through Entrez (release 15.0). Gauthier et al. (1988) found these lineages to be first and second extant outgroups, respectively, to Crocodylia.

A variation of Wheeler's (1990) test was applied to determine whether the root dictated by *Apteryx* and *Sphenodon* differed significantly from that obtained with random outgroup sequences. The length of the branch leading to an informative outgroup root will be less than the length of an uninformative (essentially randomized) root because the uninformative root will only share character states with the ingroup due to chance, whereas an informative outgroup will share states due to chance and due to common ancestry. Thus, there will be fewer changes between ingroup and outgroup with an informative root (Wheeler, 1990). The hypothesis to be tested is whether the length of the outgroup root for the proposed outgroup is shorter than the length of a root for an outgroup with randomly assigned states. The test statistic is the length of the outgroup root. Wheeler's (1990) suggestion to use the binomial distribution to assess the significance of this statistic was not followed because the length of the outgroup root depends on how character states are optimized on the tree, and it was not clear for what character state optimization (i.e., ACCTRAN, DELTRAN) a binomial distribution would be appropriate. To test the null hypothesis that the length of the proposed outgroup root is equal to (or greater than) the length expected with a random root, a null distribution of outgroup root lengths was obtained by permuting the outgroup character state distribution 99 times and finding the resulting most-parsimonious trees and outgroup root lengths (under the same character evolution optimization for all trials). The length of the outgroup root using *Sphenodon* and *Apteryx* was compared with this distribution.

The 26 taxa and 240 characters in Table 1 were also combined and analyzed with parsimony, with all characters equally weighted and ambiguous regions of the 12S data excluded. Relative support for clades was assessed with bootstrap (Felsenstein, 1985) and decay index (Bremer, 1988; Donoghue et al., 1992) analyses. Parsimony trees and tree statistics were calculated with the ingroup constrained as monophyletic. If the ingroup/outgroup root was not constrained in the combined analysis, the outgroups for the morphological data and the 12S data connected at different parts on the tree (these data sets specify different roots). Previous studies (and the partitioned analyses of this study) have shown that it is extremely unlikely that any of *Goniopholis*, *Bernissartia*, *Apteryx*, or *Sphenodon* are nested within the extant crocodilians (Benton and Clark, 1988; Gauthier et al., 1988; Clark, 1994). Therefore, these taxa were constrained as the root in the combined analysis.

A consequence of combining nine "types" of data from 10 studies with various levels of systematic coverage is that unknown states (? in the matrix) are common. However, the information gained by

including characters and operational taxonomic units (OTUs) for which some states are unknown is considerable (in this study, 18 of 22 ingroup species have unknown character states and 178 of 240 characters are not scoreable in all ingroup species) and seems to outweigh potential risks (Wiens and Reeder, 1995).

The combined tree and the trees from the five data sets were compared with the hypotheses in Figure 1. Each tree was scored as compatible or incompatible (unrooted trees could be compatible with both B and C) depending on whether the most-parsimonious tree(s) was in conflict with the considered hypothesis. If incompatible, the number of extra steps (raw and percentage of total length) needed to fit the data to that hypothesis was calculated, and Templeton's (1983) test was used to assess the significance of conflict. StatView 4.01 (Abacus Concepts, 1992) was used to calculate Wilcoxon signed-rank tests for the Templeton test because this program conveniently incorporates a correction for tied ranks. This correction is important for the application of the Wilcoxon test to comparison of trees because in that case tied ranks are common (see, e.g., Larson, 1994: table 1).

Data from albumin and parasites were also judged for compatibility with each of the three hypotheses. Phylogenies from albumin and coevolutionary parasite data were simply compared with the hypotheses in Figure 1, and alternative interpretations of these data were explored.

The tree in Figure 1 that received the strongest support from combined, separate, and uncombinable evidence was considered the best hypothesis of relationships of the four crocodilian lineages: alligatorids, crocodylids, *Tomistoma,* and *Gavialis.* Because the within-lineage (intraalligatorid and intracrocodylid) data are generally concordant and the various data sets have inconsistent within-lineage taxonomic coverage (e.g., the 12S data set included only one crocodylid), the combined analysis is considered to represent the best hypothesis of within-lineage relationships.

Quantifying Conflict

Three procedures were used to assess data set incongruence. Two of these involve the test of Farris et al. (1994), and one involves comparisons of raw values of incongruence indices proposed by Mickevich and Farris (1981) and Miyamoto (Kluge, 1989). Although these procedures are presented in terms of their ability to address specific hypotheses of incongruence, all three of them test similar properties of the data. For example, one would expect the Farris et al. test and the raw comparisons tests to agree on whether or not the morphological data set is significantly in conflict with the molecular data sets. The use of different measures to address these questions allows for comparisons of the strength of support for the tested hypotheses, the properties of each test, and the suitability of each test for different types of questions.

Farris et al. (1994) test; combined significance comparisons.—These tests were applied primarily to determine whether any individual data set(s) is significantly incongruent with the combined set of other data. For the Farris et al. test, the test statistic is the sum of the lengths of most-parsimonious trees for the compared data sets (this is a reduction of the unscaled Mickevich and Farris [1981] formula; see Farris et al., 1994). A null distribution for this sum is obtained by randomly partitioning the combined data into sets of the same size as the original data sets and calculating the sums for each partition. If the sum of the lengths of the most-parsimonious trees for the original partition is less than (e.g., 95% of) the sums for the randomized partitions, the incongruence is considered significant (Farris et al., 1994).

The Farris et al. test was applied to comparisons of each data set with the combined set of remaining data. For example, the morphological data set was compared with a combined set of data from the 18S rDNA RFLPs, 28S rDNA RFLPs, mtDNA RFLPs, and 12S mtDNA sequences. To control for the incomplete taxonomic coverage of the different data sets (Table 1),

comparisons were made using only the four taxa common to all five data sets (*Crocodylus rhombifer, Alligator mississippiensis, Tomistoma, Gavialis*). This set of tests will be referred to as the Farris et al. combined tests.

Mickevich and Farris (1981) and Miyamoto (Kluge, 1989) tests; pairwise raw comparisons.—These tests were undertaken primarily to determine whether incongruence between morphological and molecular data sets is significantly greater than incongruence between molecular data sets and whether this incongruence can be attributed primarily to the position of *Gavialis* in the morphology tree (as suggested by, e.g., Hass et al., 1992).

The Mickevich and Farris (I_{MF}) and Miyamoto (I_M) measures separate data conflict into within and between data set components and quantify conflict that is attributable to the between data set component (see Swofford, 1991, for further explanation). Both I_M and I_{MF} have the same general form:

$$I = (i_T - i_W)/i_T.$$

For data sets A and B that give most-parsimonious trees a and b, respectively, incongruence between these data sets is calculated as follows. Under I_M, i_T (total incongruence) is the sum of the extra steps required for data set A on tree b and data set B on tree a (beyond the minimum length for each data set), and i_W is the sum of the extra steps required in the most-parsimonious trees for each data set, beyond the minimum for that data set. For I_{MF}, i_W is measured the same way but i_T is the number of extra steps needed for a combined analysis of the two data sets beyond the minimum for that combined data set.

