MORPHOLOGY, FOSSILS, DIVERGENCE TIMING, AND THE PHYLOGENETIC RELATIONSHIPS OF *GAVIALIS*

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Abstract.—Although morphological data have historically favored a basal position for the Indian gharial *(Gavialis gangeticus)* within Crocodylia and a Mesozoic divergence between *Gavialis* and all other crocodylians, several recent molecular data sets have argued for a sister-group relationship between *Gavialis* and the Indonesian false gharial *(Tomistoma schlegelii)* and a divergence between them no earlier than the Late Tertiary. Fossils were added to a matrix of 164 discrete morphological characters and subjected to parsimony analysis. When morphology was analyzed alone, *Gavialis* was the sister taxon of all other extant crocodylians whether or not fossil ingroup taxa were included, and a sister-group relationship between *Gavialis* and *Tomistoma* was significantly less parsimonious. In combination with published sequence and restriction site fragment data, *Gavialis* was the sister taxon of all other living crocodylians, but the position of *Tomistoma* depended on the inclusion of fossil ingroup taxa; with or without fossils, preferred morphological and molecular topologies were not significantly different. Fossils closer to *Gavialis* than to *Tomistoma* can be recognized in the Late Cretaceous, and fossil relatives of *Tomistoma* are known from the basal Eocene, strongly indicating a divergence long before the Late Tertiary. Comparison of minimum divergence time from the fossil record with different measures of molecular distance indicates evolutionary rate heterogeneity within Crocodylia. Fossils strongly contradict a post-Oligocene divergence between *Gavialis* and any other living crocodylian, but the phylogenetic placement of *Gavialis* is best viewed as unresolved. [Combined data sets; Crocodylia; fossils; molecular clock; parsimony analysis; stratigraphy.]

The traditional phylogenetic placement of *Gavialis* ... is inconsistent with all molecular data sets and we suggest that a careful reexamination of both the extant and the fossil morphological data is warranted.

—Hass et al., 1992:193

Different phylogenetic analyses of Crocodylia are broadly congruent, but they consistently disagree on two points. Historically, morphologists have maintained that alligatorids and crocodylids are more closely related to each other than either is to the Indian gharial, *Gavialis gangeticus*, and that the lineage including *Gavialis* diverged from that including all other living crocodylians before the end of the Mesozoic. However, recent estimates based on biochemical or molecular information consistently suggest that *Gavialis* and the false gavial, *Tomistoma schlegelii*, form a clade more closely related to crocodylids than to alligatorids and that *Gavialis* and *Tomistoma* diverged from each other no earlier than the Miocene or Pliocene (Fig. 1). Although a few morphological studies have supported these results, the application of parsimony analysis to skeletal data has continued to support the earlier morphological view.

At first glance, these two hypotheses appear fundamentally different, and no alternative rooting will turn one of the trees into the other. Lost in these discussions is the fact that these diverse data sets actually produce highly congruent results (Poe, 1996). For example, in all cases Crocodylia is a monophyletic group with respect to all other amniotes, Alligatoridae is monophyletic, and the alligators are separated from the caimans. All data sets support the monophyly of *Crocodylus* and the sister-taxon relationship between *Crocodylus* and *Osteolaemus*. Most discussions are worded as if *Tomistoma* were central to the debate, but all recent analyses, regardless of the nature of the data, agree that *Tomistoma* is closer to *Crocodylus* than to *Alligator*. If *Gavialis* is disregarded, the trees are identical.

Nevertheless, two consistent and independent incongruencies can be localized. The first is topological: where do *Gavialis* and its extinct relatives fit on the phylogenetic tree of Crocodylia? The second is
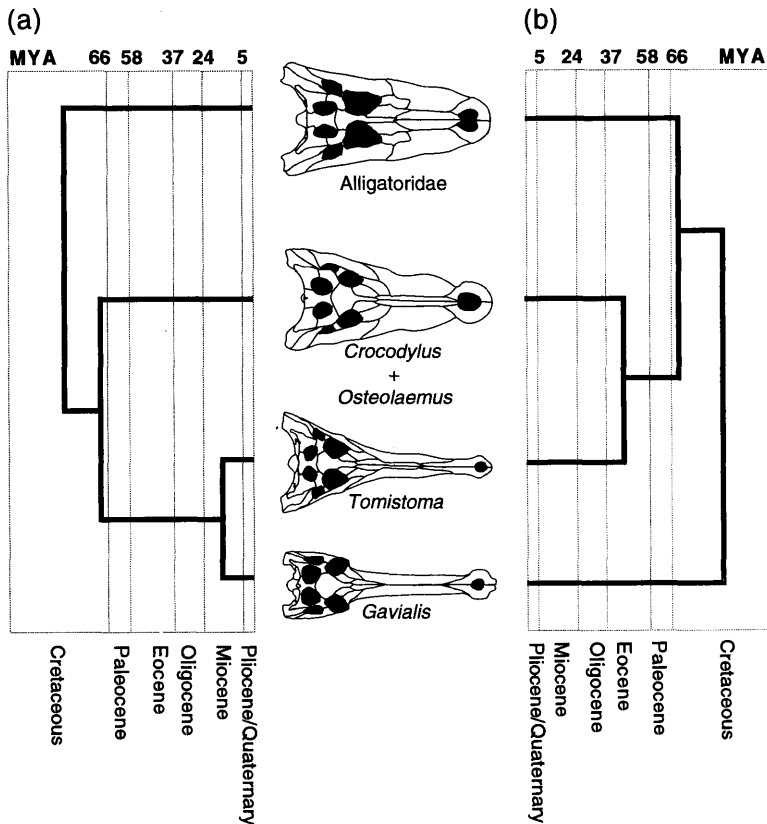
FIGURE 1.   Two competing signals among different data sets for crocodylian relationships. Several molecular data sets indicate a Late Tertiary divergence between *Gavialis* and *Tomistoma* (a), but paleontologists have long favored a more ancient divergence (as far back as the Cretaceous) between *Gavialis* and all other crocodylians. MYA = million years ago.

temporal: when did *Gavialis* diverge from its closest living relative? Although different analyses consistently suggest one answer for both questions, they can be addressed separately.

If disparity revolves around only one living taxon, why should we express concern? Because of the density of its fossil record, Crocodylia can be used to address a host of geological and evolutionary issues, including temporal diversity patterns (Hutchison, 1982; Markwick, 1994). A robust phylogenetic hypothesis is needed before questions of, for example, survivorship across mass-extinction horizons (Smith and Patterson, 1988; MacFadden, 1992; Archibald, 1993) can be addressed confidently. Expectations will differ de-

pending on both the topological and temporal issues. Finding members of one lineage in the Cretaceous implies the presence of its sister taxon in the same period, even if the oldest known members of the sister lineage are from the Eocene.

These two conflicts are often attributed to undetected convergence within morphological data sets (Densmore, 1983; Hass et al., 1992), but molecular data sets are no less prone to homoplasy (Hillis, 1987; Wyss et al., 1987; Sanderson and Donoghue, 1989; Patterson et al., 1993; Doyle, 1996). Moreover, the fact that modern crocodylian lineages have been separate since the Late Cretaceous (e.g., Norell et al., 1994; Wu et al., 1996) raises the possibility that data sets restricted to living species,

whatever the nature of the data, might be preserving a misleading signal caused by accumulation of convergent apomorphies in distantly related lineages (Felsenstein, 1978; Huelsenbeck and Hillis, 1993). Still, the most prominent hypothesis currently entertained is that convergence is misleading morphological data sets into recovering an incorrect phylogeny and overestimating the time transpired since *Tomistoma* and *Gavialis* diverged.

We can address both sides of this issue and test these hypotheses by including fossils in the analysis. The fossil record of Crocodylia is rich, including some remarkably well-preserved specimens, and extends back into the Cretaceous. Because fossils preserve primitive states modified beyond recognition in living taxa, their inclusion can increase accuracy over purely neontological analyses when extant lineages have been separated for a long time (Huelsenbeck, 1991). They also provide the means to calibrate minimum divergence time for any two living species (Norell, 1992).

In this study, I addressed Hass et al.'s (1992) invitation to reanalyze the morphological data from both living and extinct crocodylians to answer two questions: What does morphology say about the relationships of *Gavialis*, and what does it say about the timing of the divergence of *Gavialis* from other living crocodylians? A cladistic analysis of crocodylian relationships based on discrete morphological characters was performed, first from a neontological perspective and then with fossils included. Although some sequence and restriction site fragment data were used in combination with morphology for some portions of this analysis, I did not attempt to reconsider molecular analyses published to date; Poe (1996) reanalyzed the restriction site and mitochondrial DNA sequence data and provided an excellent summary of the noncladistic molecular data.

Herein, I use the phylogenetic definition of the name Crocodylia first explicitly published by Benton and Clark (1988): the crown group including the last common ancestor of alligatorids, crocodylids, and *Gavialis* and all of its descendants. "Crocodylian" is spelled with a "y" rather than an "i" to specify a member of this monophyletic group. Norell et al. (1994) expanded the phylogenetic system within Crocodylia to include three stem groups: (1) Gavialoidea (all taxa more closely related to *Gavialis* than to alligators or crocodiles), (2) Alligatoroidea (all taxa more closely related to alligators than to crocodiles or *Gavialis*), and (3) Crocodyloidea (all taxa more closely related to crocodiles than to alligators or *Gavialis*). Within each stem group is a crown group defined on the basis of extant taxa: (1) Gavialidae includes the last common ancestor of living gharials and all of its descendants; (2) Alligatoridae includes the last common ancestor of living alligators and caimans and all of its descendants; and (3) Crocodylidae includes the last common ancestor of living crocodyloids and all of its descendants.

CONFLICTING VIEWS OF *GAVIALIS* from Diverse Data Sets

Previous Hypotheses of Crocodylian Relationships

The earliest crocodylian taxonomies were based on gross similarity rather than on anatomical detail. The monophyly of Alligatoridae has never been controversial, but the relationships of nonalligatorid forms were in constant flux during the 19th century. Duméril and Bibron (1836) clustered the crocodylians known at that time such that *Gavialis* fell outside a group including all others, but later classifications, including those by evolutionists, were not always as clear. Systematists of that time frequently classified all long-snouted taxa together in a group separate from more generalized taxa (e.g., Lydekker, 1888; von Zittel, 1890), but some of the most important anatomical descriptions of that era not only considered *Tomistoma* to be a crocodylid but also classified it within *Crocodylus* (e.g., D'Alton and Burmeister, 1854; Brühl, 1862).

Early in this century, morphologists reached a broad consensus that *Gavialis*

was distantly related to all other living crocodylians (Müller, 1927a; Nopsca, 1928; Kälin, 1931; Mook, 1934). The systematic placement of *Tomistoma* and its putative extinct relatives was less certain; some authors explicitly allied them with crocodylids (Mook, 1921b, 1934; Piveteau, 1927; Kälin, 1931, 1955a, 1955b; Wermuth, 1953), whereas others left Alligatoridae + Crocodylidae + *Tomistoma* unresolved (Williston, 1925; Romer, 1956; Sill, 1968; Steel, 1973). This consensus was not unanimous (e.g., Joleaud, 1920), but by the 1950s most morphologists regarded *Gavialis* and *Tomistoma* as distant relatives. Most agreed that the lineage including *Gavialis* had diverged from that including other crocodylians before the end of the Cretaceous, and Kälin (1955b) argued for a divergence during the Jurassic, with "eusuchian" characters (pterygoid-bound choanae, procoelous vertebrae) arising independently in *Gavialis* and other members of Crocodylia.

Chromosomal studies (Cohen and Gans, 1970; King et al., 1986) have not produced results easily expressed as a tree, but they generally show that *Gavialis* has a karyotype "intermediate" between that of alligatorids and that of crocodylids. Nesting behavior was studied from a systematic standpoint by Greer (1970). His results supported a basal position for *Gavialis* but also suggested that *Osteolaemus, Tomistoma,* and alligators were all derived within *Crocodylus*; however, his study was criticized for its inclusion of ecologically plastic characters (Campbell, 1972). Phylogenetic relationships of crocodylian intestinal parasites have been extrapolated into a phylogenetic statement for Crocodylia, assuming coevolution between parasite and host (Brooks, 1979; Brooks and O'Grady, 1989), but these results suggested some heterodox relationships and have generally been criticized as reflecting a biogeographic rather than phylogenetic signal (Densmore and Owen, 1989). Coevolutionary analyses did not include *Tomistoma* but support a basal position for *Gavialis* relative to other crocodylian lineages.

Gorman et al. (1971) were the first to infer within-group crocodylian relationships

from a biochemical standpoint. Starch gel electrophoretic analysis of serum albumin indicated a shorter immunological distance between *Alligator* and *Caiman* than between *Alligator* and *Crocodylus*. Densmore (1983) conducted a much more inclusive study, using immunodiffusion analysis of serum albumin and transferrin, hemoglobin tryptic peptide "fingerprinting," and starch gel electrophoresis of 17 additional blood proteins to derive phenograms for all extant species within Crocodylia. His results diverged from more traditional morphological hypotheses in that *Tomistoma* and *Gavialis* consistently clustered together; the immunodiffusion results indicated virtually no difference between these two taxa, prompting Densmore and Dessauer (1984) to argue for a relatively recent divergence between them, perhaps as recently as the Miocene.

Several other molecular studies of crocodylian relationships have included mitochondrial and nuclear DNA restriction fragment comparison (Densmore and Owen, 1989; Densmore and White, 1991), microcomplement fixation of serum albumin (Hass et al., 1992), sequence comparison of 12S ribosomal mitochondrial DNA (Gatesy and Amato, 1992; Gatesy et al., 1993), and DNA fingerprinting (Aggarwal et al., 1994). The results of these studies were congruent with the conclusions of Densmore (1983) in that *Tomistoma* and *Gavialis* were most similar; Hass et al. (1992) argued for a divergence as recent as the Pliocene.

A few osteological studies seemed to support the molecular hypotheses, at least topologically (Aoki, 1976, 1992; Buffetaut, 1985b), but these studies have been criticized (most notably by Norell, 1989) for relying on demonstrably plesiomorphic character states to unite *Gavialis* and *Tomistoma*. Characters of tongue structure (Taplin and Grigg, 1989) and integumentary gland pores (King and Brazaitis, 1971) also support the molecular tree when viewed independently but have not been considered in more inclusive data sets. Most recent morphological analyses have instead supported the basal position of *Gavialis* and a

close relationship between *Tomistoma* and *Crocodylus* (Frey, 1988; Frey et al., 1989; Norell, 1989; Tarsitano et al., 1989; Willis, 1993; Clark, 1994; Salisbury and Willis, 1996), and even those analyses that agreed with the molecular data topologically (e.g., Buffetaut, 1985b) indicated a divergence between *Gavialis* and *Tomistoma* prior to the Eocene.

Poe (1996) combined published mitochondrial restriction site fragment data (Densmore and Owen, 1989; Densmore and White, 1991), 12S sequence data (Gatesy and Amato, 1992; Gatesy et al., 1993), and morphological, karyotypic, and behavioral characters derived from the literature (Cohen and Gans, 1970; Greer, 1970; Brazaitis, 1973; Iordansky, 1973; Ross and Mayer, 1983; Norell, 1988, 1989; Clark, 1994), using both fossil and living outgroups. This combined matrix, which ultimately included 176 molecular and 64 phenotypic (morphology, chromosome, behavior) characters, continued to support the sister-taxon relationship between *Gavialis* and *Tomistoma*. Poe (1996) emphasized the congruence among all data sets if *Gavialis* is ignored and argued that the combined tree was the best estimate for crocodylian systematics.

The Placement of Gavialis and the Role of Fossils

Why do these data sets disagree so consistently on the relationships and divergence timing of *Gavialis*? Nearly all authors of molecular studies have attributed this disagreement to undetected convergent evolution in morphological characters (Densmore, 1983; Hass et al., 1992). They correctly pointed out that crocodylian evolution has long been seen as replete with convergence, particularly with regard to snout shape (Langston, 1973). If morphological data sets rely heavily on cranial characters, as historically they have, homoplasy might be compromising attempts to accurately reconstruct relationships. Thus, when morphologists pointed to the existence of gharials in the Eocene (e.g., Hecht and Malone, 1972; Buffetaut, 1982), Hass et al. (1992) suggested that the fossils

had been misidentified. The characters used to unite *Tomistoma* and *Crocodylus* were dismissed as convergences (Hass et al., 1992) or as potential synapomorphies for all nonalligatoroid crocodylians, these synapomorphies being secondarily transformed in *Gavialis* (Densmore, 1983).

It is also entirely possible that homoplasy is projecting a misleading signal onto the molecular data. Even if rates of evolution are low, accumulation of apomorphies within long-separate lineages will erase historical information from descendant taxa and, ultimately, randomize data sets; if evolutionary rates among a group of lineages are not uniform, branches with large numbers of apomorphies may converge on each other (Felsenstein, 1978; Hendy and Penny, 1989; Sytsma and Baum, 1996). This possibility is particularly relevant given the tree reconstruction algorithms used in the distance-based crocodylian phylogenies published to date (e.g., UPGMA in the electrophoretic data of Densmore, 1983), which are known in simulation to be inaccurate when faced with long phylogenetic branches of different lengths (Huelsenbeck and Hillis, 1993; Hillis et al., 1994; Huelsenbeck, 1995).

The utility of combining disparate and conflicting data sets has been debated (Kluge, 1989; Swofford, 1991; Chippindale and Wiens, 1994; Huelsenbeck et al., 1994; de Queiroz et al., 1995; Miyamoto and Fitch, 1995; Huelsenbeck and Bull, 1996; Nixon and Carpenter, 1996). The combined approach deals with conflict at the character level but fails to properly address situations in which different data sets are producing well-supported but conflicting hypotheses of relationships (Shaffer et al., 1991; de Queiroz, 1993; de Queiroz et al., 1995). A combined approach may not accurately recover a phylogeny under these circumstances, as shown in simulation by Bull et al. (1993). The consistency and strength with which different data sets disagree on the placement and divergence timing of *Gavialis* indicates conflict between data sets, and one would expect the stronger signal, in this case that from restriction fragment length polymorphism

and sequence data, to outweigh any other signals.

If, as suggested by Hass et al. (1992) and Densmore (1983), morphological data sets are beset with convergence in extant species, one possible solution is to add fossils to morphological analyses. Fossils "prune" long branches by preserving ancestral states not recoverable in living relatives (Huelsenbeck, 1991), and their inclusion can overturn hypotheses supported by living taxa alone (Gauthier et al., 1988; Donoghue et al., 1989; Meylan and Gaffney, 1989; Novacek, 1992). To date, published parsimony analyses of Crocodylia (e.g., Norell, 1989) have essentially been analyses of living taxa. Some fossil crocodylians occur in the Late Cretaceous and represent taxa living not long after the presumed divergence of extant lineages; these taxa are important because simulations indicate that the addition of taxa to the analysis is likeliest to increase accuracy if the added taxa diverged close to the root (Kim, 1996).

If convergence is a problem for morphological data, the addition of fossils should suggest a different set of relationships than those obtained without fossils. Failure of fossils to overturn Recent-only results, of course, does not prove that morphology is not being misled by convergence but represents a failure to reject the hypothesis that morphology is being misled and bolsters confidence that the signal being drawn from morphology is consistent.

