

# A gharial from the Oligocene of Puerto Rico: transoceanic dispersal in the history of a non-marine reptile

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The Indian gharial (*Gavialis gangeticus*) is not found in saltwater, but the geographical distribution of fossil relatives suggests a derivation from ancestors that lived in, or were at least able to withstand, saline conditions. Here, we describe a new Oligocene gharial, *Aktiogavialis puertoricensis*, from deltaic-coastal deposits of northern Puerto Rico. It is related to a clade of Neogene gharials otherwise restricted to South America. Its geological and geographical settings, along with its phylogenetic relationships, are consistent with two scenarios: (i) that a single trans-Atlantic dispersal event during the Tertiary explains the South American Neogene gharial assemblage and (ii) that stem gharials were coastal animals and their current restriction to freshwater settings is a comparatively recent environmental shift for the group. This discovery highlights the importance of including fossil information in a phylogenetic context when assessing the ecological history of modern organisms.

**Keywords:** biogeography; Crocodylia; *Gavialis*; gharial; *Aktiogavialis*; phylogeny

## 1. INTRODUCTION

*Gavialis gangeticus* (the Indian gharial) is a large crocodylian with a long, tubular snout often thought to reflect a specialization for catching fishes (Langston 1973). Its historical distribution is limited to inland drainages of the Indian subcontinent (Smith 1933; Singh 1991). Although there are anecdotal reports of its occurrence in seasonally brackish bodies of water (Annandale 1915), it favours deep rivers and is viewed as a freshwater reptile. It is also thought to be the most aquatic living crocodylian with limited overland dispersal capacity (Whitaker & Basu 1983). One might thus expect a distribution for Gavialoidea (*G. gangeticus* and all crocodylians closer to it than to *Alligator mississippiensis* or *Crocodylus niloticus*; Brochu 2003), either limited in geographical scope or dominated by vicariance.

Although many Neogene fossil gavialoids occur in non-marine depositional systems (e.g. Janensch 1911; Lull 1944; Langston 1965; Langston & Gasparini 1997), their post-Oligocene geographical distribution is difficult to reconcile with a vicariance model. They appear in South America during the Miocene with no known close relatives in North America, suggesting dispersal from Africa or, less probably, Asia (Buffetaut 1982; Langston & Gasparini 1997; Brochu & Rincon 2004). Vicariance explains this distribution only if derived gavialoids have unsampled histories on multiple continents extending from the Miocene back to the Mesozoic.

Nearly all reported gavialoids from the Late Cretaceous through the Palaeocene—the so-called ‘thoracosaur’—are from shallow marine or marginal marine deposits (e.g.

Köken 1888; Troedsson 1924; Piveteau 1927; Gallagher *et al.* 1986; Schwimmer 1986; Erickson 1998; Zarski *et al.* 1998; Weems 1999; Laurent *et al.* 2000; Brochu 2004, 2006; Hua & Jouve 2004; Robb 2004; Delfino *et al.* 2005). This might support transoceanic dispersal as an important factor in explaining gavialoid distribution, but these are controversial owing to the debate over the relationships and divergence timing of extant *Gavialis*. Parsimony analyses of morphology support a clade including thoracosaur and more derived gavialoids at the base of Crocodylia, with a divergence time between *Gavialis* and any other living crocodylian minimally in the Campanian (Norell 1989; Salisbury & Willis 1996; Brochu 1997, 2003; Hua & Jouve 2004; Jouve *et al.* 2006). Molecular data consistently support a close phylogenetic relationship between *Gavialis* and another freshwater-restricted crocodylian—the Indonesian false gharial (*Tomistoma schlegelii*)—and the divergence time between them within the Tertiary (Densmore 1983; Densmore & Owen 1989; Hass *et al.* 1992; White & Densmore 2001; Gatesy *et al.* 2003; Harshman *et al.* 2003; Janke *et al.* 2005; McAliley *et al.* 2006). If molecular data are correct with respect to divergence time, thoracosaur are not gavialoids (Harshman *et al.* 2003) and are irrelevant to the debate surrounding the ecology and physiology of extinct relatives of *Gavialis*.

We describe a new fossil gavialoid from the Oligocene San Sebastián Formation of Puerto Rico (figure 1) closely related to extinct gavialoids from the Mio-Pliocene of South America. Although relationships among derived gavialoids are ambiguous about the biogeographic origin of the Neotropical clade, the presence of a member in the Greater Antilles during the Oligocene supports an African origin with a single trans-Atlantic dispersal event. The Puerto Rican gharial and other South American gharials

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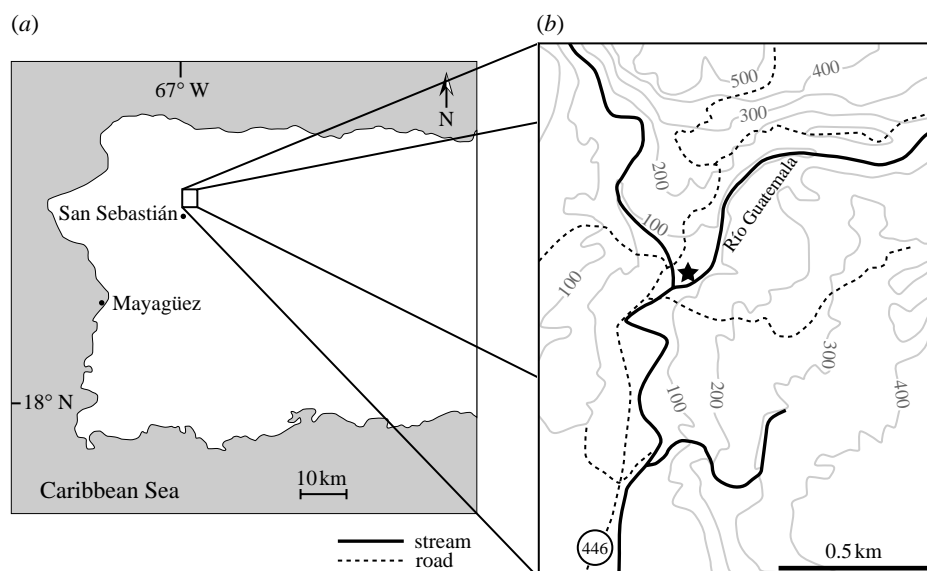


Figure 1. (a) Map of the western half of Puerto Rico showing the location of the town of San Sebastián. (b) Geologic map of the locality where UPRMP 3094 was collected. Star indicates the site where holotype was collected. Contour interval = 100 m.

are from marginal marine deposits which suggests that the ability to live in, or at least withstand, saltwater was typical among gavialoids until comparatively recently.

## 2. SYSTEMATIC PALAEONTOLOGY

CROCODYLIA Gmelin 1789 (*sensu* Benton & Clark 1988)

GRYPOSUCHINAE tax. nov.

GAVIALOIDEA Hay 1930 (*sensu* Brochu 2003)

*Aktiogavialis puertoricensis* tax. nov.

### (a) *Etymology*

*Aktios*, Gr., from the shore or beach; *gavialis*, gharial; *puertoricensis*, Puerto Rico.

### (b) *Holotype*

University of Puerto Rico Department of Geology Paleontology Collection, Mayagüez (UPRMP) 3094, incomplete skull including the braincase and skull table behind the orbits (figure 2).