To measure incongruence for comparisons between morphological and molecular data sets, incongruence indices (I_M, I_{MF}) were calculated for each pairwise comparison among the five larger data sets (18S, 28S, and mitochondrial RFLPs; 12S sequences; morphology), including only taxa common to both data sets. This procedure produced six incongruence indices for the between molecular data set comparisons and four for the morphological/molecular data set comparisons for each of I_M and I_{MF}. To assess the significance of differences in incongruence, I_M and I_{MF} for the molecular data were compared to I_M and I_{MF} for the morphological data using a Mann–Whitney *U*-test, with the null hypothesis that *I* for morphological/molecular comparisons is less than or equal to *I* for molecular/molecular comparisons. Available computer programs were unable to perform one-tailed nonparametric tests, so values were calculated by hand with reference to published tables (Conover, 1971). The expectation under the hypothesis that the morphological data are more incongruent with the molecular data than the molecular data are with each other is that I_M and I_{MF} for morphological/molecular comparisons will be significantly higher than I_M and I_{MF} for the molecular/molecular data set comparisons.

To test whether incongruence is primarily due to the separation of *Gavialis* and *Tomistoma*, the above procedure was repeated but with (1) *Gavialis* deleted from all analyses, (2) *Tomistoma* deleted, and (3) for comparison, three other taxa deleted (*A. mississippiensis, Osteolaemus, Crocodylus acutus*) in three separate analyses. These three taxa were selected as those most likely to alter results. *Alligator mississippiensis* and *C. acutus* are scored for all and most characters, respectively, and their removal would thus change more *I* values than removal of species scored for fewer character sets. The position of *Osteolaemus* in the morphological tree is different from its position in all the other trees, suggesting that it may also be a source of significant conflict. The expectation under the hypothesis that morphological incongruence is due to the separation of *Tomistoma* and *Gavialis* is that removal of either of these taxa will cause the morphological data to fail to be significantly incongruent with the molecular data. However, removal of other taxa should not affect the incongruence of the morphological data set, and morphological I_M and I_{MF} should still be significantly higher when these other taxa are removed.

This set of tests will be referred to as the raw pairwise tests.

Farris et al. (1994) test; pairwise significance comparisons.—These tests were run to determine whether significant conflict exists between any two of the individual data sets. The Farris et al. test was applied in the pairwise comparisons of the individual data sets, with analyses run including all taxa common to the compared data sets. This set of tests will be referred to as the Farris et al. pairwise tests.

Measures and Procedures

Analyses of g_1, maximum parsimony, bootstrap, consistency index (CI; Kluge and Farris, 1969), retention index (RI; Farris, 1989), decay index, and incongruence index were performed with PAUP version 3.1 (Swofford, 1993). MacClade version 3.0 (Maddison and Maddison, 1992) was used to enter data and to construct constraint trees. For parsimony analyses, heuristic searches were used with at least 20 replications of random taxon addition and PAUP's most inclusive branch-swapping option (TBR). Bootstrap parsimony analyses were performed with 100 replicates and TBR branch swapping.

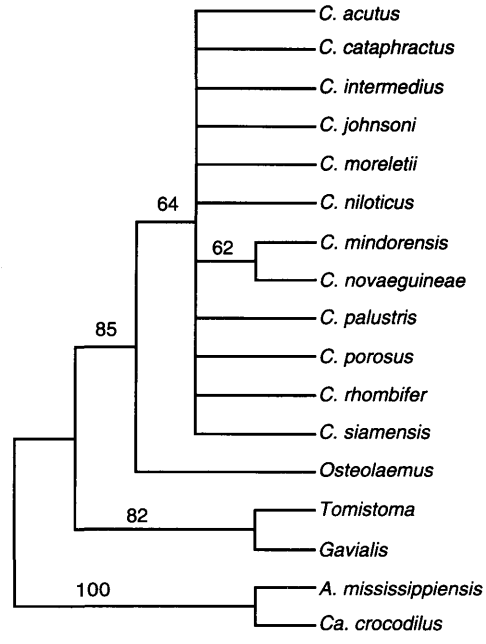

FIGURE 2. Unrooted strict consensus of most-parsimonious trees resulting from analysis of 18S nuclear rDNA restriction fragment data for crocodilians (data from Densmore and White, 1991). Numbers above branches are number of times clade occurred in 100 bootstrapped trees. *C.* = *Crocodylus*; *A.* = *Alligator*; *Ca.* = *Caiman*.

RESULTS

Partitioned and Combined Analyses

All individual data sets and the combined data set showed significant hierarchical signal, as measured by g_1 analysis of the distribution of tree lengths from 10,000 random trees, compared with the 95% confidence values presented by Hillis and Huelsenbeck (1992).

Parsimony analysis of the 18S RFLP data produced 15 most-parsimonious trees: length = 36, CI = 0.722, RI = 0.815. A strict consensus of these trees is depicted in Figure 2 with bootstrap values. Because this unrooted tree places *Gavialis* and *Tomistoma* together, it is compatible with hypotheses B and C. Hypothesis A requires two extra steps (+5.6%) beyond that required for the most-parsimonious trees. By Templeton's (1983) test, hypothesis A is not significantly different from the most-parsimonious 18S tree ($P = 0.373$, $n = 4$ ranks).

Parsimony analysis of the 28S RFLP data produced 28 trees: length = 62, CI = 0.532, RI = 0.667. A strict consensus of these trees is depicted in Figure 3 with bootstrap values. This tree is compatible with hypotheses B and C, whereas hypothesis A requires five extra steps (+8.1%) to explain the data. The most-parsimonious 28S tree is not significantly different from hypothesis A ($P = 0.0956$, $n = 9$).

Parsimony analysis of the mitochondrial RFLP data resulted in seven most-parsimonious trees: length = 90, CI = 0.422, RI = 0.475. A strict consensus of these trees is shown in Figure 4. Because *Crocodylus* is not monophyletic in two trees, the consensus tree does not conclusively support any of the hypotheses. However, five of seven trees are compatible with hypotheses B and C. Hypothesis A requires an extra step (+1.1%) to explain the data, but this hy-

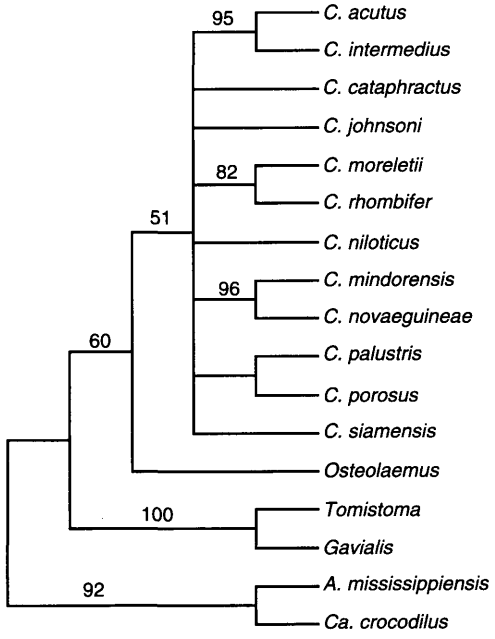

FIGURE 3. Unrooted strict consensus of most-parsimonious trees resulting from analysis of 28S nuclear rDNA restriction fragment data for crocodilians (data from Densmore and White, 1991). Numbers above branches are number of times clade occurred in 100 bootstrapped trees. *C.* = *Crocodylus*; *A.* = *Alligator*; *Ca.* = *Caiman*.