Fossils also provide a unique opportunity to calibrate the timing of lineage splitting events within Crocodylia. The oldest known occurrence of one lineage places a minimum age on both (Paul, 1982; Benton, 1990; Marshall, 1990; Norell, 1992, 1993; Archibald, 1996). If one hypothesizes that *Gavialis* and *Tomistoma* shared a common ancestor after the Oligocene, one would not expect to find fossils closer to either taxon in pre-Miocene units. Identification of such fossils forces a rejection this hypothesis. Failure to recognize pre-Miocene gavialoids or tomistomines would be consistent with a post-Oligocene divergence but would not necessarily prove it. Fossils can only provide minimum divergence

times, and the possibility of a ghost lineage must always be considered (Marshall, 1990; Norell, 1992, 1993; Springer, 1995).

METHODS

Phylogenetic Analysis: Testing the Topological Incongruence

One hundred sixty-four discrete morphological characters were subjected to maximum parsimony analysis with PAUP 3.0s (Swofford, 1990); these characters are listed in Appendix 1 (see data matrix in Appendix 2). Multistate characters were treated as unordered, and no differential character weights were used. Branch-and-bound searches were conducted when living taxa were analyzed separately, but because of the size of the matrix, heuristic searches were used when fossil taxa were added. Ten searches were done with each analysis, with the order of the taxa in the matrix randomized each time, to ensure that the search was not being trapped in a local tree-length minimum (Maddison, 1991).

Two fossil taxa, *Bernissartia fagesii* and an undescribed neosuchian from the Early Cretaceous Glen Rose Formation of Texas, were used as sequential outgroups in all analyses. Norell (1989) used *Goniopholis* + Dyrosauridae + *Eutretauranosuchus* and *Bernissartia* + *Shamosuchus* as outgroups; I was unable to examine well-preserved *Shamosuchus* material, and because the relationships among "goniopholidids" (e.g., *Goniopholis*, *Eutretauranosuchus*) are not well resolved, I excluded them. The undescribed Glen Rose form (Langston, 1974) was designated the sister taxon to Eusuchia by Benton and Clark (1988).

Poe (1996) used two extant noncrocodylians, *Sphenodon punctatus* and *Apteryx australis*, as outgroups to polarize molecular data. *Dromaius novaehollandiae* (emu) was substituted for *Apteryx* in the present study because skeletal material was available, permitting the scoring of morphological characters. The 12S ribosomal DNA (rDNA) sequence data for *Dromaius* were downloaded from GenBank (accession X67633; see Cooper et al., 1992). *Dromaius*

was used as an additional outgroup taxon when molecular and morphological data sets were combined.

Two separate types of analyses were performed. In both cases, branch-and-bound searches were done on 15 extant taxa and the two fossil outgroups, followed by heuristic searches that included the 15 extant and 44 extinct ingroup taxa (see Appendix 3). All living species within Alligatoridae were included, and *Caiman crocodilus* and *Caiman yacare* were regarded as separate species for purposes of this analysis. Only four species within *Crocodylus* (*C. cataphractus*, *C. rhombifer*, *C. porosus*, *C. niloticus*) were included in these particular analyses because other *Crocodylus* were morphologically redundant with one of these four taxa.

In the first analyses, morphological characters were analyzed separately. *Bernissartia* and the Glen Rose Form were the only outgroups, whether the ingroup was restricted to living species or included fossils. In the second, 12S rDNA sequence data (Gatesy et al., 1993) and 18S nuclear, 28S nuclear, and mitochondrial restriction site fragment data (Densmore and White, 1991) were combined with morphology and analyzed concurrently. These molecular data sets were the same ones considered by Poe (1996). For these, *Dromaius* was added as one of the outgroups. The 12S rDNA alignment published by Gatesy et al. (1993) was modified by eye to include the *Dromaius* sequence; the realigned sequence is shown in Table 1.

Nonparametric bootstrap percentages were calculated for nodes on all trees. When living taxa were analyzed separately, the bootstrap analysis consisted of separate heuristic searches of 1,000 replicate data sets. Because of the final size of the matrix with fossils included (59 taxa, 164 characters), only 100 replicate data sets were generated, and the heuristic searches were modified such that branch swapping was not used; 10 random arrangements of each replicate data set were examined.

Decay indices were calculated using TreeRot (Sorenson, 1996) for trees restricted to living taxa. These numbers were not

calculated for matrices including fossils; repeated attempts using constraint files generated by both TreeRot and AutoDecay 2.9.5 (Eriksson, 1996) were unsuccessful owing to large numbers of incomplete taxa. Because decay indices were not calculated, trees up to three steps longer were considered when fossils were included.

To compare the results obtained from these analyses with previously published hypotheses, alternative arrangements were entered as constraint trees and analyzed separately. First, the living taxa were constrained such that *Gavialis* and *Tomistoma* formed a clade more closely related to *Crocodylus* than to *Alligator*, as with previous molecular studies. With fossils included, those extinct taxa closer to either *Gavialis* or *Tomistoma* were constrained to form a clade with no internal resolution, and all other crocodylian taxa were allowed to float. These taxa were further constrained in subsequent analyses such that post-Oligocene taxa (*Gavialis gangeticus*, Siwaliks *Gavialis*, *Tomistoma lusitanica*, *Tomistoma schlegelii*) formed a clade; this constraint conformed to the hypothesis that *Gavialis* and *Tomistoma* shared a common ancestor after the Oligocene.

Templeton (1983) introduced a procedure based on the Wilcoxon signed rank test to test the significance of character state distribution difference between hypotheses (see also Larson, 1994; Poe, 1996). I used one-tailed tests in this study (but see Felsenstein, 1985), deriving significant figures from the tables of Rohlf and Sokal (1981).

Calibration of Divergence Time: Testing the Temporal Incongruence

Many of the fossil taxa considered in this analysis are known only from a single locality, effectively rendering them point occurrences for the purposes of this study. To estimate age, I determined the smallest chronostratigraphic unit to which each fossil could be assigned; for most North American fossils, this was the North American Land Mammal Age (NALMA), and for most non-North American specimens, this was stage. A few taxa could

TABLE 1. 12S rDNA sequences used in this study (taken from Gatesy et al., 1993, and modified by eye with inclusion of *Dromaius*).

Characters

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                              0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889
Taxon                         1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890

Gavialis gangeticus           GACTTGACGG TACTTCGCAC CCACCTAGAG GAGCCTGTCC TATAATCGAC AGTACTCGAT ATACCTTACC AACTTTTGCC TTAAACGT-C
Alligator sinensis            GACTTGACGG CGCTTCGAAC CACCCTAGAG GAGCCTGTCC TATAATCGAC GGTACACGAT TCACCCGACC ACCTTTAGCC C-------C
Alligator mississippiensis    GACTTGACAG TACTTTAAAC CCCCCTAGAG GAGCCTGTCC TATAATCGAA AGTACACGTT ACACCCGACC ACCTTTAGCC T---A---C
Caiman crocodilus             GACTTGACAG TACTTCAAAT CCACCTAGAG GAGCCTGTCC TATAATCGAT AGTACACGAT TCACCTAACC ACCCTTAGT- T---A---T
Caiman latirostris            GACTTGACAG CACTTCAAAT CCACCTAGAG GAGCCTGTCC TATAATCGAA AGTACACGAT TCACCTAACC ACCCCTAGTC T---A---C
Melanosuchus niger            GACTTGACAG TACTTCAAAA CCACCTAGAG GAGCCTGTCC TATAATCGAA AGTACACGAT CCACCTAACC ACCCCTGACC C-------T
Paleosuchus trigonatus        GACTTGACGG TACTTTAAAC CCACCTAGAG GAGCCTGTCTC TATAATTGAA GATACACGAT CCACCTAACC CCTCCTAGCC T-------C
Paleosuchus palpebrosus       AACTTGACGG TACTTTAAAC CCACCTAGAG GAGCCTGTCC TATAATTGAA GATACACGAT TCACCTAACC CCTCCTTGCC T-------C
Crocodylus rhombifer          GACTTGACGG TATTTCGAAC CCACCTAGAG GAGCCTGTCC TATAATCGAC AATACACGAT CCACCCAACC ACCTTTTGCC CT-AA-G--
Tomistoma schlegelii          GACTTGACGG TACTTCGCAC CCACCTAGAG GAGCCTGTCC TATAATCGAA AACACTCGAT ACACCCTACC AACTTTTGCC TTAAAC-TAC
Dromaeus novaehollandiae      GACTTGGCGG TGCCCTAAAC CCACCTAGAG GAGCCTGTTC TATAATCGAT AACCCACGAT ACACCCAGCC AA-TACAGCC ------TAC


                              0000000001 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111
                              9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778
                              1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890

Gavialis gangeticus           -TAACAGCCT GTATACCGCC GTCG-CAAAC -TAGCCC-CC TGAGGGACAA AC-A-ATTTA GTACAATAGC TTA-TT-TGA -GCTAATACG
Alligator sinensis            -T--CAGCCT GTATACCGCC GTCGCCAAGC CCGTCCC-CC TGAGGGA--G ACAA-AACGA GCACATAGC -C---TCCCA GGCTAGCACG
Alligator mississippiensis    -T--CAGTCT GTATACCGCC GTCG-CAAGC CCGTCCCCATT TGAGGGA--A ACAA-AACGC GGGCAACAGC TCA--ACCGA -GCTAACACG
Caiman crocodilus             -C--CAGTTT GTATACCGCC GTCG-CAAGC TTGTCTC-GC TGAGAGA--A ACAA-AATGA GCACAATAGC -C---CCCC GCTAAAACG
Caiman latirostris            -C--CAGTTT GTATACCGCC GTCG-CAAGC CTGTCTC-GC TGAGAGA--A ACAA-AATGG GCACAACAGC -C---TCCTA GGCTAAAACG
Melanosuchus niger            -T--CAGTCT GTATACCGCC GTCG-CAAGC TTGTCTTC-GC TGAGAGA--A ACAA-AATAA GCACAACAGC -C---TCCCA GGCTAAAACG
Paleosuchus trigonatus        -T--CAGTCT GTATACCGCC GTCG-CAAAC TTGTCCC-AC TGAAGGA--A ACAA-AACGA GTACAACAGC -C---TCCCA GGCTAATACG
Paleosuchus palpebrosus       -T--CAGTCT GTATACCGCC GTCGCCAAAC TCGTCCC-AC TGAGGGA--A ACAA-ACCTA GTGCAACAGC -C---TCCCA GGCTAATACG
Crocodylus rhombifer          ---CAGCCT GTATACCGCC GTCG-CAAGC TTAG-CC-CA TGAGGGAC-A AG-A-ACCTA GCACAATAAC TCACTTCTGA -GCTAGTACG
Tomistoma schlegelii          ATAACAGCCT GTATACCGCC GTCG-CAAAC -TAACCC-CC TGAGGGACGA AC-A-GTTAA GTGCAACAGC TCA-TT-TGA -GCTAATACG
Dromaeus novaehollandiae      ATACC-GCC- G--T-C-GCC A--GCCC-GC CTAA------ T----GA--A AGAATAGCGA GCACAATAGC -CACTT---- -GCTAA----


                              1111111111 1111111112 2222222222 2222222222 2222222222 2222222222 2222222222 2222222222 2222222222
                              8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666666
                              1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567

Gavialis gangeticus           TCAGGTCAAG GTGCAGCCAA TGAGT--GGA AGAGATGGGC TACATTTTCT -ACCACATAG AAATAGTCA CGGAGAGCCC TGTGAAA
Alligator sinensis            TCAGGTCAAG GTGCAGCCAA CAAGGT--GA AGAGATGGGC TACATTTTCT -AACCACATAG AAATATTCAA CGGAGAGCCC TGTGAAA
Alligator mississippiensis    TCAGGTCAAG GTGCAGCCAA CAAGGT-GGA AGAGATGGGC TACATTTTCT CAACATGTAG AAATATTCAA CGGAGAGTCC TATGAAA
Caiman crocodilus             TCAGGTCAAC GCGCAGCTAA TGGGGTGGGA AG--GATGTGC TACATTTTCT -AACACATAG AAATACGTGA CGGAACGTCC CGTGAAA
Caiman latirostris            TCAGGTCAAC GTGCAACTAA TGGGGTGGGA AG--GATGTGC TACATTTTCT -AACCACATAG AAATACGTGA CGGACGTCC CGTGAAA
Melanosuchus niger            TCAGGTCAAG GTGCAACTAA TGGGGTGGGA AG--GATGTGC TACATTTTCT -AACACATAG AAATAGGTAA CGGAGCGTCC CATGAAA
Paleosuchus trigonatus        TCAGGTCAAG GTGCAGCTAA CGGAGC-GGA AGAGATGTGC TACATTTTCT -AA-A-ATAG AAATACGTAA CAGAACGCCC TATGAAA
Paleosuchus palpebrosus       TCAGGTCAAG GTGCAGCTAA TGGAGC-GGT AGAGATGGGC TACATTTTCT -AA-A-ATAG AAATACGTAA CAGAACGCCC TCTGAAA
Crocodylus rhombifer          TCAGGTCAAG GTGCAGCCAA TAAGTT-GGT AGAGATGGGC TACATTTTCT -ACACCATAG AAATTGGTCA CGGAGAGCCC TGTGAAA
Tomistoma schlegelii          TCAGGTCAAG GTGCAGCCAA TAAGTT-GGA AGAGATGGGC TACATTTTCT -ACCTCATAG AAATATGTCA CGGAGAGCCC TGTGAAA
Dromaeus novaehollandiae      -----CAAG AC-AGGTCAA GGTATAGCGT AGAGATGGGC TACATTTTCT -AA--CATAG AAATAT--CA CGAAGAAGAA TGTGAAA
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only be assigned to an epoch, and some South American taxa were assignable to a South American Land Mammal Age (SAL-MA). Chronostratigraphic unit boundaries were obtained or estimated as noted in Appendix 3.

To estimate earliest known occurrence for each species, I used the midpoint of whatever chronostratigraphic unit was available for each taxon, and the temporal range of the unit was used as the error margin. For taxa known across several units of time, the midpoint of the oldest NALMA or stage was used for the origination time. Error margins on unit boundaries were not considered in this analysis; when unit boundaries were depicted as time transgressive, the most extreme limit to that unit was used. Taxa whose error margins overlapped were considered contemporary when calculating the stratigraphic consistency index (SCI) unless clear superpositional information placed one taxon above another within the same stage. I calibrated divergences between any two taxa using the oldest occurring fossil in either of the lineages as a minimum age.

The SCI is the ratio between the number of nodes consistent with known stratigraphic ranges of involved taxa and the total number of nodes (Huelsenbeck, 1994). This metric is related to the cladistic rank method of Gauthier et al. (1988; see also Norell and Novacek, 1992a, 1992b) but is able to consider all nodes simultaneously in a symmetrical tree. The SCI is only a measure of whether a particular cladogram conflicts with superpositional information and is not an indicator of the amount of conflict; for example, cases in which all taxa under consideration have the same known minimum age will give an SCI of 1.0. Also, SCI will not measure how complete the fossil record is because it only reflects relative age. In this case, however, SCI is a useful way of determining whether alternative hypotheses require more or fewer ghost lineages, as measured by deviation from the stratigraphic order of known fossils.

The SCI has been criticized as sensitive to data set size and tree shape; in particular, pectinate trees are more likely to have higher SCIs than are symmetrical trees of the same taxa (Siddall, 1996). I calculated the imbalance index *(Im)* of Heard (1992) for two completely resolved trees for each of the competing phylogenies, one that maximizes symmetry and one that minimizes it, to ensure that tree shapes were similar. The expected value of *Im* for a matrix of 59 taxa is 0.1063, following equations of Heard (1992) and Siddall (1996). SCI cannot be calculated for a consensus tree, so in both cases SCI was calculated for the most pectinate and most symmetrical trees possible from the consensus tree to give maximum and minimum *Im*.

The number of required ghost lineages can be estimated by considering the minimum implied gaps (MIG) between the first occurrences of two sequential taxa on a cladogram (Norell and Novacek, 1992a, 1992b; Weishampel and Heinrich, 1992; Storrs, 1993; Benton and Storrs, 1994, 1996; Smith and Littlewood, 1994). A sum of MIG (SMIG) for a tree indicates the sum length of ghost lineages for the entire tree. As with SCI, only fully resolved trees can be used to calculate SMIG; I therefore calculated SMIG for all trees in the set of most-parsimonious trees and averaged them. SMIG can suffer from the opposite bias of SCI: whereas SCI will favor pectinate trees, SMIG can favor symmetrical trees because long basal branches are being cut by known nodes.

Fossils exist that extend the temporal range of taxa used in the parsimony analysis. However, these fossils were not included in the analysis because they were redundant with other taxa that were included; as such, the redundant taxa contributed nothing toward resolving relationships and would have only increased the number of most-parsimonious trees (Wilkinson and Benton, 1995). Nevertheless, because these taxa were able to extend the known temporal range of their congruent taxa, they are listed at the bottom of the table in Appendix 3.

Divergence times estimated from the fossil record can be compared with those

inferred from molecular data (Hass et al., 1992). Measures of molecular distance can be plotted against minimum age of divergence, and correlations can be calculated. For this analysis, I used four different measures of distance: adjusted antigenic distance from serum albumin (Densmore, 1983), immunological distance from serum albumin (Hass et al., 1992, using the same samples as Densmore, 1983), Nei's distance *(D)* calculated from 17 different blood proteins (Densmore, 1983), and minimum number of steps between taxa for the 12S ribosomal unit of the mitochondrial genome (Gatesy et al., 1993).

Distances were read directly from the appropriate tables of Densmore (1983) and Hass et al. (1992). For Nei's *D*, pairwise comparisons between different alligatorids and nonalligatorids were not provided. Whenever possible, the distance between *Crocodylus cataphractus* and all other *Crocodylus* was used to represent the initial divergence among extant *Crocodylus*. Step matrices were generated by PAUP to calculate distance for the DNA data, and absolute distances were used.

Because we do not know the sampling distribution for many types of distance data (Hillis et al., 1996), error margins could not be calculated for antigenic distance, immunological distance, or Nei's *D*. However, molecular clock hypotheses assume that base pair substitutions accumulate following a Poisson distribution (Wilson et al., 1987; Hillis et al., 1996). Following the equation described by Hillis et al. (1996), error margins were calculated for nine different hypothetical rates of evolution (0.125, 0.25, 0.5, 0.75, 1.0, 1.25, 1.5, 1.75, and 2.0 base pair changes/million years [bpc/MY]), allowing a test of the hypothesis that all pairwise comparisons within Crocodylia are consistent with the same rate or rates of evolution. After these rates were calculated, a few divergences exceeded rates of 2.0, and so integer increments from 3.0 through 7.0 were also tested. Simple relative rate tests were also conducted with this data set following a modified version of the protocols of Mindell and Honeycutt (1990).

RESULTS

The topological results of all classes of analyses are summarized in Figure 2. Morphology, based on these results, does indicate a basal position for *Gavialis* relative to other crocodylians, but different combined analyses support different topologies and rootings.

Parsimony Analysis

Extant taxa only, morphology only.—Heuristic searches found a single most-parsimonious tree with a length of 259 (consistency index [CI] excluding uninformative characters = 0.711; retention index [RI] = 0.867) (Fig. 3a). Bootstrap percentages indicate that all ingroup nodes on this tree are robust. The monophyly of Crocodylidae, including *Tomistoma*, is supported in trees up to 6 steps longer than the most-parsimonious tree; monophyly of a group including all crocodylians except *Gavialis* is supported in trees up to 11 steps longer.