### (c) *Locality and horizon*

The holotype was collected from a medium- to coarse-grained sandstone in the lower San Sebastián Formation exposed along Río Guatemala near the town of San Sebastián (18°21'24.6" N, 66°59'41.8" W; figure 1). Exposures in the area consist of soils interbedded with marine mudstones and siltstones grading up into deltaic sands, all of which are part of the basal San Sebastián Formation (Ward *et al.* 2002). Additional vertebrate remains from the section include elasmobranchs, turtles, sirenians and rodents (MacPhee & Wyss 1990; J. V. J. & H.S. unpublished data).

Biostratigraphically informative ostracodes from mudstones in the collection area indicate an Oligocene age for the section (van den Bold 1965). Strontium isotopic ages (Johnson *et al.* 2006; Ramirez *et al.* 2006) and biostratigraphic evidence from planktic foraminifera and calcareous nannofossils (Monroe 1980; Frost *et al.* 1983; Seiglie & Moussa 1984) from the lower part

of the overlying Lares Limestone unambiguously place the San Sebastián–Lares contact within the Upper Oligocene, further indicating a pre-Miocene age for the holotype.

An isolated crocodylian caudal vertebra was collected from the same horizon as the holotype. Other crocodylian remains collected from stratigraphically lower units at this locality consist of vertebrae and scutes similar to those from other San Sebastián localities (Brochu *et al.* 2007).

### (d) *Diagnosis*

Gavialoid crocodylian with a distinct fossa extending anteriorly from the supratemporal fenestra on the dorsal postorbital surface. Absence of prootic exposure on the lateral braincase wall with at least some gryposuchines. Supratemporal fenestrae are larger anteroposteriorly than mediolaterally (could reflect ontogenetic variation).

### (e) *Description*

Although incomplete, the preserved portions are undistorted (figure 2). Water abrasion obscures some sutures.

The margins of the orbits are upturned medially and posteriorly, giving them the 'telescoped' appearance typical of more derived gavialoids. The dorsal surfaces of the fused frontals are concave between the orbits and bear an anteroposteriorly oriented groove on the ventral surface for the olfactory tract. The postorbital bars are not preserved, but the ventral surfaces of the postorbitals indicate where they descended from the skull table and indicate robust bars.

The skull table is dorsally reflected anteriorly, and the postorbitals form a pair of arches where they form the orbital margins. The supratemporal fenestrae are sub-circular with long axes oriented anterolaterally. The frontoparietal suture intersects the fenestral margins, but the parietal and postorbitals maintain robust contacts within the fenestral space. Within the supratemporal fenestrae, the quadrate forms the ventral margin of the circular temporal foramen.

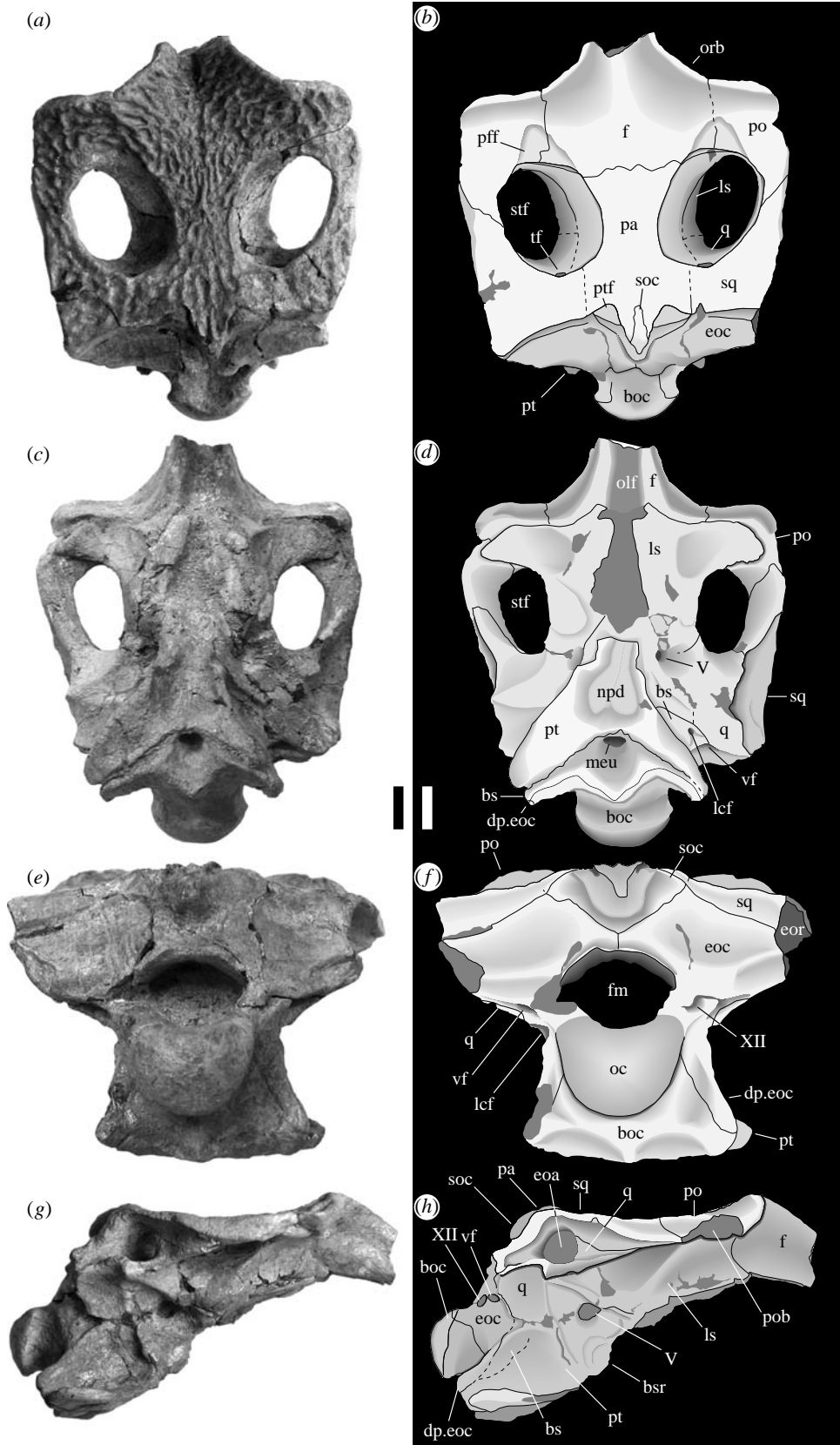


Figure 2. UPRMP 3094, holotype, *Aktiogavialis puertoricensis*: (a,b) dorsal view, (c,d) ventral view, (e,f) posterior view, and (g,h) right lateral view. Scale bar, 1 cm. boc, basioccipital; bs, basisphenoid; bsr, base of basisphenoid rostrum; dp.eoc, descending process of exoccipital; eoa, external otic aperture; eoc, exoccipital; eor, external otic recess; f, frontal; fm, foramen magnum; lcf, lateral carotid foramen; ls, laterosphenoid; meu, median Eustachian foramen; npd, roof of nasopharyngeal duct; oc, occipital condyle; olf, pathway of olfactory tract; orb, orbit; pa, parietal; pff, fossa anterior to supratemporal fenestra; po, postorbital; pob, base of postorbital bar; pt, pterygoid; ptf, post-temporal fenestra; q, quadrate; soc, supraoccipital; sq, squamosal; stf, supratemporal fenestra; tf, temporal foramen; V, trigeminal foramen; vf, vagus foramen; XII, aperture for 12th cranial nerve.

A distinct fossa extends anteriorly from the supratemporal fenestra on the dorsal postorbital surface (figure 2*a,b*). The floor of the fossa is pitted and the posterior limit corresponds with the postorbital–parietal suture. This feature is unknown in any other crocodylian.

