

PHYLOGENETIC APPROACHES TOWARD CROCODYLIAN HISTORY

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■ **Abstract** A review of crocodylian phylogeny reveals a more complex history than might have been anticipated from a direct reading of the fossil record without consideration of phylogenetic relationships. The three main extant crocodylian lineages—Gavialoidea, Alligatoidea, Crocodyloidea—are known from fossils in the Late Cretaceous, and the group is found nearly worldwide during the Cenozoic. Some groups have distributions that are best explained by the crossing of marine barriers during the Tertiary. Early Tertiary crocodylian faunas are phylogenetically composite, and clades tend to be morphologically uniform and geographically widespread. Later in the Tertiary, Old World crocodylian faunas are more endemic. Crocodylian phylogeneticists face numerous challenges, the most important being the phylogenetic relationships and time of divergence of the two living gharials (*Gavialis gangeticus* and *Tomistoma schlegelii*), the relationships among living true crocodiles (*Crocodylus*), and the relationships among caimans.

Living crocodylians include the 23 species of alligators, caimans, crocodiles, and gharials found throughout the world's tropics and warm temperate regions. The group includes the largest living reptiles and the only tetrapods known to regularly pursue humans as prey. Most populations suffered from overhunting and habitat loss during the twentieth century, but although some remain critically endangered, others are real success stories in conservation biology and have become important economic resources (Ross 1998).

Extant crocodylian diversity is low, but the group has a rich fossil record extending back to the Campanian. Known fossil crocodylians outnumber their living relatives five to one. They are found on every continent, and during the Eocene their range extended from Antarctica to Ellesmere Island (Estes & Hutchison 1980, Willis & Stilwell 2000). They are ubiquitous in continental deposits throughout the Cenozoic.

The earliest published accounts of fossil crocodyliforms emphasized differences from modern crocodylians (e.g., Cuvier 1824), but this point of view quickly changed to that typified by Buckland (1836, p. 240), who stated that “fossil reptiles of the Crocodylean family do not deviate sufficiently from living genera, to require

any description of peculiar and discontinued contrivances.” Because there have always been semiaquatic ambush predators with flattened snouts among crocodyli-forms, little fundamental change is perceived, and crocodylians are seen as having remained morphologically static since the Mesozoic.

Adoption of an evolutionary perspective had surprisingly little impact on this perception. Broad changes in crocodyliform morphology, especially in the pelvis, palate, and braincase, were viewed as powerful evidence for the theory of evolution (e.g., Eudes-Deslongchamps 1868, Huxley 1875, Woodward 1886), but beyond acknowledging a basic division into gharials, alligators, and crocodiles, groups more or less conforming to the crown group were taken as a whole. Crown-group crocodylians—members of the group including the last common ancestor of modern gharials, alligators, and crocodiles and all of its descendents—were usually seen as a coherent twig on a much larger branch, not as a complex, many-twigged bush of their own. As a result, most descriptions of fossil crocodylians written early in the twentieth century were terse, and few critical taxonomic revisions were undertaken.

Crocodyliform systematics was revived in the 1980s. The introduction of phylogenetic systematic methodology, new fossil discoveries, and new molecular information raised issues long thought resolved. Diverse sources of information, from osmoregulatory physiology to macroevolution, were integrated in ways not seen before. Paleontologists had thought the Indian gharial, *Gavialis gangeticus*, to be distantly related to other living crocodylians, but molecular datasets argued otherwise. Molecular data also indicated a Late Tertiary divergence among species of *Crocodylus* (the “true” crocodiles), a group long thought to be more ancient. Relationships among living species of *Crocodylus* and among living caimans remain poorly resolved, and while fossils seem to resolve some conflicts, they raise additional questions.

These issues address some of the central debates in modern systematics, from the efficacy of combining disparate datasets to the reliability of molecular dating methods and the comparison of different phylogenetic hypotheses with external signals, such as stratigraphy. Given the role they played in Cuvier’s catastrophist model of Earth history and in nascent transformationalist views, crocodylians have always figured in the central biological debates of the day. Crocodylia’s combination of low extant diversity, dense fossil record, and wide range of divergence times between living species makes it a model clade for the exploration of phylogenetic problems.

This paper has three purposes. First, it summarizes what we currently know about the phylogenetic history of crocodylians from a paleontological perspective. We are beginning to assemble a comprehensive phylogenetic history for the clade, and this is a group with very interesting stories to tell. Second, it discusses current problems in crocodylian phylogenetics. The “gharial problem” is foremost among these and appears to represent a genuine case of conflict between different sources of information. Third, it illustrates the central role phylogeny should play in our interpretations of the fossil record.

I ultimately hope to divorce the reader from the misconception that crocodylians are ancient holdovers from the days of the dinosaurs. However similar modern crocodylians are to some of their older relations, we cannot regard crocodylians as “living fossils.” They seem not to have changed much if we observe them at a distance, but up close, they show significant change over time. If we consider the crocodylian fossil record in a phylogenetic context, we see as dynamic a history as that of any other group of organisms.

PHYLOGENETIC NOMENCLATURE FOR CROCODYLIA

Along with a renewed interest in crocodylian systematics has come an effort to draw the taxonomy of these animals into the phylogenetic system (de Queiroz & Gauthier 1994). Supraspecific taxon names within Crocodylia can be (and are here) defined on the basis of ancestry rather than possession of characters or taxonomic content. Such definitions are more consistent with the notion of taxa as natural groups resulting from evolution rather than classes of similar objects.

The phylogenetic nomenclatural system for Crocodylia was established by Clark (1986) and expanded by later workers (Norell et al. 1994; Salisbury & Willis 1996; Brochu 1997a, 1999a, 2000). This system no longer uses Linnean ranks and is applied throughout this paper. Definitions used here are shown in Table 1 and Figure 1. Some of these—in particular, the definitions of Crocodylia, Crocodylidae, and Crocodylinae—are amendments of earlier definitions. The draft PhyloCode (Cantino & de Queiroz 2000) requires that specifiers for clade definitions be species rather than the clades that were used in some previous applications.

Criticisms of phylogenetic nomenclature often revolve around instability in content in the face of phylogenetic uncertainty (Benton 2000, Nixon & Carpenter 2000). Although this can be addressed by applying care to the naming of clades, a problem arises because of the controversy surrounding *Tomistoma* and *Gavialis*. The name Crocodylidae has historically included *Crocodylus*, *Osteolaemus*, and *Tomistoma*, with relationships as shown in Figure 1, but excluded *Gavialis*. The first definition of Crocodylidae in Table 1 reflects this historical usage (Brochu 1999a). But molecular data generally support a topology in which *Gavialis* and *Tomistoma* are sister taxa and in which Alligatoridae is the basalmost extant crocodylian clade (rather than *Gavialis*). These are the relationships reflected throughout much of this paper, including Figures 2–7. If the definitions applied to Figure 1 are instead applied to a tree supported by molecular data, Gavialoidea would be a subset of Crocodylidae and Tomistominae would be redundant with Gavialoidea. The definitions at the top of Table 1 should be applied within the phylogenetic context (Bryant 1997) of the tree shown in Figure 1. The alternate definitions shown in Table 1 would apply on the molecular tree.

The name Crocodylia is currently restricted to the crown group. It used to include a much broader assemblage of archosaurs extending back to the Early Jurassic or Late Triassic. This older usage was imprecise and had a labile lower bound—most

TABLE 1 Phylogenetic name definitions for Crocodylia

Name	Definition	Comments
In context of morphology tree		
Eusuchia (Huxley 1875)	Last common ancestor of <i>Hylaeochampsa vectiana</i> , <i>Crocodylus niloticus</i> , <i>Gavialis gangeticus</i> , and <i>Alligator mississippiensis</i> and all of its descendents	Amended definition
Crocodylia (Gmelin 1789)	Last common ancestor of <i>Gavialis gangeticus</i> , <i>Alligator mississippiensis</i> , and <i>Crocodylus niloticus</i> and all of its descendents	Amended definition
Gavialoidea (Case 1930)	<i>Gavialis gangeticus</i> and all crocodylians closer to it than to <i>Alligator mississippiensis</i> or <i>Crocodylus niloticus</i>	
Pristichampsinae (Kuhn 1968)	<i>Pristichampsus rollinatti</i> and all crocodylians closer to it than to <i>Gavialis gangeticus</i> , <i>Alligator mississippiensis</i> , or <i>Crocodylus niloticus</i>	New definition
Brevirostres (von Zittel 1890)	Last common ancestor of <i>Alligator mississippiensis</i> and <i>Crocodylus niloticus</i> and all of its descendents	If <i>Gavialis</i> and <i>Tomistoma</i> are sister taxa, <i>Brevirostres</i> is a junior synonym of Crocodylia.
Alligatoroidea (Gray 1844)	<i>Alligator mississippiensis</i> and all crocodylians closer to it than to <i>Crocodylus niloticus</i> or <i>Gavialis gangeticus</i>	
Diplocynodontinae (Brochu 1999)	<i>Diplocynodon ratelii</i> and all crocodylians closer to it than to <i>Alligator mississippiensis</i>	
Globidonta (Brochu 1999)	<i>Alligator mississippiensis</i> and all crocodylians closer to it than to <i>Diplocynodon ratelii</i>	
Alligatoridae (Cuvier 1807)	Last common ancestor of <i>Alligator mississippiensis</i> and <i>Caiman crocodilus</i> and all of its descendents	
Alligatorinae (Kälin 1940)	<i>Alligator mississippiensis</i> and all crocodylians closer to it than to <i>Caiman crocodilus</i>	
Caimaninae (Norell 1988)	<i>Caiman crocodilus</i> and all crocodylians closer to it than to <i>Alligator mississippiensis</i>	
Crocodyloidea (Fitzinger 1826)	<i>Crocodylus niloticus</i> and all crocodylians closer to it than to <i>Alligator mississippiensis</i> or <i>Gavialis gangeticus</i>	
Crocodylidae (Cuvier 1807)	Last common ancestor of <i>Crocodylus niloticus</i> , <i>Osteolaemus tetraspis</i> , and <i>Tomistoma schlegelii</i> and all of its descendents	Definition dependent on phylogenetic context.

(Continued)

TABLE 1 (Continued)

Name	Definition	Comments
Mekosuchinae (Balouet & Buffetaut 1987)	Last common ancestor of <i>Kambara murgonensis</i> , <i>Australosuchus clarkae</i> , <i>Pallimnarchus pollens</i> , <i>Baru darrowi</i> , <i>Trilophosuchus rackhami</i> , <i>Quinkana fortirostrum</i> , and <i>Mekosuchus inexpectatus</i> and all of its descendents	Definition adapted from Salisbury & Willis 1996
Tomistominae (Kälin 1955)	<i>Tomistoma schlegelii</i> and all crocodylians closer to it than to <i>Crocodylus niloticus</i>	Definition dependent on phylogenetic context.
Crocodylinae (Cuvier 1807)	<i>Crocodylus niloticus</i> and all crocodylians closer to it than to <i>Tomistoma schlegelii</i>	Definition dependent on phylogenetic context.
Osteolaeminae tax. nov.	<i>Osteolaemus tetraspis</i> and all crocodylians closer to it than to <i>Crocodylus niloticus</i>	New definition
Alternate definitions in context of molecular tree		
Crocodylidae (Cuvier 1807)	Last common ancestor of <i>Crocodylus niloticus</i> and <i>Osteolaemus tetraspis</i> and all of its descendents	
Crocodylinae (Cuvier 1807)	<i>Crocodylus niloticus</i> and all crocodylians closer to it than to <i>Osteolaemus tetraspis</i>	At present, this would be redundant with <i>Crocodylus</i>
Gavialidae (Adams 1854)	Last common ancestor of <i>Gavialis gangeticus</i> and <i>Tomistoma schlegelii</i> and all of its descendents	In a morphological context, Gavialidae would be redundant with <i>Gavialis gangeticus</i>
Tomistominae (Kälin 1955)	<i>Tomistoma schlegelii</i> and all crocodylians closer to it than to <i>Gavialis gangeticus</i>	
Gavialinae (Nopcsa 1923)	<i>Gavialis gangeticus</i> and all crocodylians closer to it than to <i>Tomistoma schlegelii</i>	

authorities included “protosuchians” and “mesosuchians,” but it may or may not have included “sphenosuchians.” The older applications of Crocodylia could thus apply to either Crocodyliformes or Crocodylomorpha. Indeed, some authorities included aetosaurs and parasuchians. There is thus no single traditional usage to which a phylogenetic definition could be applied.

REVIEW OF THE CROCODYLIAN FOSSIL RECORD

The advent of “modern” (eusuchian) crocodile morphology was traditionally linked to two features—ball and socket joints between the vertebrae (procoely) and internal nostrils (choanae) completely surrounded by the pterygoid bones of the

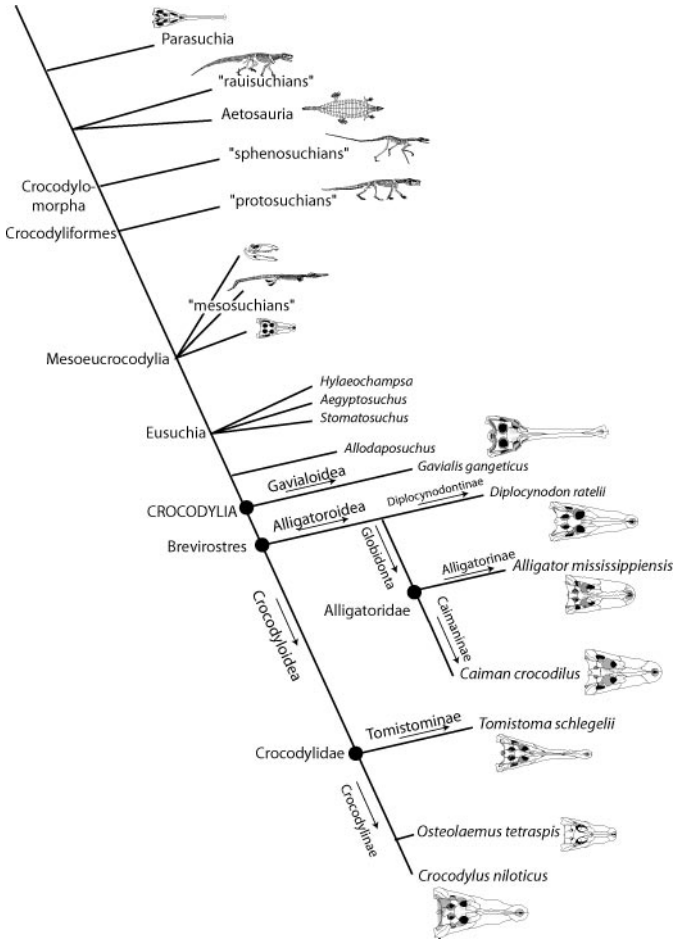


Figure 1 Diagram illustrating phylogenetic nomenclatural scheme for Crocodylia and related clades. Definitions are provided in Table 1. Arrows denote stem-based group names (groups including a species and anything more closely related to it than to another species), and black circles denote node-based group names (the last common ancestor of two or more species and all of its descendants).

palate (Huxley 1875). We now know that procoelous vertebrae occurred multiple times within Crocodyliformes (Norell & Clark 1990, Salisbury & Frey 2001), and because the palatal regions of important taxa are imperfectly preserved, the precise distribution of pterygoidal choanae is unclear (Brochu 1999a). Eusuchia is currently defined in reference to the last common ancestor of *Hylaeochampsia* and Crocodylia and all of its descendants.

The oldest eusuchian is *Hylaeochampsia vectiana* from the Barremian of the Isle of Wight (Owen 1874, Clark & Norell 1992). A stratigraphic gap separates

Hylaeochampsia from the next putative eusuchian occurrences in the Cenomanian (Stromer 1925, 1933). Character support for Eusuchia, as defined phylogenetically (Table 1), is weak; pterygoidal choanae are currently diagnostic for the group, as is the absence of a fossa on the medial wall of the supratemporal fenestra, but this diagnosis will doubtless change as new fossils are added to the analysis. Important new specimens of basal eusuchians and close eusuchian relatives (e.g., Buscalioni et al. 2001, Rogers 2003) are being described and will doubtless improve our understanding of character state distributions on that part of the tree.