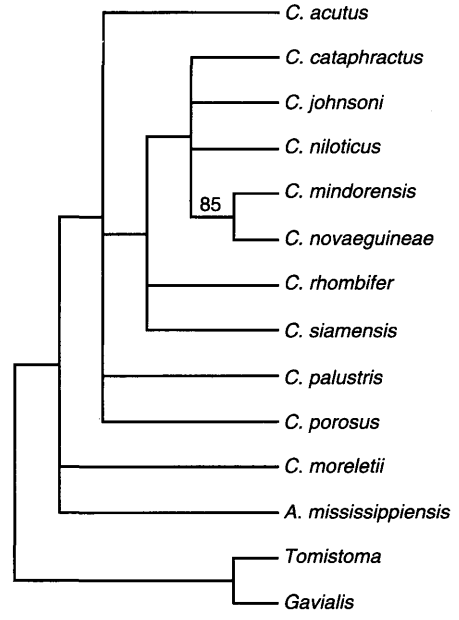

FIGURE 4. Unrooted strict consensus of most-parsimonious trees resulting from analysis of mitochondrial DNA restriction fragment data for crocodilians (data from Densmore and White, 1991). Number above branch is number of times clade occurred in 100 bootstrapped trees. *C.* = *Crocodylus*; *A.* = *Alligator*.

pothesis is not significantly suboptimal ($P = 0.0833$, $n = 3$).

In the significance test for the root of the 12S sequence data, the length of the *Apteryx* root was 27 and the length for the *Sphenodon* root was 38 under ACCTRAN optimization. The 99 randomization trials (to obtain 100 total trials for each proposed outgroup) produced a range of outgroup root lengths from 41 to 60 using ACCTRAN. Thus, both the *Sphenodon* and *Apteryx* roots were significantly shorter than random roots at a probability of 0.01, and these roots were therefore considered informative.

The cladogram obtained from the 12S sequence data is sensitive to the assumptions used. Figure 5a shows the topology resulting from parsimony analysis with transformations weighted equally and ambiguously aligned regions excluded, and Figure 5b shows the topology resulting from analyses with gaps treated as unknown or as separate character states and ambiguous regions included, with transitions and transversions weighted equally or with transversions weighted three times transitions, and with large gaps treated as single deletion/insertion events. The range of bootstrap values under each analysis is listed. Regardless of the assumptions used, the 12S results are congruent only with hypothesis B (one tree: length = 177, CI = 0.593, RI = 0.642, when characters are equally weighted and ambiguous regions excluded). Under the assumptions of equal weighting of transformations and ambiguous regions excluded, hypothesis A requires 11 extra steps (+6.2%) and hypothesis C requires 12 extra steps (+6.8%). Both of these hypotheses are significantly different from the 12S most-parsimonious tree (A: $P = 0.0045$, $n = 15$; C: $P = 0.0005$, $n = 12$).

Parsimony analysis of the morphological data resulted in 142 most-parsimonious

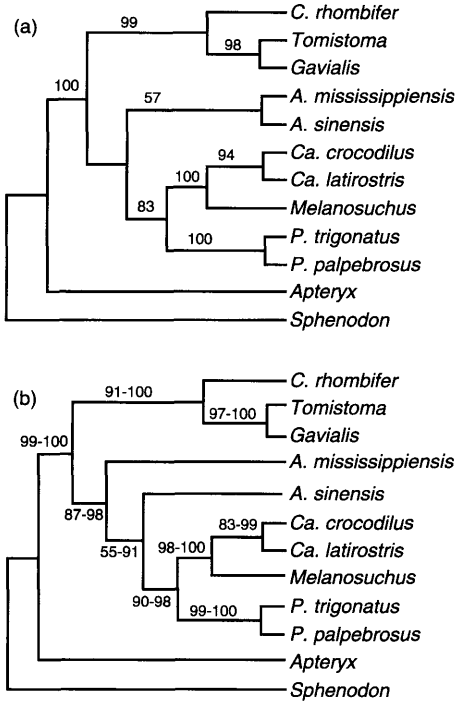

FIGURE 5. Trees from parsimony analysis of 12S mitochondrial DNA sequence data for crocodilians (Gatesy et al., 1993). Numbers above branches are number of times clade occurred in 100 bootstrapped trees. *C.* = *Crocodylus*; *A.* = *Alligator*; *Ca.* = *Caiman*; *P.* = *Paleosuchus*. (a) Tree with all transformations weighted equally and ambiguously aligned sequences excluded. (b) Tree obtained under other assumptions (see text). Ranges of bootstrap values are shown because although most-parsimonious topology was constant, bootstrap values changed under different assumptions.

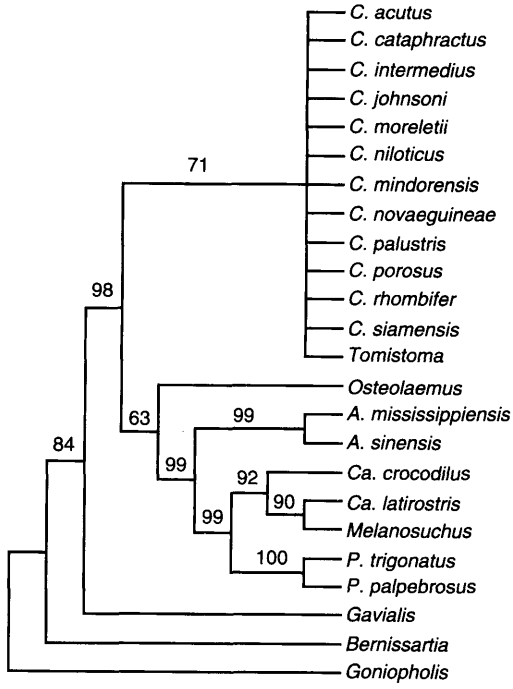

FIGURE 6. Strict consensus of most-parsimonious trees resulting from combined analysis of osteological (Norell, 1988, 1989; Clark, 1994), dentition (Iordansky, 1973), and external morphological (Brazaitis, 1973; Ross and Mayer, 1983) data for crocodilians, rooted with outgroups. Numbers above branches are number of times clade occurred in 100 bootstrapped trees. *C.* = *Crocodylus*; *A.* = *Alligator*; *Ca.* = *Caiman*; *P.* = *Paleosuchus*.

trees: length = 165, CI = 0.861, RI = 0.894. A strict consensus of these trees is shown in Figure 6, with bootstrap values. Because of the placement of *Osteolaemus* with the alligatorids, the most-parsimonious trees are not congruent with hypotheses A, B, or C. However, the traditional morphological result of Figure 1a requires only one extra step (+0.6%) to place *Osteolaemus* with *Crocodylus*. Hypotheses B and C require 11 (+6.7%) and 6 (+3.6%) additional steps, respectively. The traditional morphological tree is not significantly different (P = 0.7630, n = 8), but hypotheses B (P = 0.0009, n = 11) and C (P = 0.0339, n = 8) do give significantly different results.