The posterior margin of the skull table projects posteriorly and forms an acute process. The supraoccipital is exposed dorsally as a diamond-shaped element at the posteriormost tip of this process adjacent to the parietal. The dorsal surfaces of the post-temporal fenestrae appear not to have extended back to the posteriormost tip of this process.

The squamosal bears an indistinct, but anteriorly flaring, lateral groove for attachment of the ear flap musculature (figure 2*g,h*). The squamosal is dorsoventrally very thin immediately dorsal to the triangular external otic aperture. Within the otic recess, the squamosal forms the posterior and dorsal margins of the aperture, and the squamosal–quadrate suture intersects the apertural margin at its posteroventral corner.

Portions of the lateral braincase wall are damaged, making it difficult to trace some sutures. However, there is no trace of the prootic on either lateral braincase wall, and the surface surrounding the trigeminal foramen (where the suture would be expected in a gavialoid) is relatively well preserved on both sides (figure 2*g,h*). A notch on the laterosphenoid extending anteriorly from the trigeminal foramen probably indicates the pathway of the ophthalmic branch of the trigeminal nerve. A shallow fossa anteroventral to the trigeminal foramen constricts the braincase where the lost basisphenoid rostrum would have attached. The posterior half of the lateral braincase wall is concave behind a thin dorsoventral crest on the surfaces of the quadrate and pterygoid.

The laterosphenoid capitate processes meet the ventral surface of the skull table with anterolaterally oriented anterior margins (figure 2*c,d*). Most of the pterygoid is missing, but the dorsal surface of the nasopharyngeal duct is preserved, suggesting a posteroventrally oriented aperture with a modest dorsal septum. The medial Eustachian foramen is large and encircled by the basisphenoid, which is exposed as an anteroposteriorly broad element between the basioccipital and pterygoid.

In posterior view (figure 2*e,f*), the dorsal margin of the skull table slopes ventrally lateral to the parietal. The exoccipitals meet at the midline dorsal to the foramen magnum and bear broad descending processes that continue to the ventral surface of the basioccipital tubera. The vagus foramen is an oval slit projecting posteroventrally, and the lateral carotid foramen is a circular opening immediately ventral to the vagus foramen. A single foramen for the accessory nerve is preserved on the right side. Since the basisphenoid suture is not preserved on the lateral braincase surface, the relationship between the lateral exposure of the basisphenoid and lateral carotid foramen cannot be ascertained. The right posterior pterygoid process is a small, posteriorly projecting element lateral to the basioccipital tuber. The lateral Eustachian foramina are not preserved, but the ventral margin of the basioccipital tubera is nearly horizontal in posterior view, with deep posterior concavities between the sagittal crest and lateral sides, suggesting a placement lateral to the median Eustachian foramen.

### 3. PHYLOGENETIC ANALYSIS

#### (a) *Methods*

*Aktiogavialis* was added to a matrix of 166 morphological characters (Brochu 2004, 2006; Brochu & Rincon 2004; see electronic supplementary material). The matrix included 57 ingroup taxa including *Aktiogavialis*. The putative gavialoid *Piscogavialis jugaliperforatus* (Kraus 1998) from the Miocene of Peru was added based on codings published by Delfino *et al.* (2005) with modifications from direct observation of the type. *Bernissartia fagesii* and *Hylaeochampsia vectiana* were designated as sequential outgroups.

The matrix was subjected to a maximum parsimony analysis using PAUP\* v. 4.0b10 (Swofford 2002). One hundred heuristic searches were performed with the starting order of ingroup taxa randomized in each search. Bootstrap support, based on 100 000 replicate datasets, was assessed both globally (for the complete set of taxa used in the parsimony analysis) and locally (for a dataset restricted to the gavialoids, with *Borealosuchus sternbergii* and *H. vectiana* used as outgroups).

#### (b) *Results*

The analysis recovered 289 446 equally optimal trees, all but one within a single parsimony island (length = 449, CI without uninformative characters = 0.424, RI = 0.785). The strict consensus topology (figure 3) is consistent with previous analyses, with a monophyletic Gavialoidea at the root of Crocodylia and Tomistominae nested deeply within Crocodyloidea.

Based on these results, *A. puertoricensis* is a derived gavialoid belonging to a group otherwise occurring in the Mio–Pliocene of South America: *P. jugaliperforatus*, *Siquisiquesuchus venezuelensis* (Brochu & Rincon 2004); *Gryposuchus colombianus* (Langston 1965); and *Ikanogavialis gameroi* (Sill 1970). This group is closely related to extant *Gavialis* and Miocene *Gavialis* from the Indian subcontinent.

Bootstrap support is comparatively low (figure 3), and trees one step longer than optimal cause relationships within the clade including *Gavialis* and the South American forms to collapse. Within the South American clade, all placements of *Aktiogavialis* are equally optimal except as the sister taxon to *Ikanogavialis* or *Piscogavialis* (each of which would increase tree length by one step).

### 4. DISCUSSION

#### (a) *Nomenclature*

We define *Gryposuchinae* as a stem-based group name including *Gryposuchus jessei* (Gürich 1912) and all crocodylians closer to it than to *G. gangeticus* or *T. schlegelii*. We acknowledge the relatively low support *Gryposuchinae* currently receives, but we expect this to grow as new characters are added to the analysis and more complete fossils are described.

#### (b) *Phylogenetic relationships*

Until recently, the Tertiary record of crocodylians in Puerto Rico was limited to fragmentary material that could not be diagnosed to any particular crocodylian lineage (MacPhee & Wyss 1990). However, isolated osteoderms and a left quadrate ramus were consistent