The three primary branches of Crocodylia were distinct by the end of the Mesozoic (Figure 2). The earliest-known crocodylians are Campanian alligatoroids and gavialoids from North America and Europe (Lambe 1907; Schwimmer 1986; Williamson 1996; Wu et al. 1996; Buscalioni et al. 1997, 1999). Although crocodyloids first appear in the Maastrichtian, that lineage must also have been present in the Campanian. Moreover, the earliest alligatoroids and gavialoids include highly derived forms, indicating that the actual divergence between the three lineages was a pre-Campanian event.

The basalmost members of Alligatoroidea, Crocodyloidea, and *Borealosuchus* look like stereotypical “crocodiles,” with long, broad snouts outwardly resembling a modern American alligator or Nile crocodile. This is probably the ancestral condition for Brevirostres, and it may pertain further down the tree. Gavialoids and pristichampsines are derived when they first appear in the fossil record, but they may have also had “generalized” precursors yet to be discovered.

The split between alligators and crocodiles was traditionally based on a mixture of apomorphic and plesiomorphic “defining features.” A good example involves dental occlusion. Alligators have an overbite, and the teeth on the dentary bone of the lower jaw occlude lingual to those of the maxilla and premaxilla on the snout. In crocodiles, there is a distinct notch between the maxilla and premaxilla that receives the enlarged fourth dentary tooth. But alligator and crocodile patterns are both derived from a common ancestral condition (Brochu 1999a; Figure 3). In basal alligatoroids and crocodyloids, as well as pristichampsines, basal *Borealosuchus*, and immediate outgroups to Crocodylia, the dentary teeth occlude lingual to their maxillary counterparts—an alligator-like overbite. But there is still a notch between maxilla and premaxilla for the fourth (and sometimes third) dentary teeth. Alligatoroids ultimately lost the notch, and crocodyloids ultimately lost the overbite. A pattern much like that in derived crocodyloids also arises within Gavialoidea, *Borealosuchus*, and *Diplocynodon*. Retention of a notch between the maxilla and premaxilla (a plesiomorphy) was often confused with the lack of an overbite (an apomorphy) and led to the classification of several noncrocodyloid taxa as crocodyloids. One of the major conclusions of recent phylogenetic work is that many of the taxa we used to call “crocodylids” are actually closer to alligators or gharials, or are not members of any of the three extant lineages.

Gavialoidea

All known gavialoids are longirostrine (long-snouted) crocodylians, and many of the characters diagnosing Gavialoidea are related to the presence of a long, slender

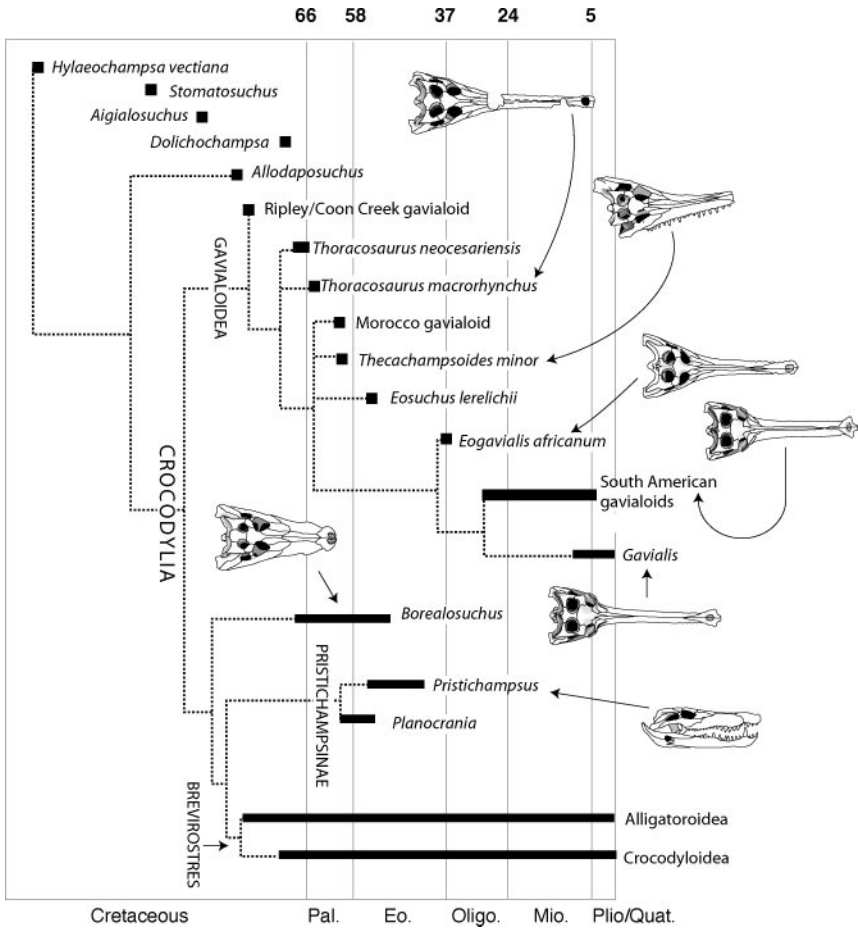


Figure 2 Basal phylogenetic relationships within Crocodylia and Gavialoidea. Topology based on Clark (1994), Brochu (1997a, 2002), and Buscalioni et al. (2001). “Ripley/Coon Creek gavialoid” is based on material in part referred to *Thoracosaurus neocesariensis* by Carpenter (1983); “Morocco gavialoid” is a new species described by Hua & Jouve (2003). The relationships of *Stomatosuchus*, *Aigialosuchus*, and *Dolicho-champsia* are uncertain, and these might not be eusuchians.

snout. Separation of the nasal bones from the narial rim, a long splenial symphysis, and a linear dentary tooththrow can all be seen as consequences of snout attenuation. But nonrostral features are also shared by members of this group, most notably a distinct forked hypophyseal keel on the axis.

The earliest long-snouted crocodylians in the fossil record are the “thoracosau- rians” of the Late Cretaceous and Paleocene (Figure 2). These were often categorized as tomistomines (e.g., Andrews 1906, Troxell 1925a, Steel 1973),

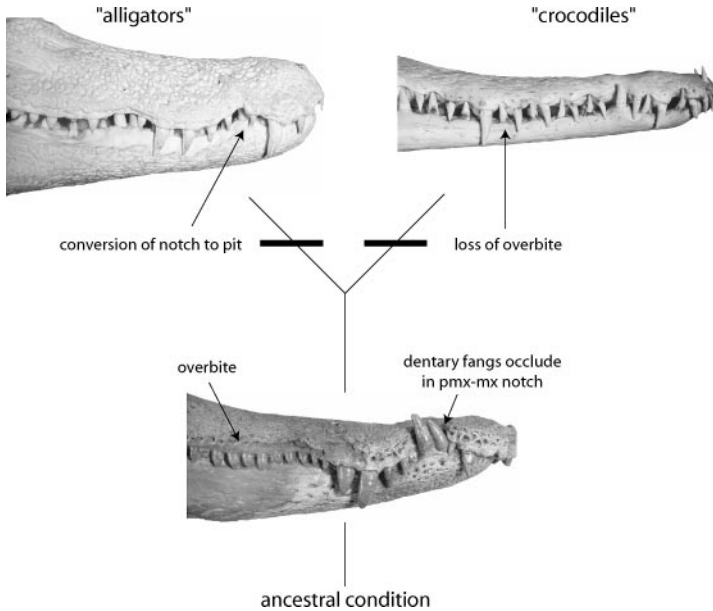


Figure 3 Polarity of occlusal transformations within Crocodylia. Specimens are, clockwise from bottom, *Leidyosuchus canadensis* (Late Cretaceous, Royal Ontario Museum 1903), *Paleosuchus trigonatus* (Recent, Field Museum 81980), *Crocodylus intermedius* (Recent, Field Museum 75659).

but phylogenetic analysis indicates a closer relationship between thoracosuars and *Gavialis*. The features that once grouped thoracosuars with *Tomistoma* are plesiomorphic; for example, the nasals and premaxillae contact each other in thoracosuars, but separation of the nasals and premaxillae is the derived condition, possibly related to continued emphasis on longirostry during gavialoid phylogeny.

The modern gharial (*Gavialis gangeticus*) is restricted to drainages on the Indian subcontinent and, with the exception of a possible historical occurrence in a brackish lagoon, is not found in saltwater (Singh & Bustard 1982, Ross 1998). But thoracosuars are usually found in marginal marine deposits (Troedsson 1924, Troxell 1925a, Piveteau 1927, Carpenter 1983, Gallagher 1993, Zarski et al. 1998, Brochu 2002, Hua & Jouve 2003, Storrs & Efimov 2000). Some later Tertiary gavialoids also occur in a nearshore context (Kraus 1998). All we can really say is that dead gavialoids were preserved in marginal marine deposits, but the large number of such occurrences suggests that they lived along the coasts and in estuaries.

Paleobiogeographic distributions suggest a capacity to cross marine barriers. Gavialoids occur as fossils in the Solomon Islands (Molnar 1982). An assemblage of gharials occurs in the Late Tertiary of South America, the closest relatives of which are from Asia and Africa. Without invoking range extensions back prior to the opening of the South Atlantic, South American gharials likely represent at least

one mid-Tertiary dispersal event from the Old World (Buffetaut 1982a, Langston & Gasparini 1997).

The present restriction of Gavialoidea to fresh water thus appears to be a comparatively recent phenomenon. Extant crocodylids have heavily keratinized oral surfaces and an elaborate set of salt-excreting glands on the tongue, features that allow prolonged exposure to high salinity. Alligatorids lack these features and are less frequently encountered in saltwater. *Gavialis* has a keratinized buccal surface, which is thought to reflect a capacity for salt tolerance in ancestral forms (Taplin & Grigg 1989, Leslie & Taplin 2001). Gavialoid capacity to cross marine barriers was thus predicted on the basis of oral morphology. Although our current understanding of gavialoid phylogeny does not require a “marine phase,” it is consistent with the idea that gavialoids were plesiomorphically capable of withstanding saltwater exposure.

***Borealosuchus* and Pristichampsinae—Outgroups to Brevirostres**

Borealosuchus is primarily known from the Late Cretaceous through Eocene of western North America (Brochu 1997b, Wu et al. 2001a; Figure 2), but fossils from the Cretaceous of the Atlantic Coastal Plain (Parris et al. 1997, Schwimmer 2002) also belong to it (C.A. Brochu, personal observation). A combination of generalized morphology and basal phylogenetic position may make *Borealosuchus* a good model of what the ancestral crocodylian looked like. Some of these, including the basalmost species (*B. sternbergii*), have been very densely sampled. *Borealosuchus* shares similarities with some basal alligatoroid lineages (Rauhe & Rossmann 1995), and most *Borealosuchus* used to be referred to the basal alligatoroid taxon *Leidyosuchus*, but the weight of character evidence draws *Borealosuchus* outside Brevirostres; similarities with early alligatoroids are shared primitive features or independent derivations (Brochu 1997b, 1999; Wu et al. 2001a,b).

Pristichampsines (Figure 2) are among the most interesting of crocodylians. These are “zipodont” taxa with laterally compressed, dorsoventrally deep snouts and laterally compressed teeth. The teeth are sometimes serrated. Well-preserved specimens are known from the Paleocene and Eocene of Eurasia and North America (Kuhn 1938, Berg 1966, Langston 1975, Li 1984, Efimov 1993). Dental remains possibly referable to Pristichampsinae may extend the temporal range of the group into the Oligocene of Eurasia (Berg 1984, Rossmann 1998). The largest examples suggest animals between 2 and 3 m in total length.

Pristichampsines are sometimes thought to have been “more terrestrial” than other crocodylians, perhaps trying to fill the large terrestrial predator niche left vacant by nonavian theropod dinosaurs at the end of the Mesozoic. Altirostral skulls with deep snouts occur in small alligatorids, including extant *Paleosuchus*. But the pristichampsine postcranial skeleton is also very derived, with somewhat blunt unguals (leading some to call pristichampsines “hoofed crocodiles”) and highly modified appendicular muscle attachments. A recent functional review of pristichampsine morphology by Rossmann (1999; 2000a,b,c) supports increased

terrestriality, at least for adult forms, even to the point of suggesting facultative bipedality.

Alligatoroidea

Alligatoroids (Figures 4 and 5) are predominantly from the Western Hemisphere, but they were common in Eurasia for parts of the Tertiary, and a single species (*Alligator sinensis*, the Chinese alligator) occurs in Asia today. A single species survives in North America (*A. mississippiensis*), and five to seven caiman species (depending on how one divides the *Caiman crocodilus* complex) occur throughout Central and South America (Ross 1998).

However distinctive living alligatorids are now, the most primitive representatives were plesiomorphic enough that they were classified closer to crocodiles. *Leidyosuchus canadensis*, from the Campanian of Alberta, is broadly similar to basal *Borealosuchus* and early crocodyloids—a long, broad, flat skull with one or two dentary teeth occluding in a notch between the maxilla and premaxilla.

Another basal alligatoroid is the gigantic *Deinosuchus*, known from both sides of the Western Interior Seaway during the Campanian (Holland 1909, Colbert & Bird 1954, Schwimmer 2002). Although previous work put the total length of this animal at over 15 m, more recent work fixes the size of the largest known specimens at between 9 and 12 m (Erickson & Brochu 1999). The restored skull often figured in books is based on a very incomplete specimen with missing portions (which is most of the skull) modeled on modern *Crocodylus*. Newly collected specimens (Schwimmer 2002) reveal a very different-looking animal, and full description of this material will clarify its relationships with other alligatoroids.

More derived alligatoroids share a lack of the occlusal notch, at least early in ontogeny (Brochu 1997b, 1999a), and can be divided into two stem-based groups: Diplocynodontinae and Globidonta. Most diplocynodontines continue to reflect the ancestral crocodylian generalist morphotype. *Diplocynodon* retains the long, broad snout found in basal brevirostrines and was a common crocodylian for most of the Tertiary in Europe (e.g., Pomel 1847, Ludwig 1877, Kuhn 1938, Berg 1966, Buscalioni et al. 1992, Vignaud 1996, Ginsburg & Bulot 1997, Brinkmann & Rauhe 1998, Pereda Suberbiola et al. 2001). *Baryphracta* is a small, blunt-snouted animal from the Eocene of Germany (Frey et al. 1987) that shares paired ventral osteoderms and some other postcranial modifications with *Diplocynodon* (Rauhe & Rossmann 1995, Brochu 1999a).

Globidontans are very derived upon their first appearance in the Campanian. Throughout the Late Cretaceous and Tertiary, they typically had short, broad snouts and enlarged teeth toward the back of the mouth, and some taxa may have been small, not exceeding 1.5 m in total length at adulthood. This suite of morphological features suggests some sort of ecological difference from modern *Alligator* or *Caiman*, but the specific functional meaning behind it is unclear. These animals are sometimes thought to have been adapted for hard-shelled prey (Abel 1928, Carpenter & Lindsey 1980).