The parsimony analysis of all methodologically compatible data produced a single most-parsimonious ingroup tree: length = 582, CI = 0.619, RI = 0.674. This tree is shown in Figure 7 with bootstrap and decay index values. This tree is compatible only with hypothesis B. Hypotheses A and C require 13 (+2.2%) and 6 (+1.0%) additional steps, respectively. The morphological hypotheses (A) is significantly suboptimal (P = 0.0374, n = 39), whereas hypothesis C is not significantly different (P = 0.1336, n = 16). The monophyly of the major lineages of crocodylids and alligatorids and of *Tomistoma* + *Gavialis* were all well supported, with decay indices of at least five steps and bootstrap support of at least 79%. Relationships among these lineages were also fairly ro-

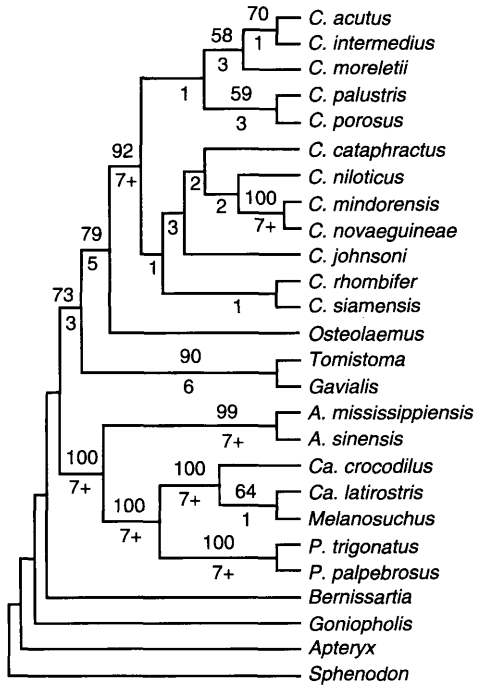

FIGURE 7. Single most-parsimonious tree resulting from combined analysis of all discrete-character crocodilian data, rooted with outgroups. Numbers above branches are number of times clade occurred in 100 bootstrapped trees. Numbers below branches are decay indices. *C.* = *Crocodylus*; *A.* = *Alligator*; *Ca.* = *Caiman*; *P.* = *Paleosuchus*.

bust (decay index ≥ 3 steps, bootstrap ≥ 73%). *Crocodylus*, *Paleosuchus*, and *Alligator* were strongly supported as monophyletic, but *Caiman* was paraphyletic relative to *Melanosuchus*. Five of six alligatorid clades were very strongly supported (decay index ≥ 7 steps, bootstrap > 98%). *Crocodylus* relationships were generally less well supported, with only one clade having bootstrap support >70%.

Tree statistics from the separate and combined analyses are summarized in Table 2.

Uncombinable Evidence

Densmore (1983) presented results from albumin immunodiffusion tests using most extant crocodilian species. He presented midpoint-rooted trees from UPGMA and Wagner analyses of these data, both of which were congruent with hypothesis B and so in conflict with hypothesis A. Rooting those trees with *Gavialis* rather than at the midpoint gives hypothesis C. However, *Gavialis* and *Tomistoma* albumins were "too similar to be distinguished" (Densmore, 1983:425), which is strongly suggestive of monophyly (B) rather than positions as sequential outgroups to the other extant crocodilians (C), because hypothesis C requires postulation of an extreme reduction in the rate of albumin evolution in these species.

Hass et al. (1992) studied crocodilian albumins with micromplement fixation techniques. Their results from reciprocal trials of each crocodilian genus except *Osteolaemus* fully support Densmore's (1983) albumin hypothesis and are in perfect accord with the combined tree presented

TABLE 2. Summary of results from combined and separate parsimony analyses of crocodilian systematic data. In addition to characters from the five data sets, the combined analysis includes data from chromosomes and ecology. Trees that are significantly different ($P < 0.05$) from the most-parsimonious tree (mpt) by Templeton's (1983) test are marked with an asterisk. G = *Gavialis*; T = *Tomistoma*; A = alligatorids; C = crocodylids.

Tree statistics	Combined	18S (RFLP)	28S (RFLP)	mt (RFLP)	12S sequences	Morphology
No. taxonomic units	26	17	17	15	12	24
Length of shortest trees	582	36	62	90	177	165
No. shortest trees	1	15	28	7	1	142
CI	0.619	0.722	0.532	0.422	0.593	0.861
RI	0.674	0.815	0.667	0.475	0.642	0.894
No. (%) extra steps needed to fit data to hypothesis[a]						
A: G(A(C, T))	13 (2.2)*	2 (5.6)	5 (8.1)	1 (1.1)	11 (6.2)*	1 (0.6)
B: A(C(G, T))	0	0	0	0 (5/7 mpt)	0	11 (6.7)*
C: G(T(C, A))	6 (1.0)	0	0	0 (5/7 mpt)	12 (6.8)*	6 (3.6)*

[a] Hypotheses A–C refer to Figure 1.

TABLE 3. Summary of whether uncombinable data sets are compatible with crocodilian hypotheses A–C in Figure 1. G = *Gavialis*; T = *Tomistoma*; A = alligatorids; C = crocodylids.

Hypothesis	Data	
	Albumin	Parasites
A: G(A(C, T))	incompatible	equivocal
B: A(C(G, T))	compatible	incompatible
C: G(T(C, A))	incompatible	equivocal

here. As Densmore (1983), Hass et al. used no outgroups and rooted by midpoint (they stated that extant outgroups would not have been informative using these techniques). However, they also found an extreme similarity of *Tomistoma* and *Gavialis* albumins (reciprocal average immunological distance = 8.5, which is comparable to that between other congeneric crocodilians, e.g., *Crocodylus*: 3–20), which is again more suggestive of *Tomistoma* / *Gavialis* monophyly than of positions as sequential outgroups to alligatorids + crocodylids. The albumin data, then, appear to unequivocally support hypothesis B and conflict with hypotheses A and C.

Brooks and O'Grady (1989) studied the digenean and nematode parasites of crocodilians. Their preferred tree (1989: fig. 14) is not congruent with any of the hypotheses in Figure 1 because of the nonmonophyly of *Crocodylus*. In addition, the parasite data suggest *Paleosuchus* + *Melanosuchus* monophyly and *Osteolaemus* + *C. cataphractus* + *C. niloticus* monophyly. The former result is strongly and independently contradicted by the 12S and morphological data and by the combined analysis, and the latter result is contradicted by all other data sets. The parasite data did recover a monophyletic alligatorid clade and, excluding the placement of *C. palustris* with *Gavialis*, a monophyletic crocodylid clade was also recovered. Discounting the unlikely result of *C. palustris* + *Gavialis* (as did Brooks and O'Grady), the parasite results are most congruent with hypotheses A and C because they suggest that *Gavialis* is the sister taxon to alligatorids and crocodylids. Unfortunately, Brooks and O'Grady were unable to include *Tomistoma*, so the possibility that the parasite data support *Gavialis* + *Tomistoma* monophyly remains. Considering these uncertainties, the parasite data are considered equivocal but more suggestive of hypotheses A and C than of B.

TABLE 4. Raw incongruence values for pairwise comparisons of crocodilian data sets. For each comparison, all taxa are included that are common to the compared data sets. Values for I_M (Kluge, 1989) are in the upper triangle; values for I_{MF} (Mickevich and Farris, 1981) are in the lower triangle. An incongruence value of zero indicates complete congruence between the compared data sets.

	18S RFLP	28S RFLP	mt RFLP	12S sequences	Morphology
18S RFLP	—	0.339	0.231	0	0.549
28S RFLP	0.093	—	0.194	0	0.500
mt RFLP	0.050	0.074	—	0	0.385
12S sequences	0	0	0	—	0.197
Morphology	0.207	0.160	0.082	0.070	—

Results from examination of the nondiscrete character evidence are summarized in Table 3.

Data Conflict

The Farris et al. (1994) combined tests showed that only the morphological data set is significantly incongruent ($P = 0.033$). Comparisons of the 18S rDNA RFLPs, 28S rDNA RFLPs, mtDNA RFLPs, and 12S mtDNA sequences to combined data sets lacking each of these sets, respectively, showed P values of ≥ 0.1.