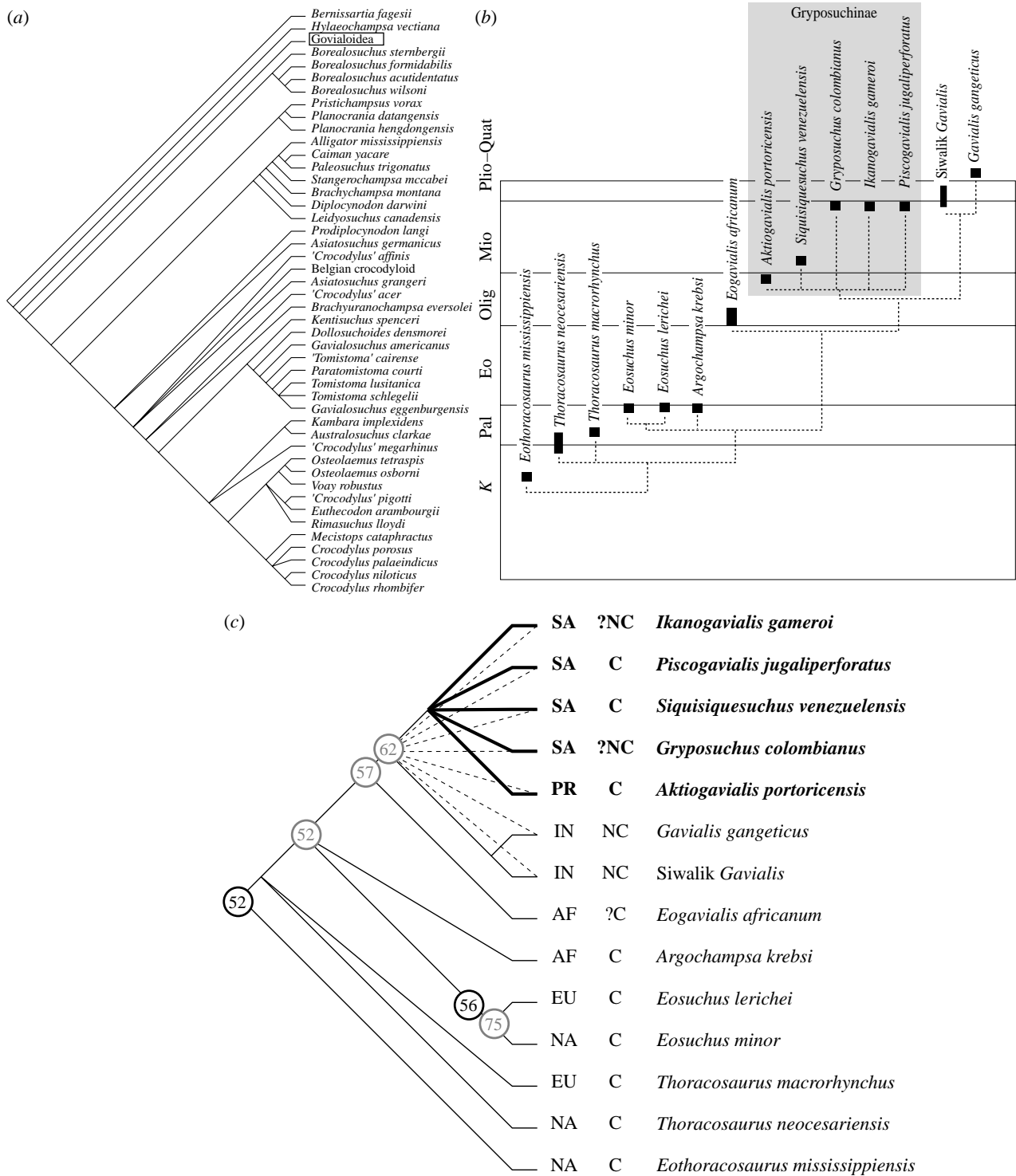


Figure 3. (a) Strict consensus of 289 446 equally optimal trees from maximum parsimony analysis; Gavialoidea collapsed. (b) Phylogenetic relationships among gavialooids in this analysis shown in stratigraphic position. (c) Phylogenetic relationships among gavialooids; gryposuchines are shown in boldface. Numbers in circles are bootstrap proportions for full (black) and restricted (grey) analyses (see text). Dashed lines indicate loss of resolution if condition of prootic in *Aktiogavialis* is coded as unknown. Columns between tree and taxon names indicate geographical occurrence (left) and whether or not taxon is from a coastal (C) or non-coastal (NC) setting. AF, Africa; EU, Europe; IN, Indian subcontinent; NA, North America; PR, Puerto Rico; SA, South America.

with corresponding parts from gavialooids. In particular, the osteoderms were rectangular, concave anteriorly in dorsal view and had small keels closer to the posterior margin than the anterior. This latter feature is typical of derived gavialooids, including Neogene gryposuchines (Brochu et al. 2007).

Although quantitative support for the position of *Aktiogavialis* among gavialooids is low, supporting characters are compelling. The descending processes of the exoccipitals lateral to the occipital condyle are anteroposteriorly broad and extend to the ventral surface of the basioccipital tubera, a feature found exclusively in

gavialoids. The basisphenoid is not exposed as a broad sheet ventral to the median Eustachian foramen, and it shares with *Eosuchus* and more derived forms an anteroposteriorly broad basisphenoid adjacent to the median Eustachian aperture. The orbital margin is telescoped, as are those of *Eogavialis*, *Gavialis* and other gryposuchines. With *Gavialis* and gryposuchines, *Aktiogavialis* shares small, posteriorly oriented posterior pterygoid processes.

Gryposuchines share a lack of a broad prootic exposure around the trigeminal foramen on the lateral braincase wall. Most gavialoids retain the plesiomorphic condition for Crocodylia, in which the prootic can be seen on the lateral braincase wall partially surrounding the trigeminal foramen. Three gavialoids—*Aktiogavialis*, *Gryposuchus* and *Piscogavialis*—lack this exposure (Langston & Gasparini 1997; Brochu & Rincon 2004; C. A. Brochu 1995, 1997; personal observations). This condition also occurs independently among derived alligatoroids and crocodyloids. The condition of the prootic is unknown in *Ikanogavialis* and *Siquisiquesuchus*. Other characters supporting gryposuchine monophyly (Brochu & Rincon 2004) are unknown in *Aktiogavialis*.

Water abrasion complicates this interpretation. Sutures are difficult to trace on the external surface, and the absence of a lateral prootic exposure could reflect non-preservation. If we recode the character expressing exposure of the prootic as unknown in *Aktiogavialis*, it can equally parsimoniously be made the sister species to any of the derived gavialoids, resulting in the collapse of the South American clade and *Gavialis* (figure 3). Discovery of additional material would clarify the matter.

Another complication is possible immaturity of the specimen. Differences in the shape of the supratemporal fenestrae, and in the extent to which the frontoparietal suture intersects the fenestral margins, are ontogenetically variable in extant crocodylians. Specific allometric changes vary among taxa, but in extant *Gavialis* the supratemporal fenestra grows comparatively wider, constricting the interfenestral bar in older animals and incorporating a frontoparietal suture that, in earlier ontogenetic stages, lies entirely on the dorsal skull table surface (Kälin 1933; Brochu 2004).

The shape of the supratemporal fenestrae approximates that of immature *Gavialis*—the long axis is oriented anterolaterally and diverges from the sagittal plane by approximately 25°. In contrast, the supratemporal fenestrae of larger gryposuchines are mediolaterally wider than long, as is the case in adult *Gavialis*. This suggests that UPRMP 3094 is from an immature animal. Likewise, the temporal foramen is circular and not a slender slit, as in mature South American gryposuchines or *Gavialis*.

Two aspects of the skull table, however, are inconsistent with ontogenetic variation as observed in modern *Gavialis*. First, the frontoparietal suture intersects the supratemporal fenestral margin in UPRMP 3094. This condition occurs in older *Gavialis* in which positive allometry in the size of the fenestra pushes its anterior limit past the suture, but not in individuals with anteroposteriorly elongate fenestrae or in individuals of approximately the same size as UPRMP 3094. Second, the shallow fossa anterior to the fenestra does not occur in other gavialoids at any ontogenetic stage.

### (c) *Historical biogeography*

The San Sebastián Formation was deposited in a basin resulting from subsidence of the Puerto Rico Trench (Monroe 1980). It consists of clay and sandy clay, with some local conglomerates and sandstones, overlying Cretaceous through Eocene rocks. The formation was predominantly formed in shallow marine, deltaic and estuarine depositional environments.

*Siquisiquesuchus* and *Piscogavialis* were also found in coastal settings (Kraus 1998; Brochu & Rincon 2004). These could be washout from inland sources, but the multiple occurrences, along with the presence of at least one form (*Aktiogavialis*) on what was then an island (Iturralde-Vinent & MacPhee 1999), argue that these occurrences might reflect the actual environment in which they lived.

The provenance of other Miocene gryposuchines is less clear. *Gryposuchus colombianus* is derived from non-marine deposits of Colombia (Kay & Madden 1997), but *Gryposuchus* and *Ikanogavialis* have been reported from the Urumaco sequence of Venezuela, which includes both marine and non-marine units (Sill 1970; Linares 2004; Sánchez-Villagra & Aguilera 2006). It is unclear whether Urumaco gavialoids are from fluvial or shallow marine portions of the sequence. Other South American gavialoids are from freshwater units (e.g. Rusconi 1935; Gasparini 1968; Bocquetin & Buffetaut 1981; Souza-Filho & Bocquetin 1989). There are no truly marine crocodylians alive today—those found in seawater also occur in freshwater (Ross 1998)—but in the absence of evidence placing fossil forms in coastal or marginal marine deposits, it is prudent to assume that these were freshwater animals.