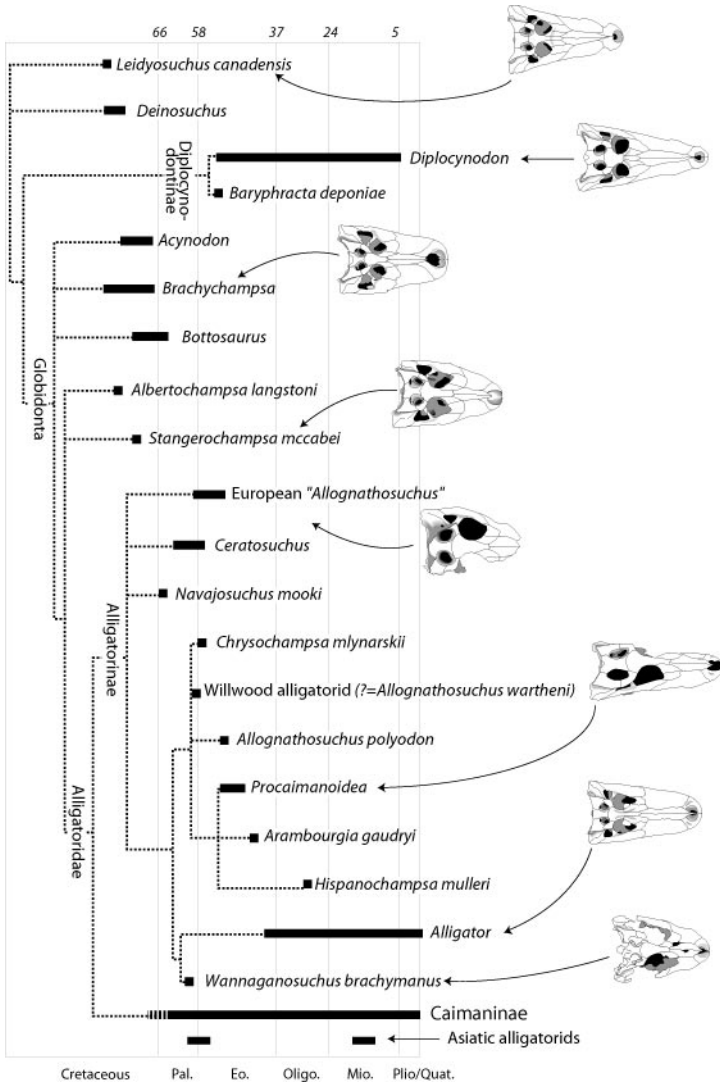


Figure 4 Basal phylogenetic relationships within Alligatoroidea and Alligatorinae. Topology based on Brochu (1999a, 2003) and Buscalioni et al. (1997, 1999).

The earliest alligatorines (Figure 4) maintained bulbous rear dentition, short snouts, and robust mandibles. The name *Allognathosuchus* is frequently given to these forms, though this assemblage is of questionable monophyly (Wu et al. 1996; Brochu 1999a, 2003). Indeed, bulbous teeth and a robust mandibular symphysis persist in the earliest species of *Alligator* from the Late Eocene, suggesting that the

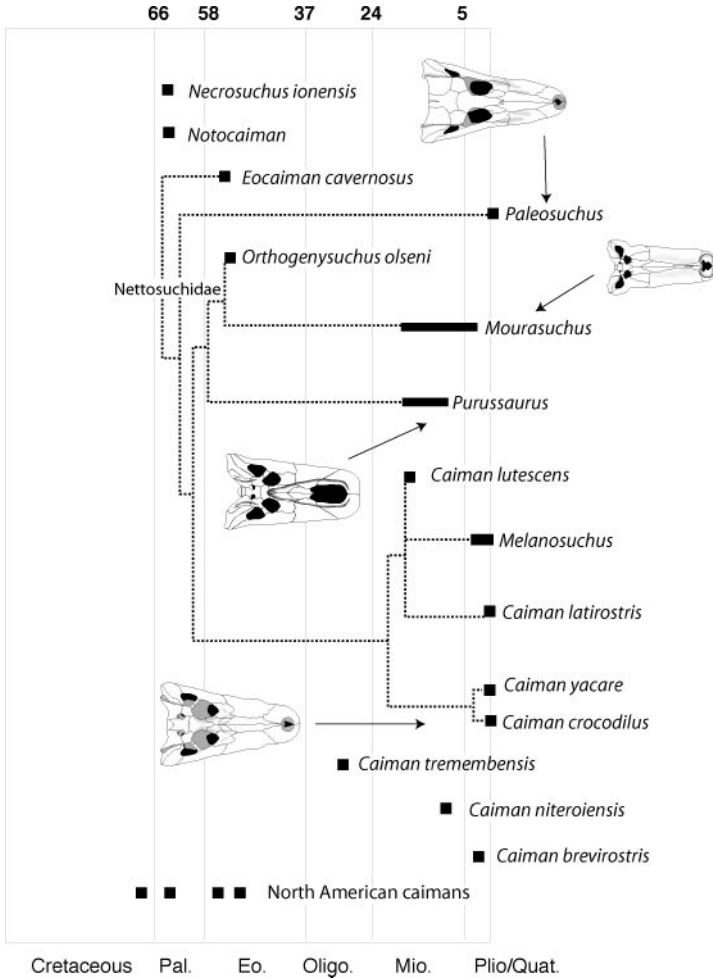


Figure 5 Phylogenetic relationships among caimans. Topology based on Brochu (1999a).

generalized condition of later *Alligator* (including *A. mississippiensis*) is a reversal. At least one other digression from the ancestral alligatorine bauplane occurred in *Procaimanoidea*, which has a rather deep snout closely resembling that of modern *Paleosuchus* and laterally compressed (but unserrated) teeth.

Alligatorines are present in the Tertiary of Europe, where they represent at least two dispersal events from North America (Brochu 1999a, 2003). After the Oligocene, the alligatorine record is dominated by North American *Alligator*. The systematics of Late Tertiary *Alligator* need revision, but *A. mississippiensis* appears to have been present from at least the Pleistocene (Preston 1979, Holman 1995).

The fossil record of caimans (Figure 5) is the least complete of any crocodylian lineage. The earliest known alligatorines are from the Early Paleocene (Brochu 1999a), demonstrating that the alligatorine-caimanine split had occurred at least by then. A few caimans are known from the Paleocene and Eocene (and possibly Late Cretaceous) of North America (Busbey 1989, Bryant 1989), but with one exception, their relationships with South American caimans are untested. The terrestrial stratigraphic record of South America is less complete than that of North America, and only a handful of caimans are known from pre-Miocene deposits (e.g., Rovereto 1912, Simpson 1933, Rusconi 1937, Langston 1965, Chiappe 1988, Souza Filho & Bocquetin 1991, Gasparini 1996), few of which have been included in phylogenetic analyses.

When caimans finally appear in substantial numbers in South America, they include some of the most bizarre crocodylians of all time. Included among these are the nettosuchids, with absurdly long, broad, flat snouts and large numbers of very small teeth (Price 1964, Langston 1965, Bocquetin 1984). The large South American nettosuchid *Mourasuchus* resembled the putative eusuchian *Stomatosuchus* from the Late Cretaceous of Egypt (Stromer 1925). An Early Eocene fossil from North America (*Orthogenysuchus olseni*) apparently represents a North American nettosuchid (Brochu 1999a). *Mourasuchus* and *Orthogenysuchus* were clearly specialized for something, but we have yet to understand what that could be.

Another caiman oddball is *Purussaurus* (Bocquetin et al. 1991). Although a close nettosuchid relative (Brochu 1999a), *Purussaurus* seems to be the antinettosuchid—where *Mourasuchus* had an extremely flat skull with tiny teeth, *Purussaurus*' rostrum was broad and deep and the teeth were robust. The external naris (nostril) was very large relative to skull size, and in the most derived form (*P. brasiliensis* from the Miocene of Brazil), the nasal bones are very small. One can literally put one's head in the narial aperture and look around. Some specimens of *Purussaurus* were large enough to rival *Deinosuchus* in size, and *Mourasuchus* reached impressive dimensions as well.

The origins of modern caiman species are paleontologically obscure. The lineage including the dwarf caiman (*Paleosuchus*) is unknown from fossils, even though it dates back to at least the Early Eocene on the basis of fossil occurrences elsewhere among caimans. A form related to the broad-snouted caiman (*C. latirostris*) and black caiman (*Melanosuchus*) is known from the Miocene (Langston 1965), and *Melanosuchus* itself first appears in the Pliocene (Medina 1976). Additional caimans are known from the Neogene (Patterson 1936, Souza Filho 1987, Cione et al. 2000, Piña & Argañaraz 2000) that may be related to extant species.

Crocodyloidea

Only a single crocodyloid is known from the Cretaceous—the Maastrichtian *Prodiplocynodon langi* from Wyoming (Mook 1941). *Prodiplocynodon* is known from a single skull without the lower jaw, and most cranial sutures are not visible.

As fragmentary as our knowledge of *Prodiplocynodon* is, it nonetheless reveals an animal not fundamentally different in overall body shape from the most primitive alligatoroids.

Crocodyloids (Figure 6) occur throughout the Northern Hemisphere during the Early Tertiary (Mook 1921a,b, 1940; Troxell 1925b; Young 1964; Berg 1966; Vasse 1992a,b; Efimov 1993; Angielczyk & Gingerich 1998) and are sometimes referred to as *Asiatosuchus*. The type species (*A. grangeri*) from Mongolia is imperfectly

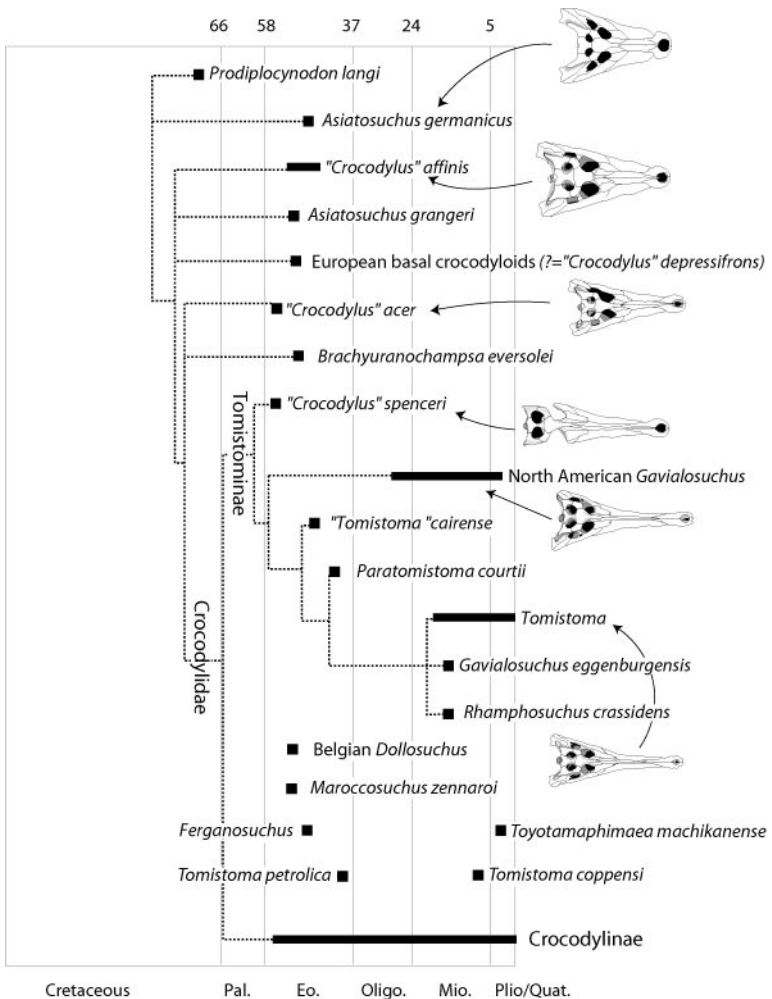


Figure 6 Basal phylogenetic relationships among crocodyloids and tomistomines. Topology based on Brochu (1997a, 2000), Brochu & Gingerich (2000), and Head (2001).

known, but it shares some derived character states with Eocene crocodyloids from North America and Europe that are lacking in the best-known species assigned to *Asiatosuchus*, *A. germanicus* from the Eocene of Germany. Most notably, *A. grangeri* and these more derived forms share a lack of a splenial symphysis, a frontoparietal suture completely excluded from the supratemporal fenestrae, and the beginnings of an interfingering occlusion (Brochu 1997a, 2000).

Relationships at the base of Crocodylidae are unclear (Figures 6 and 7). “*Crocodylus*” *megarhinus* is a common crocodile from the Eocene-Oligocene Fayum sequence in Egypt (Andrews 1906, Mook 1927, Müller 1927), and I regard “*C.*” *articeps* as a junior synonym. Mekosuchines were regarded as the sister group to Crocodylidae by Salisbury & Willis (1996) and as basal crocodylines by Brochu (1997a, 2000).

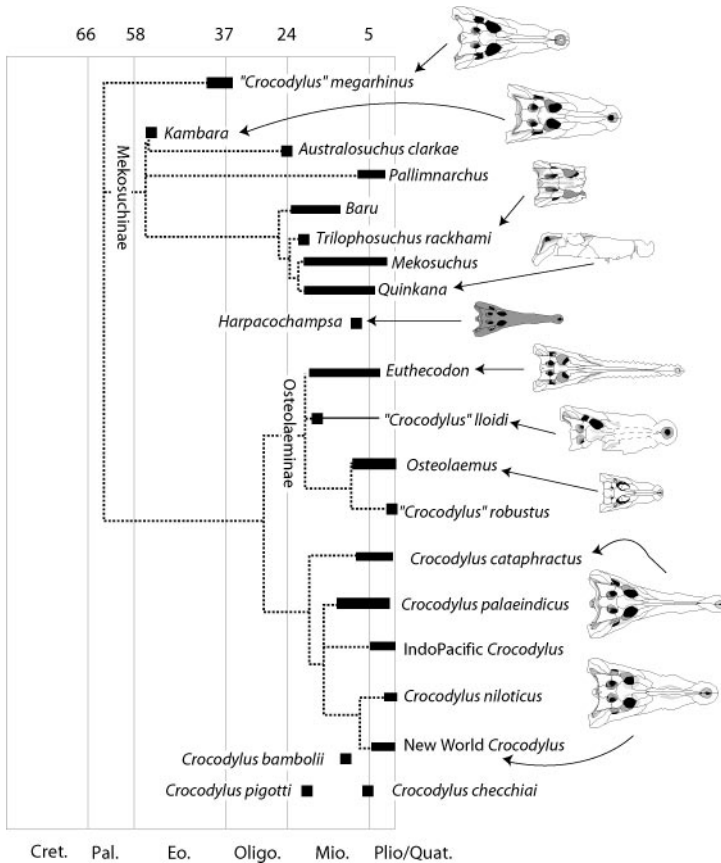


Figure 7 Phylogenetic relationships among crocodylines. Topology based on Salisbury & Willis (1996) and Brochu (1997a, 2000). The skull of *Harpacochampsia* shown in this figure is hypothetical; the skull of this taxon is imperfectly known.

Among new crocodylian discoveries of the late twentieth century, Mekosuchinae may be the most important, not only because it added to our knowledge of Late Tertiary crocodylian diversity, but also because it led to the discovery of Late Tertiary crocodyloid endemism. The group was initially based on a strange small animal from the Holocene of New Caledonia (Buffetaut 1983, Balouet & Buffetaut 1987). Named *Mekosuchus*, it displayed an odd combination of derived and ancestral features and was initially thought to be a late-surviving member of a non-crocodylian group. It was also evidently part of the menu of the inhabitants of New Caledonia prior to European contact. More complete *Mekosuchus* material has since been found in Australia, along with a diverse assemblage of closely related crocodylians that seem to form an endemic assemblage in Australia (Willis et al. 1990; Willis & Molnar 1991; Willis 1993, 1997a,b, 2001; Megirian 1994; Figure 7). The earliest and basal-most forms were generalized in appearance (Willis et al. 1993, Salisbury & Willis 1996), but by the end of the Tertiary the group included pristichampsine-like predators with serrated teeth, small blunt-snouted forms similar to extant *Osteolaemus* or extinct *Allognathosuchus*, and possibly a longirostrine form (Megirian et al. 1991). They persisted until the Quaternary in Australia. Mekosuchines are also known from Vanuatu and Fiji (Worthy et al. 1999, Mead et al. 2002, Molnar et al. 2002) and may have been present in New Guinea (de Vis 1905, Plane 1967).

Mekosuchinae is not the only endemic crocodyloid radiation of the Tertiary. Ginsburg & Buffetaut (1978) and Buffetaut (1985) regarded the bizarre longirostrine crocodylian *Euthecodon*, with laterally protruding alveoli that make the skull resemble the head of a sawfish, as an endemic African taxon closer to *Crocodylus* than to *Tomistoma*, with which it had formerly been allied (Steel 1973). Several other African crocodylians are closely related to *Euthecodon*, including the living African dwarf crocodile, *Osteolaemus tetraspis* (Brochu 2000). This group is herein called Osteolaeminae. *Osteolaemus* rarely exceeds 2 m in total length and has a blunt snout reminiscent of a dwarf caiman. Other osteolaemines include "*Crocodylus*" *robustus* from the Holocene of Madagascar, which looks like an oversized *Osteolaemus* with horns (Barbour 1918, Mook 1921c), and "*Crocodylus*" *lloidi*, which resembles modern *Crocodylus* in its overall appearance (Maccagno 1948, Tchernov 1986, Pickford 1996).