This tree is largely congruent with all previous analyses of Crocodylia, regardless of the type of data used. *Crocodylus* is monophyletic and is the closest living relative of *Osteolaemus*; Alligatoridae is monophyletic, as are the caimans; the sister-taxon relationship between *Caiman latirostris* and *Melanosuchus niger* was supported by Norell (1988) and Poe (1996), and all other topological arrangements within Alligatoridae are in agreement with previous analyses; and *Tomistoma* is closer to *Crocodylus + Osteolaemus* than it is to Alligatoridae. A sister-group relationship is indicated between *Crocodylus cataphractus* and all other *Crocodylus*, in accord with some immunological data (e.g., Densmore, 1983), although different data sets do not agree on the relationships within *Crocodylus* (Poe, 1996).

This data set supports previous morphological cladistic studies of Crocodylia (e.g., Norell, 1989) in that *Gavialis* is unequivocally the sister taxon of all other crocodylians. By constraining *Gavialis* and *Tomistoma* as sister taxa, tree length increases from 259 to 273. This is an increase of 5.13%, and based on Templeton's test (one-tailed),
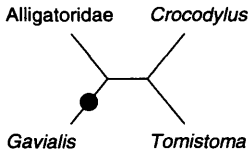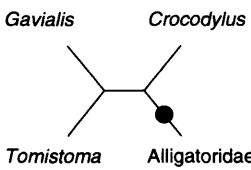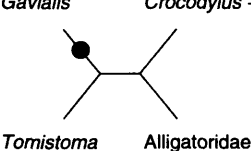
Alligatoridae *Crocodylus + Osteolaemus* ● *Gavialis* Tomistoma	morphology, recent only ✳
	morphology, with fossils ✳
	combined, with fossils
Gavialis *Crocodylus + Osteolaemus* ● *Tomistoma* Alligatoridae	molecular, recent only ✳ (Poe, 1996)
	combined, no fossils, *Dromaius* only outgroup (in part)
Gavialis *Crocodylus + Osteolaemus* ● *Tomistoma* Alligatoridae	combined, no fossils, *Dromaius* and fossil outgroups
	combined, no fossils, *Dromaius* only outgroup (in part)

FIGURE 2. Summarized results of different parsimony analyses for Crocodylia. ● = preferred root. The asterisk indicates a situation in which the preferred topology is significantly more parsimonious than competing topologies based on Templeton's test. See Poe (1996) for results of parsimony analyses of molecular data alone.

the difference is significant ($P < 0.025$, Ts = 273, $n = 41$).

Fossils included, morphology only.—The strict consensus of the 1,620 most-parsimonious trees recovered had a length of 472 (Figs. 4a, 5a). The relationships among living crocodylians are entirely congruent with those of Figure 3a. *Gavialis* and its closest extinct putative relatives form the basalmost clade within Crocodylia; Alligatoroidea and Crocodyloidea, including *Tomistoma* and several extinct tomistomines, are sister taxa.

In most ways, this tree agrees topologically with previous analyses of fossil crocodyliform systematics. *Hylaeochampsa vectiana* is the sister taxon to Crocodylia, as proposed by Clark and Norell (1992). The crocodyloid identity of such taxa as *Asiatosuchus germanicus*, "*Crocodylus*" *affinis*, and *Brachyuranochampsa eversolei* is in agreement with the proposals of Norell and Storrs (1986) and Salisbury and Willis (1996). The placement of *Diplocynodon* close to but not within Alligatoridae was supported by Norell et al. (1994), and the

gavialoid affinities of *Eogavialis africanum* were supported by Hecht and Malone (1972) and Buffetaut (1982).

Nevertheless, there are some unexpected results. Most important of these from a paleontological perspective is the nonmonophyly of "*Leidyosuchus*," a widespread assemblage of generalized eusuchians from the Late Cretaceous through the Eocene of North America (Lambe, 1907; Gilmore, 1910; Erickson, 1976; Brochu, in press). As shown here, *Leidyosuchus canadensis* is a basal alligatoroid, but other "*Leidyosuchus*" lie outside Alligatoroidea + Crocodyloidea. "*Allognathosuchus*," an assemblage of broad-snouted alligatorids from the Tertiary of North America and Europe (e.g., Simpson, 1930; Berg, 1966), is also not monophyletic; *Allognathosuchus wartheni* is more closely related to *Alligator* than is "*Allognathosuchus*" *mooki*.

The gavialoid identity of *Thoracosaurus macrorhynchus* was likewise unexpected. Most 20th century authors have considered *Thoracosaurus* to be a tomistomine (Piveteau, 1927; Steel, 1973; Carpenter, 1983).
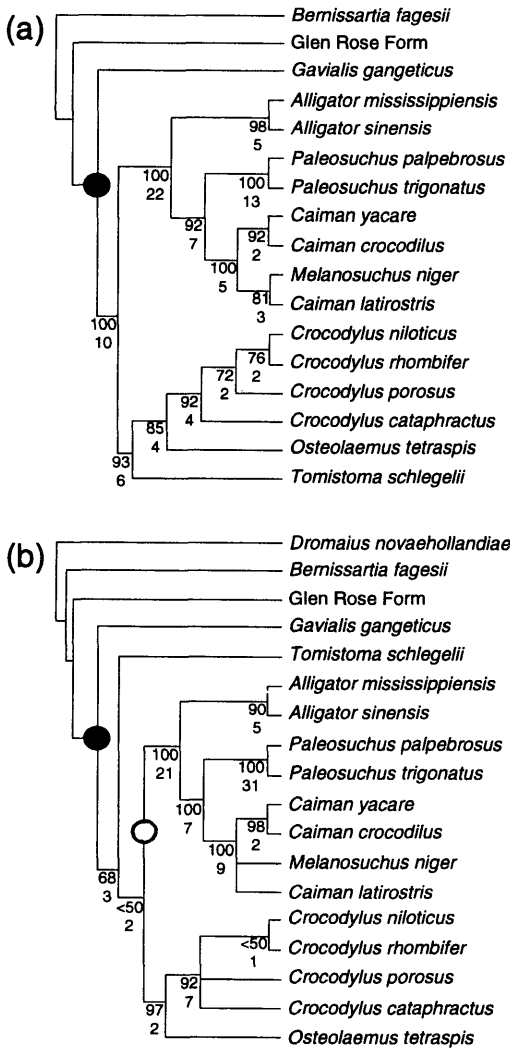
FIGURE 3. Results of strict parsimony analysis on matrix including living crocodylian ingroup taxa only. Numbers near the nodes are bootstrap percentages (upper) and decay indices (lower). (a) Single most-parsimonious tree (length = 259, CI [excluding uninformative] = 0.711, RI = 0.867) when morphological characters were used exclusively; ● = root. (b) Strict consensus of four most-parsimonious trees (length = 625, CI [excluding uninformative] = 0.670, RI = 0.750) when the combined data set was considered. ● = preferred root when *Dromaius* and fossil outgroups were used concurrently; ○ = equally parsimonious root when the fossil outgroups are pruned.

The relationship proposed here is not strictly new; 19th century paleontologists (e.g., LeMoine, 1884; Köken, 1888) regarded *Thoracosaurus* as a close relative of *Gavialis*. Although *T. macrorhynchus* itself is from the lowermost Paleocene (Troedsson, 1924; Piveteau, 1927), congruent forms are known from the Late Cretaceous (Leidy, 1864; Troxell, 1925; Carpenter, 1983; Schwimmer, 1986).

Tomistominae, whose name is defined in reference to all crocodylians more closely related to *Tomistoma* than to *Crocodylus*, *Alligator*, or *Gavialis*, includes *T. schlegelii* and a series of extinct forms extending into the Lower Tertiary. The oldest of these is "*Crocodilus*" *spenceri* from the lowermost Eocene (Ypresian) of England, originally described by Buckland (1836) and later redescribed and illustrated by Owen (1850). *Tomistoma cairense*, known from the Middle Eocene Mokattam Formation of Egypt (Müller, 1927b; Buffetaut, 1982), is also a tomistomine according to this analysis.

In general, nodes supported by high bootstrap percentages in the Recent-only tree were either more weakly supported or not supported at all in the Recent + fossils tree, probably because the large suites of characters supporting taxa in the Recent-only tree were being shared by a larger number of nodes. The 12 unambiguous synapomorphies diagnosing Crocodylidae in the Recent-only analysis, for example, were distributed over five to seven nodes in the Recent + fossils tree. Nevertheless, the monophyly of Gavialoidea, including pre-Miocene taxa, received very high support (100%).

Taxa designated as gavialoids or tomistomines in the analysis with fossils were constrained to form a clade; heuristic searches under this constraint recovered 14,648 most-parsimonious trees with a length of 492, an increase of 4.07%. The strict consensus of these was similar to that in Figures 4a and 5a, with the exception that Gavialoidea (including tomistomines) was the sister taxon of the clade including "*Crocodylus*" *megarhinus*, *Australosuchus clarkae*, and more derived crocodylids. Putative tomistomines were sister taxa to the last
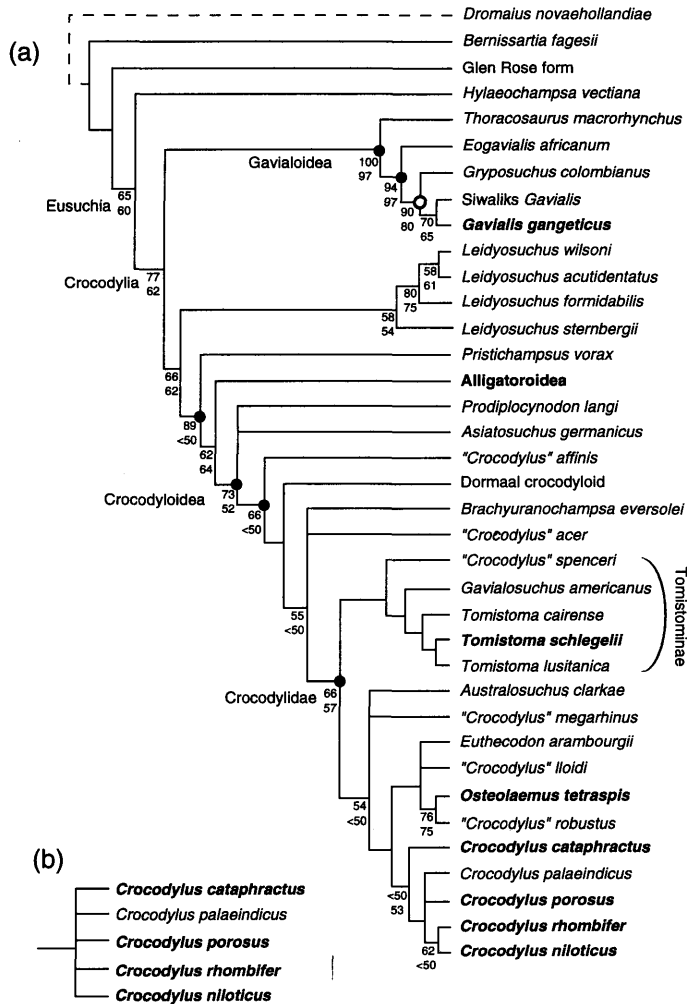
FIGURE 4. Strict consensus trees for crocodylians and outgroups. Extant taxa are shown in bold. (a) Strict consensus of 1,620 most-parsimonious trees (length = 472, CI [excluding uninformative] = 0.431, RI = 0.827) recovered when fossil and living ingroup taxa were analyzed with morphology alone. Alligatoroidea has been collapsed and is shown in detail in Figure 5. Numbers at the nodes are bootstrap percentages for the morphology-only analysis (upper) and combined analysis (lower). Decay indices could not be calculated. ● = nodes preserved in trees three or more steps longer than the most-parsimonious trees; ○ = nodes preserved in trees two steps longer. (b) The strict consensus of 7,560 trees (length = 841, CI [excluding uninformative] = 0.475, RI = 0.781) recovered when the combined matrix was used; it is congruent with tree a, but there was loss of resolution within *Crocodylus*. *Dromaius* was used as an additional outgroup, as indicated by the dashed line leading to *Dromaius* in tree a.

common ancestor of *Thoracosaurus* and *Gavialis* (Fig. 6). Although the percentage of tree-length increase is smaller with fossils than without, the unconstrained tree is still significantly more parsimonious ($P < 0.025$, $Ts = 424$, $n = 51$).

Extant taxa only, combined matrix.—The combined matrix produced four most-parsimonious trees with a length of 624 steps. *Gavialis* is placed at the base of Crocodylia, as with the morphology-only analyses, but *Tomistoma* is also close to the root (Fig. 3b). In effect, the unrooted network supported by the combined matrix is the same as
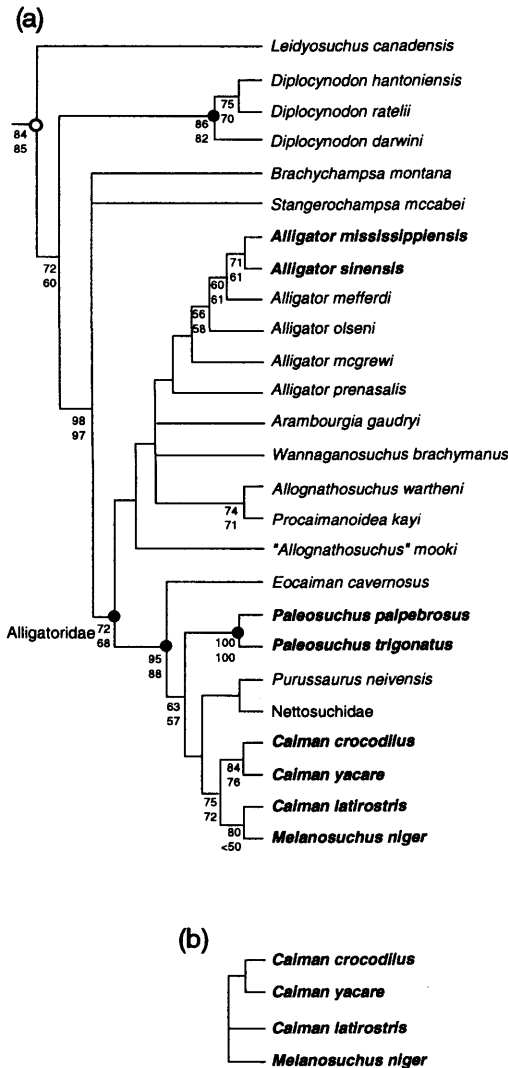
(a)

(b)

FIGURE 5. Relationships among alligatoroids when morphological data were analyzed alone. Extant taxa are shown in bold. (a) Expansion of tree in Figure 4a. Numbers at the nodes are bootstrap percentages for the morphology-only analysis (upper) and combined analysis (lower). Decay indices could not be calculated. ● = nodes preserved in trees three or more steps longer than the most-parsimonious trees. (b) Loss of resolution within *Caiman* when combined matrix was used.
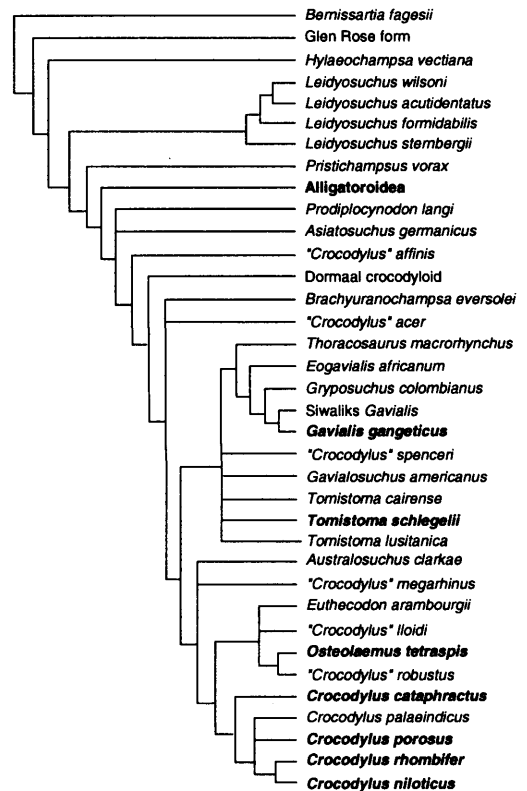
FIGURE 6. Strict consensus of 14,648 most-parsimonious trees (length = 492, CI [excluding uninformative] = 0.420, RI = 0.810) when the morphological data set was constrained to make *Gavialis* and *Tomistoma* closer to each other than either is to other living crocodylians.

with molecular data alone, but morphological information strongly supports a rooting on *Gavialis* rather than Alligatoridae.

This tree also differs from the morphology-only tree in that *Crocodylus cataphractus*

and *C. niloticus* are sister taxa. This node is not robust, and trees supporting a sister-group relationship between *C. cataphractus* and other *Crocodylus* are only one step longer. Some of the molecular data indicate a close relationship between *Caiman latirostris* and *Caiman crocodilus* + *Caiman yacare*, and resolution is reduced in this portion of the tree.

Trees supporting the morphological placement of *Tomistoma* are 628 steps long, regardless of the placement of *C. cataphractus*. The preferred molecular tree, in which *Gavialis* and *Tomistoma* are sister taxa, is 631 steps long. The lengths of both of these trees are <1% greater than the length of the optimal tree, and neither tree is significantly less parsimonious with Templeton's

test ($Ts = 539$, $n = 48$, combined vs. preferred morphology; $Ts = 418$, $n = 43$, combined vs. preferred molecular). However, the preferred morphological and molecular topologies are significantly different from each other ($P < 0.001$, $Ts = 760.5$, $n = 78$).

When the fossil outgroups are pruned from the analysis, two different rootings become equally parsimonious, one on *Gavialis* and one on Alligatoridae. These trees are 592 steps in length, only eight steps shorter than the preferred morphology tree. These three topologies are not significantly different ($Ts = 490$, $n = 48$, preferred morphology tree vs. most-parsimonious result rooted on *Gavialis*; $Ts = 1382.5$, $n = 78$, preferred morphology tree vs. most-parsimonious result rooted on Alligatoridae).

Fossils included, combined matrix.—This analysis produced 7,560 most-parsimonious trees with a length of 841. The strict consensus of these is completely congruent with the set of most-parsimonious trees favored by morphology alone. However, there is loss of resolution within the caimans (Fig. 5b) and *Crocodylus* (Fig. 4b). This set of trees is only three steps longer than the set of trees in which gavialoids and tomistomines are constrained as close relatives. This difference is not significant ($Ts = 1,332$, $n = 74$).

Timing of Divergence within Crocodylia

For the tree as a whole, concordance with stratigraphy is good (average SCI = 0.8679; Figs. 7, 8a), although there are some prominent exceptions. For example, *Pristichampsus* is known only from the Eocene (Berg, 1966; Langston, 1975; Busbey, 1986), but if the phylogeny in Figure 4 is correct, its lineage must extend back to the Cretaceous. Likewise, the lineage including *Diplocynodon* must extend into the Cretaceous, even though remains have not been described for this taxon prior to the Eocene (Berg, 1966; Buscalioni et al., 1992).

The most-parsimonious relationships within Gavialoidea are in perfect agreement with known stratigraphic ranges, and if Late Cretaceous *Thoracosaurus* are

included, the node joining Gavialoidea with all other crocodylians is consistent with stratigraphy. Within Tomistominae, *Gavialosuchus* is the only taxon out of place, with an inferred gap of 10.7 MY.