Table 4 shows I_M and I_{MF} values for the raw pairwise tests for which no specific taxon was removed. I_M for the morphological/molecular data set comparisons was significantly higher than that for the molecular/molecular data set comparisons (null hypothesis of I_M for morphology comparisons being less than or equal to molecular/molecular I_M was rejected at $P < 0.025$). Removal of *Gavialis* or *Tomistoma* brought morphological and molecular values closer such that differences in I_M were not significant ($P > 0.10$, $P > 0.05$), whereas differences remained significant with the removal of other taxa ($P < 0.05$, $P < 0.025$, $P < 0.025$). As with I_M, I_{MF} for com-

TABLE 5. P values for incongruence (I) comparisons of morphological and molecular crocodilian data sets using one-tailed Mann–Whitney U-tests with various taxa removed. Null hypothesis: morphological $I \leq$ molecular I. Asterisk indicates rejection of the null hypothesis at the 95% confidence level.

Taxon omitted	I_M	I_{MF}
None	<0.025*	<0.05*
Gavialis	>0.10	>0.10
Tomistoma	>0.05	>0.10
Crocodylus acutus	<0.05*	<0.05*
Alligator mississippiensis	<0.025*	<0.05*
Osteolaemus	<0.025*	<0.05*

TABLE 6. P values for comparisons of incongruence between crocodilian data sets using the Farris et al. (1994) test. Asterisk signals significant incongruence at the 95% confidence level.

Comparison	P
Morphology/18S RFLP	0.069
Morphology/28S RFLP	0.088
Morphology/12S sequences	0.033*
Morphology/mt RFLP	>0.10
18S RFLP/28S RFLP	>0.10
18S RFLP/mt RFLP	>0.10
18S RFLP/12S sequences	>0.10
28S RFLP/mt RFLP	>0.10
28S RFLP/12S sequences	>0.10
mt RFLP/12S sequences	>0.10

parisons involving morphological data was significantly higher than that for the molecular data ($P < 0.05$). Removal of *Gavialis* or *Tomistoma* renders the differences insignificant ($P > 0.10$ for both), but removal of other taxa does not ($P < 0.05$ for all three other taxa). Significance results for the raw pairwise tests are summarized in Table 5.

Table 6 summarizes the results of the Farris et al. pairwise tests. Only the 12S versus morphology comparison showed significant conflict.

A sequential Bonferroni correction (e.g., Rice, 1989) applied to the Farris et al. test results has no effect on conclusions because each of these shows only one significant P value. Application of a Bonferroni correction to all cells of Table 5 (raw comparisons P) would render all values insignificant. However, a more appropriate application would be to correct the first three rows (because these are all that are required for the hypotheses) of each column (because these are distinct tests) individually, which has no effect on results. Regardless of how the post hoc correction is applied, the hypotheses are maintained by application of Fisher's (1954) combining probabilities test applied to the P values obtained independently via both I_M and I_{MF} tests (see, e.g., Sokal and Rohlf, 1981).

DISCUSSION

Support for Hypotheses

Hypothesis B, originally posited by Densmore (1983), appears to be best supported by the criteria of combined and separate analyses and by the analysis of uncombinable data. Parsimony trees from the 18S, 28S, and 12S data support this hypothesis, as does the combined analysis. Furthermore, the albumin data are compatible only with hypothesis B. Only the morphological data are significantly incongruent with this tree, requiring 13 extra steps beyond that required for its most-parsimonious tree. The mitochondrial RFLP data do not support this tree in all its most-parsimonious trees, but neither do they support the other hypotheses.

Without a root, hypothesis C is the same as hypothesis B. However, none of the rooted trees (12S, morphology, combined) suggest hypothesis C, which is therefore considered less likely to be the true tree than is hypothesis B.

Hypothesis A, the traditional morphology tree, is not compatible with the most-parsimonious trees from any of the separate or combined analyses or with the results from albumin data. However, it is nearly compatible with the most-parsimonious morphological trees (only one extra step required), and the parasite data are suggestive of this hypothesis. The 18S, 28S, and mitochondrial RFLP data sets do not significantly conflict with hypothesis A. However, the 12S and combined trees and the albumin data are unequivocal in their support for hypothesis B, and a combined analysis of 18S and 28S data (probably a reasonable "process partition," sensu Bull et al., 1993) produces a most-parsimonious

character distribution that is significantly suboptimal compared with the morphological hypothesis, using Templeton's (1983) test ($P = 0.0114$, $n = 10$, tree not shown). Because acceptance of hypothesis A requires postulation of additional homoplasy besides that required for the most-parsimonious trees in all individual data sets and in the combined tree, hypothesis A seems unlikely to be the true tree.

The best-supported hypothesis of crocodilian relationships, then, requires that a less than most-parsimonious morphological tree is the true tree and thus that several features are homoplastically shared by *Gavialis* and the outgroups. In particular, *Gavialis* and both outgroups possess an anterior postorbital spine, a massive postorbital bar, and axial diapophyses, which are absent in other extant crocodilians (Norell, 1989). It is disheartening that the best-supported hypothesis of crocodilian relationships requires considerable additional homoplasy in morphology. However, adoption of any particular hypothesis of crocodilian phylogeny requires postulation of additional homoplasy in more than one independent data set. For example, although they conflict with the remaining data, the morphological trees and incongruent mitochondrial RFLP trees (two of the seven most-parsimonious mtDNA RFLP trees require extra steps in hypothesis B) are not congruent with each other, and adoption of either of these hypotheses would necessitate postulation of additional homoplasy in all other data sets. Selection of hypothesis B over alternative hypotheses minimizes homoplasy, both in terms of the number of less parsimonious data sets and the number of additional steps needed within data sets, and signals the most-parsimonious combined tree as the best hypothesis of relationships.

The congruence of four of the potentially independent data sets (18S RFLPs, 28S RFLPs, 12S sequences, albumin) with the combined tree is powerful evidence for the veracity of that tree (e.g., Hillis, 1995), as is the fact that the conflicting data sets (morphology, mitochondrial RFLPs, parasites) do not give concordant results with each other. Evaluation of all available evidence has allowed not only finer assessment of hypotheses of relationships but also identification of previously unsuspected conflict (e.g., mitochondrial RFLP data). Other taxonomic groups for which many data and many data sets are available might benefit from this multifaceted approach (Swofford, 1991).

Reevaluation of the Data Sets

Results of some analyses were congruent with results presented in the original papers. However, in some cases the parsimony analyses presented here produced different results from those originally obtained from the same data.

Not surprisingly, parsimony analyses of the 18S, 28S, and mitochondrial RFLP data sets produced results that were generally concordant with those presented by Densmore and White (1991: figs. 3–5) from their compatibility and "compatible parsimony" analyses. They noted that the mitochondrial data appeared to have less resolving power than the nuclear data. Parsimony analysis of the mitochondrial data resulted in a tree with only one node supported at bootstrap values >50% and with results within one step of being compatible with all three hypotheses in Figure 1 (Table 2), thus supporting this contention and suggesting that these data alone are of little help in choosing among alternative hypotheses of crocodilian phylogeny.

Gatesy et al. (1993) noted that their analysis of 12S sequence data produced results in conflict with the well-supported morphological result of a monophyletic *Alligator* (Norell, 1989). Gatesy et al.'s trees depicted *A. sinensis* as more closely related to *Caiman*, *Paleosuchus*, and *Melanosuchus* than to *A. mississippiensis*. Gatesy et al. also found conflict in their caiman (=*Caiman*, *Paleosuchus*, *Melanosuchus*) topology, but whereas this topology was unstable depending on alignment used, *Alligator* was paraphyletic for all alignments. The parsimony analyses presented here show that the *Alligator* topology obtained with the 12S data is sensitive to the assumptions

used. Under most assumptions tried, *Alligator* is paraphyletic (Fig. 5b). However, under equal weighting of all transformations and exclusion of ambiguously aligned sites, parsimony analysis gives a monophyletic *Alligator* (Fig. 5a), in accord with results from morphology.