Crocodylus

Fossils as old as the Cretaceous have long been classified as *Crocodylus*. The characters used to do so were largely plesiomorphic—retention of a maxillary-premaxillary notch, exclusion of the prefrontal from the maxilla, broad snout tapering toward the naris, and so on (e.g., Steel 1973). This led to the view that *Crocodylus* was an ancient and conservative genus.

But *Crocodylus* is a much more recent radiation. Protein distance analyses in the early 1980s (Densmore 1983) indicated very low levels of divergence between modern species. More recent DNA sequence-based analyses are congruent with

this result (White & Densmore 2001). Stratigraphic estimates of the longevity of *Crocodylus* were 20 times older, but this reflects the vague meaning of *Crocodylus* in the older paleontological literature. Phylogenetic analysis of fossil crocodylians reveals a distant relationship between extant *Crocodylus* and the majority of fossils called *Crocodylus* (Brochu 2000). This is a striking example of the need for clear phylogenetic nomenclature—the “conflict” had nothing to do with the data and everything to do with different applications of the name *Crocodylus*.

According to some datasets (Densmore & White 1991, Brochu 2000), the basal-most species within *Crocodylus* is the African sharp-nosed crocodile, *Crocodylus cataphractus* (Figure 7). This has long been viewed as an aberrant species, and not all workers agreed that it belonged to *Crocodylus* (e.g., Aoki 1976, 1992). Interestingly, some recent sequence analyses based on both mitochondrial and nuclear genes draw *C. cataphractus* closer to *Osteolaemus* than to other *Crocodylus* (White & Densmore 2001). This would make *C. cataphractus* part of the endemic African lineage. Fossils related to *C. cataphractus* are known from the Miocene and Pliocene of Africa (Tchernov 1986, Aoki 1992, Pickford 1994).

The fossil record for the rest of *Crocodylus* is sparse. It is well known from the Mio-Pliocene Siwaliks sequence of the Indian subcontinent. These may represent a single fossil species, and although it resembles the modern Indian mugger (*C. palustris*) in some respects, it also lacks features that draw *C. palustris* closer to a group including other *Crocodylus* from the Indian and Pacific oceans, including the world’s most dangerous reptile, the saltwater crocodile (*C. porosus*). Monophyly of an Indopacific *Crocodylus* assemblage is modestly supported by morphology and some molecular information. Fossils putatively belonging to this group are from the Pleistocene of Java (Janensch 1911) and Pliocene or Pleistocene of Australia (Willis 1997b).

Likewise, some datasets suggest that the four living species of *Crocodylus* in the New World form a clade, and that the Nile crocodile (*C. niloticus*) is closely related to it (Figure 7). First appearance of *Crocodylus* in the New World is at around 4 Ma ago (Miller 1980), and first demonstrable *C. niloticus* are between 2 and 3 Ma ago (Tchernov 1986). A Neogene radiation within *Crocodylus* implies at least one crossing of a major marine barrier; if the New World assemblage last shared an ancestor with other *Crocodylus* within the past 10 to 15 Ma, dispersal across either the Atlantic or (less likely) the Pacific is necessary.

Tomistominae

Tomistoma schlegelii is the only living member of this group, and it is found in freshwater lakes and rivers of Southeast Asia and parts of Indonesia. Like *Gavialis*, it has a long, slender rostrum. Although long snouts are thought to be adaptations for catching fish, *Tomistoma*’s diet is not as fish-centered as that of *Gavialis* (Ross 1998).

The oldest fossils attributable to Tomistominae are from the Early Eocene of Europe and northern Africa (Owen 1850, de Zigno 1880, Swinton 1937, Jonet

& Wouters 1977; Figure 6). These are just barely tomistomines—they resemble basal crocodyloids, especially *Brachyuranochampsa*, and in at least some the nasal bones still contact the narial rim. But there is a long splenial symphysis, and like other tomistomines (but unlike gavialoids), the splenial is very constricted in the symphyseal region, forming a very slender “V.” These animals also share features with crocodylids not found in gavialoids, such as an enlarged fifth maxillary alveolus, and do not have some of the crocodylian-level plesiomorphies found in gavialoids, such as robust postorbital bars (Norell 1989, Brochu 1997a).

Tomistomines are known from the Neogene of North America (Mook 1921d, Auffenberg 1954, Myrick 2001). Most have been called *Gavialosuchus*, and they first appear in mainland deposits in the Oligocene (Erickson & Sawyer 1996), but the lineage had to have been present in the Eocene. The type species of *Gavialosuchus* (*G. eggenburgensis* from the Miocene of Austria) is closer to *Tomistoma* than to New World “*Gavialosuchus*” (Brochu & Gingerich 2000). A probable tomistomine is also known from the Eocene of Jamaica (Berg 1969). Tomistomines have been reported from the Tertiary of South America (Langston 1965, Gasparini 1996), but a close relationship with *Tomistoma* has not been tested phylogenetically.

Tomistomines were broadly distributed throughout the Old World, including Europe, mainland Asia, Africa, and Japan (e.g., Li 1975, Aoki 1983, Mlynarski 1984, Buffetaut et al. 1984, Efimov 1993, Pickford 1994, Rossmann et al. 1999, Rossmann 2000d). The geographic distribution of tomistomines resembles that of gavialoids in certain respects. In particular, some groups seem to have been residents of coastal and estuarine settings, despite the restriction of modern *Tomistoma* to fresh water. This is true for New World “*Gavialosuchus*” and an array of derived Miocene tomistomines from the Mediterranean region (Hulke 1871; Lydekker 1886; Antunes 1961, 1987). Like gavialoids, tomistomine distribution in the Tertiary implies the crossing of marine barriers (Brochu 2001a).

CONTROVERSIES AND UNFINISHED BUSINESS

Molecules Versus Morphology: Relationships of *Gavialis*

Morphologists have long favored a distant relationship between *Gavialis* and all other living crocodylians, and an ancient divergence, in the Cretaceous or even Jurassic, between *Gavialis* and any other living crocodylian (Kälin 1931, 1955; Tarsitano et al. 1989; Norell 1989; Brochu 1997a). But molecular datasets overwhelmingly support a sister-taxon relationship between *Gavialis* and *Tomistoma* (Densmore 1983; Densmore & Owen 1989; Densmore & White 1991; Gatesy & Amato 1992; Hass et al. 1992; Gatesy et al. 1993, 2003; White & Densmore 2001; Harshman et al. 2003; D. Ray & L. Densmore, personal communication), and some molecular analyses put the divergence between *Gavialis* and any other living crocodylian in the Late Tertiary (Densmore & Dessauer 1984, Hass et al. 1992). The Indian gharial thus presents us with two distinct conflicts (Figures 8 and 9):

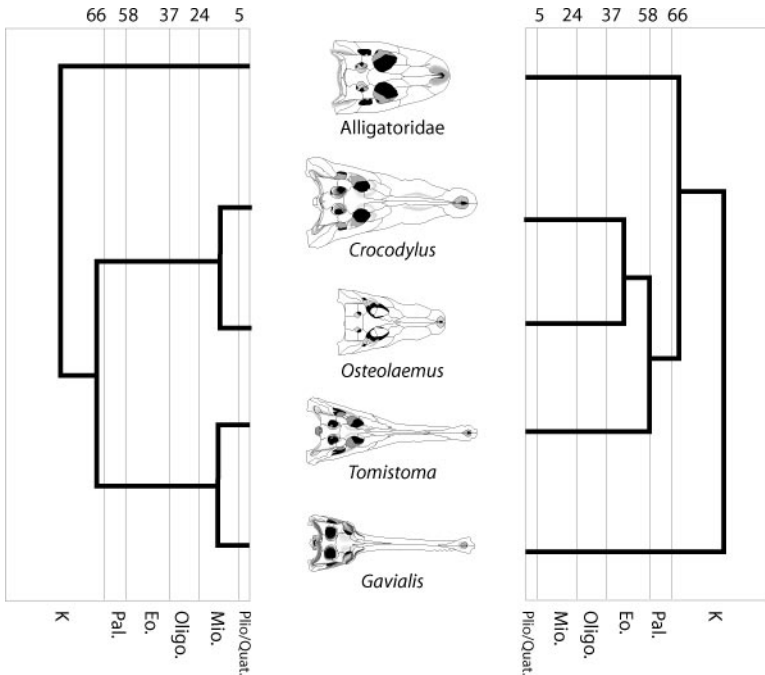


Figure 8 Conflict between morphological (*left*) and most molecular (*right*) datasets with regard to crocodylian phylogeny and divergence timing.

topological (the relationships of *Gavialis* to other crocodylians) and temporal (the divergence time between *Gavialis* and any other living crocodylian).

Molecules and morphology are both heritable and, ultimately, share the same phylogenetic history. They should be telling us the same thing—and for the most part, they are. Removal of *Gavialis* from the analysis results in nearly identical results regardless of source of data. Alligatoridae is monophyletic, caimans form a coherent group, *Paleosuchus* is outside a clade including other caimans, and alligators and caimans represent an ancient divergence at or near the Cretaceous-Tertiary boundary. *Crocodylus* is monophyletic (mostly) and recently diverged, *Osteolaemus* is its closest living relative, and *Tomistoma* is closer to *Crocodylus* than to *Alligator*. Forcing the morphological hypothesis on any given molecular dataset (or vice versa) usually results in tree length increases of less than 4%, and Wilcoxon signed rank tests usually fail to detect a statistically significant difference between hypotheses (Brochu & Densmore 2001). However, addition of *Gavialis* renders the competing topologies inconsistent with each other (Figure 9).

The first morphological analyses to take advantage of modern phylogenetic methods were limited with respect to taxon and character sampling. This raised the specter of a morphological version of the long-branch attraction

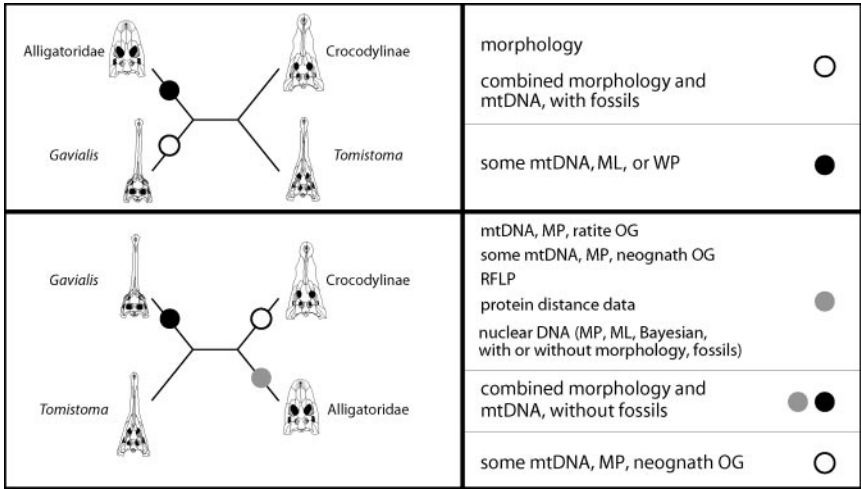


Figure 9 Topological conflict between various data sets for Crocodylia. Dots indicate different rooting placements (the inferred position of the base of the tree). Information on nuclear DNA analyses from Gatesy et al. (2003) and Harshman et al. (2003); all other analyses described in Brochu & Densmore (2001). Abbreviations: ML, maximum likelihood; MP, maximum parsimony; mtDNA, mitochondrial DNA; OG, outgroup; WP, weighted parsimony.

problem—*Tomistoma* and *Crocodylus* independently acquired similarities that overwhelmed any similarity between *Gavialis* and *Tomistoma*. If this were the case, inclusion of fossils might have supported a fundamentally different tree with respect to living taxa. As one gets closer to the root of a clade, taxa are expected to more closely reflect the ancestral condition, effectively pruning any long phylogenetic branches. To date, addition of fossils has not changed the underlying relationships among living crocodylians (Salisbury & Willis 1996; Brochu 1997a, 2002; Brochu & Gingerich 2000; Buscalioni et al. 2001; Hua & Jouve 2003).

The first molecular analyses on crocodylians (Densmore 1983, Densmore & Owen 1989, Densmore & White 1991, Hass et al. 1992) all supported essentially the same tree, with *Gavialis* closer to *Tomistoma*, but applied methods thought to be less reliable when divergences are very old or when branch lengths are heterogeneous (e.g., Huelsenbeck 1995). If the problem is methodological, application of sequence-based approaches should tip the balance. So far, this has not happened. Mitochondrial sequence data usually support the *Gavialis*-*Tomistoma* linkage (Gatesy et al. 1993, White & Densmore 2001, Ray et al. 2001), although some of this can be made to support a morphological topology with weighted parsimony or maximum likelihood methods (Brochu & Densmore 2001). Nuclear genes also strongly support a *Gavialis*-*Tomistoma* clade when analyzed using

maximum parsimony, maximum likelihood, and Bayesian analysis (Gatesy et al. 2003, Harshman et al. 2003; D. Ray & L. Densmore, personal communication). Thus, molecular data are as stable as morphology in the face of new data and new methods.

The most puzzling aspect of this debate is that although *Gavialis* and *Tomistoma* are very similar in overall shape, they are being drawn together not by morphology, but by molecules. It is usually the other way around (e.g., Marshall 1992, McCracken et al. 1999, Naylor & Adams 2001)—when molecular data suggest a more distant relationship between similar-looking organisms traditionally classified together, a closer look at the morphological details reveals overlooked differences or a functional linkage related to independently evolved ecological similarities. If the gharial problem followed the same pattern, molecular data would have argued against a monophyletic group including *Gavialis* and *Tomistoma* based on morphology.

Similarities between *Gavialis* and *Tomistoma* are largely centered on the snout and jaw apparatus, and these similarities diminish as more primitive gavialoids and tomistomines are considered (Trueman 1998, Brochu 1999b, Gatesy et al. 2003). Support for clades including *Tomistoma* and excluding *Gavialis* (e.g., Crocodylidae, Brevirostres) is spread throughout the skeleton, from the skull to the hip. Gavialoid and tomistomine snouts are outwardly similar, but they differ in detail—for example, gavialoids have more teeth than other living crocodylians, suggesting that teeth were added as the snout lengthened, but *Tomistoma* has the same dental formula as *Crocodylus*, with the tooth sockets spread farther apart. Morphological evidence strongly argues against homology of the long-snouted condition in *Gavialis* and *Tomistoma*, even if they are the closest living relatives.

The results of a combined analysis depend heavily on the relative amounts of information included. Poe (1997) combined 97 RFLP characters, 12s rDNA sequence data (79 informative bases), and 64 nonmolecular characters (mostly osteological), and the resulting most parsimonious trees were congruent with the standard molecular topology. Brochu (1997a) used the same molecular information but instead included 164 morphological characters. When fossils were excluded from the ingroup, the result was congruent with the standard molecular hypothesis. When fossils were included in the ingroup, the preferred topology was consistent with that preferred by morphology alone (Figure 9). Ongoing total evidence analyses, including additional mitochondrial and nuclear genes, indicate that a bolstered molecular component results in a preferred topology for extant taxa consistent with that preferred by individual molecular datasets, with tomistomines forming an unresolved assemblage at the base of Gavialoidea (Brochu & Densmore 2001, Gatesy et al. 2003, Harshman et al. 2003). In this case, the tree is very similar to that obtained when the morphological dataset, with fossils, is constrained to make *Gavialis* and *Tomistoma* close relatives (Figure 10; Brochu 1997a).