Post-Palaeogene fossils unambiguously closer to *G. gangeticus* than to Gryposuchinae derive from the southern Asian mainland (Lull 1944) or Java (Janensch 1911; Delfino & de Vos 2006). All are from freshwater deposits, and Java was sometimes connected to the Asian mainland during the Neogene and the Quaternary (Voris 2000; Hall 2001). But derived gavialoids have been found in Neogene coastal deposits of the Arabian Peninsula (Rauhe *et al.* 1999) and the Quaternary of the Solomon Islands (Molnar 1982). Relationships of these forms to either Gryposuchinae or *Gavialis* are unknown, but they suggest a more complicated biogeographic scenario for Gavialoidea than ecology of the single living species would indicate.

*Eogavialis africanum* is from Late Eocene–Oligocene deposits in the Fayum Depression of Egypt that also represent both marine and non-marine deposits (Bown & Kraus 1988; Gingerich 1992; Gagnon 1997). It has been sampled from multiple horizons throughout the sequence (Andrews 1906; Buffetaut 1982), but we do not know whether the museum specimens observed come from both shallow marine and fluvial deposits.

Uncertainty over provenance, combined with unresolved phylogenetic relationships among gryposuchines, makes it difficult to assess whether the last common ancestor of *Gavialis* and gryposuchines was a coastal animal. But if we resolve gryposuchine relationships according to stratigraphic occurrence, with *Aktiogavialis* and *Siquisiquesuchus* forming successive outgroups to remaining members of the group, and if we assume that *Eogavialis* was a coastal form, then the last common

ancestor of gryposuchines and *Gavialis* is most parsimoniously presumed to have occurred in a coastal setting.

Whether the ancestors of Gryposuchinae are of African or Asian origin is ambiguous on current phylogenetic estimates (Brochu & Rincon 2004), but an African origin has been preferred historically (e.g. Langston 1965; Buffetaut 1982; Langston & Gasparini 1997) largely because the Atlantic would be a much smaller barrier to cross than the Pacific and warm equatorial Atlantic currents run from east to west. The results of this analysis do not resolve the phylogenetic ambiguity, but the fact that the oldest member of the group (*Aktiogavialis*) is from the Greater Antilles rather than a Pacific locality supports the trans-Atlantic scenario.

Strictly speaking, the gavialoid fossil record does not falsify the hypothesis that vicariance explains the distribution of Neogene gavialoids. The fossil record is incomplete. But South America was isolated from the rest of Gondwana by the end of the Mesozoic, and although crocodyliforms are prominent members of Cretaceous Gondwanan faunas (e.g. Gasparini 1996; Buckley et al. 1997, 2000; Goman 1997; Larsson & Gado 2000; Krause 2003; Sereno et al. 2003; Turner 2004; Pol & Apesteguía 2005; Candeiro & Martinelli 2006; Salisbury et al. 2006; Zaher et al. 2006), nothing related to *Gavialis* has been reported. Range extensions of roughly 75 Myr in South America and 65 Myr in Africa would be required to accommodate vicariance.

A coastal dispersal route along the North Atlantic is also problematic. Thoracosaurids are found in marginal marine deposits on both sides of the North Atlantic, but these are distantly related to gryposuchines (figure 3). Long-snouted crocodylians from coastal North America and Europe after the Early Eocene are tomistomines unrelated to gryposuchines (e.g. Auffenberg 1954; Antunes 1961; Buffetaut et al. 1984; Erickson & Sawyer 1996; Brochu 2001).

Other secondarily aquatic tetrapods are thought to have dispersed between Africa and the Neotropics since the Eocene, including seals (Deméré et al. 2003; Fyler et al. 2005), manatees and dugongs (Domning 2001; Vianna et al. 2006), and crocodiles (*Crocodylus*; Brochu 2001). The same is true for several non-aquatic tetrapods, including monkeys (Schrägo & Russo 2003), rodents (Poux et al. 2006), geckos (Carranza et al. 2000) and skinks (Carranza & Arnold 2003). Clear examples of low-latitude dispersal across the Pacific to South America of coastal or freshwater tetrapods are lacking.

The oral cavity of extant *Gavialis* is keratinized. This is thought to limit osmotic loss of water in hypersaline environments among living crocodylians, and its presence in freshwater crocodylians (including *Gavialis*) was thought to be the evidence that crocodylians passed through a marine phase early in their history (Taplin et al. 1985; Taplin & Grigg 1989). This suggests at least partial tolerance of saltwater. But like living alligatorids (which, with rare exception, avoid saltwater), *Gavialis* lacks the large salt-excreting glands found on the tongues of crocodylids (Taplin et al. 1982; Taplin & Grigg 1989; Taylor et al. 1995; Jackson et al. 1996; Leslie & Taplin 2001). Whether absence in *Gavialis* is plesiomorphic or a derived loss is unknown, but if *Gavialis* is secondarily limited to freshwater, lingual salt glands (which leave

no trace on the skeleton) might be expected in saltwater predecessors.

We therefore have a clade of derived gavialoids, at least some found in former coastal areas, in areas geographically separated from the ranges of known relatives in Africa and Asia. The fossils expected with vicariance- or circum-Atlantic dispersal-based models have not been found, and the oral morphology of *Gavialis* is consistent with saltwater tolerance. Taken together, these observations lend support for earlier suggestions that Neotropical gavialoids are descended from ancestors that crossed the Atlantic (Buffetaut 1982; Langston & Gasparini 1997).

Ongoing fieldwork in Puerto Rico will hopefully reveal more complete remains of *Aktiogavialis* and help resolve its relationships with other gavialoids, but fieldwork in South America and Africa is needed to allow a more complete and robust picture of gavialoid history throughout the Cenozoic. Further phylogenetic work on all crocodylians, living and extinct, is necessary to allow the integration of biogeographic information from fossils with physiological information from their living descendants.

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## REFERENCES

- Andrews, C. W. 1906 *A descriptive catalogue of the tertiary vertebrata of the Fayûm, Egypt*. London, UK: British Museum (Natural History).
- Annandale, N. 1915 Fauna of the Chilka lake: reptiles and batrachia. *Mem. Ind. Mus.* 5, 167–174.
- Antunes, M. T. 1961 *Tomistoma lusitanica*, crocodilien du Miocène du Portugal. *Revista da Faculdade de Ciências de Lisboa (ser. 2)* 9, 5–88.
- Auffenberg, W. 1954 Additional specimens of *Gavialosuchus americanus* (Sellards) from a new locality in Florida. *Q. J. Fl. Acad. Sci.* 17, 185–209.
- Benton, M. J. & Clark, J. M. 1988 Archosaur phylogeny and the relationships of the Crocodylia. In *The phylogeny and classification of the tetrapods*, vol. 1 (ed. M. J. Benton) *Amphibians, reptiles, birds*, pp. 295–338. Oxford, UK: Clarendon Press.
- Bocquetin, J. C. & Buffetaut, E. 1981 *Hesperogavialis cruxenti* n. gen., n. sp., nouveau gavialide (Crocodylia, Eusuchia) du Miocène Supérieur (Huayquerien) d'Uruguay (Venezuela). *Géobios* 14, 415–419.
- Bown, T. M. & Kraus, M. J. 1988 Geology and paleoenvironment of the Oligocene Jebel Qatrani Formation and adjacent rocks, Fayum Depression, Egypt. *US Geol. Survey Prof. Pap.* 1452, 1–60.
- Brochu, C. A. 1997 Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Syst. Biol.* 46, 479–522. (doi:10.2307/2413693)
- Brochu, C. A. 2001 Congruence between physiology, phylogenetics, and the fossil record on crocodylian historical biogeography. In *Crocodylian biology and evolution* (eds G. Grigg, F. Seebacher & C. E. Franklin), pp. 9–28. Sydney, Australia: Surrey Beatty and Sons.
- Brochu, C. A. 2003 Phylogenetic approaches toward crocodylian history. *Annu. Rev. Earth Planet. Sci.* 31, 357–397. (doi:10.1146/annurev.earth.31.100901.141308)
- Brochu, C. A. 2004 A new gavialoid crocodylian from the Late Cretaceous of eastern North America and