Morphological results were somewhat different from those previously reported, not because of differing methodology but because the total morphological database had never been combined in a single analysis. Many of Clark's (1994) and Norell's (1988, 1989) characters appear to be independent, and the external data (Brazaitis, 1973; Ross and Mayer, 1983) have not been analyzed with numerical systematic analyses, so it was appropriate to combine these data to obtain a single morphological hypothesis. Specifically, the morphological placement of *Osteolaemus* with alligatorids is surprising and counter to traditional interpretations of morphology. The placement of *Osteolaemus* with the alligatorids results mainly from Norell's (1988) characters. Clark (1994) and Norell (1989) treated *Osteolaemus* as part of a crocodylid OTU and so coded it identically to all *Crocodylus*. Parsimony analysis of Norell's (1988) data grouped *Osteolaemus* with most alligatorids in the most-parsimonious trees (results not shown). Because Norell (1988) treated this taxon as an outgroup (and so apparently rooted his tree on the branch leading to alligatorids), he made no note of the *Osteolaemus*/alligatorid similarity. Regardless of the source of this conflict, placement of *Osteolaemus* with the alligatorids is not strongly supported (bootstrap = 63%, decay index = 1 step).

Some data sets apparently are more useful than others for reconstructing crocodilian phylogeny. For example, the mitochondrial RFLP data are more or less congruent with all three tested hypotheses and with several others. Like the mitochondrial data set, some uncombinable data in their present form do not appear to be useful for reconstructing crocodilian phylogeny. The parasite data set has potential for offering independent evidence for phylogeny, but this data set is hampered by the absence of *Tomistoma*, and the phylogeny produced differs from that obtained from other data sets. Stratigraphic information is another potential source of independent evidence for phylogeny. The stratigraphic consistency index of Huelsenbeck (1994) was applied to data of Taplin and Grigg (1989) and Benton (1993) and the trees in Figure 1, but because of a lack of variation in stratigraphic ranks and a paucity of informative nodes, significant results could not be obtained (data not shown). Finer stratigraphic information and assessments of the position of critical fossil taxa could offer insight. However, a perhaps more promising use of the fossil data would be the incorporation of fossil taxa into a cladistic analysis. This approach would seem to offer sorely needed insight into the morphological evolution of the group, especially given the ability of fossil data to overturn phylogenies based on extant taxa alone (e.g., Gauthier et al., 1988; Donoghue et al., 1989).

In addition to the data sets evaluated here, still more uncombinable data exist in the form of blood protein allozymes, hemoglobin peptide fingerprints, transferrin immunodiffusion distances (Densmore, 1983), and DNA fingerprints from a Bkm-derived probe (Aggarawal et al., 1994). However, these studies did not produce results useful to the goals of this study. Densmore (1983) found that some transferrin reactions did not form detectable precipitin lines and so mapped results of within-lineage comparisons onto his albumin phenogram. Hemoglobin electrophoretic comparisons were based upon "crocodilian affinities suggested by the evidence from albumins and transferrins" (1983:430). Allozyme data were analyzed with separate genetic distance matrices for the alligatorid and the crocodylid + *Tomistoma* + *Gavialis* assumed lineages (these data could not be reanalyzed because for each matrix, characters were coded relative to the other species in that matrix instead of relative to crocodilians as a whole). Because none of these results were obtained independently of the albumin results, it is not surprising that they were found to

support the albumin hypothesis. Aggarawal et al.'s study is commendable for its use of a novel source of characters; however, they used a phenetic approach and no outgroups (they cited additional parsimony and bootstrap tests but presented no results), they presented no table of raw data, and their presented tree has extremely long branches and short internodes (1994: fig. 4). Their results could be interpreted to support hypotheses B and C or they could be viewed as equivocal.

Intralineage Relationships

In the combined tree, within-lineage relationships were strongly supported in the alligatorids apparently because the Norell (1988) and Gatesy et al. (1993) data, which contribute most to alligatorid relationships, are generally congruent. All nodes in this clade except *C. latirostris* + *Melanosuchus* were supported by ≥99% bootstrap values and decay indices of ≥7 steps (the maximum measured in this analysis). Thus, this alligatorid topology found by Densmore (1983) based on albumin and by Norell (1988) based on osteology forms a strong foundation for future comparative work.

In spite of poorly resolved trees from separate analyses (Figs. 2–6), the combined tree shows fully resolved crocodylid relationships. That the combined tree has resolved relationships when separate analyses are more or less equivocal is testament to the usefulness and power of the combined approach. But, although only a single most-parsimonious tree was found, most *Crocodylus* relationships were not robustly resolved (e.g., only one clade with bootstrap support >70%). This lack of support is not due to poor taxonomic sampling. Character information was available for *Crocodylus* (all *Crocodylus* could be scored for at least 121 of 240 characters) but phylogenetically useful variation was not. The morphology and mtDNA data sets each produced poorly resolved *Crocodylus* relationships, and the 18S and 28S data sets, which resolved four clades between them, had zero and three *Crocodylus* clades, respectively, with bootstrap values > 70%.

A potential reason for the lack of informativeness in the *Crocodylus* characters is that the *Crocodylus* radiation is recent (Densmore, 1983) and these data may simply not be evolving fast enough to provide phylogenetically useful information. However, if mitochondrial data are not suitable, just what type of data is appropriate? Sequence data from mitochondria and from any rapidly evolving region of the nuclear genome might be appropriate. The excellent alligatorid work of Norell (1988) has not been followed by a comprehensive morphological cladistic analysis of the crocodylids. Cladistic coding of the several osteological and external features that have served crocodilian systematists well since the time of Duméril (1806) would be eminently useful.

Incongruence Hypotheses: Real Data Conflict

The hypothesis that the morphological data set conflicts with the molecular data sets was supported. This contention was demonstrated convincingly by the Farris et al. (1994) combined tests, in which only the morphological data set was significantly in conflict, and by the raw pairwise tests, in which morphological/molecular comparisons showed significantly greater incongruence than molecular/molecular comparisons by both I_M and I_{MF} indices (Table 5).

Although morphology was clearly in conflict with the other data sets, pairwise comparisons showed that among individual data sets only the 12S versus morphology comparison showed significant conflict. Apparently, although the other molecular data sets are not robust enough to offer significant conflict to morphology individually, when combined their concordance produces a robust hypothesis that results in significant molecular/morphological conflict.

The hypothesis that morphological incongruence is primarily due to the placement of *Gavialis* separate from *Tomistoma* was supported decisively by the raw comparisons test, in which removal of *Gavialis* or *Tomistoma* lowered incongruence such that the morphology *I* was no longer sig-

nificantly different, but removal of other taxa had no effect on significance (Table 5).

Test Evaluations

I evaluated the tests used here based on how well they addressed the following questions: (1) Is one (or more) data set significantly incongruent with the other data? (2) Is morphological/molecular incongruence greater than molecular/molecular incongruence? (3) Are the individual data sets significantly incongruent with each other? (4) Can incongruence be localized to specific taxa? These evaluations focused on the suitability of these measures in the crocodilian case, but the potential for wider use was also examined. The properties of these tests that emerged in the course of this study are discussed here.