Combined analyses are always informative, regardless of whether we view the results as the hypothesis maximizing the explanatory power of all available information (and thus the best estimate of phylogeny) or as a reflection

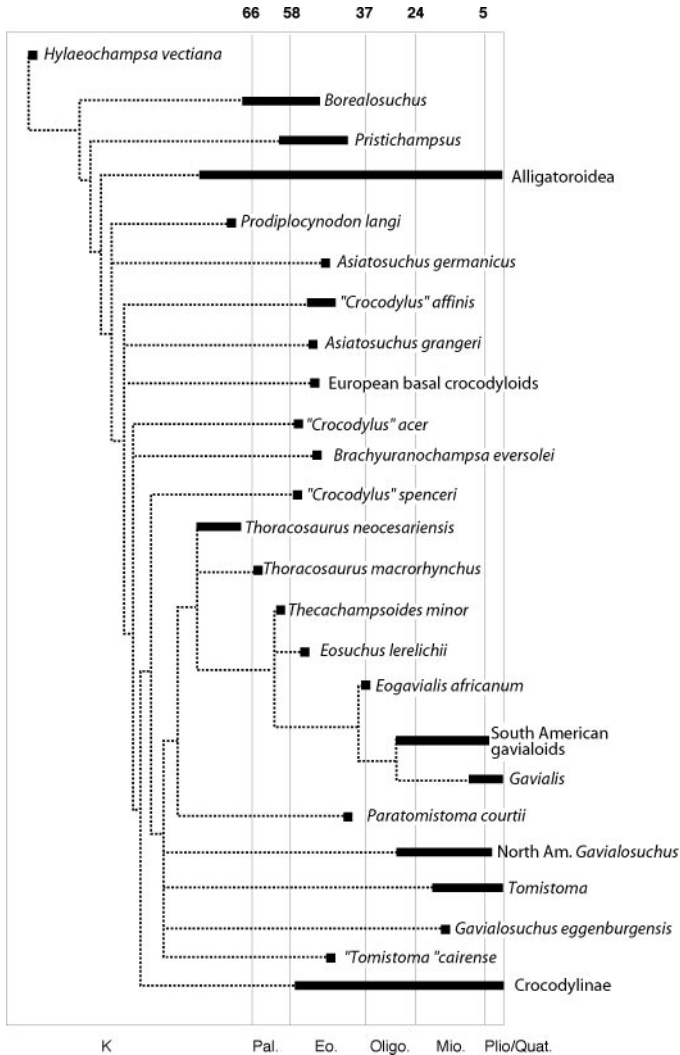


Figure 10 Phylogenetic relationships among fossil crocodylians based on morphology if the analysis is constrained to support the standard molecular hypothesis with respect to *Tomistoma* and *Gavialis*. Results based on a parsimony analysis of 164 morphological characters; matrices provided in Brochu (1999a, 2000) and Brochu & Gingerich (2000).

of the strongest of two or more competing signals. But we must continue to improve our available pool of data. Inclusion of new genes is an obvious direction, and this is underway. We can also improve our morphological dataset, both by including new information from soft tissue or from the complex internal details now made available by imaging technology (e.g., Rowe et al. 1999)

and by including the fossils that have not yet been included in a phylogenetic analysis.

Molecules Versus Morphology: Divergence Timing of *Gavialis*

The temporal aspect of the *Gavialis* problem is odd. The more celebrated disputes, such as the origins of modern mammal and bird lineages, involve molecular divergence estimates much older than those supported by the fossil record. In this case, the molecular divergence estimate is much younger than what fossils indicate (Figure 8). Some protein divergence levels between *Gavialis* and *Tomistoma* were low enough to imply a split within the past 10 Ma (Densmore & Dessauer 1984). This is roughly 40 Ma after the earliest known tomistomines and 70 Ma after the earliest known gavialoids. A recent mitochondrial DNA sequence analysis supports an older divergence, but still within the Tertiary (Brochu & Densmore 2001).

Timing disputes are fundamentally different from topological dataset incongruence. Such disputes have less to do with the data and more to do with expectations. We either expect our methods based on molecular data to provide reliable estimates of absolute divergence time or we expect the fossil record to provide a roughly accurate reflection of speciation dates. Both expectations are likely to be off: We know molecular dating techniques are imperfect, and we know the fossil record is incomplete.

We can quantify the fit between a particular phylogenetic hypothesis and the stratigraphic distribution of ingroup taxa. Some approaches measure relative congruence and ask whether the order of appearance on a cladogram matches the order of appearance in the stratigraphic record, regardless of the amount of time involved (e.g., Huelsenbeck 1994). Using these, the preferred morphological hypothesis is virtually indistinguishable from one designed to reflect the molecular hypothesis by constraining *Gavialis* and *Tomistoma* as close relatives (Brochu 1997a). Other approaches consider absolute time and the amount of missing records implied by extending the stratigraphic ranges of some taxa to the first appearance data of their closest relatives (e.g., Benton & Storrs 1994, Siddall 1998, Pol & Norell 2001). In this case, the different hypotheses are quite different—the preferred molecular topology requires 25% more range extension and cannot be distinguished from a random distribution of first appearance data (Brochu 1997a).

Why do these hypotheses differ with respect to absolute time expectations but not order of appearance? For the most part, both hypotheses are the same. Thoracosaurids are closer to *Gavialis* than to *Tomistoma*, whether tomistomines are gavialoids or not (Figure 10). This extends the range of several lineages minimally from the Eocene to the Late Cretaceous. It also renders Tomistominae in the morphological sense paraphyletic (Figure 10). These alterations have little impact on the fit between clade rank and age rank, but greatly increase the amount of missing record.

Crocodylians live in their own depositional environments and have dense skeletons. One would expect some sort of phylogenetic reflection in their stratigraphic

mirror, and the morphological hypothesis does fit the stratigraphic distribution of crocodylians better than the molecular competitor. Nevertheless, there are some significant gaps in the crocodylian record. The South American, Australian, and African records are especially spotty for the Paleogene. We also face ghost lineages for New World "*Gavialosuchus*," and the record for crocodyloids between the Maastrichtian and the Ypresian is sparse. The most significant, however, is the gap between the oldest eusuchians in the Barremian and the earliest known crocodylians in the Campanian. The derived nature of the earliest known gavialoids and globidontans indicates an unsampled history of unknown duration, and the few eusuchian occurrences in the middle Cretaceous are fragmentary (Stromer 1925, 1933; Persson 1960). For this reason, we should not reject a phylogenetic hypothesis purely on stratigraphic grounds.

Uncertain Relationships Within *Crocodylus*

Most datasets agree on monophyly of *Crocodylus*. They also agree on a Late Tertiary divergence among living species (Brochu 2000). But there is little consensus on within-group relationships. Some molecular data (Densmore 1983, Densmore & White 1991) and morphology (Brochu 2000) support a sister-group relationship between *Crocodylus cataphractus* and all other living *Crocodylus*. But not all datasets support this (Densmore & Owen 1989), and some sequence-based analyses actually favor a close relationship between *C. cataphractus* and *Osteolaemus* (White & Densmore 2001). Morphology (Brochu 2000) and some molecular data (White & Densmore 2001) recover a monophyletic New World assemblage related to the Nile crocodile (*C. niloticus*) and a monophyletic Indopacific assemblage, but support for these clusters is very weak.

Lack of signal among published datasets for *Crocodylus* may relate to the recency of divergence among living species. For the 12S rRNA gene, less than 1% sequence difference exists between *Crocodylus rhombifer* (Gatesy et al. 1993) and *C. acutus* (Mindell et al. 1996). Insufficient divergence has occurred in the time since speciation, and no robust tree can be recovered. For a signal to be discerned, rapidly evolving genes must be used.

Morphological data can also be bolstered. Thus far, morphological datasets have been predominantly osteological, and soft-tissue differences are known that would doubtless be informative when approached phylogenetically (e.g., Brazaitis 1973, Ross & Ross 1974). More importantly, the African fossil record of Late Tertiary crocodylians includes species not yet considered in phylogenetic analysis, such as *Crocodylus checchiai* and *C. pigotti*. Moreover, "*Crocodylus*" *lloidi* has been reported from numerous localities all over Africa (Tchernov 1986; Pickford 1994, 1996); the position of "*C.*" *lloidi* in Figure 7 is based on material from the type locality in Libya, but material from other localities should be included. Additional specimens from Asia and the Greater Antilles might also prove illuminating (MacPhee & Wyss 1990, Rauhe et al. 1999, Head 2001).

Uncertain Relationships Among Caimans

A basal division between dwarf caimans (*Paleosuchus*) and all other caimans appears robust, but relationships among these animals are otherwise poorly resolved (Gatesy et al. 1993, Brochu 1999a, White & Densmore 2001). Some datasets support *Caiman* monophyly (two to four living species), but others support a close relationship between *Caiman latirostris* and *Melanosuchus niger*. The problem here is similar to that for *Crocodylus*—the issue is nonresolution rather than conflicting robust signals.

This limitation impacts our understanding of molecular rates of evolution among crocodylians. Although relative rate tests on some ribosomal genes sometimes support faster evolutionary rates within Alligatoridae, actual rates calculated by assuming a Poisson distribution of mutations over time and using fossil calibrations are at least two orders of magnitude higher among caimans than among other crocodylian groups (Brochu 1997a). This is likely a reflection of the fragmentary fossil record—range extensions reduce absolute rate estimates (e.g., Springer 1995, Bromham et al. 1998, Huchon et al. 2000). But further work is needed, both with respect to the fossil record and sequence data, to study the impact range extensions have on rate estimations.

How did the Chinese Alligator Get to China?

The Chinese alligator (*A. sinensis*) is a biogeographic puzzle (Xu & Huang 1984). *Alligator sinensis* is rather derived within *Alligator*. Based on first appearance data and molecular information, it last shared a common ancestor with *A. mississippiensis* within the past 20 Ma. It also shares with other alligatorids the lack of anatomical features that allow prolonged exposure to salt water (Taplin & Grigg 1989), making a direct crossing of the Pacific Ocean unlikely.

An overland route (presumably through Beringia) is the shortest approach from North America to Asia. But by the Miocene, the high latitudes were already temperate enough to possibly exclude crocodylians (Markwick 1998a). A European route would present the same problems, and the alligatorines found there are unrelated to any species of *Alligator* (Brochu 1999a).

On further reflection, the Beringian route may not be as problematic as it first appears. *Alligator sinensis* is the most cold-adapted of all living crocodylians, and it overwinters in a complex set of burrows (Ross 1998). Although not described in depth in the literature, alligatorids possibly referable to *Alligator* are known from California and Oregon during the Tertiary (Bramble & Hutchison 1971; Repenning & Vedder 1961; Hanson 1996; C.A. Brochu, personal observation); if this scenario is correct, we should eventually discover alligators from Late Tertiary deposits of Alaska.

Globidontans are known from the Asian Tertiary (Young 1964, Efimov 1976), including a form referred to *Alligator* from the Miocene (Li & Wang 1987), but relationships to extant *Alligator* are unclear. These fossils need to be incorporated into phylogenetic analysis.

CROCODYLIAN HISTORY: SYNTHESIS AND THE IMPORTANCE OF PHYLOGENY

Higher crocodylian taxonomic names were not always used consistently. There was broad understanding that most could be divided into an “alligator” category and a “crocodile” category, but the criteria used to make this distinction fluctuated. Very often, “crocodile” in a paleontological sense simply meant “not an alligator.” Long-snouted crocodylians could be “gavialids” if they had certain derived conditions (such as separation of the nasals from the premaxillae), but “tomistomines” if they did not. This system effectively combined categories based on derived conditions with others based on plesiomorphy. It also treated taxa as coherent assemblages that could be viewed as a unit and not as a hierarchy.

My contention is not that phylogeny fundamentally changes the story of crocodylian diversity over time, but that a phylogenetic perspective can add immeasurably to a macroevolutionary study based on counts of taxa over long stretches of geological time. Examples of this point are shown below.

The crocodylian record shows two peaks of high diversity—one in the Early Eocene, the other in the Early Miocene (Hutchison 1982, 1992; Taplin 1984; Markwick 1998b; Vasse & Hua 1998). These are usually thought to reflect global climate, as the Early Eocene and Early Miocene diversity peaks are correlated with global mean temperature maxima (Hutchison 1982, Markwick 1998a). Crocodylians seem to have escaped the Cretaceous-Tertiary extinction event relatively unscathed (Buffetaut 1980, 1990; Vasse & Hua 1998), and the Eocene maximum may be a continuation of diversification from the Cretaceous. Consideration of the phylogenetic relationships among fossil crocodylians reveals an added level of complexity to this pattern.

Crocodylian diversity was higher in the past than now, but most fossil crocodylian faunas are no more diverse than the most speciose crocodylian faunas today. They usually include one or two “generalized” crocodylians with long, broad snouts, more or less like those of extant *Alligator* or *Crocodylus*; one or two small crocodylians with blunt snouts and bulbous rear teeth; one or two long-snouted taxa; and one or two examples of a morphotype not seen today, such as a terrestrial ziphodont form or one of the bizarre duck-faced caimans of the Tertiary (Brochu 2001b). This is especially true of the Early Eocene and Miocene, the periods of maximum worldwide crocodylian diversity.

Crocodylian faunas of the Early Eocene peak tend to be phylogenetically composite, with components often sharing a closer relative on another continent than in the same fauna. For example, the crocodylians found in Early Eocene European deposits (e.g., Messel) include generalized forms (*Diplocynodon* and a basal crocodyloid), a blunt-snouted alligatorine, a ziphodont pristichampsine, and a tomistomine or gavialoid (Berg 1966, Rauhe & Rossmann 1995, Rossmann et al. 1999). *Diplocynodon* is endemic to Europe, but the crocodyloid, pristichampsine, alligatorine, and longirostrine crocodylians are each more closely related to crocodylians from North America or Europe (Brochu 1999, 2001b).

The groups themselves tend to be geographically widespread but morphologically uniform. Many of the small blunt-snouted alligatorines from North America and Europe are called *Allognathosuchus* because of their overall similarity, and Rossmann (1998) considers North American and European *Pristichampsus* to be the same species. Whatever “*Allognathosuchus*” and *Pristichampsus* were specialized for, they found a solution to a problem and spread it far and wide.

Crocodylian faunas of the Miocene peak tend to be more endemic. This is especially true in Australia and Africa, where endemic clades of crocodyloids dominate the crocodylian fauna. These are morphologically diverse—the Australasian mekosuchines include a ziphodont form (*Quinkana*) (Molnar 1977, Megirian 1994, Willis & Mackness 1996) and a small blunt-snouted animal (*Trilophosuchus*) (Willis 1993), and if *Harpacochampsia* is a mekosuchine, the group also includes a longirostrine taxon. Osteolaeminae includes a blunt-snouted form that persists to the Recent (*Osteolaemus*), generalized forms (“*C.*” *lloidi*), and at least one longirostrine taxon (*Euthecodon*). Isolated ziphodont crocodyliiform teeth are known from the Late Tertiary of Africa (Andrews 1914), raising the possibility that ziphodonty was also a component of the osteolaemine radiation.

The South American crocodyliiform fauna of the Late Tertiary is composite as a whole, but the components themselves represent endemic groups by the Miocene. Gavialoids have a worldwide distribution throughout the Cenozoic, but the gavialoids found in South America may represent an endemic group (Buffetaut 1982a). Similarly, ziphodont sebecosuchians (which are not crown-group crocodylians) are found outside South America in Late Mesozoic through Eocene units, but not after the Oligocene (Buffetaut 1982b, Gasparini 1996).

The phylogenetic distribution of endemism is illustrated in Figures 11 and 12. Endemism in Figure 11 is measured as the percentage of taxa in a particular time bin that have their closest relative in the same region, with the regions being continents. In Figure 12, the distribution of head shapes is mapped over a calibrated cladogram to illustrate the relative morphological diversity of later Tertiary radiations (Brochu 2001b).

Alligatoroids have always been relatively endemic. For crown-group alligatorids, this may reflect the absence of the elaborate osmoregulatory system that allows other crocodylian lineages to handle excess salt (Taplin & Grigg 1989, Leslie & Taplin 2001); without these tissues, extant alligatorids are less able to withstand prolonged exposure to salt water. This may have limited alligatorid capacity to cross significant marine barriers and kept them restricted to the Americas and Europe for most of their history.