There is general agreement between the data sets regarding divergence time. For example, molecular data have supported an ancient split between the alligators and caimans (Gorman et al., 1971; Densmore, 1983; Densmore and Owen, 1989; Hass et al., 1992; Kumazawa and Nishida, 1995). Based on the presence of *"Allognathosuchus" mooki* in the lower Paleocene (Simpson, 1930; Sullivan et al., 1988), the alligator–caiman split occurred at or shortly after the Cretaceous–Tertiary boundary. Although the oldest caiman considered in this study is from the Eocene, putative caimans are known from the Paleocene of Argentina (Rusconi, 1937) and Texas (Brochu, 1996); furthermore, a headless skeleton from the Hell Creek Formaton may represent a Late Cretaceous caiman and thus may draw this divergence into the Cretaceous (Bryant, 1989).

Molecular distances have also implied a relatively recent divergence among living species of *Crocodylus* and between the two modern species of *Alligator* (Densmore, 1983). The oldest arguable members of the crown-group *Crocodylus* are from the Miocene (Tchernov, 1986; Pickford, 1994; Leakey et al., 1996), and the divergence between *Alligator mississippiensis* and *A. sinensis* was probably in the Miocene, based on the presence of *A. mississippiensis* in the Barstovian (middle Miocene; Malone, 1979).

The distribution of fossil taxa in Figure 7 is problematic if, as suggested by some protein distances (Densmore and Dessauer, 1984; Hass et al., 1992), *Gavialis* and *Tomistoma* diverged from each other in the Miocene or Pliocene. Gavialoidea can be recognized in the Late Cretaceous based on the presence of *Thoracosaurus* in the Campanian (Lavocat, 1955; Schwimmer, 1986), and tomistomines are known in the Eocene (*"Crocodilus" spenceri*, *Tomistoma cairense*). The fossils discussed by Hass et al. (1992) were used in this analysis, and
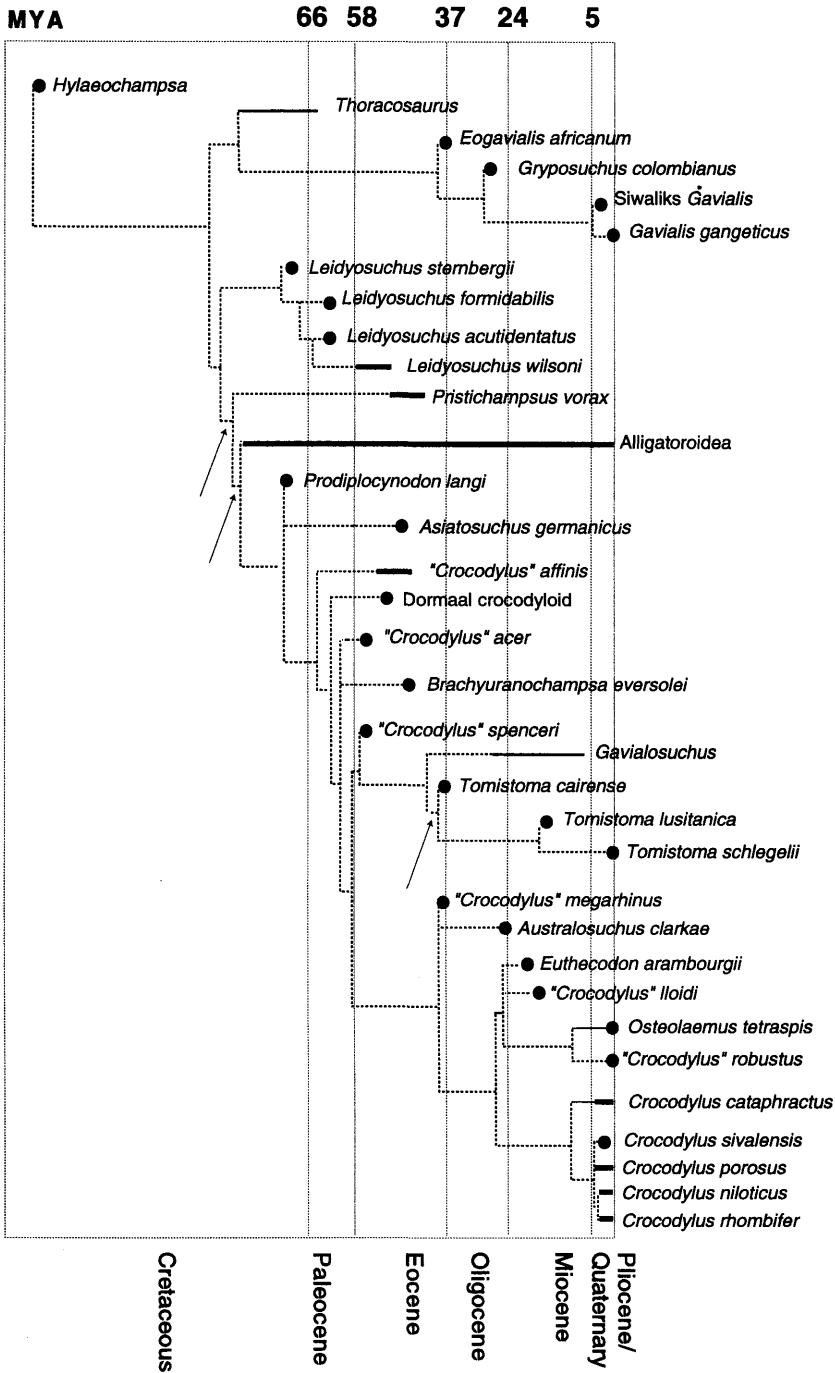
FIGURE 7. Stratigraphic distribution of fossil and living crocodylians. Alligatoroidea has been collapsed and is shown in Figure 8a. ● = occurrences within a single formation or limited time range; solid lines indicate continuous time ranges; MYA = million years ago. Arrows indicate nodes inconsistent with the phylogeny proposed in Figure 4. All polytomies include some topologies inconsistent with the proposed phylogeny.
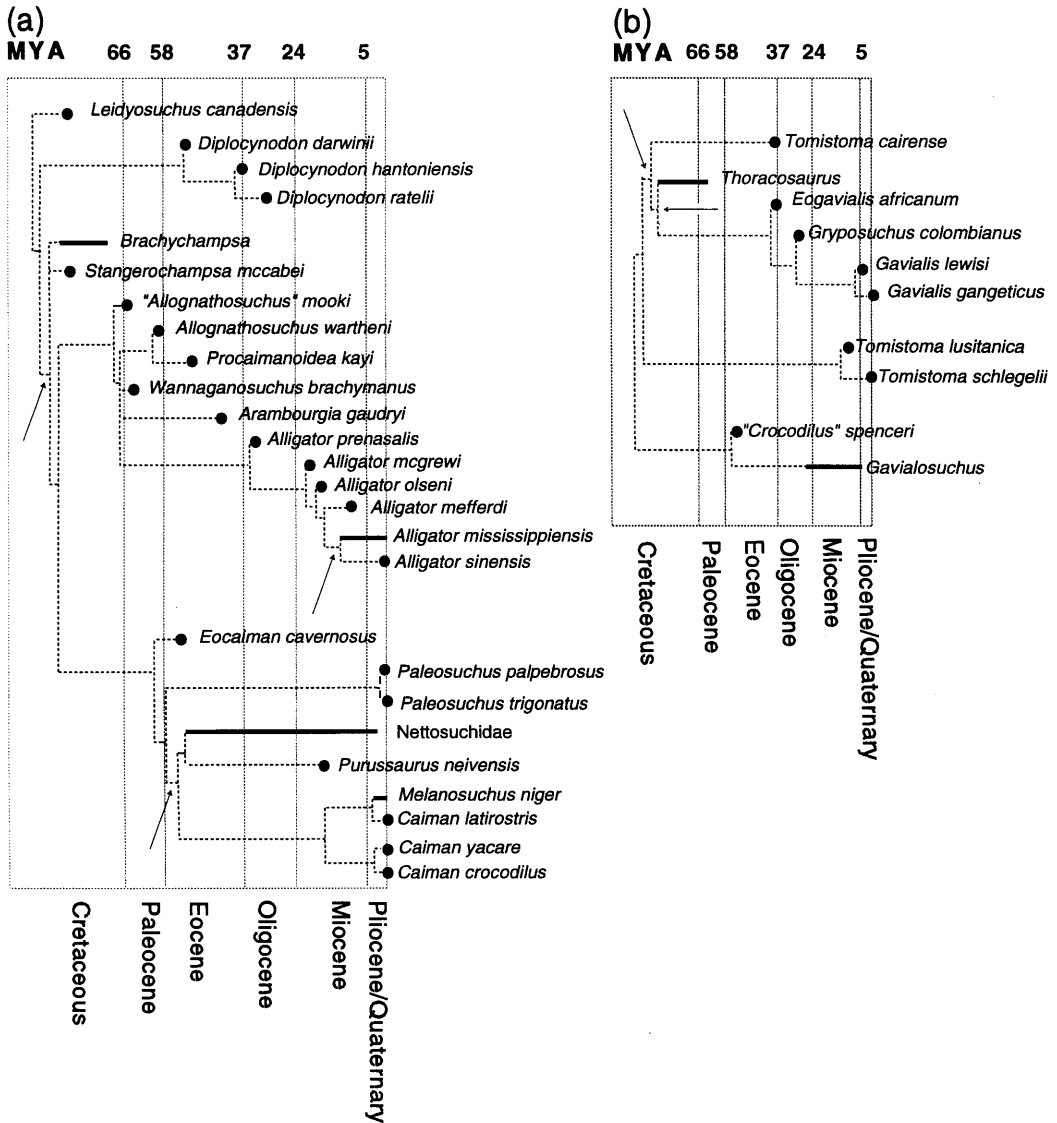
FIGURE 8. Stratigraphic distribution of alligatoroid, gavialoid, and tomistomine taxa. ● = occurrences within a single formation or limited time range; solid lines indicate continuous time ranges; MYA = million years ago. Arrows indicate nodes stratigraphically inconsistent with the proposed phylogeny in Figures 4 and 5. (a) Alligatoroid taxa. (b) Gavialoid and tomistomine taxa when *Gavialis* and *Tomistoma* are constrained as close relatives. Note that the earliest divergence between *Gavialis* and *Tomistoma* is still Late Cretaceous.

without any a priori constraint, Eocene and Oligocene taxa thought to be gavialoids in 1992 are still gavialoids. Indeed, when some "misidentified" taxa are properly assigned, e.g., *Thoracosaurus*, the disparity between phenetic distance and temporal range grows.

With fossils included, the range of *Im* indicates slightly more symmetry in the constrained tree over the preferred morphology tree, but the ranges overlap (0.224–0.300 for constrained tree, 0.246–0.298 for preferred morphology tree), and the tree shapes in the competing topologies can be

considered similar for purposes of this analysis. In both cases, the set of trees is less symmetrical than would be expected for the number of taxa analyzed (expected $Im = 0.1063$).

The constrained tree fits the relative stratigraphic distribution of taxa nearly as well as the unconstrained tree, and average SCI values are close (average SCI = 0.866 for constrained tree). However, the amount of missing time is much greater for the constrained as compared with the unconstrained tree. Average SMIG for the most-parsimonious set of trees is 734.26; in the case of the *Gavialis–Tomistoma* constraint, average SMIG = 984.90, a difference of nearly 25.5%.

The most-parsimonious arrangement allowing a close relationship between *Gavialis* and *Tomistoma* still indicates a Late Cretaceous divergence between these two taxa. *Thoracosaurus* is still most-parsimoniously seen as closer to *Gavialis* than to *Tomistoma*. The most-parsimonious arrangement permitting a post-Eocene divergence between *Gavialis* and *Tomistoma* increases tree length by 52 steps (9.9%) with morphology only and 36 steps (4.1%) with the combined matrix and is significantly less parsimonious in both cases ($P < 0.001$, $Ts = 277.5$, $n = 59$, morphology only; $P < 0.001$, $Ts = 1165.5$, $n = 86$, combined matrix). Either of these arrangements further implies long ghost lineages for noncrocodylid crocodyloids.

The pre-Campanian record for eusuchians generally is poor, and an approximately 25-MY gap exists between *Hylaeochampsa*, the oldest known eusuchian, and the next oldest eusuchian occurrences in the Cenomanian (Stromer, 1925, 1933). However, this gap exists during a time of marine highstand, and terrestrial deposits are not common for most of the middle Cretaceous. The stratigraphic record is much more dense for the Tertiary, when sea levels were lower and nonmarine deposits are more widespread (Raup, 1976; Haq et al., 1988). The gaps implied by the constraint tree encompass much of the Tertiary, when we would not expect long gaps for continental lineages.
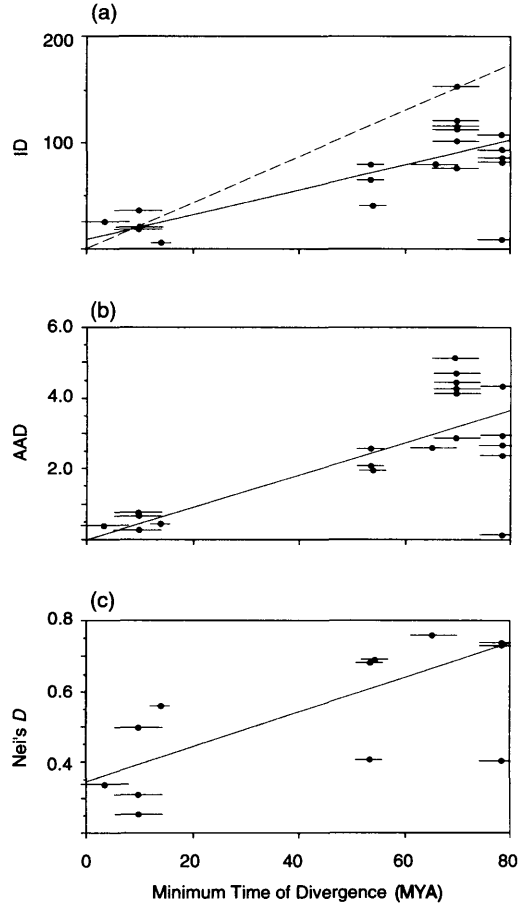

FIGURE 9. Comparison between minimum time of divergence (million years ago [MYA]) based on fossil occurrences and three different measures of protein distance. Points indicate pairwise comparisons between living lineages; see Table 2. (a) Immunological distance (ID), with the dashed line as the proposed rate curve, from Hass et al. (1992). (b) Adjusted antigenic distance (AAD) from Densmore (1983). (c) Nei's D from Densmore (1983).

Comparison of Molecular Distances with Fossil Divergence Time

The two distance measures derived from albumin (adjusted antigenic distance [AAD] and immunological distance [ID]; Figs. 9a, 9b; Table 2) show a general correspondence with minimum divergence time as predicted by fossils. Relatively recent divergences (*A. mississippiensis–A. sinensis*, *Crocodylus–Osteolaemus*, *Crocodylus cataphractus*–all other *Crocodylus*) correspond

TABLE 2. Protein distance data used in this analysis. ID from Hass et al., 1992; Nei's *D* and AAD from Densmore, 1983. Minimum time of divergence (TOD) calibrated as in Appendix 3.

Divergence	ID	Nei's *D*	AAD	TOD
Alligator–all caiman	79.00	0.762	2.54	65.8
A. mississippiensis–*A. sinensis*	5.00	0.560	0.43	14.0
Crocodylus–*Osteoleamus*	36.00	0.498	0.67	9.7
C. cataphractus–other *Crocodylus*	19.00	0.253	0.26	9.7
Crocodylus–*Tomistoma*	78.90	0.408	2.57	53.3
Osteolaemus–*Tomistoma*	65.00	0.682	2.07	53.3
Paleosuchus–(*Caiman* + *Melanosuchus*)	40.30	0.686	1.93	53.8
Osteolaemus–*Gavialis*	86.00	0.730	2.36	78.5
Crocodylus–*Gavialis*	81.00	0.737	2.58	78.5
Tomistoma–*Gavialis*	8.50	0.404	0.03	78.5
Melanosuchus–*Caiman latirostris*	21.00	0.337	0.39	3.4
(*M. niger* + *C. latirostris*)–*C. crocodilus*	23.38	0.311	0.72	9.7
Alligator–*Crocodylus*	114.00		4.12	69.5
Alligator–*Gavialis*	93.00		2.94	78.5
Alligator–*Tomistoma*	76.00		2.86	78.5
All caiman–*Crocodylus*	112.00		4.68	69.5
All caiman–*Gavialis*	107.00		4.33	78.5
All caiman–*Tomistoma*	100.67		4.41	69.5
Alligator–*Osteolaemus*	120.00		4.24	69.5
All caiman–*Osteolaemus*	153.00		5.13	69.5

to low AAD or ID; more ancient divergences typically correspond to higher AAD or ID. Both measures indicate an ancient divergence between *Alligator* and the caimans, between *Crocodylus* and *Tomistoma*, and between most nongavialoid crocodylians and *Gavialis*.

However, the low AAD and ID between *Gavialis* and *Tomistoma* are in stark contrast with a minimum divergence time in the Late Cretaceous. In both cases, AAD and ID grossly underestimate the divergence time between these two taxa. Because error margins cannot be calculated for these comparisons, it is unclear whether this point is a significant outlier in the statistical sense; it clearly falls far from other points with both measures.

Hass et al. (1992), using a similar plot for ID and a molecular clock estimated from salamander phylogeny, argued that the oldest fossils putatively considered gavialoids (Oligocene, in their case) represented misidentified taxa unrelated to *Gavialis* or *Tomistoma*. However, a parsimony reanalysis continues to support the gavialoid identity of these fossils, and an explanation other than misidentification should be sought. Conversely, both the distances and divergence time between these

two taxa could be accepted at face value, a rate curve could be estimated from the origin through the *Gavialis*–*Tomistoma* point, and then ghost lineages could be extrapolated for all other points until they intersected the rate curve. This process would require ghost lineages for some pairwise comparisons as old as 1 billion years, implying the existence of Crocodylia prior to the Cambrian Explosion.

Other interesting patterns arise from close inspection of Figure 9. In particular, both AAD and ID appear to overestimate divergences between nonalligatorids and alligatorids generally, especially between nonalligatorids and caimans. Thus, the distance between *Alligator* and any nonalligatorid should be very similar to the distance between the caimans and the same nonalligatorid because the last common ancestor shared between *Alligator* and, for example, *Crocodylus* was the same last common ancestor shared between caimans and *Crocodylus*. Instead, AAD and ID consistently indicate greater distances when caimans are involved.

Nei's *D* does not correspond as well with time as do the albumin distance measures, particularly for recent divergences (Fig. 9c). Nevertheless, Nei's *D* underesti-

mates the divergence between *Gavialis* and *Tomistoma*. Because pairwise comparisons between alligatorids and nonalligatorids could not be made, the overestimation of caiman divergence time seen with AAD and ID could not be tested.

Comparison of Sequence Data with Fossil Divergence Time

Simple relative rates tests for pairwise comparisons between extant crocodylian species (Table 3) indicate that the 12S ribosomal sequence data are generally internally consistent with the same rate of evolution, but some comparisons between some caimans, in particular *Melanosuchus niger*, *Caiman latirostris*, and *Paleosuchus palpebrosus*, and noncaiman crocodylians indicate significantly higher rates of evolution for some caimans. Comparisons with *Gavialis* do not reflect differential rates, with the exception of two of the caiman comparisons.

