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 extent 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) can be addressed confidently. Expectations will differ depending 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. Dumeril 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; Kalin, 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; Kalin, 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 Kalin (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; Tarstano 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; Systsma 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 (Sorensen, 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
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only be assigned to an epoch, and some South American taxa were assignable to a South American Land Mammal Age (SALMA). 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 contemporaneous 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; 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 \( \text{Crocodylus cataphractus} \) and all other \( \text{Crocodylus} \) was used to represent the initial divergence among extant \( \text{Crocodylus} \). 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 \( [\text{bp}/\text{MY}] \)\), allowing a test of the hypothesis that all pairwise comparisons within \( \text{Crocodylia} \) 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 \( \text{Gavialis} \) 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 \( \text{Crocodylii} \), including \( \text{Tomistoma} \), is supported in trees up to 6 steps longer than the most-parsimonious tree; monophyly of a group including all crocodylians except \( \text{Gavialis} \) is supported in trees up to 11 steps longer. This tree is largely congruent with all previous analyses of \( \text{Crocodylia} \), regardless of the type of data used. \( \text{Crocodylus} \) is monophyletic and is the closest living relative of \( \text{Osteolaemus} \); \( \text{Alligatoridae} \) is monophyletic, as are the caimans; the sister-taxa relationship between \( \text{Caiman latirostris} \) and \( \text{Melanosuchus niger} \) was supported by Norell (1988) and Poe (1996), and all other topological arrangements within \( \text{Alligatoridae} \) are in agreement with previous analyses; and \( \text{Tomistoma} \) is closer to \( \text{Crocodylus} + \text{Osteolaemus} \) than it is to \( \text{Alligatoridae} \). A sister-group relationship is indicated between \( \text{Crocodylus cataphractus} \) and all other \( \text{Crocodylus} \), in accord with some immunological data (e.g., Densmore, 1983), although different data sets do not agree on the relationships within \( \text{Crocodylus} \) (Poe, 1996).

This data set supports previous morphological cladistic studies of \( \text{Crocodylia} \) (e.g., Norell, 1989) in that \( \text{Gavialis} \) is unequivocally the sister taxon of all other crocodylians. By constraining \( \text{Gavialis} \) and \( \text{Tomistoma} \) 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

morbidity, recent only **

morphology, with fossils **

combined, with fossils

Tomistoma

Gavialis

Crocodylus + Osteolaemus

molecular, recent only

(Poe, 1996)

combined, no fossils,
Dromaius only outgroup

(in part)

Gavialis

Crocodylus + Osteolaemus

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 tomistomes, 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 *Asiaotosuchus 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 palaeontological 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 (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).
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 "Crocodylus" 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 clarkei, 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
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
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).

**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 *Diplocaulus* 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 Formation 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; Leacy 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 Des-sauer, 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 (*"Crocodylus" spenceri, Tomistoma cairene*). 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.
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

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**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.
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 Gavi-
alis 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 di-
vergence 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 signifi-
cantly 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 arrange-
ments further implies long ghost lineages for noncrocodylid crocodyloids.

The pre-Campanian record for eusuchians generally is poor, and an approximat-
ely 25-MY gap exists between Hylaeochampsa, the oldest known eusuchian, and the
next oldest eusuchian occurrences in the Cenomanian (Stromer, 1925, 1933). How-
ever, 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 con-
tinental lineages.

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 cor-
respondence with minimum divergence time as predicted by fossils. Relatively re-
cent divergences (A. mississippiensis–A. sinensis, Crocodylus–Osteolaemus, Crocodylus ca-
taphractus–all other Crocodylus) correspond

![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).](https://academic.oup.com/sysbio/article-abstract/46/3/479/1651365)
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.

<table>
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<tr>
<th>Divergence</th>
<th>ID</th>
<th>Nei's D</th>
<th>AAD</th>
<th>TOD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alligator–all caiman</td>
<td>79.00</td>
<td>0.762</td>
<td>2.54</td>
<td>65.8</td>
</tr>
<tr>
<td>A. mississippiensis–A. sinensis</td>
<td>5.00</td>
<td>0.560</td>
<td>0.43</td>
<td>14.0</td>
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<td>Crocodylus–Osteoleamus</td>
<td>36.00</td>
<td>0.498</td>
<td>0.67</td>
<td>9.7</td>
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<td>C. cataphractus–other Crocodylus</td>
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<td>0.253</td>
<td>0.26</td>
<td>9.7</td>
</tr>
<tr>
<td>Crocodylus–Tomistoma</td>
<td>78.90</td>
<td>0.408</td>
<td>2.57</td>
<td>53.3</td>
</tr>
<tr>
<td>Osteoleamus–Tomistoma</td>
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<td>0.682</td>
<td>2.07</td>
<td>53.3</td>
</tr>
<tr>
<td>Paleosuchus–(Caiman + Melanosuchus)</td>
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<td>0.686</td>
<td>1.93</td>
<td>53.8</td>
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<td>78.5</td>
</tr>
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<td>0.404</td>
<td>0.03</td>
<td>78.5</td>
</tr>
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<td>Melanosuchus–Caiman latirostris</td>
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<td>0.337</td>
<td>0.39</td>
<td>3.4</td>
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<tr>
<td>(M. niger + C. latirostris)–C. crocodilus</td>
<td>23.38</td>
<td>0.311</td>
<td>0.72</td>
<td>9.7</td>
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<td>Alligator–Crocodylus</td>
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<td>153.00</td>
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</table>