But endemism increases sharply for Gavialoidea and Crocodyloidea during the Tertiary. Three particular clades are responsible for most of this endemism—the endemic South American gavialoid group and the endemic crocodyloid clades (Mekosuchinae and Osteolaeminae). Crocodyloids and gavialoids ancestrally have the osmoregulatory structures for salt tolerance (or at least the indications of

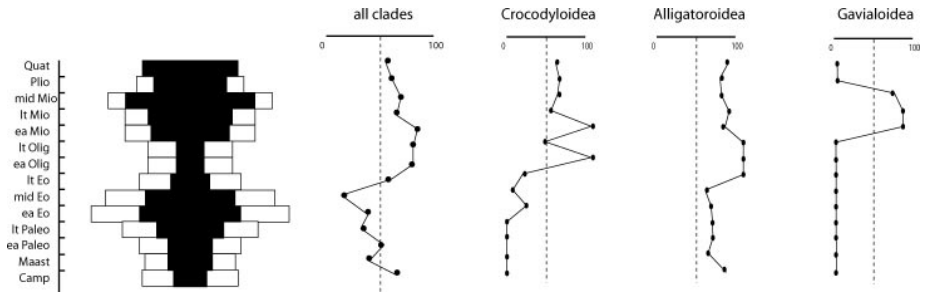


Figure 11 Patterns of crocodylian endemicity over time. Line graphs reflect the percentage of a particular clade whose closest relative is in the same continent during a given period of time. The spindle diagram reflects crocodylian species-level diversity over time, with black bars indicating known species and white extensions indicating ghost lineages inferred from phylogeny; data modified from Markwick (1998b).

them; Taplin & Grigg 1989), and as discussed earlier, crocodyloid and gavialoid history is sometimes best explained with the invocation of an oceanic dispersal event. But these marine barriers were somewhat larger in the Miocene than in the Eocene, suggesting that tectonics may be partially responsible for the phylogenetic difference between the Eocene and Miocene diversity peaks.

A weakness in this argument is the incompleteness of the early mekosuchine and osteolaemine records. Maximum known diversity for these groups is in the Miocene, but we do not know how far back these groups go. These radiations might have longer temporal durations, with the Miocene peak being more apparent than real.

Another interesting aspect is the fact that the African and Australian radiations are largely extinct and have been replaced by *Crocodylus*. Whether *Crocodylus* outcompeted these groups or simply filled voids left by local extinction is unknown. But *Crocodylus* itself almost seems to represent at least two endemic radiations—one in the Indopacific and another in the Caribbean. Snout shape is diverse in *Crocodylus*, and both the Indopacific and New World assemblages include at least one member with a comparatively narrow snout (*C. johnstoni* in Australia, *C. intermedius* in northern South America).

Looking at the Late Cretaceous and Cenozoic as a whole, a limited number of morphotypes reappear in distantly related lineages. Different clades will fill the same presumed ecological role in a given area at different times. This is not, by itself, a novel conclusion (e.g., Langston 1973). But when the phylogenetic relationships of these crocodylians are mapped over geography and stratigraphy, we see not one radiation, but many. Tabulation of the number of crocodylian species over time shows us the broad pattern of diversity, but the more complex history underlying it is only recoverable with phylogenetics.

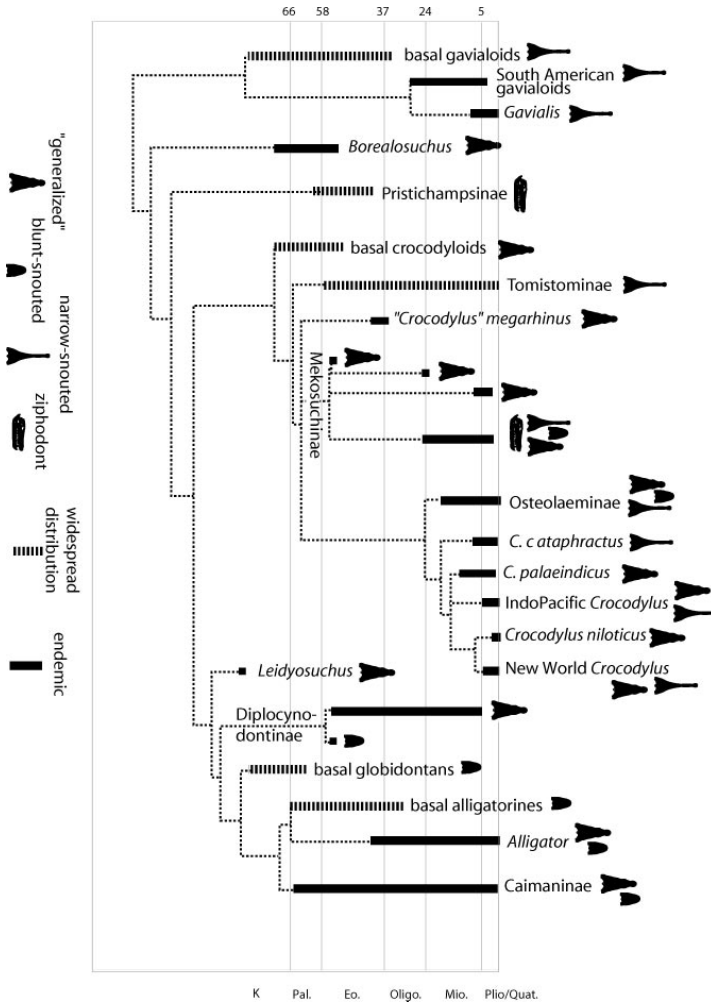


Figure 12 Patterns of crocodylian skull shape over time. Some basal clusters are collapsed for purposes of this diagram, and *Harpacochampsia* is assumed to be mekosuchine. Caimans are treated as endemic; in fact, scattered occurrences in North America render the biogeographic history of the group more complicated. Phylogeny based on morphological data only. Based on Brochu (2001a,b).

CONCLUSIONS

The study of fossil crocodyliforms is almost as old as vertebrate paleontology itself. Many of the ideas expressed here are refinements of those made by many researchers for nearly 200 years. But the synthesis of molecular biology,

morphology, paleontology, and physiology is allowing the construction and testing of hypotheses that were previously made invisible by the insular nature of our sciences. Multiple derivations of a long, slender snout is an old idea; that some of these long, slender snouts may be part of comparatively recent, morphologically diverse endemic radiations is not.

The solution of current problems in crocodylian phylogenetics lies in the continued effort to gather information. New fossils await discovery, and new genes await sequencing. Our technology will improve, but the real answer will always be found in museum collections, and it is there that our efforts must be strongest. Our phylogenetic matrices are summaries of observations, not of morphology; the real data are in drawers or bottles of preservative. We will learn much about both molecules and morphology by working at these issues.

Crocodylians bear the unfair label of “living fossil” for no other reason than the maintenance of a *gestalt* that happens to work quite well. Crocodylians are an “evolutionary canon”—a basic body shape may persist through history, but its character becomes noticeably more sophisticated over time, and individual lineages occasionally break from the mold and do something different. Like a musical canon, the underlying musical phrase is maintained but becomes more elaborate. The song remains the same, but more instruments join the orchestra and there are more notes per measure.

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LITERATURE CITED

- Abel O. 1928. *Allognathosuchus*, ein an de che-loniphage Nahrungsweise angepaßter Krokodiltypus des nordamerikanischen Eozäns. *Paläontol. Zeitschr.* 9:367–74
- Alroy J. 2001. How many named species are valid? *Proc. Natl. Acad. Sci. USA* 99:3706–11
- Andrews CW. 1906. *A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt*. London: Bri. Mus. (Natl. Hist.). 324 pp.
- Andrews CW. 1914. On the Lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. *Q. J. Geol. Soc. London* 70:163–86
- Angielczyk KD, Gingerich PD. 1998. New

- specimen of cf. *Asiatosuchus* (Crocodyloidea) from the middle Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan). *Contrib. Mus. Paleontol. Univ. Mich.* 30:163–89
- Antunes MT. 1961. *Tomistoma lusitanica*, crocodilien du Miocène du Portugal. *Rev. Fac. Cien. Lisboa* 9(Ser. 2):5–88
- Antunes MT. 1987. Affinities and taxinomial status of Miocene longirostrine crocodilians from western Europe with remarks on phylogeny, paleoecology, and distribution. *Commun. Serv. Geol. Port.* 73:49–58
- Aoki R. 1976. On the generic status of *Mecistops* (Crocodylidae), and the origin of *Tomistoma* and *Gavialis*. *Bull. Atagawa Inst.* 6/7:23–30
- Aoki R. 1983. A new generic allocation of *Tomistoma machikanense*, a fossil crocodilian from the Pleistocene of Japan. *Copeia* 1983:89–95
- Aoki R. 1992. Fossil crocodilians from the late Tertiary strata in the Sinda Basin, eastern Zaire. *Afr. Study Monogr.* 17:67–85
- Auffenberg W. 1954. Additional specimens of *Gavialosuchus americanus* (Sellards) from a new locality in Florida. *Q. J. Fla. Acad. Sci.* 17:185–209
- Balouet JC, Buffetaut E. 1987. *Mekosuchus inexpectatus*, n. g., n. sp., crocodilien nouveau de l'Holocène de Nouvelle Calédonie. *C. R. Acad. Sci. Paris* 304:853–56
- Barbour T. 1918. Amphibia and Reptilia. *Bull. Mus. Comp. Zool.* 14:479–89
- Benton MJ. 2000. Stems, nodes, crown-clades, and rank-free lists: is Linnaeus dead? *Biol. Rev.* 75:633–48
- Benton MJ, Storrs GW. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology* 22:111–14
- Berg DE. 1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus?*, aus dem Eozän von Messel bei Darmstadt/Hessen. *Abh. Hess. Landesamtes Bodenforsch.* 52:1–105
- Berg DE. 1969. *Charactosuchus kugleri*, eine neue Krokodilart aus dem Eozän von Jamaica. *Elcogae Geol. Helv.* 62:731–35
- Berg DE. 1984. Amphibien und Reptilien im “prae-aquitaniens” Tertiär des Mainzer Beckens. *Mainzer Geowiss. Mitteil.* 13:115
- Bocquetin JC. 1984. Un nuevo Nettosuchiidae (Crocodylia, Eusuchia) proveniente da la Formación Urumaco (Mioceno Superior), Venezuela. *Ameghiniana* 21:3–8
- Bocquetin JC, Souza Filho JP, Buffetaut E, Negri FR. 1991. Nova interpretação do genero *Purussaurus* (Crocodylia, Alligatoridae). *Anais XI Congr. Bras. Paleontol.* pp. 427–38
- Bramble DM, Hutchison JH. 1971. Biogeography of continental Tertiary Chelonia and Crocodylia of far-western United States. *Geol. Soc. Am. Abstr. Prog.* 3:86–87
- Brazaitis P. 1973. The identification of living crocodilians. *Zoologica* 59:59–88
- Brinkmann W, Rauhe M. 1998. *Diplocynodon ratelii* Pomel, 1847 (Crocodylia, Leidyosuchidae) aus dem Unter-Oligozän von Céreste (Südfrankreich). *Neus Jahrb. Geol. Paläontol. Abh.* 209:295–321
- Brochu CA. 1997a. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Syst. Biol.* 46:479–522
- Brochu CA. 1997b. A review of “*Leidyosuchus*” (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. *J. Vertebr. Paleontol.* 17:679–97
- Brochu CA. 1999a. Phylogeny, systematics, and historical biogeography of Alligatoroidea. *Soc. Vertebr. Paleontol. Mem.* 6:9–100
- Brochu CA. 1999b. Taxon sampling and reverse successive weighting. *Syst. Biol.* 48:808–13
- Brochu CA. 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. *Copeia* 2000:657–73
- Brochu CA. 2001a. Congruence between physiology, phylogenetics, and the fossil record on crocodylian historical biogeography. See Grigg et al. 2001, pp. 9–28
- Brochu CA. 2001b. Crocodylian snouts in space and time: phylogenetic approaches toward adaptive radiation. *Am. Zool.* 41:564–85

- Brochu CA. 2002. *Thecachampsoides* minor and early gavialoid history: coastal Atlantic origins of longirostrine crocodylians. *J. Vertebr. Paleontol.* 22:39A
- Brochu CA. 2003. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. *J. Vertebr. Paleontol.* In press
- Brochu CA, Densmore LD. 2001. Crocodile phylogenetics: a review of current progress. See Grigg et al. 2001, pp. 3–8
- Brochu CA, Gingerich PD. 2000. New tomitomine crocodylian from the middle Eocene (Bartonian) of Wadi Hitán, Fayum Province, Egypt. *Cont. Mus. Paleontol. Univ. Mich.* 30:251–68
- Bromham L, Rambaut A, Fortey R, Cooper A, Penny D. 1998. Testing the Cambrian explosion hypothesis by using a molecular dating technique. *Proc. Natl. Acad. Sci. USA* 95:12386–89
- Bryant HN. 1997. Cladistic information in phylogenetic definitions and designated phylogenetic contexts for the use of taxon names. *Biol. J. Linn. Soc.* 62:495–503
- Bryant LJ. 1989. Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary Boundary in northeastern Montana. *Univ. Calif. Publ. Geol. Sci.* 134:1–107
- Buckland W. 1836. *Geology and Mineralogy Considered with Reference to Natural Theology*. London: Pickering
- Buffetaut E. 1980. Détermination de la nature des événements de la transition Crétacé-Tertiaire: la contribution de l'étude des crocodiliens. *Mém. Soc. Geol. Fr.* 139:47–52
- Buffetaut E. 1982a. Systematique, origine et évolution des Gavialidae Sud-Américains. *Geobios Mém. Spec.* 6:127–40
- Buffetaut E. 1982b. Radiation évolutive, paléooécologie et biogéographie des crocodiliens mesosuchiens. *Mém. Soc. Geol. Fr.* 60:1–88
- Buffetaut E. 1983. Sur la persistance tardive d'un crocodilien archaïque dans le Pleistocène de l'île des Pins (Nouvelle-Calédonie) et sa signification biogéographique. *C. R. Acad. Sci. Paris* 297:89–92
- Buffetaut E. 1985. Zoogeographical history of African crocodilians since the Triassic. In *Proceedings of the International Symposium on African Vertebrates: Systematics, Phylogeny and Evolutionary Ecology*, ed. K-L Schuchmann, pp. 453–69. Bonn: Selbstverlag
- Buffetaut E. 1990. Vertebrate extinctions and survival across the Cretaceous-Tertiary boundary. *Tectonophysics* 171:337–45
- Buffetaut E, Crouzel F, Juillard F, Stigliani F. 1984. Le crocodilien longirostre *Gavialosuchus* dans le Miocène moyen de Polastron (Gers, France). *Geobios* 17:113–17
- Busbey AB. 1989. An Eocene caiman from the Texas Gulf Coast. *J. Vertebr. Paleontol.* 9:A15
- Buscalioni AD, Ortega F, Vasse D. 1997. New crocodiles (Eusuchia: Alligatoidea) from the Upper Cretaceous of southern Europe. *C. R. Acad. Sci. Paris Sci. Terre Planét.* 325:525–30
- Buscalioni AD, Ortega F, Vasse D. 1999. The Upper Cretaceous crocodilian assemblage from Lano (northcentral Spain): implications in the knowledge of the finicretaceous European faunas. *Est. Mus. Cien. Nat. Alava* 14:213–33
- Buscalioni AD, Ortega F, Weishampel DB, Jianu CM. 2001. A revision of the crocodyliiform *Allodaposuchus precedens* from the Upper Cretaceous of the Hateg Basin, Romania. Its relevance in the phylogeny of Eusuchia. *J. Vertebr. Paleontol.* 21:74–86
- Buscalioni AD, Sanz JL, Casanovas ML. 1992. A new species of the eusuchian crocodile *Diplocynodon* from the Eocene of Spain. *Neues Jahrb. Geol. Paläontol. Abh.* 187:1–29
- Cantino PD, Queiroz KD. 2000. PhyloCode: A Phylogenetic Code of Biological Nomenclature. <http://www.ohiou.edu/phylocode/>
- Carpenter K. 1983. *Thoracosaurus neocariensis* (De Kay, 1842) (Crocodylia: Crocodylidae) from the Late Cretaceous Ripley Formation of Mississippi. *Miss. Geol.* 4:1–10
- Carpenter K, Lindsey D. 1980. The dentary of *Brachychampsia montana* Gilmore (Alligatorinae; Crocodylidae), a Late Cretaceous