Relative rate tests have the advantage of being independent of topology and fossil divergence estimates (Mindell and Thacker, 1996), but fossil occurrences can be used to obtain rough divergence estimates and to test apparent absolute rates further. Figure 10 shows the relationship between minimum divergence time from fossils and the number of steps between any two crocodylian taxa for the 12S data (Gatesy et al., 1993; Table 3). Lines radiating from the origin correspond to hypothetical rates of evolution as indicated.

Two pairwise distances, those between *Gavialis* and *Tomistoma* and between *Gavialis* and *Crocodylus rhombifer*, are consistent with an evolutionary rate of 0.25 bpc/MY but lie outside the error margins for all other rates. The *Gavialis–Tomistoma* distance is also consistent with a rate of 0.125 bpc/MY, and all other points lie well outside the error margins for this rate. Most other points lie within the error margins for 0.5 bpc/MY and/or 0.75 bpc/MY.

Late Tertiary divergences within Alligatoridae indicate considerably faster rates of evolution. The distance between the two living species of *Alligator* is consistent with rates of 1.5–2.0 bpc/MY. Comparisons

among caimans suggest even faster rates, e.g., the distance between *Melanosuchus niger* and *Caiman latirostris* is consistent with rates of 3.0–7.0 bpc/MY.

There are two caveats with this type of analysis. First, the calculated error margins on molecular rates assume a Poisson distribution of substitutions, and recent studies indicate that this assumption is not always met (Gillespie, 1986; Sullivan et al., 1995). Second, the disparity between some comparisons might be an artifact of an incomplete fossil record (Springer, 1995). Projection of ghost lineages will draw any of these comparisons into slower apparent rates of evolution. For caimans, the pre-Miocene fossil record is very poor, and the anomalously high rates calculated from caiman divergences might reflect the nonpreservation of speciation events in the Eocene or Paleocene.

Nevertheless, the rate calculated from *Gavialis* and *Tomistoma* raises some interesting questions. If the maximum rate for this comparison (0.25 bpc/MY) is taken as a conservative rate estimate for all crocodylian lineages, then other divergences can be projected back in time until they are consistent with that rate. This procedure results in some ghost lineages, in particular those involving caimans, that extend into the lowermost Upper Jurassic (Oxfordian), roughly 40 MY before the first known eusuchian. Conversely, the *Gavialis–Tomistoma* divergence is consistent with a rate of 0.5 bpc/MY only if it occurred after the Eocene, which is inconsistent with the existence of fossils from both lineages prior to the Oligocene.

DISCUSSION

What Does Morphology Say about the Relationships of Gavialis?

A thorough review supports the signal reflected by earlier anatomical studies; morphology really does indicate that *Gavialis* is the sister taxon of all other extant crocodylians. The addition of fossils has no effect on the tree topology resulting from analysis of modern taxa. Thus, the hypothesis that morphological data are be-

TABLE 3. Pairwise 12S rDNA sequence distances for crocodylian taxa; data from Gatesy et al. (1993; see Table 1). Bold numbers indicate significant branch length difference; the difference between taxon branches is two standard deviations away from this value. A. Upper: raw distances (base pair changes/million years [bpc/MY]) between taxa; lower: minimum age of divergence (MY). B. Upper: corrected distances using an outgroup sequence (*Dromaius*); lower: expected binomial values for these distances, using the equation of Mindell and Honeycutt (1990).

A.

	1	2	3	4	5	6	7	8	9	10
1. *Alligator sinensis*	—	**33[a,b]**	**38[a,b]**	**26[c]**	**37[a]**	**35[a]**	**40[a,b]**	**34[a]**	**32[a]**	**37[a]**
2. *Melanosuchus niger*	65.8	—	**34[a,b]**	**40[a,b]**	**18[d]**	**35[a,b]**	**19[d]**	**44[a,b]**	**43[a]**	**45[a,b]**
3. *Paleosuchus trigonatus*	65.8	53.8	—	**40[a,b]**	**33[a,b]**	**12[e]**	**36[b]**	**49[a,b]**	**44[a]**	**45[a,b]**
4. *Alligator mississippiensis*	14.0	65.8	65.8	—	**43[a,b]**	**43[a,b]**	**47[a,b]**	**44[a]**	**40[a]**	**39[a]**
5. *Caiman latirostris*	65.8	3.4	53.8	65.8	—	**36[b]**	**11[e]**	**52[b]**	**46[a]**	**49[a,b]**
6. *Paleosuchus palpebrosus*	65.8	53.8	?0[e]	65.8	53.8	—	**37[b]**	**47[a,b]**	**41[a]**	**39[a]**
7. *Caiman crocodilus*	65.8	9.7	53.8	65.8	?0[e]	53.8	—	**49[a,b]**	**45[a]**	**50[a,b]**
8. *Crocodylus rhombifer*	69.5	69.5	69.5	69.5	69.5	69.5	69.5	—	**26[f]**	**28[a]**
9. *Gavialis gangeticus*	78.5	78.5	78.5	78.5	78.5	78.5	78.5	78.5	—	**14[f,g]**
10. *Tomistoma schlegelii*	69.5	69.5	69.5	69.5	69.5	69.5	69.5	53.3	78.5	—

B.

	1	2	3	4	5	6	7	8	9	10
1. *Alligator sinensis*	—	**12**	5	5	**10**	**11**	7	2	2	0
2. *Melanosuchus niger*	**0.248**	—	7	7	2	1	3	**14**	**10**	**12**
3. *Paleosuchus trigonatus*	1.780	1.134	—	0	5	6	2	7	3	5
4. *Alligator mississippiensis*	1.266	1.372	0.125	—	5	6	2	7	3	5
5. *Caiman latirostris*	**0.622**	0.167	0.091	0.091	—	1	3	**12**	8	**10**
6. *Paleosuchus palpebrosus*	**0.024**	0.132	**0.054**	1.729	2.377	—	4	**13**	9	**11**
7. *Caiman crocodilus*	1.371	0.161	0.125	2.635	0.161	1.967	—	9	5	7
8. *Crocodylus rhombifer*	0.128	**0.013**	0.069	1.522	**0.028**	**0.020**	0.050	—	4	2
9. *Gavialis gangeticus*	0.132	**0.814**	2.403	2.269	**0.059**	**0.047**	0.090	0.115	—	2
10. *Tomistoma schlegelii*	2.443	**0.533**	0.090	0.093	1.005	0.027	1.734	0.140	0.183	—

[a] Consistent with 0.5 bpc/MY.
[b] Consistent with 0.75 bpc/MY.
[c] Consistent with 1.0–2.0 bpc/MY.
[d] Consistent with 3.0–7.0 bpc/MY.
[e] No fossil record; no rate hypotheses tested.
[f] Consistent with 0.25 bpc/MY.
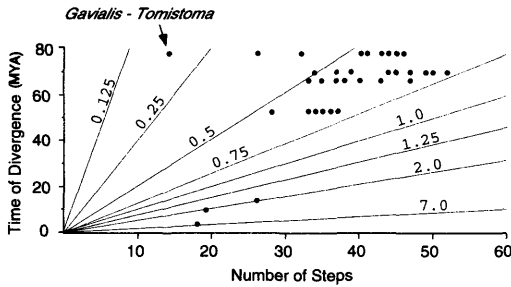[g] Consistent with 0.125 bpc/MY.

FIGURE 10.   Comparison between 12S ribosomal sequence difference and minimum time of divergence (million years ago [MYA]) between crocodylian taxa. Points indicate pairwise comparisons between living species; see Table 3A. Lines radiating from the origin are tested substitution rates, ranging from 0.125 to 7.0 base pair changes/million years.

ing misled by convergence when living taxa are analyzed separately cannot be rejected.

One possible criticism is that because these fossils were all incomplete to some degree they did not support relationships that would otherwise have been recovered with complete taxa. Although some analyses have shown decreases in accuracy with the addition of incomplete taxa (Wiens and Reeder, 1995), most paleontologists have found that the completeness of a fossil has little bearing on whether it will alter relationships (Gauthier et al., 1988; Simmons, 1993; Wilkinson and Benton, 1995), and very incomplete taxa are more likely to reduce resolution (Wheeler, 1992; Livezey, 1996). Furthermore, some of these fossils (e.g., "*Leidyosuchus*" *formidabilis*, *Diplocynodon hantoniensis*, "*Crocodylus*" *affinis*) were almost as morphologically complete as the modern taxa (Appendix 3), and many extant taxa were also incomplete because complete molecular data were not available.

What Does the Fossil Record Say about Divergence Timing within Crocodylia?

The presence of fossil gavialoids in the Cretaceous and fossil tomistomines in the Eocene falsifies the hypothesis that extant *Gavialis* and *Tomistoma* shared a common ancestor as recently as the Late Tertiary. This conclusion is independent of the re-

lationships between living *Gavialis* and *Tomistoma*; constraining the analysis to draw these genera close together still indicates a Cretaceous divergence, and even the combined analyses significantly reject a topology that would permit a post-Oligocene divergence.

This conflict is a more interesting than the topological issue. Significant topological disagreement among data sets centers on only one extant lineage, and given the consistency with which independent molecular data sets agree on the position of *Gavialis*, the topological conflict could be dismissed as an artifact of morphological convergence. However, the sequence of fossils extending Gavialoidea into the Campanian must be explained if *Gavialis* and *Tomistoma* diverged from each other within the past 22 MY.

Both topologies fit the known stratigraphic sequence of fossils approximately as well. However, making *Gavialis* and *Tomistoma* sister taxa increases the amount of missing time by over 250 MY, and a minimum 56 MY discrepancy separates molecular and fossil estimates for the divergence of these taxa. Measures of clade rank and missing time show no correlation, which is not unexpected because they measure very different things: fit between branching order and stratigraphic appearance and the amount of stratigraphic gap between occurrences, respectively (Hitchin and Benton, 1997). I do not accept the conclusion that long ghost lineages in the set of most-parsimonious trees should be cause to prefer a suboptimal tree (contra Wagner, 1995), but in this case the preferred morphology trees are considerably better at explaining the absolute temporal distribution of fossils.

Some interesting questions arise regarding interpretations of molecular distance data and assumptions of clocklike evolution within Crocodylia. Mitochondrial DNA substitution rates are not uniform throughout the group (Table 3; Fig. 9). Although the extremely high rates implied for caimans by minimum divergence times are probably being inflated by an incomplete fossil record, other measures indicate

higher rates in caimans than in other croc-
odylian lineages.

Kumazawa and Nishida (1995) found
that rates for tRNA evolution were higher
in crocodylians than in other amniote lin-
eages, and their data suggest a slightly
longer branch in *Caiman* than in *Alligator*
or *Crocodylus*. The mitochondrial genome
of *Crocodylus porosus* has a longer cyto-
chrome *b* sequence than do those of non-
crocodylian amniotes and, apparently, a
pseudogene derived from the tRNA[Phe]
gene (Quinn and Mindell, 1996). *Caiman
crocodilus* also has an additional noncoding
region inserted between the ND4 and
tRNA[Ser(AGY)] genes (Macey et al., 1997). To-
gether with the 12S rDNA rate heteroge-
neity proposed here, these observations
indicate a complex history for the
crocodylian mitochondrial genome.

A recent analysis by Wu et al. (1996)
supported a placement of *Hylaeochampsa*
deep within Alligatoridae, which would
draw the divergence between Alligatoridae
and Crocodylidae into the Lower Creta-
ceous and would support much lower
rates of evolution for alligatorid taxa. How-
ever, this comparison must be made cau-
tiously because Wu et al.'s analysis exclud-
ed many taxa, such as gavialoids and
tomistomines, that could overturn their
tree (Brochu, in press). No caimans were
included, so the presence of *Hylaeochampsa*
close to *Brachychampsa* and *Stangerochampsa*
provides no information about the diver-
gence between *Alligator* and *Caiman*. The
relationships for *Hylaeochampsa* supported
by Wu et al. are strongly rejected by the
morphological matrix used in the present
analysis (4.6% tree length increase; $P <
0.005$, $Ts = 45$, $n = 29$).

Is a Combined Approach the Answer?

The conclusions of the combined analy-
ses presented here differ from those of Poe
(1996) in two ways. First, Poe's combined
matrix significantly rejected a sister-group
relationship between *Gavialis* and all other
living crocodylians, whereas the analyses
presented here either do not significantly
reject it or prefer it (Fig. 2); in either case,
the competing hypotheses are not signifi-

cantly different. Second, the inclusion of
fossils shows that the conflict is no longer
restricted to a single species only; *Gavialis*
produced the only consistent conflict in
Poe's analyses (1996), but competing hy-
potheses must also consider such extinct
taxa as *Thoracosaurus*, *Eogavialis*, and *Gavi-
alosuchus*, especially if the fossil record is
to be reconciled with molecular distance
data.

The combined analyses presented here
reflect the strong disparity between differ-
ent morphological and molecular data sets
for the position of *Gavialis* more than they
uphold one over another. However congru-
ent the available data are for most parts of
the crocodylian tree, they strongly dis-
agree on the placement of *Gavialis* and its
extinct relatives. The total evidence tree in
Figures 4 and 5 is currently the best avail-
able hypothesis for crocodylian relation-
ships, but alternative topologies supported
by other data sets are not significantly less
parsimonious, and the inclusion of new
data sets or fossil taxa might very well
overturn these trees.

Nonsignificance of tree-length difference
between topologies leads to the suspicion
that combined analyses alone will not re-
solve this particular issue. There are two
conflicting signals represented in the com-
bined matrix, and whichever is stronger in
a particular analysis will dominate the re-
sulting combined signal. Poe (1996) found
the preferred molecular tree to be better
supported than the morphology tree, but
he used more than twice as many molec-
ular as morphological characters. A bol-
stered morphological data set led either to
a different rooting (for the Recent-only tree
with fossil outgroups) or a different topol-
ogy altogether (when fossils are included).
The change in root can be seen as a com-
promise result: the molecular data are
strongly enforcing a four-taxon network in
which *Gavialis* and *Tomistoma* are close to-
gether, but the morphological data are
rooting it on *Gavialis*. The complete change
in topology is reflecting a stronger mor-
phological signal with the addition of fos-
sils. One would expect the addition of a

large sequence data set to tip the balance in favor of the molecular tree again.

There is value to combining data sets; weakly supported relationships in different partitions might become more robust in the combined analysis, and as illustrated by Pennington (1996), different partitions will resolve different regions of the tree. But, with respect to *Gavialis*, a combined analysis will reflect either the stronger of the two signals or a compromise between them. Because we cannot know a priori which of these signals is the correct one, we can only state that the resulting tree indicates the best estimate from two conflicting signals, and it would be prudent to bear the unstable placement of *Gavialis* in mind when discussing crocodylian relationships.

Prospectus

Although some possible reasons (in particular, long-branch attraction) for morphology to reflect a misleading signal appear unlikely given the data presented here, the fossil record for crocodylians remains incomplete, and the addition of newly collected fossils could overturn these results. In particular, the eusuchian record between the Barremian and Campanian is virtually barren, and the effects of fossils from this time period could be significant. Some known crocodylian fossils may be well-preserved enough to allow extraction of nucleic acids sufficient for sequencing; if so, molecular data from extinct crocodylians would be an important contribution.

Several fossils greatly predate the predicted divergence of two taxa based on protein distance, which argues against a molecular clock for Crocodylia, and evolutionary rate heterogeneity should be considered by future investigators. However, certain fossil discoveries could recalibrate several lineages and resurrect the hypothesis of clocklike evolution for crocodylians. The discovery of a fossil in the Oligocene that draws *Gavialis* and *Tomistoma* together would clearly falsify the morphological hypothesis presented here.

Given a long time of lineage separation

and evolutionary rate heterogeneity, long-branch attraction in molecular data should be explored as a possible cause of the topological disparity. Positive recognition of long-branch attraction with real data is not possible, although circumstances under which it is suspected can be identified (Allard and Miyamoto, 1992; Halanych, 1996). In Figures 9a and 9b, the distance between *Gavialis* and *Tomistoma* is less than expected, but the distance between Alligatoridae and *Crocodylus* or *Osteolaemus* is greater than expected. With sequence data, comparisons between *Gavialis* and either *Tomistoma* or *Crocodylus* are consistent with slow rates of evolution, but comparisons of any of these taxa, particularly *Tomistoma* and *Crocodylus*, with any alligatorid suggest a faster substitution rate.

I echo the hope expressed by Hass et al. (1992) that the morphological characters relevant to crocodylian systematics, including those used here, will be closely scrutinized. However, the results of this study indicate that a closer examination of the molecular data is likewise warranted. We are faced with two equally compelling signals, and the issue remains unsettled. The reason for this tree of conflict amid a forest of congruence should be sought, and possibilities other than the unreliability of morphological data should be considered.

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APPENDIX 1
CHARACTER LIST

1. Ventral tubercle of proatlas at least one half (0) or less than one half (1) the width of the dorsal crest.
2. Proatlas boomerang shaped (0), strap shaped (1), or massive and block shaped (2).
3. Posterior half of axis neural spine wide (0) or narrow (1).
4. Axis neural arch lacks (0) or possesses (1) a lateral process ("diapophysis"). (Adapted from Norell, 1989, character 7.)
5. Atlas intercentrum wedge shaped in lateral view with insignificant parapophyseal processes (0) or plate shaped in lateral view with prominent parapophyseal processes at maturity (1). (Modified from Clark, 1994, character 89.)
6. Axial hypapophysis located toward the center of centrum (0) or toward the anterior end of centrum (1).
7. Hypapophyseal keels extend to 11th vertebra behind atlas (0), 12th vertebra behind atlas (1), or 10th vertebra behind atlas (2).
8. First postaxial cervical vertebra with prominent

hypapophysis (0) or lacks prominent hypapo-physis (1). (Adapted from Norell, 1989, character 12; Norell and Clark, 1990, character 11; Clark, 1994, character 91.)

9. Neural spine on first postaxial cervical vertebra wide with dorsal tip at least half the length of the centrum without the cotyle (0) or narrow with dorsal tip acute and less than half the length of the centrum without the cotyle (1).

10. Proatlas with prominent anterior process (0) or lacks anterior process (1).

11. Anterior half of axis neural spine oriented horizontally (0) or slopes anteriorly (1).

12. Axis neural spine crested (0) or not crested (1).

13. Anterior sacral capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0) or anterior margins of tuberculum and capitulum nearly in same plane and capitulum largely obscured dorsally (1).

14. Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1).

15. Atlantal ribs lack (0) or possess (1) large articular facets for each other at anterior ends.

16. Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end.

17. Proatlas has tall dorsal keel (0) or lacks tall dorsal keel and has a smooth dorsal side (1).

18. Presacral centra amphicoelous (0) or procoelous (1). (Adapted from several previous analyses, e.g., Benton and Clark, 1988; Norell and Clark, 1990, characters 8, 10; Clark, 1994, characters 92, 93.)

19. Axial hypapophysis with (0) or without (1) deep fork.

20. Axial rib tuberculum wide with broad dorsal tip (0) or narrow with acute dorsal tip (1).

21. Axial rib tuberculum contacts diapophysis late in ontogeny if at all (0) or early in ontogeny (1).

22. Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel with minimal dorsal flare at maturity (1). (Adapted from Benton and Clark, 1988.)

23. Deltoid crest of scapula very thin at maturity with sharp margin (0) or very wide at maturity with broad margin (1).

24. Scapulocoracoid synchondrosis closes very late in ontogeny (0) or relatively early in ontogeny (1).

25. Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa and tapering anteriorly (1).

26. Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1).