The Farris et al. combined tests were undertaken to examine whether any of the individual data sets is significantly incongruent with the other data as a whole. The advantages of this method are that it addresses this question directly (rather than indirectly, as in the pairwise raw tests) and that it controls for the effects of differing numbers of taxa. The main disadvantages of this method resulted from the differing taxonomic coverages of the data sets. First, the taxon removal experiments were not informative with this test in the crocodilian case because only four taxa are scored for all characters and hence removal of any taxon results in a three-taxon tree. Second, much information is lost by omitting the incompletely scored taxa. If, as the other tests have shown, *Gavialis* and *Tomistoma* are responsible for morphological incongruence, then the Farris et al. combined tests in fact maximize morphological incongruence by including precisely those species for which morphology conflicts. If other taxa for which morphology does not conflict could be scored for all characters and thus included, morphology might not be significantly incongruent. However, this possibility is not supported by the results of the other tests in this study.

The pairwise raw tests were undertaken mainly to see whether morphological/molecular incongruence could be localized to *Gavialis* but also to see whether morphological/molecular incongruence is significantly greater than molecular/molecular incongruence. The advantage of this procedure for exploring these questions is that it is a more direct test than is the Farris et al. pairwise test because it gives clear results based on a single statistical test, whereas the Farris et al. test would require an additional test to answer these questions. For example, in the Farris et al. pairwise tests, one can speculate that the morphological data set is probably most incongruent relative to the molecular data sets based on the 12S/morphology incongruence (Table 6) and the general concordance of the molecular trees (Figs. 2–5), but because of the insignificant results with the other molecular/morphology comparisons (Table 6), one would need a further statistical test (e.g., a Mann–Whitney *U*-test comparing *P* values) to assess this source of incongruence rigorously. The advantage of the raw pairwise tests relative to the Farris et al. combined tests for examining overall morphological incongruence is that the raw pairwise tests include information from all scored taxa rather than from just those taxa scored for all characters.

Disadvantages of the pairwise raw tests are the low statistical power resulting from the small number of comparisons possible with five data sets and the potential effect of number of taxa on I_M and I_{MF}. These indices probably are positively correlated with number of taxa compared, because more taxa give more opportunities for incongruence between data sets (e.g., two independent four-taxon trees have a 1/3 chance of showing zero incongruence, whereas two five-taxon trees have a 1/15 chance). However, the quantitative effects of this association remain to be demonstrated, and it is not clear whether and to what degree this phenomenon also affects the Farris et al. significance tests. If these indices are significantly correlated with number of taxa, then a correction for this correlation would have to be applied to each raw value before the raw pairwise tests could be considered valid. As with the Farris et al. combined tests, the raw

pairwise tests are unable to address questions of individual data set incongruence.

The Farris et al. pairwise tests were employed to examine whether any pairs of individual data sets show significant incongruence. Furthermore, the Farris et al. pairwise tests were expected to give additional perspective on the other questions asked. These tests are the only ones that address the question of incongruence between the individual data sets. However, the Farris et al. pairwise tests are less useful for addressing the question of morphological/molecular data set incongruence. If the Farris et al. pairwise tests had found all four morphological/molecular data set comparisons to be significantly incongruent and further that all six molecular/molecular comparisons were insignificantly incongruent, then the pairwise raw tests would not have been necessary because the conclusion of significant morphological/molecular incongruence would be unavoidable. Because this result was not obtained, the pairwise raw tests were used to assess the significance of the differing results with morphology.

Comparison of the Farris et al. and raw pairwise tests suggests further interesting points. First, the Farris et al. and raw pairwise tests address subtly different properties of the data, namely, magnitude of incongruence (raw) versus significance of incongruence (Farris et al.) (C. Marshall, pers. comm.). Thus, even though only one molecular data set is significantly incongruent with morphology (Table 6), the *I* values for morphological comparisons are significantly greater than those for molecular comparisons (Table 5). Second, although the two pairwise tests suggest identical conclusions, they do not show complete concordance. The three comparisons that show the lowest *P* values (Table 6) are not the comparisons with the three highest incongruence values (Table 4). This result could be related to the effect of number of taxa on these measures or to some other property of one or both of these tests.

In sum, the Farris et al. combined test most rigorously examines individual data set incongruence with the whole of the data, the raw comparisons test best examines the effect of different taxa on the incongruence of morphological/molecular comparisons relative to molecular/molecular comparisons, and the Farris et al. pairwise test is suitable for questions of incongruence between individual data sets. The use of multiple methods to assess incongruence is a consequence of the diversity of questions asked, but it also reflects the difficulties that follow from the incomplete taxonomic coverage of the crocodilian data sets. If all five data sets had complete taxonomic coverage, the more interesting hypotheses evaluated in this paper could be concisely addressed by applying just the Farris et al. combined test. This test could determine which, if any, data sets are incongruent with the whole of the other data and (by taxon removal experiments) where any discovered incongruence is located. Given complete taxonomic coverage, the Farris et al. combined test is certainly the most general and useful of the tests used here to address questions of multiple data set incongruence. It should find widespread use in the future.

Implications of Incongruence

These results suggest that the conflict between morphology and the other data sets is real but that it is concentrated in the placement of *Gavialis* (both morphology and other data place *Tomistoma* with crocodylids), not in the morphological data as a whole. This contention is supported by the nearly complete congruence of the morphology tree with the remaining trees (cf. Figs. 5–7). Unlike many cases where supposedly conflicting data sets can be shown to be essentially congruent when consistent methodology is applied (e.g., Hillis, 1985; Omland, 1994), it is apparent that the conflict between crocodilian data sets is real and is not a methodological artifact. It is appropriate to ask, as Hass et al. (1992) did, why the morphology gives aberrant phylogeny results with regard to *Gavialis* and to seek explanation for this discordance in biological rather than methodological sources. Other pertinent questions include why the mitochondrial RFLP data give no

strongly supported results and why the parasite data conflict (Tables 2, 3, 6).

The discordant results from the morphological data may suggest that it is inappropriate to combine these data with the other data in a single analysis (Swofford, 1991; Bull et al., 1993; Miyamoto and Fitch, 1995). However, although the morphological data are discordant, this discordance can be localized to a small part of the tree (*Gavialis* and *Tomistoma*). Excluding the morphological data would exclude some conflicting data, but it would also weaken relationships that would otherwise be extremely well supported (e.g., alligatorid relationships). In this case, a combined analysis is favored over consensus analysis in spite of some strong disagreement between part of the data sets. The expectation is that the congruent areas of the tree will be especially well supported and that the discordant areas will be overwhelmed by other congruent data (Donoghue and Sanderson, 1992), an occurrence that seems especially likely given the many crocodilian data sets. This phenomenon appears to have occurred in the combined tree of this paper; *Gavialis* and *Tomistoma* come out monophyletic (contra morphology), and the congruent relationships of alligatorids and monophyletic *Crocodylus* are among the most strongly supported nodes on the tree.

In this paper, I have demonstrated the use of incongruence indices to test specific hypotheses of data set incongruence. The identification of conflicting data sets is an issue of current importance in systematics (Huelsenbeck et al., 1994; Wiens and Chippindale, 1994). The results presented here suggest that localization of conflict within an incongruent data set may also be useful. In this study, removal of taxa and comparisons of incongruence indices were used to test a hypothesis of localized incongruence. More general comparisons are possible, e.g., by removing each taxon from a conflicting data set and measuring incongruence to assess whether any particular taxon is responsible or if instead the data set in general is incongruent. The study of incongruence is in its incipient stages (Hillis, 1995; Miyamoto and Fitch, 1995), and continued development of incongruence indices and uses for them should enable further rigorous testing of hypotheses of data set conflict.