- turtle-eating alligator. *J. Paleontol.* 54:1213–17
- Carroll RL. 1988. *Vertebrate Paleontology and Evolution*. New York: Freeman. 698 pp.
- Chiappe L. 1988. Un nuevo *Caiman* (Crocodylia, Alligatoridae) de la Formación Tremembé (Oligoceno), Estado de São Paulo, Brasil, y su significado paleoclimático. *Paula-Coutiana* 3:49–66
- Cione AL, Azpelicueta M, Bond M, Carlini AA, Casciotta JR, et al. 2000. Miocene vertebrates from Entre Ríos province, eastern Argentina. In *El Neógeno de Argentina*, ed. FG Acenolaza, R Herbst, pp. 255–61. Tucumán: Inst. Super. Correl. Geol.
- Clark JM. 1986. *Phylogenetic relationships of the crocodylomorph archosaurs*. PhD thesis. Univ. Chicago
- Clark JM. 1994. Patterns of evolution in Mesozoic Crocodyliformes. In *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, ed. NC Fraser, H-D Sues, pp. 84–97. New York: Cambridge Univ. Press
- Clark JM, Norell MA. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsia vectiana* from the Wealden of the Isle of Wight. *Am. Mus. Novit.* 3032:1–19
- Colbert EH, Bird RT. 1954. A gigantic crocodile from the Upper Cretaceous beds of Texas. *Am. Mus. Novit.* 1688:1–22
- Cuvier G. 1824. *Ossemens Fossiles*. Paris: G. Doufour Ed. D'Ocagne. 547 pp.
- Densmore LD. 1983. Biochemical and immunological systematics of the order Crocodylia. In *Evolutionary Biology*, ed. MK Hecht, B Wallace, GH Prance, pp. 397–465. New York: Plenum
- Densmore LD, Dessauer HC. 1984. Low levels of protein divergence detected between *Gavialis* and *Tomistoma*: evidence for crocodylian monophyly. *Comp. Biochem. Physiol. B* 77:715–20
- Densmore LD, Owen RD. 1989. Molecular systematics of the order Crocodylia. *Am. Zool.* 29:831–41
- Densmore LD, White PS. 1991. The systematics and evolution of the Crocodylia as suggested by restriction endonuclease analysis of mitochondrial and nuclear ribosomal DNA. *Copeia* 1991:602–15
- de Quieroz K, Gauthier J. 1994. Toward a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* 9:27–31
- de Vis CW. 1905. Fossil vertebrates from New Guinea. *Ann. Qld. Mus.* 6:26–31
- de Zigno A. 1880. Sopra un cranio di cocodrillo scoperto nel terreno eoceno del Veronese. *Atti R. Accad. Naz. Lincei Mem. Cl. Sci. Fis. Math. Nat.* 5(Ser. 3):65–72
- Efimov MB. 1976. On first occurrence of *Alligator* (Crocodylia) in the Lower Paleogene of Mongolia. *Trudy Somest. Sov.-Mongol. Paleontol. Exp.* 3:105–6
- Efimov MB. 1993. The Eocene crocodiles of the GUS—a history of development. *Kaupia* 3:23–25
- Erickson BR, Sawyer GT. 1996. The estuarine crocodile *Gavialosuchus carolinensis* n. sp. (Crocodylia: Eusuchia) from the Late Oligocene of South Carolina, North America. *Monogr. Sci. Mus. Minn. (Paleontol.)* 3:1–47
- Erickson GM, Brochu CA. 1999. How the “terror crocodile” grew so big. *Nature* 398:205–6
- Estes R, Hutchison JH. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 30:325–47
- Eudes-Deslongchamps E. 1868. Observations faites sur le foetus de caïman à museau de brochet et constatation d'un fait très important dans l'anatomie des crocodiles. *Bull. Soc. Linn. Normandie Ser. 2* 3:22–225
- Frey E, Laemmert A, Riess J. 1987. *Baryphracta deponiae* n. g. n. sp. (Reptilia, Crocodylia), ein neues Krokodil aus der Grube Messel bey Darmstadt (Hessen, Bundesrepublik Deutschland). *Neues Jahrb. Geol. Paläontol. Monatsh.* 1987:15–26
- Gallagher WB. 1993. The Cretaceous/Tertiary mass extinction event in the northern Atlantic Coastal Plain. *Mosasaur* 5:75–154
- Gasparini Z. 1996. Biogeographic evolution of the South American crocodylians. *Münchner Geowiss. Abh.* 30:159–84

- Gatesy J, Amato GD. 1992. Sequence similarity of 12S ribosomal segment of mitochondrial DNAs of gharial and false gharial. *Copeia* 1992:241–44
- Gatesy J, Amato G, Norell M, De Salle R, Hayashi C. 2003. Total evidence support for extreme taxic atavism in gavialine crocodylians. *Syst. Biol.* In press
- Gatesy J, De Salle R, Wheeler W. 1993. Alignment-ambiguous nucleotide sites and the exclusion of systematic data. *Mol. Phylogen. Evol.* 2:152–57
- Ginsburg L, Buffetaut E. 1978. *Euthecodon arambourgii* n. sp., et l'évolution du genre *Euthecodon*, crocodylien du Néogène d'Afrique. *Géol. Méditerr.* 5:291–302
- Ginsburg L, Bulot C. 1997. Les *Diplocynodon* (Reptilia, Crocodylia) de l'Orléanien (Miocène inférieur à moyen) de France. *Geodiversitas* 19:107–28
- Grigg G, Seebacher F, Franklin CE, eds. 2001. *Crocodylian Biology and Evolution*. Chipping Norton, NSW: Surrey Beatty
- Hanson CB. 1996. Stratigraphy and vertebrate faunas of the Bridgerian-Duchesnean Clarno Formation, north-central Oregon. In *The Terrestrial Eocene-Oligocene Transition in North America*, ed. DR Prothero, RJ Emry, pp. 206–39. New York: Cambridge Univ. Press
- Harshman J, Huddleston CJ, Bollback JP, Parsons TJ, Braun MJ. 2003. True and false gharials: a nuclear gene phylogeny of Crocodylia. *Syst. Biol.* In press
- Hass CA, Hoffman MA, Densmore LD, Maxson LR. 1992. Crocodylian evolution: insights from immunological data. *Mol. Phylogen. Evol.* 1:193–201
- Head JJ. 2001. Systematics and body size of the gigantic, enigmatic crocodyloid *Rhamphosuchus crassidens*, and the faunal history of Siwalik Group (Miocene) crocodylians. *J. Vertebr. Paleontol.* 31:A59
- Holland WJ. 1909. *Deinosuchus hatcheri*, a new genus and species of crocodile from the Judith River Beds of Montana. *Ann. Carnegie Mus.* 6:281–94
- Holman JA. 1995. *Pleistocene Amphibians and Reptiles in North America*. New York: Oxford Univ. Press. 243 pp.
- Hua S, Jouve S. 2003. A primitive gavialoid from the Paleocene of Morocco. *J. Vertebr. Paleontol.* In press
- Huchon D, Catzeflis FM, Douzery EJP. 2000. Variance of molecular datings, evolution of rodents and the phylogenetic affinities between Ctenodactylidae and Hystricognathi. *Proc. R. Soc. London Ser. B* 267:393–402
- Huelsenbeck JP. 1991. When are fossils better than extant taxa in phylogenetic analysis? *Syst. Zool.* 40:458–69
- Huelsenbeck JP. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* 20:470–83
- Huelsenbeck JP. 1995. Performance of phylogenetic methods in simulation. *Syst. Biol.* 44:17–48
- Hulke JW. 1871. Note on some fossil reptiles from Gozo. *Q. J. Geol. Soc.* 27:29–33
- Hutchison JH. 1982. Turtle, crocodylian, and champsosaur diversity changes in the Cenozoic of the north-central region of western United States. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 37:149–64
- Hutchison JH. 1992. Western North American reptile and amphibian record across the Eocene-Oligocene boundary and its climatic implications. In *Eocene-Oligocene Climatic and Biotic Evolution*, ed. DR Prothero, WA Berggren, pp. 451–63. Princeton: Princeton Univ. Press
- Huxley TH. 1875. On *Stagonolepis robertsoni*, and on the evolution of the Crocodylia. *Q. J. Geol. Soc.* 31:423–38
- Janensch W. 1911. Die Reptilienreste (exkl. Schildkröten). In *Die Pithecanthropus-Schichten auf Java*, ed. ML Selenka, M Blanckenhorn, pp. 61–74. Leipzig: Engelmann
- Jonet S, Wouters G. 1977. *Marccosuchus zenaroi*, crocodylien eusuchien nouveau des phosphates du Maroc. *Notes Serv. Geol. Maroc* 38:177–202
- Kälin JA. 1931. Ueber die Stellung der Gavialiden im System der Crocodylia. *Rev. Suisse Zool.* 38:379–88

- Kälin JA. 1955. Zur Stammesgeschichte der Crocodilia. *Rev. Suisse Zool.* 62:347–56
- Kim J. 1996. General inconsistency conditions for maximum parsimony: effects of branch lengths and increasing numbers of taxa. *Syst. Biol.* 45:363–74
- Kraus R. 1998. The cranium of *Piscogavialis jugaliperforatus* n. gen., n. sp. (Gavialidae, Crocodylia) from the Miocene of Peru. *Paläontol. Zeitschr.* 72:389–406
- Kuhn O. 1938. Die Crocodilier aus dem mittleren Eozän des Geiseltales bei Halle. *Nova Acta Leopold. N.F.* 39:313–28
- Lambe LM. 1907. On a new crocodilian genus and species from the Judith River Formation of Alberta. *Trans. R. Soc. Can.* 4:219–44
- Langston W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *Univ. Calif. Publ. Geol. Sci.* 52:1–152
- Langston W. 1973. The crocodilian skull in historical perspective. In *Biology of the Reptilia*, ed. C Gans, T Parsons, pp. 263–84. London: Academic
- Langston W. 1975. Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. *Feldiana Geol.* 33:291–314
- Langston W, Gasparini Z. 1997. Crocodilians, *Gryposuchus*, and the South American gavials. In *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*, ed. RF Kay, RH Madden, RL Cifelli, JJ Flynn, pp. 113–54. Washington, DC: Smithsonian Inst.
- Leslie AJ, Taplin LE. 2001. Recent developments in osmoregulation of crocodilians. See Grigg et al. 2001, pp. 265–79
- Li J. 1984. A new species of *Planocrania* from Hengdong, Hunan. *Vertebr. Palasiat.* 22:123–33
- Li J, Wang B. 1987. A new species of *Alligator* from Shanwang, Shandong. *Vertebr. Palasiat.* 7:199–207
- Li J-L. 1975. New material on *Tomistoma petrolica* of Maoming, Kwantung. *Vertebr. Palasiat.* 13:190–91
- Ludwig R. 1877. Fossile Crocodiliden aus der Tertiärformation des mainzer Beckens. *Paleontogr. Suppl.* 3:1–52
- Lydekker R. 1886. On the occurrence of the crocodilian genus *Tomistoma* in the Miocene of the Maltese Islands. *Q. J. Geol. Soc.* 42:20–22
- Maccagno AM. 1948. Descrizione di una nuova specie di “*Crocodylus*” del giacimento di Sahabi (Sirtica). *Atti R. Accad. Naz. Lincei Mem. Cl. Sci. Fis. Math. Nat. Ser.* 81:63–96
- MacPhee RDE, Wyss AR. 1990. Oligo-Miocene vertebrates from Puerto Rico, with a catalog of localities. *Am. Mus. Novit.* 2965:1–45
- Markwick PJ. 1998a. Crocodilian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. *Paleobiology* 24:470–97
- Markwick PJ. 1998b. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 137:205–71
- Marshall CR. 1992. Character analysis and the integration of molecular and morphological data in an understanding of sand dollar phylogeny. *Mol. Biol. Evol.* 9:309–22
- McCracken KG, Harshman J, McClellan DA, Afton AD. 1999. Data set incongruence and correlated character evolution: an example of functional convergence in the hind-limbs of stiff-tail diving ducks. *Syst. Biol.* 48:683–714
- Mead JJ, Steadman DW, Bedford SH, Bell CJ, Spriggs M. 2002. New extinct mekosuchine crocodile from Vanuatu, South Pacific. *Copeia* 2002:632–41
- Medina CJ. 1976. Crocodilians from the Late Tertiary of northwestern Venezuela: *Melanosuchus fisheri* sp. nov. *Breviora* 438:1–14
- Megirian D. 1994. A new species of *Quinkana* (Eusuchia: Crocodylidae) from the Miocene Camfield Beds of northern Australia. *Beagle* 11:145–66
- Megirian D, Murray PF, Willis P. 1991. A new crocodile of the gavial ecomorph morphology from the Miocene of northern Australia. *Beagle* 8:135–58

- Miller WE. 1980. The Late Pliocene Las Tunas Local Fauna from southernmost Baja California, Mexico. *J. Paleontol.* 54:762–805
- Mindell DP, Knight A, Baer C, Huddleston CJ. 1996. Slow rates of molecular evolution in birds and the metabolic rate and body temperature hypothesis. *Mol. Biol. Evol.* 13:422–26
- Mlynarski M. 1984. Notes on the amphibian and reptilian faunas of the Polish Miocene. *Acta Zool. Cracov.* 27:127–48
- Molnar RE. 1977. Crocodile with laterally compressed snout: first find in Australia. *Science* 197:62–64
- Molnar RE. 1982. A longirostrine crocodylian from Murua (Woodlark), Solomon Sea. *Mem. Qld. Mus.* 20:675–85
- Molnar RE, Worthy TH, Willis PMA. 2002. An extinct Pleistocene endemic mekosuchine crocodylian from Fiji. *J. Vertebr. Paleontol.* 22:612–28
- Mook CC. 1921a. Description of a skull of a Bridger crocodylian. *Bull. Am. Mus. Nat. Hist.* 44:111–16
- Mook CC. 1921b. The skull of *Crocodylus acer* Cope. *Bull. Am. Mus. Nat. Hist.* 44:117–21
- Mook CC. 1921c. Description of a skull of the extinct Madagascar Crocodile, *Crocodylus robustus* Vaillant and Grandidier. *Bull. Am. Mus. Nat. Hist.* 44:25–33
- Mook CC. 1921d. Skull characters and affinities of the extinct Florida gavial, *Gavialosuchus americana* (Sellards). *Bull. Am. Mus. Nat. Hist.* 44:33–41
- Mook CC. 1927. The skull characters of *Crocodylus megarhinus* Andrews. *Am. Mus. Novit.* 289:1–8
- Mook CC. 1940. A new fossil crocodylian from Mongolia. *Am. Mus. Novit.* 1097:1–3
- Mook CC. 1941. A new crocodylian from the Lance Formation. *Am. Mus. Novit.* 1128:1–5
- Müller L. 1927. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. V. Tertiäre Wirbeltiere. 1. Beiträge zur Kenntnis der Krokodilier des ägyptischen Tertiärs. *Abh. Bayer. Akad. Wiss. Math.-Naturwiss. Abt.* 31:1–96
- Myrick AC. 2001. *Thecachampsia antiqua* (Leidy, 1852) (Crocodylidae, Thoracosaurinae) from fossil marine deposits at Lee Creek Mine, Aurora, North Carolina, USA. *Smithson. Contrib. Paleobiol.* 90:219–25
- Naylor GJP, Adams DC. 2001. Are the fossil data really at odds with the molecular data? Morphological evidence for Cetartiodactyla phylogeny reexamined. *Syst. Biol.* 50:444–53
- Nixon KC, Carpenter JM. 2000. On the other “phylogenetic systematics.” *Cladistics* 16:298–318
- Norell MA. 1988. *Cladistic approaches to paleobiology as applied to the phylogeny of alligatorids*. PhD thesis. Yale Univ., New Haven
- Norell MA. 1989. The higher level relationships of the extant Crocodylia. *J. Herpetol.* 23:325–35
- Norell MA, Clark JM. 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bull. Inst. R. Sci. Nat. Belg.* 60:115–28
- Norell MA, Clark JM, Hutchison JH. 1994. The Late Cretaceous alligatoroid *Brachychampsia montana* (Crocodylia): new material and putative relationships. *Am. Mus. Novit.* 3116:1–26
- O’Leary MA. 2001. The phylogenetic position of cetaceans: further combined data analyses, comparisons with the stratigraphic record and a discussion of character optimization. *Am. Zool.* 41:487–506
- Owen R. 1850. *Monograph on the Fossil Reptilia of the London Clay, and of the Bracklesham and Other Tertiary Beds, Part II: Crocodilia (Crocodylus, etc.)*. London: Paleontogr. Soc. 50 pp.
- Owen R. 1874. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. VI. *Hylaeochampsia*. *Palaontogr. Soc. Monogr.* 27:1–7
- Parris DC, Grandstaff BS, Denton RK, Dobie JL. 1997. *Diplocynodon* (Alligatorinae) in the Cretaceous of eastern North America. *J. Vertebr. Paleontol.* 17:A69
- Patterson B. 1936. *Caiman latirostris* from the Pleistocene of Argentina, and a summary of