27. Olecranon process of ulna narrow and subangular (0) or wide and rounded (1).

28. Dorsal margin of iliac blade rounded with smooth border (0), rounded with modest dorsal indentation (1), rounded with strong dorsal indentation (wasp-waisted) (2), narrow with dorsal

indentation (3), or rounded with smooth border and posterior tip of blade very deep (4).

29. *M. teres major* and *M. dorsalis scapulae* insert separately on humerus and scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon and single insertion scar (1).

30. Interclavicle flat along length without dorsoventral flexure (0), with moderate dorsoventral flexure (1), or with severe dorsoventral flexure (2).

31. Anterior end of interclavicle flat (0) or rodlike (1).

32. Supraacetabular crest narrow (0) or broad (1).

33. Limb bones relatively robust and hind limb much longer than forelimb at maturity (0) or limb bones very long and slender and forelimb and hind limb more equal in length at maturity (1).

34. Iliac anterior process prominent (0) or virtually absent (1). (Adapted from Benton and Clark, 1988; Clark, 1994, character 84; although the transformation recorded here is different.)

35. Dorsal osteoderms not keeled (0) or keeled (1). (Adapted from Buscalioni et al., 1992, character 22.)

36. Dorsal midline osteoderms rectangular (0) or square or equant (1). (Adapted from Norell and Clark, 1990, character 16; Clark, 1994, character 95.)

37. Four (0), 6 (1), 8 (2), or 10 (3) contiguous dorsal osteoderms per row at maturity. (Adapted from Norell and Clark, 1990, character 12; Clark, 1994, character 97.)

38. Nuchal shield grades continuously into dorsal shield (0), differentiated from dorsal shield with four nuchal osteoderms (1), differentiated from dorsal shield with six nuchal osteoderms, four central and two lateral (2), or differentiated from dorsal shield with eight nuchal osteoderms in two parallel rows (3).

39. Ventral armor absent (0), present and osteoderms single (1), or present and osteoderms consist of paired ossifications that suture together (2). (Adapted from Buscalioni et al., 1992, character 21.)

40. Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth and without process (1). (Adapted from Norell and Clark, 1990, character 13; Clark, 1994, character 96.)

41. Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1). (Adapted from Norell, 1988, character 15; Norell, 1989, character 8.)

42. Mandibular ramus of cranial nerve V exits splenial anteriorly only (0), splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1), or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2). (Adapted from Norell, 1988, character 15; Norell, 1989, character 8.)

43. Splenial participates in mandibular symphysis and splenial symphysis adjacent to no more than five dentary alveoli (0), splenial excluded from

mandibular symphysis and anterior tip of splenial passes ventral to Meckelian groove (1), splenial excluded from mandibular symphysis and anterior tip of splenial passes dorsal to Meckelian groove (2), deep splenial symphysis, longer than five dentary alveoli, and splenial forms wide "V" within symphysis (3), or deep splenial symphysis, longer than five dentary alveoli, and splenial constricted within symphysis and forms narrow "V" (4). (Adapted from Clark, 1994, character 77.)

44. Articular–surangular suture simple (0), with anterior process dorsal to lingual foramen ("crocodyline process" of Aoki, 1992) (1), or with anterior process ventral to lingual foramen (2).

45. Lingual foramen for articular artery and alveolar nerve on surangular entirely (0), on surangular/angular suture (1), or on angular entirely (2).

46. Coronoid bounds posterior half of foramen intermandibularis medius (0), completely surrounds foramen intermandibularis medius at maturity (1), or obliterates foramen intermandibularis medius at maturity (2). (Adapted from Norell, 1988, character 12.)

47. Angular–surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1). (Adapted from Norell, 1988, character 40.)

48. Anterior processes of surangular unequal (0) or subequal to equal (1).

49. Foramen aerum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1). (Adapted from Norell, 1988, character 16.)

50. Retroarticular process projects posteriorly (0) or projects posterodorsally (1). (Adapted from Benton and Clark, 1988; Norell and Clark, 1990, character 7; Clark, 1994, character 71.)

51. Surangular extends to posterior end of retroarticular process (0) or is pinched off anterior to tip of retroarticular process (1). (Adapted from Norell, 1988, character 42.)

52. Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0) or fourth alveolus larger than third and alveoli are separated (1).

53. Anterior dentary teeth strongly procumbent (0) or project anterodorsally (1).

54. Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1).

55. Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1).

56. Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1).

57. Dorsal projection of hyoid cornu flat (0) or rodlike (1).

58. Dorsal projection of hyoid cornu narrow with parallel sides (0) or flared (1).

59. Process of splenial separates angular and coronoid (0) or there is no splenial process between angular and coronoid (1).

60. Sulcus between articular and surangular (0) or articular flush against surangular (1).

61. Surangular with spur bordering the dentary toothrow lingually for at least one alveolus length (0) or lacking such spur (1).

62. External mandibular fenestra absent (0) or present (1). (Clark, 1994, character 75.)

63. Dorsal anterior projection of coronoid longer than ventral (0) or ventral projection longer than dorsal (1).

64. External mandibular fenestra small and foramen intermandibularis caudalis not visible laterally (0) or external mandibular fenestra large and foramen intermandibularis caudalis visible laterally (1). (Adapted from Norell, 1988, character 14.)

65. Surangular–dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) or at posterodorsal corner (1).

66. Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis and anterior tip acute (0) or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis and anterior tip very blunt (1).

67. Surangular–angular suture lingually meets articular at ventral tip (0) or dorsal to ventral tip (1).

68. Dentary gently curved (0), deeply curved (1), or linear (2) between 4th and 10th alveoli.

69. Spina quadratojugalis prominent at maturity (0) or greatly reduced or absent at maturity (1). (Adapted from Norell, 1989, character 1.)

70. Postorbital bar massive (0) or slender (1). (Norell, 1989, character 3.)

71. Anterior border of the internal choana is comprised of the palatines (0) or choana entirely surrounded by pterygoids (1). (Benton and Clark, 1988; Norell and Clark, 1990, character 1; Clark, 1994, character 43.)

72. Choana projects posteroventrally (0) or anteroventrally (1) at maturity.

73. Pterygoid surface lateral and anterior to internal choanal flush with choanal margin (0) or pushed inward to form "neck" (1).

74. Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1). (Adapted from Norell, 1989, character 5).

75. Quadratojugal forms posterior angle of infratemporal fenestra (0), jugal forms posterior angle of infratemporal fenestra (1), or quadratojugal–jugal suture lies at posterior angle of infratemporal fenestra (2). (Adapted from Norell, 1989, character 10.)

76. Postorbital contacts neither quadrate nor quadratojugal medially (0), contacts quadratojugal but not quadrate medially (1), contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2), or contacts quadratojugal with significant descending process (3).

77. Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in pit between premaxilla and maxilla

and there is no notch early in ontogeny (1). (Norell, 1988, character 29.)

78. All dentary teeth occlude lingual to maxillary teeth (0), occlusion pit between 7th and 8th maxillary teeth and all other dentary teeth occlude lingally (1), or dentary teeth occlude in line with maxillary toothrow (2). (Adapted from Norell, 1988, character 5; Willis, 1993, character 1.)

79. Naris projects anterodorsally (0) or dorsally (1).

80. Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra and quadrate participates in fenestra (1). (Adapted from Buscalioni et al., 1992, character 6.)

81. Frontoparietal suture deeply within supratemporal fenestra and frontal prevents broad contact between postorbital and parietal (0), suture makes modest entry into supratemporal fenestra at maturity and postorbital and parietal are in broad contact (1), or suture on skull table entirely (2).

82. Supraoccipital exposure on dorsal skull table small (0), absent (1), large (2), or large such that parietal is excluded from posterior edge of table (3). (Norell, 1988, character 11.)

83. Quadratojugal sends long anterior process along lower temporal bar (0) or sends modest process or none at all along lower temporal bar (1).

84. Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1).

85. Palatine–pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra.

86. Frontoparietal suture concavoconvex (0) or linear (1).

87. Supratemporal fenestra with fossa and dermal bones of skull roof do not overhang rim at maturity (0), dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (1), or supratemporal fenestra closes during ontogeny (2). (Adapted from Norell, 1988, character 9.)

88. Suborbital fenestra without (0) or with (1) posterior notch.

89. Largest maxillary alveolus is no. 3 (0), no. 5 (1), or no. 4 (2), no. 4 and no. 5 are same size (3), or maxillary teeth homodont (4). (Adapted from Norell, 1988, character 1.)

90. Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing a shelf (1). (Adapted from Norell, 1988, character 2.)

91. Ectopterygoid abuts maxillary toothrow (0) or maxilla broadly separates ectopterygoid from maxillary toothrow (1). (Norell, 1988, character 19.)

92. Shallow fossa at anteromedial corner of supratemporal fenestra (0) or no such fossa and anteromedial corner of supratemporal fenestra smooth (1).

93. Lacrymal makes broad contact with nasal and there is no posterior process of maxilla (0), maxilla sends posterior process within lacrymal (1), or maxilla sends posterior process between lacrymal and prefrontal (2).

94. Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1).

95. External naris bisected by nasals (0), nasals contact external naris but do not bisect it (1), nasals excluded, at least externally, from naris and nasals and premaxillae still in contact (2), or nasals and premaxillae not in contact (3). (Adapted from Norell, 1988, character 3; Clark, 1994, characters 13, 14.)

96. Palpebral forms from single ossification (0) or from multiple ossifications (1). (Adapted from Norell, 1988, character 8; Clark, 1994, character 65.)

97. Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny. (Norell, 1988, character 17.)

98. Posterior pterygoid processes tall and prominent (0), small and project posteroventrally (1), or small and project posteriorly (2).

99. Palatine smooth dorsally anterior to prefrontal pillar (0) or with prominent thin ridge on palatine running anterior to prefrontal pillar (1).

100. Prefrontals separated by frontals and nasals (0) or prefrontals meet medially (1). (Norell, 1988, character 27.)

101. Dorsal surface of rostrum curves smoothly (0) or bears medial dorsal boss (1).

102. Posterior margin of otic aperture smooth (0) or invaginate (1).

103. Margin of orbit flush with skull surface (0), dorsal edge of orbit upturned (1), or orbital margin telescoped (2).

104. Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1). (Norell, 1988, character 51.)

105. Lateral edge of suborbital fenestra straight (0) or bowed medially (1).

106. Lacrymal much longer than broad (0) or wide and short and nearly as broad as long (1).

107. Posterior rim of internal choana not deeply notched (0) or deeply notched (1).

108. Anterior face of palate process rounded or pointed anteriorly (0) or invaginate (1).

109. Anterior ectopterygoid process tapers to a point (0) or is forked (1).

110. Palatine process extends (0) or does not extend (1) significantly beyond anterior end of suborbital fenestra. (Adapted from Willis, 1993, character 2.)

111. Maxillary foramen for palatine ramus of CN-V small or not present (0) or very large (1).

112. Quadrate with small ventrally reflected medial hemicondyle (0), with small medial hemicondyle and dorsal notch for foramen aerum (1), with prominent dorsal projection between hemicondyles (2), or with expanded medial hemicondyle (3).

113. Basisphenoid thin (0) or anteroposteriorly wide (1) ventral to basioccipital.

114. Spina quadratojugalis low and near posterior angle of infratemporal fenestra (0) or high and be-

tween posterior and superior angles of infratemporal fenestra (1).

115. Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process or palatine (1).

116. Ectopterygoid–pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1).

117. Lacrymal longer than prefrontal (0), prefrontal longer than lacrymal (1), or lacrymal and prefrontal both elongate and nearly the same length (2). (Modified from Norell, 1988, character 7.)

118. Palatine process generally broad anteriorly (0) or in form of thin wedge (1).

119. Basisphenoid not broadly exposed ventral to basioccipital at maturity and pterygoid short ventral to median eustachian opening (0) or basisphenoid exposed as broad sheet ventral to basioccipital at maturity and pterygoid tall ventral to median eustachian opening (1).

120. Medial jugal foramen small (0) or very large (1).

121. Quadrate foramen aerum on mediodorsal angle (0) or on dorsal surface (1) of quadrate.

122. Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth with no sulcus (1).

123. Skull table surface slopes ventrally from sagittal axis (0) or is planar (1) at maturity.

124. Incisive foramen small and less than half the greatest width of premaxillae (0), large and more than half the greatest width of premaxillae (1), or large and intersects premaxillary–maxillary suture (2).

125. Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary–maxillary suture (1). (Adapted from Norell, 1988, character 22.)

126. Vomer entirely obscured by maxillae and palatines (0) or exposed on palate between palatines (1).

127. Significant ventral quadrate process on lateral braincase wall (0) or quadrate–pterygoid suture linear from basisphenoid exposure to foramen ovale (1).

128. Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid lateral exposure at maturity.

129. Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall anterior to foramen ovale. (Adapted from Norell, 1989, character 5.)

130. Capitate process of laterosphenoid oriented laterally (0) or anteroposteriorly (1) toward midline.

131. Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0), parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1), or parietal and squamosal meet along posterior wall of supratemporal fenestra (2).

132. Squamosal–quadrate suture extends dorsally along posterior margin of external auditory me-

atus (0) or extends only to posteroventral corner of external auditory meatus (1).

133. Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1).

134. Two prominent projections (0) or single projection that is generally not prominent (1) on postorbital bar. (Adapted from Norell, 1989, character 2.)

135. Maxillary toothrow curves medially or linear (0) or curves laterally broadly (1) posterior to first six maxillary alveoli. (Adapted from Clark, 1994, character 79.)

136. Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1).

137. Dorsal half of prefrontal pillar narrow (0) or expanded anteroposteriorly in dorsal half (1). (Adapted from Norell, 1988, character 41.)

138. Medial process of prefrontal pillar wide (0) or constricted (1) at base.

139. Ventral margin of orbit gently circular (0) or with prominent notch (1).

140. Mature skull table with broad curvature and short squamosal prongs (0) or with nearly horizontal sides and significant squamosal prongs (1).

141. Exoccipital with very prominent boss on paroccipital process and process lateral to cranioquadrate opening short (0) or exoccipital with small or no boss on paroccipital process and process lateral to cranioquadrate opening long (1).

142. Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1).

143. Canthi rostrales absent or very modest (0) or very prominent (1) at maturity. (Norell, 1988, character 34.)

144. Preorbital ridges absent or very modest (0) or very prominent (1) at maturity.

145. Dorsal premaxillary processes short and not extending beyond third maxillary alveolus (0) or long and extending beyond third maxillary alveolus (1).

146. Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1). (Adapted from Benton and Clark, 1988; Norell and Clark, 1990, character 3.)

147. Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal. (Adapted from Norell, 1988, character 46.)

148. Surface of maxilla within narial canal imperforate (0) or with multiple cecal recesses (1). (See Witmer, 1995.)

149. Ectopterygoid extends (0) or does not extend (1) to posterior tip of lateral pterygoid flange at maturity. (Adapted from Norell, 1988, character 32.)

150. Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of exoccipital and quadrate.

151. Otoccipitals terminate dorsal to basioccipital tubera (0), send robust process ventrally and participate in basioccipital tubera (1), or send slender process ventrally to basioccipital tubera (2).

(Adapted from Norell, 1988, character 20; Clark, 1994, characters 57 and 60.)

152. Internal choana not septate (0), with septum that remains recessed within choana (1), or with septum that projects out of choana (2).

153. Incisive foramen completely situated far from premaxillary toothrow at the level of the second or third alveolus (0), abuts premaxillary toothrow (1), or projects between first premaxillary teeth (2).

154. Parietal with sinus communicating with pneumatic system (0) or solid and without sinus (1).

155. Ventral scales have (0) or lack (1) follicle gland pores. (Poe, 1996.)

156. Ventral collar scales not enlarged relative to other ventral scales (0), in a single enlarged row (1), or in two parallel enlarged rows (2). (Poe, 1996.)

157. Median pelvic keel scales form two parallel rows along most of tail length (0), form single row along tail (1), or merge with lateral keel scales to form Y-shaped keel (2). (Poe, 1996.)

158. Lingual osmoregulatory pores small (0) or large (1). (Taplin and Grigg, 1989.)

159. Tongue with (0) or without (1) keratinized surface. (Taplin and Grigg, 1989.)

160. *M. caudofemoralis* with single head (0) or with double head (*longus* and *brevis*) (1). (Frey et al., 1989.)

161. Naris circular or keyhole shaped (0) or wider than long (1).

162. Surangular–articular suture oriented anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa.

163. Postorbital–squamosal suture oriented ventrally (0) or passes medially (1) ventral to skull table.

164. Anterior foramen for palatine ramus of cranial nerve VII ventrolateral (0) or ventral (1) to basisphenoid rostrum.

APPENDIX 2. Data matrix used in the analysis of crocodylians and outgroups. ? = missing data; N = unscorable conditions.