...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 non-preservation 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).

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<td>—</td>
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<td>69.5</td>
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<td>1.372</td>
<td>0.125</td>
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<td>0.047</td>
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<td>0.533</td>
<td>0.090</td>
<td>0.093</td>
<td>1.005</td>
<td>0.027</td>
<td>1.734</td>
<td>0.140</td>
<td>0.183</td>
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* Consistent with 0.5 bpc/MY.
* Consistent with 0.75 bpc/MY.
* Consistent with 1.0-2.0 bpc/MY.
* Consistent with 3.0-7.0 bpc/MY.
* No fossil record; no rate hypotheses tested.
* Consistent with 0.25 bpc/MY.
* 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, Diplcynodon 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 relationships 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 crocodylian lineages.

Kumazawa and Nishida (1995) found that rates for tRNA evolution were higher in crocodylians than in other amniote lineages, and their data suggest a slightly longer branch in *Caiman* than in *Alligator* or *Crocodylus*. The mitochondrial genome of *Crocodylus porosus* has a longer cytochrome *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). Together with the 12S rDNA rate heterogeneity 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 Crocodyliidae into the Lower Cretaceous and would support much lower rates of evolution for alligatorid taxa. However, this comparison must be made cautiously because Wu et al.'s analysis excluded 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 divergence 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 analyses 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 significantly 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 hypotheses must also consider such extinct taxa as *Thoracosaurus*, *Eogavialis*, and *Gaviatlosuchus*, especially if the fossil record is to be reconciled with molecular distance data.

The combined analyses presented here reflect the strong disparity between different morphological and molecular data sets for the position of *Gavialis* more than they uphold one over another. However congruent the available data are for most parts of the crocodylian tree, they strongly disagree on the placement of *Gavialis* and its extinct relatives. The total evidence tree in Figures 4 and 5 is currently the best available hypothesis for crocodylian relationships, 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 resolve this particular issue. There are two conflicting signals represented in the combined matrix, and whichever is stronger in a particular analysis will dominate the resulting 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 molecular as morphological characters. A bolstered morphological data set led either to a different rooting (for the Recent-only tree with fossil outgroups) or a different topology altogether (when fossils are included). The change in root can be seen as a compromise result: the molecular data are strongly enforcing a four-taxon network in which *Gavialis* and *Tomistoma* are close together, but the morphological data are rooting it on *Gavialis*. The complete change in topology is reflecting a stronger morphological signal with the addition of fossils. 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 (Allad 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.

ACKNOWLEDGMENTS

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Sliddall, M. E. 1996. Stratigraphic consistency and


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 Novacek, 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 hypapophysial keels extend to 11th vertebra behind atlas (0) or toward the anterior end of centrum (1).

7. Hypapophysial 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

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hypapophysis (0) or lacks prominent hypapophysis (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 diaphysis 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, 1998, 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 ("crocodileline 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 lags 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 rod-like (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 choana 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 lingually (1), or dentary teeth occlude in line with maxillary tooththrow (2). (Adapted from Norell, 1988, character 5; Willis, 1993, character 1.)
79. Nasal 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 tooththrow (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 posterocaudally (1), or small and project posteriorly (2).
99. Palatine smooth dorsally anterior to prefrontal pillar (0) or with prominent thin ridge on palate 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 palatine 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 hemicondyly (0), with small medial hemicondyly and dorsal notch for foramen aerum (1), with prominent dorsal projection between hemicondyly (2), or with expanded medial hemicondyly (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-
131. Parietal and squamosal widely separated by lateral (0) or with ascending process or palatine (1).

132. Squamosal-quadrate suture extends dorsally without actually making contact (1), or parietal and squamosal meet along posterior wall of supratemporal fenestra (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 dorsally (0) or anteromedially (1).

137. Dorsal half of prefrontal pillar narrow (0) or expanded anteromedially 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 eustachian canal (0) or inset from lateral orbital bar. (Adapted from 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. Premaxilla toothrow curves medially or linear (0) or curves laterally broadly (1) posterior to first six maxillary alveoli. (Adapted from Clark, 1994, character 32.)