- the phylogenetic relationships of thoracosaurus. *J. Vert. Paleontol.* **24**, 610–633. (doi:10.1671/0272-4634(2004)024[0610:ANLCCG]2.0.CO;2)
- Brochu, C. A. 2006 Osteology and phylogenetic significance of *Eosuchus minor* (Marsh 1870), new combination, a longirostrine crocodylian from the Late Paleocene of North America. *J. Paleontol.* **80**, 162–186. (doi:10.1666/0022-3360(2006)080[0162:OAPSOE]2.0.CO;2)
- Brochu, C. A. & Rincon, A. D. 2004 A gavialoid crocodylian from the Lower Miocene of Venezuela. *Spec. Pap. Palaeontol.* **71**, 61–78.
- Brochu, C. A., Nieves-Rivera, A., Vélez-Juarbe, J., Daza-Vaca, J. D. & Santos, H. 2007 Tertiary crocodylians from Puerto Rico: evidence for Late Tertiary endemic crocodylians in the West Indies? *Geobios* **40**, 51–59. (doi:10.1016/j.geobios.2005.10.008)
- Buckley, G. A., Brochu, C. A. & Krause, D. W. 1997 Hyperdiversity and the paleobiogeographic origins of the Late Cretaceous crocodyliforms of Madagascar. *J. Vert. Paleontol.* **17**, 34A.
- Buckley, G. A., Brochu, C. A., Krause, D. W. & Pol, D. 2000 A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature* **405**, 941–944. (doi:10.1038/35016061)
- Buffetaut, E. 1982 Systematique, origine et évolution des Gavialidae Sud-Américains. *Geobios, Memoire Special* **6**, 127–140.
- Buffetaut, E., Crouzel, F., Juillard, F. & Stigliani, F. 1984 Le crocodylien longirostre *Gavialosuchus* dans le Miocène moyen de Polastron (Gers, France). *Geobios* **17**, 113–117. (doi:10.1016/S0016-6995(84)80009-1)
- Candeiro, C. R. A. & Martinelli, A. G. 2006 A review of paleogeographical and chronostratigraphical distribution of mesoeucrocodylian species from the upper Cretaceous beds from the Bauru (Brazil) and Neuquén (Argentina) groups, southern South America. *J. South Am. Earth Sci.* **22**, 116–112. (doi:10.1016/j.jsames.2006.08.001)
- Carranza, S. & Arnold, E. N. 2003 Investigating the origin of transoceanic distributions: mtDNA shows *Mabuya* lizards (Reptilia: Scincidae) crossed the Atlantic twice. *Syst. Biodiv.* **1**, 275–282. (doi:10.1017/S1477200003001099)
- Carranza, S., Arnold, E. N., Mateo, J. A. & Lopez-Jurado, L. F. 2000 Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proc. R. Soc. B* **267**, 637–649. (doi:10.1098/rspb.2000.1050)
- Delfino, M. & de Vos, J. 2006 A revision of Dubois crocodylians: *Gavialis bengawanicus* and *Crocodylus ossifragus* from the Early Pleistocene *Homo* beds of Java. *J. Vert. Paleontol.* **26**, 55A.
- Delfino, M., Piras, P. & Smith, T. 2005 Anatomy and phylogeny of the gavialoid *Eosuchus lerichei* from the Paleocene of Europe. *Acta Palaeontologica Polonica* **50**, 565–580.
- Deméré, T. A., Berta, A. & Adam, P. J. 2003 Pinnipedimorph evolutionary biogeography. *Bull. Am. Mus. Nat. Hist.* **279**, 32–76.
- Densmore, L. D. 1983 Biochemical and immunological systematics of the order Crocodylia. In *Evolutionary biology*, vol. 16 (eds M. K. Hecht, B. Wallace & G. H. Prance), pp. 397–465. New York, NY: Plenum Press.
- Densmore, L. D. & Owen, R. D. 1989 Molecular systematics of the order Crocodylia. *Am. Zool.* **29**, 831–841.
- Domning, D. P. 2001 Evolution of the Sirenia and Desmostylia. In *Secondary adaptation of tetrapods to life in water* (eds J.-M. Mazin & V. Buffrenil), pp. 151–168. Munich, Germany: Verlag Dr. Friedrich Pfeil.
- Erickson, B. R. 1998 Crocodylians of the Black Mingo Group (Paleocene) of the South Carolina Coastal Plain. *Trans. Am. Phil. Soc.* **88**, 196–214. (doi:10.2307/1006674)
- Erickson, B. R. & Sawyer, G. T. 1996 The estuarine crocodile *Gavialosuchus carolinensis* n. sp. (Crocodylia: Eusuchia) from the Late Oligocene of South Carolina, North America. *Monogr. Sci. Mus. Minn. (Paleontology)* **3**, 1–47.
- Frost, S. H., Harbour, J. L., Beach, D. K., Realini, M. J. & Harris, P. M. 1983 Oligocene reef tract development, southwestern Puerto Rico. *Sedimenta* **9**, 1–144.
- Fyler, C. A., Reeder, T. W., Berta, A., Antonelis, G., Aguilar, A. & Androukaki, E. 2005 Historical biogeography and phylogeny of monachine seals (Pinnipedia: Phocidae) based on mitochondrial and nuclear DNA data. *J. Biogeogr.* **32**, 1267–1279. (doi:10.1111/j.1365-2699.2005.01281.x)
- Gagnon, M. 1997 Ecological diversity and community ecology in the Fayum sequence (Egypt). *J. Human Evol.* **32**, 133–160. (doi:10.1006/jhev.1996.0107)
- Gallagher, W. B., Parris, D. C. & Spamer, E. E. 1986 Paleontology, biostratigraphy, and depositional environments of the Cretaceous–Tertiary transition in the New Jersey Coastal Plain. *The Mosasaur* **3**, 1–35.
- Gasparini, Z. 1968 Nuevas restos de *Rhamphostomopsis neogaeus* (Burm.) Rusconi 1933 (Reptilia, Crocodylia) del “Mesopotamiense” (Plioceno medio-superior) de Argentina. *Ameghiniana* **5**, 299–311.
- Gasparini, Z. 1996 Biogeographic evolution of the South American crocodylians. *Münchener Geowissenschaftliche Abhandlungen* **30**, 159–184.
- Gatesy, J., Amato, G., Norell, M., DeSalle, R. & Hayashi, C. 2003 Combined support for wholesale taxic atavism in gavialine crocodylians. *Syst. Biol.* **52**, 403–422. (doi:10.1080/10635150390197037)
- Gingerich, P. D. 1992 Marine mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: stratigraphy, age, and paleoenvironments. *Univ. Mich. Pap. Paleontol.* **30**, 1–84.
- Gomani, E. M. 1997 A crocodyliform from the Early Cretaceous Dinosaur Beds, northern Malawi. *J. Vert. Paleontol.* **17**, 280–294.
- Gürich, G. 1912 *Gryposuchus jessei*, ein neues schmalsnauziges Krokodil aus den jüngeren Ablagerungen des oberen Amazonas-Gebietes. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* **29**, 59–71.
- Hall, R. 2001 Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. In *Faunal and floral migrations and evolution in SE Asia–Australia* (eds I. Metcalfe, J. M. B. Smith, M. Morwood & I. D. Davidson), pp. 35–56. Lisse, The Netherlands: A.A. Balkema.
- Harshman, J., Huddleston, C. J., Bollback, J. P., Parsons, T. J. & Braun, M. J. 2003 True and false gharials: a nuclear gene phylogeny of Crocodylia. *Syst. Biol.* **52**, 386–402. (doi:10.1080/10635150390197028)
- Hass, C. A., Hoffman, M. A., Densmore, L. D. & Maxson, L. R. 1992 Crocodylian evolution: insights from immunological data. *Mol. Phylogenet. Evol.* **1**, 193–201. (doi:10.1016/1055-7903(92)90015-9)
- Hua, S. & Jouve, S. 2004 A primitive gavialoid from the Paleocene of Morocco. *J. Vert. Paleontol.* **24**, 341–350. (doi:10.1671/1104)
- Iturralde-Vinent, M. A. & MacPhee, R. D. E. 1999 Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bull. Am. Mus. Nat. Hist.* **238**, 1–95.
- Jackson, K., Butler, D. G. & Brooks, D. R. 1996 Habitat and phylogeny influence salinity discrimination in crocodylians: implications for osmoregulatory physiology and historical biogeography. *Biol. J. Linn. Soc.* **58**, 371–383. (doi:10.1006/bjll.1996.0042)