Taxon	Characters					
	0000000000 0000000001 1234567890	0000000000 1111111112 1234567890	0000000000 2222222223 1234567890	0000000000 3333333334 1234567890	0000000000 4444444445 1234567890	0000000000 5555555556 1234567890
Dromaius novaehollandiae	010100N101	100NNN1N1N	N10100N00N	N010NNNN0N	0N111N0000	1NNNNN01N1
Glen Rose Form	??????????	??0?????1??	?00000?00?	?000000??0	000???N0??	?10???????
Bernissartia fagesii	??11?1210?	010????00?	?0?0?0000?	?000100010	0000??N?00	100??????1
Hylaeochampsa vectiana	??????????	??????????	??????????	??????????	??????????	??????????
Leidyosuchus formidabilis	0000010100	1100??01?0	0000000010	0010000?20	0000000?01	0010?00100
Leidyosuchus sternbergii	??0001?10?	110000?100	0000000010	001000???0	0000?0001	001??00?0
Leidyosuchus acutidentatus	??????????	??????????	?????70???	??????????	??????????	??????????
Leidyosuchus wilsoni	???????10?	??0?????1??	?00000001?	?10000?20	??10200001	0010?0???0
Leidyosuchus canadensis	??????????	????????1??	?????1?01?	??01111??11	0?000?01?1	10???????
Thoracosaurus macrorhynchus	??11?1?1??	0??????11?	?????0??0?	???000???0	??300??001	11??????0
Eogavialis africanus	?????1????	??0?????11	??????????	??0?????0	?030??10?1	111??????1
Gryposuchus colombianus	??1?0?????	00??????1??	??000?????	??????????0	?030000001	111100???0
Siwaliks *Gavialis*	??????????	??0????????	??????????	??????????	??30???0?1	??????????
Gavialis gangeticus	0211010110	0000000110	0000001001	0000?00000	0030000001	1110000100
Pristichampsus vorax	??000101??	01?????10?	?000000111?	?000100??1	00001?0??1	?11???????
Diplocynodon darwini	100000?000	0101000101	?000?1141?	?001001121	0010100111	101??000?1
Diplocynodon ratelii	??0?0????	??0?????10?	??00?11410	0001100?221	10101?0111	101??????1
Diplocynodon hantoniensis	1000?01000	010???0101	?000?11411	?001101?221	1010100111	101??????1
Alligator mississippiensis	1000110001	0101001101	1110111110	0001112101	1120100111	1111000011
Alligator sinensis	1000111001	1101001101	1110111110	0001112111	1120100111	111?00??11
Alligator mefferdi	??????????	??????????	?????????1	???11?1???	0120100111	1111000001
Alligator olseni	?????1????	????????101	?10011111?	?00?11????	0100?0111	111??????1
Alligator mcgrewi	100011?000	0100000101	100011??11	0?01111???	0100?0111	111100???1
Alligator prenasalis	????1?????	??0?????101	100011??1?	?001112111	0100?0?111	1101??00?1
Allognathosuchus mooki	??????????	??0?????101	?0???11?1?	?01111111	0100?0?1?1	111???????
Allognathosuchus wartheni	????1?????	??0?????1??	?000?1101?	?001?11??1	01000?0111	111100???1
Wannaganosuchus brachymanus	??001?????	1?0?????10?	?000?11010	00011?1??1	0?000?0?11	?11???????
Procaimanoidea kayi	????1?????	??01???101	??00?1101?	??01111111	?1?00?0111	1??100????
Arambourgia gaudryi	??????????	??????????	??????????	??????????	??0???0111	111???????
Stangerochampsa mccabei	??00?1?00?	010???011?	?000?11010	000101??11	0100?001??	111???????
Brachychampsa montana	10001??001	11?100017?1	0?00011010	000?103111	10100?0111	111??700?1
Eocaiman cavernensis	??????????	??????????	??????????	??????????	??2???11??	?1?????????
Purussaurus neivensis	100011?0?1	00?0??1111	1???01??1?	??0?11??1	?1?0011111	11?010???1
Nettosuchidae	10?01?700?	00?????1?1	1?0?01?31?	?00111???1	1120000111	011??????0
Caiman yacare	1000110001	1001011101	1101111110	0001111221	1122011111	1110100111
Caiman crocodilus	1000110001	1001011101	1101111110	0001111221	1122011111	1110100111
Caiman latirostris	1000110001	1000011101	110?111110	0001111221	1122011111	111010??1?
Melanosuchus niger	1000110001	1?01011101	1101111110	0001111221	1122011111	111010??11
Paleosuchus trigonatus	1000111000	0101111101	1001111312	1001111321	1220021111	1111110111
Paleosuchus palpebrosus	1000111010	0101111101	1001111312	1001111321	1220021111	11111101??
Crocodylus cataphractus	101001000?	001100?101	0100111212	0001111101	1011101001	011100100?
Crocodylus rhombifer	0010010011	1010001101	0100111112	0001111201	1011101001	0111001001
Crocodylus porosus	??10011011	001???1101	0100011212	0001111201	1011101001	011100??01
Crocodylus niloticus	1010010011	1010001101	0100111212	0001111201	1011101001	0111001001
Crocodylus palaeindicus	??????????	??1?????1??	??????????	??1??????	1011?01001	?111?0?001
Osteolaemus tetraspis	??10011001	00100?1101	0100111112	0101111111	1011101001	0111001001
Crocodylus robustus	??????????	??1?????10?	?????111?	?101????1	1011100011	011100??01
Crocodylus lloidi	??????????	??????????	??????????	??????????	??1??????	??????????
Crocodylus megarhinus	?????????0?	????????1??	??????????	??????????	101???0001	011??????1
Australosuchus clarkae	?????1?0??	????????1??	?????1??1?	??0?10??71	??111?00??	?11??????1
Euthecodon arambourgii	??????????	??????????	??????????	??????????	??0???????	??????????
Tomistoma schlegelii	0210010011	0010001101	0000111111	0001101301	1040001001	0110000000
Tomistoma lusitanica	??????????	??????1??	??????????	????10???1	??4??700001	01???????
Tomistoma cairense	??????????	??????????	??????????	??????????	??402????1	01??????0
Crocodylus spenceri	??????????	????????1??	??????????	??????????	??411?0?01	??1??????1
Gavialosuchus americanus	021001?000	0010000010?	?01011?11?	??01?0???1	??412????1	0111000???
Brachyuranochampsa eversolei	??????????	??????????	??????????	??????????	??????????	??????????
Dormaal crocodyloid	??????700?	???700?10?	?00?71111?	?00110??71	1010070001	011??????1
Crocodylus acer	??????????	??????????	??????????	??????????	??????????	??????????
Crocodylus affinis	0000010001	1011001101	0000011110	000110??71	1010000001	0111000001
Asiatosuchus germanicus	0010017011	00????1101	?000?11?1?	??01?????1	000??70001	011??00??
Prodiplocynodon langi	??????????	??????????	??????????	??????????	?? ????????	??????????

Characters

Taxon						
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	6666666667	7777777778	8888888889	9999999990	0000000001	1111111112
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Dromaius novaehollandiae	N1N0000N1N	N000NNNN01	N00N1120N0	NN000NNNNN	000N0001N0	001NNNN00N
Glen Rose Form	10?NN0?0?0	000??1000?	00?0100000	0020?0000	0010010000	0?0?000010
Bernissartia fagesii	10?NN0?000	0??0?0000	0??0?10030	1??0??00?0	?0001?0?00	?00??0?0??
Hylaeochampsa vectiana	?????????0	100??1?0?0	00?0100?0	0110???0?0	0020010000	?00??0101?
Leidyosuchus formidabilis	1100000001	100?0?0200	0000110030	0100200?0	0000000000	0000?02110
Leidyosuchus sternbergii	0100000001	1000010100	0000100130	01012?0000	0000000000	0000?00011
Leidyosuchus acutidentatus	???0000001	????0?020?	1000?10?3?	01002?00?0	000000??0?	?0????2???
Leidyosuchus wilsoni	11?0000001	1000010200	100?110030	01002?00?0	0000000?00	?00000211?
Leidyosuchus canadensis	?1?0000001	100?010000	0000100130	11012?0000	0100100000	0101000010
Thoracosaurus macrorhynchus	?100000200	100?010210	0001110040	01002??0?0	0010000000	0000?1010?
Eogavialis africanus	?1?0000200	1000010210	1101100040	0100?20000	0020000000	0010000100
Gryposuchus colombianus	0100000200	1001010210	1001110041	01102?02?0	0020000000	?010000100
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Gavialis gangeticus	0100000200	1000010210	1001110040	0110300200	0020000000	0010000100
Pristichampsus vorax	?1?00000?1	100?010000	2000100030	01001?00?0	0010000000	020?000010
Diplocynodon darwini	?1?0000011	1?0?011000	0000110131	?1002?00?0	0100000000	?101?00010
Diplocynodon ratelii	1100000011	1000011110	0000100131	11002?00?0	0000000000	0101?00011
Diplocynodon hantoniensis	1100000011	1000011110	0000110031	11002?00?0	0100000000	0101?00011
Alligator mississippiensis	1101000011	1101021010	2100010121	1110000010	0110010000	0101101010
Alligator sinensis	1101000011	1101021010	2100000121	1110000010	0110110000	0101101010
Alligator mefferdi	1101000011	1101021010	2100000?21	11100?00?0	0110010000	?101?01010
Alligator olseni	11?1000011	111?021010	2100000121	11110?00?0	0110010?00	?101?010??
Alligator mcgrewi	1100000111	1101021000	2100000121	1110000000	0100110000	0101?01010
Alligator prenasalis	1100000111	1101021000	2000000121	11100?0000	0100110000	0101?01010
Allognathosuchus mooki	?1000??1?1	110?02100?	20000?0?21	11101?00?0	0100?10?00	?1???00??0
Allognathosuchus wartheni	1100100111	1101021000	2000?00021	11101?00?0	0100010000	0101??1010
Wannaganosuchus brachymanus	?10?00?1?1	1??????101?	20?0?00?2?	11101?00?0	010?110000	?10???101?
Procaimanoidea kayi	?1001001?1	110?0210?0	21000000?1	1110?00?0	0100010000	?10??01010
Arambourgia gaudryi	?1?000?111	11??021000	20?0?10?2?	1?1?1?00?0	0100?10?00	?101??101?
Stangerochampsa mccabei	11?0110011	1101021010	1000000121	11202?00?0	0?000100?0	0101?0001?
Brachychampsa montana	11?00?0011	1101021010	1200000111	11201?0010	0100010100	0101000010
Eocaiman cavernensis	?1?0??0071	???????0??	?30?0?0???	1??0???0??	???1???0	?????0?0??
Purussaurus neivensis	11?1011011	1101021011	2?00001121	0101?0001	011?001?00	01?10110?0
Nettosuchidae	11?00?1211	110?0?1010	230?011141	11002?0000	0?1?0111?0	0101??1010
Caiman yacare	0100011011	1101021111	2300001121	1110100001	0111111000	0101010010
Caiman crocodilus	0100011011	1101021111	2300001121	1110100000	0111111000	0101010010
Caiman latirostris	0100011011	1101021111	2300011121	1110100000	0111111000	0101010010
Melanosuchus niger	1100011011	1101021011	2300011121	1110100000	0111111000	0101010010
Paleosuchus trigonatus	1100011011	1101021011	2200111121	1101111010	011?011100	0101000010
Paleosuchus palpebrosus	?100011011	1101021011	2200111121	1101111010	011?011100	0101010010
Crocodylus cataphractus	0100000001	1001100211	2010100110	0100200100	0110000010	0300000101
Crocodylus rhombifer	1100000001	1001100211	2010100110	0110100100	1110000010	0300000001
Crocodylus porosus	1100000001	1001100211	2010100110	0100100100	0110000000	0300000001
Crocodylus niloticus	1110000001	1001100211	2010100110	0110100100	0110000010	0300000001
Crocodylus palaeindicus	1100000001	1001100211	2110000010	01001?0100	011000?010	0300?00001
Osteolaemus tetraspis	1100000001	1011100210	2010111110	0101011100	0110100000	0300000011
Crocodylus robustus	1100000001	1011100211	2110101110	01011?0100	0110000001	0300000001
Crocodylus lloidi	?????????01	10?1100211	2010?00?1?	011?1?01?0	011000?000	0300??00?1
Crocodylus megarhinus	11?0000001	10002?0211	2?101?0130	01201?01?0	0110000000	?300000001
Australosuchus clarkae	11?00??0?1	????100211	2010?000?1?	0100?1?0?0	0?1000?000	03?0??00?1
Euthecodon arambourgii	?????????1	????101211	2010?10?10	01?02?0?0?0	0110001000	0301??00?1
Tomistoma schlegelii	0100000201	1000010210	2010110010	0110200100	0110000001	0300000001
Tomistoma lusitanica	?1?0000201	1000010210	20?1110010	01002?01?0	0110000000	0300000101
Tomistoma cairense	?1?00002?0	100?0102??	20?0100040	?1002?????0	1?10000000	?30?00?10?
Crocodylus spenceri	?1?0000??1	100?0?0210	20?0100010	01101?0??0	0?1000?000	?30??001??
Gavialosuchus americanus	?10000002?1	1000010212	21?1100?10	0?102?01?0	0110000000	030?0000?1
Brachyuranochampsa eversolei	?????????1	100?0?0210	2000110110	01001??000	0100000?0?	030??00?0?
Dormaal crocodyloid	11?0000001	1000010110	2000100?10	?1?01?0000	0100000001	?3010?0001
Crocodylus acer	?????????01	100?0?0211	2000?00?10	01001?00?0	0?00000000	030000000?
Crocodylus affinis	1100000001	100?01011?	2000100110	01001?0000	0100000001	130?000000
Asiatosuchus germanicus	11?00000?1	100?010000	1000?10?10	010?1?00?0	0100000001	130??000??
Prodiplocynodon langi	?????????1	100?0?001?	10001?013?	01?01?000?	01000?0001	130?00?01?

	Characters				
	1111111111	1111111111	1111111111	1111111111	1111
Taxon	2222222223	3333333334	4444444445	5555555556	6666
	1234567890	1234567890	1234567890	1234567890	1234
Dromaius novaehollandiae	100N00N101	N0NNNNNN00	0000NNN0N1	01N1NNNN10	000N
Glen Rose Form	?0?000???1	0?0?00?000	0000010?00	0010??????	0?0?
Bernissartia fagesii	0??0??????	????00??00	0000000?0?	0?1???????	00??
Hylaeochampsa vectiana	??0??000?1	0000?0?000	0?000000?0	00????????	??0?
Leidyosuchus formidabilis	0?100000??	000?101001	0000010?10	001???????	000?
Leidyosuchus sternbergii	0010000001	00011?1?01	1000010010	0010??????	0000
Leidyosuchus acutidentatus	??10???0??	????1???01	1????1??0	001???????	000?
Leidyosuchus wilsoni	?01????0??	00001?1?01	1????1??10	001???????	000?
Leidyosuchus canadensis	1010000?1	0??10?1?01	1000010?10	001???????	000?
Thoracosaurus macrorhynchus	000000?0?0	?0000?0?01	1000100?10	100???????	000?
Eogavialis africanus	000?00?0?0	0000N00011	1000100?10	100???????	000?
Gryposuchus colombianus	0000000000	0000N???11	1000100?10	100???????	000?
Siwaliks *Gavialis*	000??000?	0000N???11	1????00?10	100???????	000?
Gavialis gangeticus	0000000000	0000N00011	1000100010	1000000000	0000
Pristichampsus vorax	0?1000?1?1	01010???01	1000010?10	001???????	010?
Diplocynodon darwini	1?1000?0??	11?10???01	1000010?10	001???????	000?
Diplocynodon ratelii	1010001001	10010???01	1000010010	0010??????	0001
Diplocynodon hantoniensis	1?1000?0?1	10010?1?01	1????1??01	0010??????	000?
Alligator mississippiensis	1010000001	2111011001	1100010010	0210110011	0011
Alligator sinensis	1010000001	2111011001	1100010010	0210111011	0011
Alligator mefferdi	1?100000??	21110???01	1100010?10	021???????	001?
Alligator olseni	1?1000000?	21110???01	1????1??01	0210??????	001?
Alligator mcgrewi	1?1000000?	21110?1001	1100010?10	021???????	001?
Alligator prenasalis	1010000001	2111011001	1100010?10	021???????	001?
Allognathosuchus mooki	1?11???0?1	21110???01	1000010?10	0?1???????	001?
Allognathosuchus wartheni	1010000?01	21110?1?01	1000010010	011???????	001?
Wannaganosuchus brachymanus	1?1000????	???10???01	1????1??10	0?1???????	001?
Procaimanoidea kayi	1?1????0??	21110???01	1000010?10	01???????	0?1?
Arambourgia gaudryi	1?1??0????	2??1001001	1000017?10	01???????	0?1?
Stangerochampsa mccabei	1?1200????	??10???01	1000110?1?	011???????	000?
Brachychampsa montana	1012000001	11110?1?01	1000110?10	011???????	000?
Eocaiman cavernensis	??????????	?????????01	1?????????	2?????????	0???
Purussaurus neivensis	101100?001	21110???01	1000010?10	212???????	001?
Nettosuchidae	1?1000??1	??10?1?01	1001110?1?	?12???????	101?
Caiman yacare	1010000001	2111011001	1000010010	2120111011	0011
Caiman crocodilus	1010000001	2111011001	1000010010	2120111011	0011
Caiman latirostris	1010000001	2111011001	1010010010	2120121011	0011
Melanosuchus niger	1010100001	2111011001	1010010010	2120121011	0011
Paleosuchus trigonatus	1010000001	2111011001	1000010010	2110112011	0011
Paleosuchus palpebrosus	1010000001	2111011001	1000010010	2110112011	0011
Crocodylus cataphractus	0110001111	0001011101	1000010110	0011010101	0101
Crocodylus rhombifer	0110001111	0001011101	1000011101	0011010101	0101
Crocodylus porosus	0110001111	0001011101	1001011110	0011010101	0101
Crocodylus niloticus	0110001111	0001011101	1000011110	0011010101	0101
Crocodylus palaeindicus	0010001111	0001011101	1000011?10	001???????	010?
Osteolaemus tetraspis	0110001111	0001011101	1001010011	0011010101	0101
Crocodylus robustus	0?1000?111	0001011101	1001010011	001???????	0101
Crocodylus lloidi	011000?111	00?1011101	1001010??1	0?1???????	0?0?
Crocodylus megarhinus	011000?11?	00010???01	1000010?10	001???????	010?
Australosuchus clarkae	0?1000??71	0?010?1?01	100001??1?	??1???????	010?
Euthecodon arambourgii	0?1000?1?1	0001011101	1001110??1	0?0???????	0?0?
Tomistoma schlegelii	0110011111	0001011101	1000110010	0011010101	0101
Tomistoma lusitanica	011001?111	0001?11?01	1000110?10	001???????	0?0?
Tomistoma cairense	011??0?1??	00?1????01	1????1??0	001???????	010?
Crocodylus spenceri	??100011??	???10???01	1000110?10	001???????	0?0?
Gavialosuchus americanus	??1000?1??	0001????01	1000110?10	0011??????	010?
Brachyuranochampsa eversolei	0?1?00?1??	???10???01	1000110?10	001???????	0?0?
Dormaal crocodyloid	0110001101	00010?1?01	1000010?10	001???????	010?
Crocodylus acer	011000?1??	00010?1?01	1000110?10	001???????	0?0?
Crocodylus affinis	011000?1??	00010???01	1000010?10	0011??????	010?
Asiatosuchus germanicus	0?100??1??	00?10???01	1000010?10	001???????	000?
Prodiplocynodon langi	01100001?1	???10?1001	1000?10?10	001???????	0?0?

APPENDIX 3. Number of scored morphological characters (No. morph), morphological completeness (% morph), total completeness, including morphological and molecular characters (% total), chronostratigraphic units of occurrence (strat. unit), age, and temporal range for crocodylian and outgroup taxa. MY = million years. Specimens or references used in calibrations and rationale for some taxonomic lumping are indicated in the notes.

TAXON	No. morph	% morph	% total	Strat. unit	Age (MY)	Range (MY)	Note no.
Parsimony analysis							
Dromaius novaehollandiae	96	58.5	60.6	Recent	0	0	1, 2
Glen Rose Form	97	59.1	23.2	Albian/Aptian[a]	111	13.8	1, 3
Bernissartia fagesii	89	54.3	21.2	Berriasian/Albian[a]	129	16.8	1, 4
Hylaeochampsa vectiana	61	37.2	14.6	Barremian[a]	128	3.7	5, 6
Leidyosuchus formidabilis	141	86.0	33.7	Tiffanian[b]	61.3	1.75	5, 6
Leidyosuchus sternbergii	140	85.4	33.4	Maestrichtian[a]	69.5	4.5	1, 6
Leidyosuchus acutidentatus	51	31.1	12.2	Tiffanian[b]	61.3	1.75	5, 6
Leidyosuchus wilsoni	107	65.2	25.5	Wasatchian–Bridgerian[b]	54	3.5	5, 6
Leidyosuchus canadensis	106	64.6	25.3	Campanian[a]	78.5	4.5	1, 7
Thoracosaurus macrorhynchus	105	64.0	25.1	Danian[a]	62.8	2.3	1, 8
Eogavialis africanum	105	64.0	25.1	Priabonian–Rupelian[a]	36.1	1.1	1, 9, 10
Gryposuchus colombianus	113	68.9	27.0	Chattian[a]	26.3	3	1, 11
Siwaliks Gavialis	67	40.9	16.0	Pliocene[c]	3.4	1.8	12, 13
Gavialis gangeticus	162	98.8	99.5	Recent	0	0	12
Pristichampsus vorax	115	70.1	27.4	Bridgerian–Uintan,[b] Lutetian[a]	49.5	1.5	5, 14
Diplocynodon darwini	130	79.3	31.0	Lutetian[a]	46.1	4	1, 15
Diplocynodon ratelii	125	76.2	29.8	Aquitanian[a]	22.4	1.8	1, 15
Diplocynodon hantoniensis	129	78.7	30.8	Priabonian[a]	37	1.6	1, 15
Alligator mississippiensis	164	100.0	100.0	Barstovian[b]–Recent	14	2.5	5, 16
Alligator sinensis	161	98.2	99.3	Recent	0	0	
Alligator mefferdi	107	65.2	25.5	Upper Clarendonian[b]	9	1	5, 17
Alligator olseni	105	64.0	25.1	Upper Hemmingfordian[b]	16.8	0.3	5, 18
Alligator mcgrewi	140	85.4	33.4	Hemmingfordian[b]	18.3	1.8	5, 19
Alligator prenasalis	131	79.9	31.3	Chadronian[b]	34	5	5, 20
Allognathosuchus mooki	94	57.3	22.4	Puercan[b]	65.8	0.8	5, 21
Allognathosuchus wartheni	120	73.2	28.6	Clarkforkian[b]	58.3	0.8	5, 22
Wannaganosuchus brachymanus	86	52.4	20.5	Tiffanian[b]	61.3	1.75	5, 23
Procaimanoidea kayi	104	63.4	24.8	Bridgerian[b]	49.5	1.5	5, 24
Arambourgia gaudryi	72	43.9	17.2	Bartonian[a]	40.4	1.8	1, 25
Stangerochampsa mccabei	112	68.3	26.7	Campanian[a]	78.5	4.5	1, 26
Brachychampsa montana	139	84.8	33.2	Maestrichtian[a]	69.5	4.5	1, 27
Eocaiman cavernensis	25	15.2	6.0	Casamayoran[d]	53.8	2.8	28, 29
Purussaurus niecevensis	122	74.4	29.1	Upper Miocene[c]	9.7	4.5	1, 30
Nettosuchidae	108	65.9	25.8	Wasatchian[b]–Pliocene[c]	54	3.5	1, 31
Caiman yacare	164	100.0	39.1	Recent	0	0	

APPENDIX 3. Continued.