Conclusions and Taxonomy

1. The hypothesis of crocodilian relationships originally posited by Densmore (1983) is well supported by combined analysis, separate analyses, and uncombinable data. Although this hypothesis requires additional homoplasy in morphological data beyond that required in the most-parsimonious trees, other hypotheses require even more homoplasy, and any particular hypothesis of crocodilian phylogeny requires additional homoplasy in more than one data set.
2. The morphological data set conflicts more with the molecular data sets than the molecular data sets do with each other, and this incongruence may be localized to the placement of *Gavialis*.
3. Alligatorid relationships are robustly supported by the combined tree and the congruence of 12S data (Gatesy et al., 1993), osteology (Norell, 1988), and albumin data (Densmore, 1983). None of the individual crocodilian data sets produce well-resolved *Crocodylus* relationships, but *Crocodylus* relationships are fully resolved in the combined tree. *Crocodylus* relationships are less robustly resolved overall.
4. The 12S sequence data, which have been interpreted to conflict with morphology relative to *Alligator* relationships, can be analyzed such that results congruent with those from morphology are obtained. The mitochondrial restriction fragment data set is not strongly suggestive of any particular hypothesis.

Because the monophyly of alligatorids, of crocodylids, and of *Gavialis* + *Tomistoma* was well supported, recognition of these three lineages is warranted. The names Crocodylidae Cuvier, 1807 (*Osteolaemus* + *Crocodylus*), Alligatoridae Gray, 1844 (*Alligator* + *Caiman* + *Paleosuchus* + *Melanosuchus*), and Gavialidae Adams, 1854 (*Gavialis* + *Tomistoma*) have been used for these

lineages as families within the order Eusuchia Huxley, 1875. Furthermore, if taxonomy is to reflect phylogeny (Hennig, 1966), either *Melanosuchus niger* should be synonymized with *Caiman* or *Caiman latirostris* should be renamed, in recognition of the paraphyly of *Caiman*. Norell (1988) elected the latter approach and suggested the name *Jacaretinga litirostris* Vaillant, 1898 for *Caiman latirostris*. For reasons of stability (the *Caiman* + *Melanosuchus* clade is extremely well supported) and precedence (*Caiman* is the oldest of these generic names to be applied to either *Caiman* or *Melanosuchus*; Mook and Mook, 1940), I suggest the alternative of assigning *Melanosuchus niger* to the genus *Caiman*.

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APPENDIX
CHARACTER LIST

Characters published in matrix form and used in numerical systematic analyses are listed by reference and character type only. Characters taken from published tables or descriptions that have not been used in numerical systematic analyses until now are described here. These features were selected for coding from a large body of documented variation because characterization was straightforward. Potentially phylogenetically informative variation in size (e.g., Brazaitis, 1973; Steel, 1973), color (e.g., Brazaitis, 1973), scutellation (e.g., Brazaitis, 1973; Ross and Mayer, 1983), physiology (e.g., Deeming and Ferguson, 1989), ecology (e.g., Shine, 1988), osmoregulatory anatomy and ability (Taplin and Grigg, 1989), dentition (e.g., Brazaitis, 1973; Iordansky, 1973), musculature (e.g., Shumacher, 1973; Frey et al., 1989), and osteology (e.g., Hecht and Malone, 1972; Iordansky, 1973; Steel, 1973; Tarsitano et al., 1989) was not included because of characterization problems due to continuous variation, conflicting reports of states, or lack of phylogenetic informativeness due to unknown polarity (states present in one ingroup taxon are informative if present in at least one outgroup taxon; some characters were excluded because a single ingroup taxon differed from the others but the outgroup condition was unknown) or because hypotheses of homology were impossible from literature descriptions. Many of the omitted characters have traditionally been important in crocodilian taxonomy (e.g., nuchal scales). Reexamination of these features with the goal of cladistic characterization would be useful. Only characters informative for these taxa were used. Characters were treated as unordered unless otherwise stated. Characters are grouped by reference.

1–26.—18S nuclear rDNA restriction fragments (Densmore and White, 1991: table 1).

27–59.—28S nuclear rDNA restriction fragments (Densmore and White, 1991: table 1).

60–97.—mtDNA restriction fragments (Densmore and White, 1991: table 2).

98–106.—Osteological characters 2–4, 6–10, and 12 (Norell, 1989: appendix 1). Norell's (1989) OTUs were *Tomistoma*, *Gavialis*, "crocodylids," and "alligatorids." He listed the contents of these groups but gave no list of specimens examined. In this study, which uses species as taxonomic units, the alligatorid state was assigned to each alligatorid species and the crocodylid state was assigned to each crocodylid species. Some of Norell's (1989) characters were omitted becauese they are duplicated by Norell (1988) or Clark (1994).

107–109.—Chromosome characters (Cohen and Gans, 1970: table 1). *107.* Complement of large metacentric (lmc), small metacentric (smc), submetacentric (sbmc), and telocentric (tc) chromosomes (coded state = no. lmc, no. smc, no. sbmc, no. tc): 0 = 0, 10, 6, 26; 1 = 0, 12, 6, 24; 2 = 0, 16, 4, 22; 3 = 10, 14, 4, 4; 4 = 10, 10, 8, 4; 5 = 8, 10, 6, 10; 6 = 8, 12, 4, 10; 7 = 8, 10, 6, 8; 8 = 8, 10, 8, 6; 9 = 8, 12, 6, 6; A = 10, 10, 8, 2; B = 10, 12, 6, 2; C = 4, 10, 6, 18; D = 10, 14, 2, 6. *108.* Satellite submetacentric chromosome. 0 = absent; 1 = present. *109.* Secondary constriction telocentric chromosome. 0 = absent 0; 1 = present.

110.—Nest type (Greer, 1970: table 1). 0 = mound; 1 = hole.

111.—Number of premaxillary teeth (Iordansky, 1973: table 1). 0 = five; 1 = four. This character was also used by Norell (1988).

112–115.—External morphological characters (taxonomic diagnoses of Brazaitis, 1973). *112.* Front feet. 0 = webbed; 1 = unwebbed. Species described as "slightly webbed" were assigned state 0. *113.* Ventral follicle glands. 0 = present; 1 = absent. *114.* Subcaudal scales. 0 = large uniform transverse rows; 1 = rows interrupted by several irregular groups of small scales. *115.* Ventral collar scales. 0 = not enlarged; 1 = one enlarged row; 2 = two enlarged rows.

116.—Median pelvic keel rows (Ross and Mayer, 1983). 0 = do not form Y-shaped caudal keel and remain paired posteriorly; 1 = do not form Y-shaped caudal keel and become singular posteriorly; 2 = merge with lateral pelvic keel row to become Y-shaped caudal keel.

117–120.—Osteological characters 43, 45, 71, and 89 (Clark, 1994).

121–161.—Morphological (mainly osteological) characters 1–16, 19–21, 23–26, 29, 30, 33, 34, 36–39, 41–46, 48, 49, 51, and 52 (Norell, 1988). Character 36, prootic exposure, is coded as a composite of two nonindependent characters, one from Norell (1989) and one from Norell (1988) (Norell coded the earlier character more finely to deal specifically with alligatorid relationships rather than all extant crocodilians). 0 = extensive; 1 = small; 2 = almost nonexistent. Ordered.

162–240.—12S mtDNA sequences (Gatesy and Amato, 1992; Gatesy et al., 1993). Only informative, unambigous sites are included in the combined matrix.