- Janensch, W. 1911 Die Reptilienreste (exkl. Schildkröten). In *Die Pithecanthropus-Schichten auf Java* (eds M. L. Selenka & M. Blanckenhorn), pp. 61–74. Leipzig, Germany: Wilhelm Engelmann.
- Janke, A., Gullberg, A., Hughes, S., Aggarwal, R. K. & Arnason, U. 2005 Mitogenomic analyses place the gharial (*Gavialis gangeticus*) on the crocodile tree and provide pre-K/T divergence times for most crocodylians. *J. Mol. Evol.* **61**, 620–626. (doi:10.1007/s00239-004-0336-9)
- Johnson, C. C., Ramirez, W. R., Leckie, R. M., Hernandez, S. Y., Barrow, E. A., Hegewald, M. & Velez, J. 2006 Oligocene reef deposits linked to ODP site 999 with strontium isotope stratigraphy. *Geol. Soc. Am. Abstr. Prog.* **38**, 557.
- Jouve, S., Iarochene, M., Bouya, B. & Amaghazaz, M. 2006 New material of *Argochampsa krebsi* (Crocodylia: Gavialoidea) from the Lower Paleocene of the Oulad Abdoun Basin (Morocco): phylogenetic implications. *Geobios* **39**, 817–832. (doi:10.1016/j.geobios.2005.07.003)
- Kälin, J. A. 1933 Beiträge zur vergleichenden Osteologie des Crocodylienschädels. *Zoologische Jahrbücher* **57**, 535–714.
- Kay, R. F. & Madden, R. H. 1997 Paleogeography and paleoecology. In *Vertebrate paleontology in the neotropics: the Miocene fauna of La Venta, Colombia* (eds R. F. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn), pp. 520–550. Washington, DC: Smithsonian Institution Press.
- Köken, E. 1888 *Thoracosaurus macrorhynchus* Bl. aus der Tuffkreide von Maastricht. *Abdruck a.d. Zeitschrift der Deutschen geologische Gessellschaft* **1888**, 754–773.
- Kraus, R. 1998 The cranium of *Piscogavialis jugaliperforatus* n. gen., n. sp. (Gavialidae, Crocodylia) from the Miocene of Peru. *Paläontologische Zeitschrift* **72**, 389–406.
- Krause, D. W. 2003 Late Cretaceous vertebrates of Madagascar: a window into Gondwanan biogeography at the end of the age of dinosaurs. In *The natural history of Madagascar* (eds S. M. Goodman & J. P. Benstead), pp. 40–47. Chicago, IL: University of Chicago Press.
- Langston, W. 1965 Fossil crocodylians from Colombia and the Cenozoic history of the Crocodylia in South America. *Univ. Calif. Publ. Geol. Sci.* **52**, 1–152.
- Langston, W. 1973 The crocodylian skull in historical perspective. In *Biology of the reptilia*, vol. 4 (eds C. Gans & T. Parsons) *Morphology D*, pp. 263–284. London, UK: Academic Press.
- Langston, W. & Gasparini, Z. 1997 Crocodylians, *Gryposuchus*, and the South American gavials. In *Vertebrate paleontology in the neotropics: the Miocene fauna of La Venta, Colombia* (eds R. F. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn), pp. 113–154. Washington, DC: Smithsonian Institution.
- Larsson, H. C. E. & Gado, B. 2000 A new Early Cretaceous crocodyliiform from Niger. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **217**, 131–141.
- Laurent, Y., Buffetaut, E. & Le Loeff, J. 2000 Un crane de thoracosaurine (Crocodylia, Crocodylidae) dans le Maastrichtien Supérieur du sud de la France. *Oryctos* **3**, 19–27.
- Leslie, A. J. & Taplin, L. E. 2001 Recent developments in osmoregulation of crocodylians. In *Crocodylian biology and evolution* (eds G. Grigg, F. Seebacher & C. E. Franklin), pp. 265–279. Chipping Norton, UK; Sydney, Australia: Surrey Beatty and Sons.
- Linares, O. J. 2004 Bioestratigrafía de la fauna de mamíferos de las Formaciones Socorro, Urumaco y Codore (Mioceno Medio–Plioceno Temprano) de la región de Urumaco, Falcon, Venezuela. *Paleobiología Neotropical* **1**, 1–26.
- Lull, R. S. 1944 Fossil gavials from India. *Am. J. Sci.* **242**, 417–430.
- MacPhee, R. D. E. & Wyss, A. R. 1990 Oligo–Miocene vertebrates from Puerto Rico, with a catalog of localities. *Am. Mus. Novit.* **2965**, 1–45.
- McAliley, L. R., Willis, R. E., Ray, D. A., White, P. S., Brochu, C. A. & Densmore, L. D. 2006 Are crocodylians really monophyletic?—evidence for subdivisions from sequence and morphological data. *Mol. Phylogenet. Evol.* **39**, 16–32. (doi:10.1016/j.ympev.2006.01.012)
- Molnar, R. E. 1982 A longirostrine crocodylian from Murua (Woodlark), Solomon Sea. *Mem. Queensl. Mus.* **20**, 675–685.
- Monroe, W. H. 1980 Geology of the middle Tertiary formations of Puerto Rico. *US Geol. Survey Prof. Pap.* **953**, 1–93.
- Norell, M. A. 1989 The higher level relationships of the extant Crocodylia. *J. Herpetol.* **23**, 325–335. (doi:10.2307/1564042)
- Piveteau, J. 1927 Études sur quelques amphibiens et reptiles fossiles, II: Reptile du Montien. *Annales de Paléontologie* **16**, 29–37.
- Pol, D. & Apesteguía, S. 2005 New *Araripesuchus* remains from the Early Late Cretaceous (Cenomanian–Turonian) of Patagonia. *Am. Mus. Novit.* **3490**, 1–38. (doi:10.1206/0003-0082(2005)490[0001:NARFTE]2.0.CO;2)
- Poux, C., Chevret, P., Huchon, D., de Jong, W. W. & Douzery, E. J. P. 2006 Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. *Syst. Biol.* **55**, 228–244. (doi:10.1080/10635150500481390)
- Ramirez, W. R., Johnson, C. C., Martinez, M., Torres, M. C. & Ortiz, V. 2006 Strontium isotope stratigraphy from *Kuphus incrassatus*, Cretaceous limestones, Puerto Rico. *Geol. Soc. Am. Abstr. Prog.* **38**, 90.
- Rauhe, M., Frey, E., Pemberton, D. S. & 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* (eds P. J. Whybrow & A. Hill), pp. 163–185. New Haven, CT: Yale University Press.
- Robb, A. J. 2004 Vertebrate fossils from the Upper Cretaceous (Merchantville Formation: Early Campanian) Graham Brickyard Locality of New Jersey. *The Mosasaur* **7**, 75–88.
- Ross, J. P. 1998 *Crocodyles—status survey and conservation action plan*. Gland, Switzerland: International Union for the Conservation of Nature.
- Rusconi, C. 1935 Observaciones sobre los gaviales fosiles Argentinos. *Anales de la S.C. Argentina* **119**, 203–214.
- Salisbury, S. W. & Willis, P. M. A. 1996 A new crocodylian from the Early Eocene of southeastern Queensland and a preliminary investigation of the phylogenetic relationships of crocodylians. *Alcheringa* **20**, 179–227.
- Salisbury, S. W., Molnar, R. E., Frey, E. & Willis, P. M. A. 2006 The origin of modern crocodylians: new evidence from the Cretaceous of Australia. *Proc. R. Soc. B* **273**, 2439–2448. (doi:10.1098/rspb.2006.3613)
- Sánchez-Villagra, M. R. & Aguilera, O. A. 2006 Neogene vertebrates from Urumaco, Falcón State, Venezuela: diversity and significance. *J. Syst. Palaeontol.* **4**, 213–220. (doi:10.1017/S1477201906001829)
- Schrago, C. G. & Russo, C. A. M. 2003 Timing the origin of New World monkeys. *Mol. Biol. Evol.* **20**, 1620–1625. (doi:10.1093/molbev/msg172)
- Schwimmer, D. R. 1986 Late Cretaceous fossils from the Blufftown Formation (Campanian) in western Georgia. *The Mosasaur* **3**, 109–123.
- Seiglie, G. A. & Moussa, M. T. 1984 Late Oligocene–Pliocene transgressive–regressive cycles of sedimentation in northwestern Puerto Rico. *Am. Assoc. Petrol. Geol. Mem.* **36**, 89–95.
- Sereno, P. C., Sidor, C. A., Larsson, H. C. E. & Gado, B. 2003 A new notosuchian from the Early Cretaceous of Niger. *J. Vert. Paleontol.* **23**, 477–482. (doi:10.1671/0272-4634(2003)023[0477:ANNFTE]2.0.CO;2)