TAXON	No. morph	% morph	% total	Strat. unit	Age (MY)	Range (MY)	Note no.
Caiman crocodilus	164	100.0	90.9	Recent	0	0	32
Caiman latirostris	159	97.0	75.7	Pleistocene–Recent	0.82	0.82	33
Melanosuchus niger	161	98.2	76.1	Recent	0	0	
Paleosuchus trigonatus	163	99.4	76.6	Recent	0	0	
Paleosuchus palpebrosus	160	97.6	75.9	Recent	0	0	
Crocodylus cataphractus	161	98.2	61.6	Pliocene[c]	3.4	1.8	34
Crocodylus rhombifer	164	100.0	100.0	Pleistocene[c]–Recent	0.82	0.82	35
Crocodylus porosus	157	95.7	60.6	Zanclian–Recent	4	0.6	1, 36
Crocodylus niloticus	164	100.0	62.3	Piacenzian[a]–Recent	2.5	9	1, 37
Crocodylus palaeindicus	110	67.1	26.3	Pliocene[c]	3.4	1.8	13
Osteolaemus tetraspis	161	98.2	52.5	Recent	0	0	38
Crocodylus robustus	123	75.0	29.4	Recent	0	0	39
Crocodylus lloidi	72	43.9	17.2	Burdigalian[a]	17.5	0.5	1, 40
Crocodylus megarhinus	96	58.5	22.9	Priabonian[a]	37	1.6	1, 10
Australosuchus clarkae	82	50.0	19.6	Chattian/Aquitanian[a]	23.3	7.8	1, 41
Euthecodon arambourgii	67	40.9	16.0	Burdigalian[a]	18.9	2.6	1, 42
Tomistoma schlegelii	164	100.0	100.0	Recent	0	0	
Tomistoma lusitanica	97	59.1	23.2	Serravallian[a]	12.3	1.9	1, 43
Tomistoma cairense	69	42.1	16.5	Priabonian–Rupelian[a]	36.1	1.1	1, 44
Crocodylus spenceri	75	45.7	17.9	Ypresian[a]	53.3	3.3	1, 45
Gavialosuchus americanus	117	71.3	27.9	Hemphillian[b]	6.5	1.5	5, 46
Brachyuranochampsa eversolei	64	39.0	15.3	Uintan[b]	45.3	3.3	5, 47
Dormaal crocodyloid	117	71.3	27.9	Ypresian/Lutetian[a]	49.3	7.2	1, 48
Crocodylus acer	75	45.7	17.9	Wasatchian[b]	54	3.5	5, 49
Crocodylus affinis	143	87.2	34.1	Bridgerian–Uintan[b]	49.5	1.5	5, 50
Asiatosuchus germanicus	110	67.1	26.3	Lutetian[a]	46.1	4	1, 51
Prodiplocynodon langi	67	40.9	16.0	Maestrichtian[a]	69.5	4.5	1, 52
Other taxa[e]							
Melanosuchus fisheri				Huayquerian[d]	3.4	1.8	28, 33
Caiman lutescens				Upper Miocene[c]	9.7	4.5	32
Thoracosaurus neocesariensis				Campanian[a]	78.5	4.5	1, 8
Gavialosuchus carolinensis				Chattian[a]	26.3		31, 46
Osteolaemus sp.				Upper Miocene[c]	9.7	4.5	1, 38
Crocodylus ndokoensis				Zanclian[a]	4.3	0.9	1, 34

a Stage.
b North American Land Mammal Age.
c Epoch.
d South American Land Mammal Age.
e Taxa not included in parsimony analyses but used to calibrate minimum divergence times.

Notes

1. Calibration from Harland et al. (1990).
2. The Glen Rose Form derives its name from the Glen Rose Formation (Albian–Aptian) of central Texas (Langston, 1974).
3. The Bernissart locality in Belgium has not been precisely localized in the Lower Cretaceous; the indicated range is taken from Norell and Clark (1990). A well-preserved skull of *Bernissartia* was described from the Barremian of Spain (Buscalioni and Sanz, 1990), but its identity with *B. fagesii* has not been established.
4. Age derived from Clark and Norell (1992).
5. Calibration from Woodburne (1987: fig. 10.1).
6. A more thorough review of these taxa was given by Brochu (in press). *Leidyosuchus formidabilis, L. wilsoni,* and *L. sternbergii* are among the most complete fossil crocodylians known (Erickson, 1976; Bryant, 1989). The date used for the lineage as a whole is based on *L. sternbergii* from the Lance Formation (Gilmore, 1910) and correlative Hell Creek Formation (Estes, 1964; Bryant, 1989).
7. All known material of *Leidyosuchus canadensis* is from the Campanian Judith River Group of Alberta (Lambe, 1907; Eberth and Brinkman, 1997). Reports of *L. canadensis* from the Paleocene (Greenwald, 1979) are spurious (Bryant, 1989).
8. *Thoracosaurus neocesariensis* is widespread in the Maestrichtian (uppermost Cretaceous) of North America (Troxell, 1925; Carpenter, 1983). Less complete *Thoracosaurus* remains are also known from the Campanian of North America (Schwimmer, 1986) and Africa (Lavocat, 1955). Codings in the matrix are based primarily on Paleocene material from France and Sweden.
9. Based on "*Tomistoma*" *africanum* and "*Tomistoma*" *gavialoides* (Andrews, 1906), which are not morphologically separable. The original distinction was stratigraphic; "*T.*" *gavialoides* came from slightly younger sediments in the Fayûm sequence. The name *Eogavialis* was first applied by Buffetaut (1982).
10. The Fayûm Depression of Egypt contains a thick sequence covering the uppermost Eocene and lowermost Oligocene. The chronology is derived from Kappelman et al. (1992).
11. Based on material first described (as *Gavialis colombianus*) by Langston (1965; Langston and Gasparini, 1997), who accepted a Late Oligocene age for the fauna from which it was derived.
12. Gavialoid remains are prominent in the Upper Miocene through Quaternary sediments of the Siwaliks Group of Pakistan (Lydekker, 1888; Pilgrim, 1912; Lull, 1944). Steel (1973) referred some of these to *G. gangeticus*, but this identification is not accepted here. Several other species have been described, but they probably represent one or at most two valid species.
13. Crocodylians are ubiquitous throughout the Siwaliks Series. Because locality information was not very specific for the specimens actually studied, I was unable to pinpoint the age of first oc-

currence for Siwaliks gavialoids or *C. palaeindicus.* Upper and lower bounds for the Siwaliks were taken from Opdyke et al. (1979).
14. The indicated date is for the Bridgerian, within which the holotype of *Pristichampsus vorax* was collected (Langston, 1975). *Pristichampsus* has also been recorded from younger sediments (Uintan NALMA) in North America (Busbey, 1986) and in units more or less correlative with the Bridgerian in Europe (Kuhn, 1938). A possible Paleocene relative, *Planocrania,* has been described from China (Li, 1984).
15. *Diplocynodon darwini* is from the Lutetian Messel locality of Germany (Ludwig, 1877; Berg, 1966). Codings for *Diplocynodon hantoniensis* are based on material from the Lower Headon Beds (Lower Oligocene; Benton and Spencer, 1995) in England, although fossils from elsewhere have been referred to *D. hantoniensis* (Gramann, 1958; Vignaud et al., 1996) in units of approximately the same age. *Diplocynodon ratelii* is from the Aquitanian of France (Pomel, 1847; Vaillant, 1872).
16. Based on the holotype of *Alligator thompsoni* (Mook, 1923) from Nebraska and undescribed material from Texas. Both are from the Barstovian NALMA. I follow Malone (1979) and regard *A. thompsoni* as a junior synonym of *A. mississippiensis.* Fossils indistinguishable from modern *A. mississippiensis* are well documented through the Pleistocene (Preston, 1979; Holman, 1995).
17. *Alligator mefferdi* is based on a skull and jaws from Nebraska (Mook, 1946). Malone (1979) considered it synonymous with *A. mississippiensis,* but a clade including *A. mississippiensis* and *A. sinensis* can be diagnosed on the absence of the anterior foramen intermandibularis oralis, a feature plesiomorphically retained in *A. mefferdi.*
18. Based on material from Florida (White, 1942).
19. Scorings indicated here were based on the holotype in the Field Museum of Natural History and several specimens at the American Museum of Natural History, all from the Hemingfordian of Nebraska (Schmidt, 1941). Malone (1979) also reported *A. mcgrewi* from the younger Barstovian NALMA.
20. *Alligator prenasalis* is one of the best-known fossil crocodylians, known from several well-preserved skeletons from the Chadronian of South Dakota (Loomis, 1904; Mook, 1932; Higgins, 1972).
21. Based on material described by Simpson (1930) from the lowermost Paleocene of New Mexico.
22. The taxonomy of "*Allognathosuchus*" is in need of revision. The blunt-toothed alligatorine from the Willwood Formation of Wyoming (*Allognathosuchus wartheni*: Case, 1925; Bartels, 1983; Gunnell et al., 1992) is one of the best represented.
23. Based on a skeleton from the same Paleocene locality as "*Leidyosuchus*" *formidabilis* (Erickson, 1982).
24. Based on a skeleton from the Bridger Formation of Wyoming (Mook, 1941a). *Procaimanoidea* has

also been described from the Uintan NALMA of Utah (Gilmore, 1946).

25. Based on a skull and partial mandible from the Oligocene of France (Kälin, 1939).

26. Based on a well-preserved skull and skeleton from the Judith River Group of Alberta (Wu et al., 1996). Although the skull of *S. mccabei* shows proportions different from those of the holotype of *Albertochampsa langstoni* from the same unit (Erickson, 1972), *Stangerochampsa* and *Albertochampsa* were redundant for purposes of this study.

27. Both the holotype (Gilmore, 1911) and a well-preserved skeleton described by Norell et al. (1994) came from the uppermost Cretaceous Hell Creek Formation.

28. South American Land Mammal Ages are not well calibrated. Upper and lower bounds of the Casamayoran are adapted from Wyss et al. (1993), with the understanding that they are extremely approximate. I was unable to find absolute dates for the Huayquerian, so the date and range indicated are for the Pliocene, using the calibration of Harland et al. (1990).

29. Caimans are probably the most poorly represented lineage in this study, at least from a paleontological perspective. *Eocaiman cavernensis*, from the Lower Eocene of Patagonia (Simpson, 1933), is regarded as the oldest reasonably preserved caiman, although poorly preserved fossils are known from the Paleocene of Argentina (Rusconi, 1937; Langston, 1965) and Texas (Brochu, 1996). *Eocaiman* has been reported from the Paleocene (Gasparini, 1981), but calibrations in this study are based only on Eocene material.

30. *Purussaurus neivensis* is part of an assemblage of large caimans from the Mio-Pliocene of northern South America that have extremely large narial openings; Langston (1965) referred the La Venta Fauna, from which *P. neivensis* is known, to the Late Miocene.

31. Nettosuchids are among the most bizarre crocodylians known, characterized by long, broad skulls with a large number of very small teeth (Price, 1964; Langston, 1965; Bocquetin and de Souza Filho, 1990). Most are known from the Miocene and Pliocene of South America, where the oldest is *Mourasuchus atopus* from the La Venta Fauna (Langston, 1965). However, *Orthogenysuchus olseni* from the Wasatchian NALMA of New Mexico (Mook, 1924) possesses not only the broad snout and small maxillary alveoli but also the transversely wide external naris characteristic of South American nettosuchids and draws this lineage, as well as the divergence of *Paleosuchus* from other extant caimans, at least to the base of the Eocene. Fossils are not known from the lineage including *Paleosuchus* to the exclusion of other living caimans.

32. Our knowledge of *Caiman latirostris* is, for purposes of this study, restricted to the Quaternary. A partial snout from the Pleistocene of Argentina was referred to this species by Patterson (1936). *Caiman lutescens* from the La Venta Fauna has been referred to this species (Gasparini, 1981; Langston and Gasparini, 1997), but the holotype of this taxon can be distinguished from *C. latirostris* on the basis of a much larger external naris. *Caiman lutescens* was not included in the parsimony analyses but is congruent with both *C. latirostris* and *Melanosuchus niger* and shares the presence of well-developed rostral ridges with both living species, indicating a divergence between *C. latirostris* + *M. niger* and *C. crocodilus* + *C. yacare* by the beginning of the Pliocene.

33. There is no fossil record for extant *Melanosuchus niger*, but *M. fisheri* is based on a Pliocene skull from Venezuela preserving the characteristic diamond-shaped exposure of the vomer on the palate (Medina, 1976).

34. Skulls attributable to *Crocodylus cataphractus* have been described from the Pliocene Lake Rudolf deposits (Tchernov, 1986). *Crocodylus ndokoensis* is a form described by Pickford (1994) from the Miocene of Uganda; it shares an attenuated snout and exclusion of the nasals from the naris with *C. cataphractus*.

35. Relatively complete cranial material from the Pleistocene of Cuba can be referred to *Crocodylus rhombifer* (Varona, 1984). Subfossil remains belonging to *C. rhombifer* have been found on Grand Cayman Island (Morgan et al., 1993) but are probably not older than a few thousand years. Varona (1966, 1984) referred less complete material from the Pleistocene of Cuba to *Crocodylus antilliensis*.

36. A partial snout from the Miocene of Australia was referred to *Crocodylus porosus* by Molnar (1979).

37. This particular record is based on remains from Lake Rudolf (Tchernov, 1986).

38. Miocene *Osteolaemus* have been described (Antunes, 1962; Aoki, 1992; Pickford, 1994), but they may not be *O. tetraspis*. The date for fossil *Osteolaemus* is from Pickford (1994).

39. *"Crocodylus" robustus* from Madagascar is extinct, but most authorities (e.g., Dewar, 1984) regard all Cenozoic Malagasy terrestrial deposits as Holocene.

40. *"Crocodylus" lloidi* has been described from several African localities from the Miocene and Pliocene (Tchernov, 1986; Leakey et al., 1996; Pickford, 1996), but the tangibility of some of these identifications is questionable. The scorings for this analysis were based on material from the Wadi Moghara in Egypt, dated to 17–18 MYA by Miller and Simons (1996).

41. Willis and Molnar (1991) based *Australosuchus clarkae* on material considered to be of Late Oligocene or Early Miocene age. For this study, I have taken the age of the Oligocene–Miocene boundary from Harland et al. (1990) as the approximate age of *A. clarkae*, with the bounds of the Chattian and Aquitainian as the range. *Australosuchus clarkae* might be part of an insular Australian lineage dating back to the lower Eocene (Willis et al., 1993; Salisbury and Willis, 1996).

42. *Euthecodon arambourgii* is the oldest and presum-

ably the least derived of the species of *Euthecodon* (Ginsburg and Buffetaut, 1978).

43. Antunes (1961) referred *Tomistoma lusitanica* from Portugal to the Burdigalian. Late Miocene tomistomine skulls from northern Africa and elsewhere in Europe (e.g., *T. dowsoni, T. calaritanus*) are not morphologically distinguishable from *T. lusitanica*, and all probably represent a single species.

44. Based on material from the Middle Eocene of Mokattam, Egypt (Müller, 1927b). Hecht and Malone (1972) regarded it as part of the Eocene African gavialoid assemblage, but Buffetaut (1982) considered it to be tomistomine.

45. Originally described by Buckland (1836) and later illustrated by Owen (1850). The specimens on which this analysis are based are from the London Clay, assigned to the Ypresian by Benton and Spencer (1995). A possible close relative was described by Swinton (1937) from younger Eocene beds in Belgium.

46. The scorings in the matrix are based primarily on *Gavialosuchus americanus* from the Pliocene of Florida (Auffenberg, 1954). Congruent material is known from the Oligocene and Miocene of eastern North America; the date used here is for *G. carolinensis* from the Oligocene of South Carolina (Erickson and Sawyer, 1996). *Gavialosuchus* is also known from the Miocene and Pliocene of Europe (Toula and Kail, 1885; Buffetaut et al., 1984).

47. Based on a skull from the Washakie Formation of Wyoming (Zangerl, 1944).

48. The specimens used in this analysis were from the Eocene Dormaal locality of Belgium (Buffetaut, 1985a); they were labeled as *"Crocodylus" depres-* *sifrons*. This assignment must be made carefully because the holotype of *"C." depressifrons*, although well-illustrated by Blainville (1850), is now completely pyritized. Material from beds in the Paris Basin correlative to those from which the holotype were collected probably represents *"C." depressifrons*; if so, the referral of the Belgian material to this taxon may be valid.

49. Based on a skull from the Bridger Formation (Mook, 1921a).

50. The concept of *"Crocodylus" affinis* used here includes a large number of named crocodylian taxa from the Eocene of North America. Norell and Storrs (1986) synonymized most North American Bridgerian *"Crocodylus"* (e.g., *"C." grinnelli, "C." brevicollis, "C." liodon*) with *"C." affinis*. Furthermore, the holotype and only known specimen of *Brachyuranochampsa zangerli*, also from the Bridgerian of Wyoming (Mook, 1962), cannot be distinguished from *"C." affinis*. *"Crocodylus" clavis* is derived from somewhat younger units than is the type material for *"C." affinis* but is distinguishable only in minor differences in the shape of the palatine process.

51. *"Asiatosuchus" germanicus* is derived from the Messel locality of Germany (Berg, 1966). It retains the plesiomorphic states of a frontoparietal suture that barely enters the supratemporal fenestra and a splenial symphysis, states not seen in *Asiatosuchus grangeri* from Mongolia (Mook, 1940) or in *"Crocodylus" depressifrons*, with which Vasse (1992) synonymized *"A." germanicus*.

52. Based on a skull from the Late Cretaceous Lance Formation of Wyoming (Mook, 1941b).