- South American Cenozoic Crocodylia. *Herpetologica* 1:43–54
- Pereda Suberbiola X, Murelaga X, Astibia H, Badiola A. 2001. Restos fósiles del cocodrilo *Diplocynodon* (Alligatoroidea) en el Mioceno Inferior de las Bardenas Reales de Navarra. *Rev. Espan. Paleontol.* 16:223–42
- Persson PO. 1960. Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). *Arkiv Mineral. Geol.* 2:431–78
- Pickford M. 1994. Late Cenozoic crocodiles (Reptilia: Crocodylidae) from the Western Rift, Uganda. In *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire, Vol. II—Palaeobiology*, pp. 137–55. Orléans: CIFEG Occas. Publ.
- Pickford M. 1996. Fossil crocodiles (*Crocodylus lloydi*) from the Lower and Middle Miocene of southern Africa. *Ann. Paleontol.* 82:235–50
- Piña CI, Argañaraz B. 2000. Presencia del género *Caiman* (Crocodylia: Alligatoridae) en la Formación Ituzaingó (Mioceno Superior-Plioceno), Entre Ríos, Argentina. In *El Neógeno de Argentina*, ed. FG Acenolaza, R Herbst, pp. 255–61. Tucumán: Inst. Super. Correl. Geol.
- Piveteau J. 1927. Études sur quelques amphibiens et reptiles fossiles, II: Reptile du Montien. *Ann. Paleontol.* 16:29–37
- Plane MD. 1967. Stratigraphy and vertebrate fauna of the Otibanda Formation, New Guinea. *Bull. Bur. Min. Res. Aust.* 85:1–64
- Poe S. 1997. Data set incongruence and the phylogeny of crocodylians. *Syst. Biol.* 45:393–414
- Pol D, Norell M. 2001. Comments on the Manhattan Stratigraphic Measure. *Cladistics* 17:285–89
- Pomel A. 1847. Note sur les animaux fossiles découverts dans le département de l'Allier. *Bull. Soc. Geol. Fr.* 4(Ser. 2):378–85
- Preston RE. 1979. Late Pleistocene cold-blooded vertebrate faunas from the mid-continental United States. I. Reptilia; Testudines, Crocodylia. *Univ. Mich. Mus. Paleontol. Pap. Paleontol.* 19:1–53
- Price LI. 1964. Sobre o cranio de um grande crocodilideo extinto do Alto Rio Jurua, Estado do Acre. *Anais Acad. Bras. Cienc.* 36:59–66
- Rauhe M, Frey E, Pemberton DS, Rossmann T. 1999. Fossil crocodylians from the Late Miocene Baynunah Formation of the Emirate of Abu Dhabi, United Arab Emirates: Osteology and palaeoecology. In *Fossil Vertebrates of Arabia*, ed. PJ Whybrow, A Hill, pp. 163–85. New Haven, CT: Yale Univ. Press
- Rauhe M, Rossmann T. 1995. News about fossil crocodiles from the middle Eocene of Messel and Geiseltal, Germany. *Hallesches Jahrb. Geowiss.* 17:81–92
- Ray DA, White PS, Duong HV, Cullen T, Densmore LD. 2001. High levels of genetic variability in West African dwarf crocodiles *Osteolaemus tetraspis tetraspis*. See Grigg et al. 2001, pp. 58–63
- Repenning CA, Vedder JG. 1961. Continental vertebrates and their stratigraphic correlation with marine mollusks, eastern Caliente Range, California. *US Geol. Surv. Prof. Pap.* 424:235–39
- Rogers JV. 2003. A procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas. *J. Vertebr. Paleontol.* In press
- Ross FD, Ross CA. 1974. Caudal scalation of Central American *Crocodylus*. *Proc. Biol. Soc. Wash.* 87:231–33
- Ross JP. 1998. *Crocodyles—Status Survey and Conservation Action Plan*. Gland, Switz.: Int. Union Conserv. Nature. 96 pp.
- Rossmann T. 1998. Studien an känozoischen Krokodilen: 2. Taxonomische Revision der Familie Pristichampsidae Efimov (Crocodylia: Eusuchia). *Neues Jahrb. Geol. Paläontol. Abh.* 210:85–128
- Rossmann T. 1999. Studien an känozoischen Krokodilen: 1. Die paläoökologische Bedeutung des eusuchen Krokodils *Pristichampus rollinatus* (Gray) für die Fossilagerstätte Grube Messel. *Cour. Forsch. Senckenberg* 216:85–96
- Rossmann T. 2000a. Eine neue Krokodil-Spezies aus dem Geiseltalium (Mittleres

- Eozän, MP 11) der Grube Messel. *Terra Nostra* 70:98
- Rossmann T. 2000b. Skelettanatomische Beschreibung von *Pristichampsus rollinatii* (Gray) (Crocodilia, Eusuchia) aus dem Paläogen von Europa, Nordamerika und Ostasien. *Cour. Forsch. Senckenberg* 221:1–107
- Rossmann T. 2000c. Studien an känozoischen Krokodilen: 4. Biomechanische Untersuchung am Schädel und der Halswirbelsäule des paläogenen Krokodils *Pristichampsus rollinatii* (Eusuchia: Pristichampsidae). *Neues Jahrb. Geol. Paläontol. Abh.* 215:397–432
- Rossmann T. 2000d. Studien an känozoischen Krokodilen: 5. Biomechanische Untersuchung am postkranialen Skelett des paläogenen Krokodils *Pristichampsus rollinatii* (Eusuchia: Pristichampsidae). *Neues Jahrb. Geol. Paläontol. Abh.* 217:289–330
- Rossmann T, Berg DE. 1999. Die eozäne Krokodil-Fauna Kataloniens im Vergleich zu der von Messel, Eckfeld und Geiseltal: Paläoökologische Implikationen. *Terra Nostra* 69:65
- Rossmann T, Berg DE, Salisbury SW. 1999. Studies on Cenozoic crocodiles: 3. *Gavialosuchus* cf. *gaudensis* (Eusuchia: Tomistomidae) from the Lower Miocene of south Germany. *Neues Jahrb. Geol. Paläontol. Monat.* 1999:321–30
- Rovereto C. 1912. Los crocodilos fósiles en las capas del Paraná. *An. Mus. Nac. Buenos Aires Ser.* 3 22:339–69
- Rowe T, Brochu CA, Kishi K, Merck JW, Colbert MW. 1999. *Alligator*: Digital Atlas of the Skull. Soc. Vertebr. Paleontol., CDROM
- Rusconi C. 1937. Nuevo aligatorino del Paleoceno Argentino. *Bol. Paleontol. Buenos Aires* 8:1–5
- Salisbury SW, Frey E. 2001. A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodylians. See Grigg et al. 2001, pp. 85–134
- Salisbury SW, Willis PMA. 1996. A new crocodylian from the Early Eocene of southeastern Queensland and a preliminary investigation of the phylogenetic relationships of crocodyloids. *Alcheringa* 20:179–227
- Schwimmer DR. 1986. Late Cretaceous fossils from the Blufftown Formation (Campanian) in western Georgia. *Mosasauro* 3:109–23
- Schwimmer DR. 2002. *King of the Crocodylians: The Paleobiology of Deinosuchus*. Bloomington: Indiana Univ. Press. 220 pp.
- Siddall ME. 1998. Stratigraphic fit to phylogenies: a proposed solution. *Cladistics* 14:201–8
- Simpson GG. 1933. A new crocodylian from the Notostylops Beds of Patagonia. *Am. Mus. Novit.* 623:1–9
- Singh LAK, Bustard HR. 1982. Geographical distribution of the gharial *Gavialis gangeticus* (Gmelin) in Orissa, India. *Br. J. Herpetol.* 6:259–60
- Souza Filho JP. 1987. *Caiman brevirostris* sp. nov., um novo Alligatoridae da formação Solimões (Pleistoceno) do Estado do Acre, Brasil. In *Anais X Congr. Bras. Paleontol.*, pp. 173–80. Rio de Janeiro: Soc. Bras. Paleontol.
- Souza Filho JP, Bocquetin JC. 1991. *Caiman niteroiensis*, sp. nov., Alligatoridae (Crocodylia) do Neogeno do Estado do Acre, Brasil. In *Anais XII Congr. Bras. Paleontol.*, p. 37. Rio de Janeiro: Soc. Bras. Paleontol.
- Springer MS. 1995. Molecular clocks and the incompleteness of the fossil record. *J. Mol. Evol.* 41:531–38
- Steel R. 1973. *Handbuch der Paleoherpetologie*, Vol. 16: *Crocodylia*. Portland, OR: Fischer-Verlag. 116 pp.
- Storrs GW, Efimov MB. 2000. Mesozoic crocodyliiforms of north-central Eurasia. In *The Age of Dinosaurs in Russia and Mongolia*, ed. MJ Benton, MA Shishkin, DM Unwin, EN Kurochkin, pp. 402–19. Cambridge: Cambridge Univ. Press
- Stromer E. 1925. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens, II: Wirbeltier-Reste der Baharije-Stufe (Unterest es Cenoman), 7: *Stomatosuchus inermis* Stromer, ein schwach bezahnter Krokodilier. *Abh. Bayer. Akad. Wissen. Math.-Naturwiss. Abt.* 30:1–9

- Stromer E. 1933. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. 12: Die Procölen Crocodilia. *Abh. Bayer. Akad. Wissen. Math.-Naturwiss. Abt. N. F.* 15:1–55
- Swinton WE. 1937. The crocodile of Maransart (*Dollosuchus dixoni* [Owen]). *Mem. Mus. R. Hist. Nat. Belg.* 80:1–46
- Taplin LE. 1984. Evolution and zoogeography of crocodylians: a new look at an ancient order. In *Vertebrate Zoogeography and Evolution in Australasia*, ed. M Archer, G Clayton, pp. 361–70. Victoria Park, West. Aust.: Hesperian
- Taplin LE, Grigg GC. 1989. Historical zoogeography of the eusuchian crocodylians: a physiological perspective. *Am. Zool.* 29:885–901
- Tarsitano SF, Frey E, Riess J. 1989. The evolution of the Crocodilia: a conflict between morphological and biochemical data. *Am. Zool.* 29:843–56
- Tchernov E. 1986. *Evolution of the Crocodiles in East and North Africa*. Paris: CNRS. 65 pp.
- Troedsson GT. 1924. On crocodylian remains from the Danian of Sweden. *Lunds Univ. Årsskr. N. F.* 20:1–75
- Troxell EL. 1925a. *Thoracosaurus*, a Cretaceous crocodile. *Am. J. Sci. 5th Ser.* 10:219–33
- Troxell EL. 1925b. The Bridger crocodiles. *Am. J. Sci. 5th Ser.* 9:29–72
- Trueman JWH. 1998. Reverse successive weighting. *Syst. Biol.* 47:733–37
- Vasse D. 1992a. Les crocodiles de l'Aude: Aperçu du matériel connu et présentation de quelques nouvelles pièces. *Bull. Soc. Étud. Sci. Aude* 92:37–41
- Vasse D. 1992b. Un crâne d'*Asiatosuchus germanicus* du Lutétien d'Issel (Aude). Bilan sur le genre *Asiatosuchus* en Europe. *Geobios* 25:293–304
- Vasse D, Hua S. 1998. Diversité des crocodyliens du Crétacé Supérieur et du Paléogène. Influences et limites de la crise Maastrichtien-Paléocène et des "Terminal Eocene Events." *Oryctos* 1:65–77
- Vignaud P, Brunet M, Guevel B, Jehenne Y. 1996. Un crâne de *Diplocynodon* (Crocodylomorpha, Alligatoridae) de l'Oligocène inférieur de Dordogne (France). *C. R. Acad. Sci. Paris Ser. Ila* 322:595–601
- White PS, Densmore LD. 2001. DNA sequence alignments and data analysis methods: their effect on the recovery of crocodylian relationships. See Grigg et al. 2001, pp. 29–37
- Williamson TE. 1996. *Brachychampsia sealeyi*, sp. nov., (Crocodylia, Alligatoroidea) from the Upper Cretaceous (lower Campanian) Menefee Formation, northwestern New Mexico. *J. Vertebr. Paleontol.* 16:421–31
- Willis PMA. 1993. *Trilophosuchus rackhami* gen et sp. nov., a new crocodylian from the early Miocene limestones of Riversleigh, northwestern Queensland. *J. Vertebr. Paleontol.* 13:90–98
- Willis PMA. 1997a. New crocodylians from the Late Oligocene White Hunter Site, Riversleigh, northwestern Queensland. *Mem. Qld. Mus.* 41:423–38
- Willis PMA. 1997b. Review of fossil crocodylians from Australia. *Austr. Zool.* 30:287–98
- Willis PMA. 2001. New crocodylian material from the Miocene of Riversleigh (northwestern Queensland, Australia). See Grigg et al. 2001, pp. 64–74.
- Willis PMA, Mackness BS. 1996. *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the Early Pliocene Bluff Downs Local Fauna, northern Australia with a revision of the genus. *Proc. Linn. Soc. NSW* 116:143–51
- Willis PMA, Molnar RE. 1991. A new middle Tertiary crocodile from Lake Palankarina, South Australia. *Rec. South Aust. Mus.* 25:39–55
- Willis PMA, Molnar RE, Scanlon JD. 1993. An early Eocene crocodylian from Murgon, southeastern Queensland. *Kaupia* 3:27–33
- Willis PMA, Murray PF, Megirian D. 1990. *Baru darrowi* gen. et sp. nov., a large broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in northern Australia. *Mem. Qld. Mus.* 29:521–40

- Willis PMA, Stilwell JD. 2000. A probable piscivorous crocodile from Eocene deposits of McMurdo Sound, East Antarctica. *Antarct. Res. Ser.* 76:355–58
- Woodward AS. 1886. The history of fossil crocodiles. *Proc. Geol. Assoc.* 9:1–57
- Worthy TH, Anderson AJ, Molnar RE. 1999. Megafaunal expression in a land without mammals—the first fossil faunas from terrestrial deposits in Fiji (Vertebrata: Amphibia, Reptilia, Aves). *Senck. Biol.* 79:237–42
- Wu X-C, Brinkman DB, Fox RC. 2001a. A new crocodylian (Archosauria) from the basal Paleocene of the Red Deer River valley, southern Alberta. *Can. J. Earth Sci.* 38:1689–704
- Wu X-C, Brinkman DB, Russell AP. 1996. A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians. *Palaeontology* 39:351–75
- Wu X-C, Russell AP, Brinkman DB. 2001b. A review of *Leidyosuchus canadensis* Lambe, 1907 (Archosauria: Crocodylia) and an assessment of cranial variation based upon new material. *Can. J. Earth Sci.* 38:1665–87
- Xu Q, Huang C. 1984. Some problems in evolution and distribution of *Alligator*. *Vertebr. Palasiat.* 22:49–53
- Young CC. 1964. New fossil crocodiles from China. *Vertebr. Palasiat.* 8:189–210
- Zarski M, Jakubowski G, Gawor-Biedowa E. 1998. The first Polish find of Lower Paleocene crocodile *Thoracosaurus* Leidy, 1852: Geological and palaeontological description. *Geol. Q.* 42:141–60