- Sill, W. D. 1970 Nota preliminar sobre un nuevo gavial del Plioceno de Venezuela y una discusión de los gaviales sudamericanos. *Ameghiniana* 7, 151–159.
- Singh, L. A. K. 1991 Distribution of *Gavialis gangeticus*. *Hamadryad* 16, 39–46.
- Smith, M. A. 1933 *The reptiles of British India, including Ceylon and Burma: reptilia and amphibia. Loricata, Testudines*, vol. 1. London, UK: Taylor and Francis.
- Souza-Filho, J. P. & Bocquetin, J. C. 1989 *Brasilosuchus mendesi*, n.g., sp. nov., um novo representante da familia Gavialidae no Neogene do Acre, Brasil. *Anais do XI Congresso Brasileiro de Paleontologia*, pp. 457–463.
- Swofford, D. L. 2002 *PAUP\*. Phylogenetic analysis using parsimony (\*and Other Methods), version 4.0b10*. Sunderland, MA: Sinauer Associates.
- Taplin, L. E. & Grigg, G. C. 1989 Historical zoogeography of the Eusuchian crocodylians: a physiological perspective. *Am. Zool.* 29, 885–901.
- Taplin, L. E., Grigg, G. C., Harlow, P., Ellis, T. M. & Dunson, W. A. 1982 Lingual salt glands in *Crocodylus acutus* and *C. johnstoni*, and their absence from *Alligator mississippiensis* and *Caiman crocodylus*. *J. Comp. Physiol.* 149, 43–47.
- Taplin, L. E., Grigg, G. C. & Beard, L. 1985 Salt gland function in fresh water crocodiles: evidence for a marine phase in Eusuchian evolution? In *Biology of Australasian frogs and reptiles* (eds G. Grigg, R. Shine & H. Ehmann), pp. 403–410. Sydney, Australia: Surrey Beatty and Sons.
- Taylor, G. C., Franklin, C. E. & Grigg, G. C. 1995 Salt loading stimulates secretion by the lingual salt glands in unrestrained *Crocodylus porosus*. *J. Exp. Zool.* 272, 490–495. (doi:10.1002/jez.1402720611)
- Troedsson, G. T. 1924 On crocodylian remains from the Danian of Sweden. *Lunds Universitets Årsskrift N.F.* 20, 1–75.
- Turner, A. H. 2004 Crocodyliform biogeography during the Cretaceous: evidence of Gondwanan vicariance from biogeographical analysis. *Proc. R. Soc. B* 271, 2003–2009. (doi:10.1098/rspb.2004.2840)
- van den Bold, W. A. 1965 Middle Tertiary Ostracoda from northwestern Puerto Rico. *Micropaleontology* 11, 381–414. (doi:10.2307/1484777)
- Vianna, J. A. *et al.* 2006 Phylogeography, phylogeny and hybridization in trichechid sirenians: implications for manatee conservation. *Mol. Ecol.* 15, 433–447. (doi:10.1111/j.1365-294X.2005.02771.x)
- Voris, H. K. 2000 Maps of Pleistocene sea levels in southeast Asia: shorelines, river systems and time durations. *J. Biogeogr.* 27, 1153–1167. (doi:10.1046/j.1365-2699.2000.00489.x)
- Ward, W. C., Scharlach, R. A. & Hartley, J. R. 2002 Geology of the North Coast ground-water Province of Puerto Rico. In *Geology and hydrogeology of the Caribbean Islands aquifer system of the Commonwealth of Puerto Rico and the U.S. Virgin Islands*, (eds R. A. Renken, W. C. Ward, I. P. Gill, F. Gomez-Gomez & J. Rodriguez-Martinez), pp. 45–76. U.S. Geological Survey Professional Paper 1419.
- Weems, R. E. 1999 Reptile remains from the Fisher/Sullivan site. *Vir. Div. Miner. Resour. Publ.* 152, 101–121.
- Whitaker, R. & Basu, D. 1983 The gharial (*Gavialis gangeticus*): a review. *J. Bombay Nat. Hist. Soc.* 79, 531–548.
- White, P. S. & Densmore, L. D. 2001 DNA sequence alignments and data analysis methods: their effect on the recovery of crocodylian relationships. In *Crocodylian biology and evolution* (eds G. Grigg, F. Seebacher & C. E. Franklin), pp. 29–37. Sydney, Australia: Surrey Beatty and Sons.
- Zaher, H., Pol, D., Carvalho, A. B., Riccomini, C., Campos, D. A. & Nava, W. 2006 Redescription of the cranial morphology of *Mariliasuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). *Am. Mus. Novit.* 3512, 1–40. (doi:10.1206/0003-0082(2006)3512[1:ROTCMO]2.0.CO;2)
- 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, 141–160.