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

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).
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 basi- sphenoid rostrum.
APPENDIX 2. Data matrix used in the analysis of crocodylians and outgroups. ? = missing data; N = unscorable conditions.
Dromalus novaehollandiae
Glen Rose Form
Bernissartia fagesi
Hylaeochampsa vectiana
Leidyosuchus formidabilis
Leidyosuchus sternbergi
Leidyosuchus acutidentatus
Leidyosuchus wilsoni
Leidyosuchus canadensis
Thoracosaurs macrorhynchus
Boygavisauriscus africanus
Gryposuchus colombianus
Sivalisca Gavialis
Gavialis gangeticus
Pristichampas vorax
Diplocynodon darwini
Diplocynodon ratelii
Diplocynodon hantoniensis
Alligator mississippiensis
Alligator sinensis
Alligator meffardi
Alligator osaeni
Alligator mcgregori
Alligator prenasalis
Allognathosuchus mookii
Allognathosuchus wartheni
Wannagonsuchus brachymanus
Procamainoidea kaiy
Arambourgia gaudryi
Stangerochampsa mccabeii
Brachycephosaurus montana
Eocalamus cavernensis
Purussaurus gavialis
Nectosuchidae
Caiman yacare
Caiman crocodilus
Caiman latirostris
Melanosuchus niger
Paleosuchus trigonatus
Paleosuchus palpebrosus
Crocodilus captafractus
Crocodilus rhombifer
Crocodilus porosus
Crocodilus niloticus
Crocodilus palaeindicus
Osteolepis tetrapsis
Crocodilus robustus
Crocodilus lioi
Crocodilus megahus
Australosuchus clarkae
Ruthecodon arambourgi
Tomistoma schlegeli
Tomistoma lusitanica
Tomistoma cairensae
Crocodilus spenceri
Gavialosuchus americanus
Brachyurochampsa eversei
Dormael crocodylodon
Crocodilus acer
Crocodilus affinis
Asiatosuchus germanicus
Prodiplocynodon longi
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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.

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*Note: Mya = million years. Note nos. indicate references used in calibrations.*

**APPENDIX 3. Continued.**

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<th>% total</th>
<th>Strat. unit</th>
<th>Age (MY)</th>
<th>Range (MY)</th>
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**Other taxa a**

- *Melanosuchus fisheri*  
  - Huayquerian d  
  - Upper Miocene c  
- *Caiman lutescens*  
  - Upper Miocene c  
- *Thoracosaurus neocesariensis*  
  - Campanian a  
- *Gavialisuchus carolinensis*  
  - Chattian a  
- *Osteolaemus sp.*  
  - Upper Miocene c  
- *Crocodylus ndokoensis*  
  - Zanclian a

---

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

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 (Buscaldi and Sanz, 1990), but its identity with B. gavialides has not been established.
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. Thracosaurus neocesariensis is widespread in the Maastrichtian (uppermost Cretaceous) of North America (Troxell, 1925; Carpenter, 1983). Less complete Thracosaurus 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" africanaum and "Tomistoma" gavialides (Andrews, 1906), which are not morphologically separable. The original distinction was stratigraphic; "T." gavialoides came from slightly younger sediments in the Fayum sequence. The name Eogavialis was first applied by Buffetaut (1982).
10. The Fayum 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 occurrence for Siwaliks gavialoids or C. palaendicus. 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 torax 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 mantoniensis 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. mantoniensis (Gramann, 1958; Vignaud et al., 1996) in units of approximately the same age. Diplocynodon ratelli 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. Scoring 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. mcgregori 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 "Alligatorosuchus" is in need of revision. The blunt-toothed alligatorine from the Willwood Formation of Wyoming (Alligatorosuchus 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). Procaimanoida has
25. Based on a skull and partial mandible from the Uintan NALMA of Utah (Gilmore, 1946).
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. mccabeii shows proportions different from those of the holotype of Albertochampsa langstoni from the same unit (Erlickson, 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 Casmayoran 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 catherinei, 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 Moursuchus 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 ofPaleosuchus 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 ndokensis is a form described by Pickford (1994) from the Miocene of Uganda; it shares an attenuated snout and exclusion of the nasals 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 antillensis.
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" lloydii 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 clarkei 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. clarkei, with the bounds of the Chattian and Aquitainian as the range. Australosuchus clarkei might be part of an insular Australian lineage dating back to the lower Eocene (Willis et al., 1993; Salisbury and Willis, 1996).
42. Euthedon arambourgi 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* depressifrons". 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.* lidon") with "*C.* affinis." Furthermore, the holotype and only known specimen of *Brachyuranochamps 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).