

New Miocene Caribbean gavialoids and patterns of longirostry in crocodylians

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Gavialoidea is a clade of slender- and long-snouted crocodylomorphs with a single living species, the Indian gharial *Gavialis gangeticus*. Because elongated snouts (longirostry) have evolved independently in several crocodylomorph clades, this head shape has been interpreted as an ecological adaptation. How this condition affected patterns of diversification and how longirostrine-associated cranial features changed through adaptive radiations remain poorly understood. Two new small gryposuchine gavialoids, *Dadagavialis gunai* gen. et sp. nov. (early Miocene, Panama) and *Aktiogavialis caribesi* sp. nov. (late Miocene, Venezuela), evidence remarkable Miocene diversification of longirostrine forms in the Neotropics and support transmarine biogeographical relations between northern South America, the Caribbean, and southernmost North America before the Isthmus of Panama was fully established. By integrating phylogenetics and geometric morphometrics, we focus on this gavialoid diversity to investigate patterns of longirostry across the crown group of crocodylomorphs (Crocodylia). Analyses revealed that the snout shape of gavialoids has occupied a small, distinct and almost invariable morphospace since the Cretaceous, in contrast with the morphologically labile snout shape of other crocodylians (crocodyloids and alligatoroids). Our results suggest iterative environmental shift occupations throughout gavialoid evolution without major changes in snout proportions, but involving conspicuous rearrangements of the circumorbital bones. The longirostrine gavialoid morphotype is a distinct adaptation for seizing small prey and typically includes short and wide premaxillae and enlarged ‘caniniform’ teeth only at the tip of the snout. In longirostrine crocodyloids (*Tomistoma*, *Crocodylus intermedius*), the conservation of powerful bites and ‘caniniforms’ closer to the jaw joints allowed them to exploit a wider range of prey sizes, which could explain their snout shape plasticity. Therefore, the Mio–Pliocene extirpation of gryposuchine gavialoids from the Caribbean by the arrival of *Crocodylus* is quite unlikely. The last gryposuchine survived throughout the Pliocene in the south-eastern Pacific, where *Crocodylus* has never been documented.

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Introduction

Five out of 27 extant crocodylian species possess long, tubular and slender snouts (longirostry), including *Gavialis gangeticus* (Gmelin 1789), *Tomistoma schlegelii* (Muller 1838), *Mecistops cataphractus* (Cuvier 1825), *Crocodylus johnstoni* (Kreff 1873) and *Crocodylus intermedius* (Graves 1819). If *Gavialis* (Gavialoidea) is only distantly related to *Tomistoma* (Crocodyloidea), as suggested by morphological data, then the elongation of the snout evolved independently at least four times among extant crocodylians (Brochu 2003). Convergent evolution of craniomandibular features (relatively large supratemporal fenestrae, long dentary symphysis, long nasals having no contact with the external nares, a great number of teeth, homodont

maxillary teeth) seems to be ecologically driven as it is consistent with similar freshwater predatory ecologies and piscivorous diets (Thorbjarnarson *et al.* 1992; Grigg & Kirshner 2015). However, this is at odds with results from morphometric and biomechanical analyses which regard extant longirostrine forms as dissimilar functional and ecological entities (Pierce *et al.* 2008; Erickson *et al.* 2012). The fossil record suggests that longirostrine crocodylians and their early relatives (Crocodylomorpha) explored different ecologies and roamed many aquatic environments, including oceanic and coastal marine areas (Hua 1994; Busbey 1995; Pierce & Benton 2006; Pierce *et al.* 2009a, b; J. E. Martin *et al.* 2014), but how the evolution of a long and slender snout affected their diversification and habitat preferences is still poorly understood (Brochu 2001).

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The diversification and extinction of gavialoids in the Neotropics represents a rich case study to explore aspects of longirostrine crocodylian evolution. Palaeontological evidence suggests that neotropical gavialoids, namely gryposuchines (*sensu* Vélez-Juarbe *et al.* 2007), might have originated in the early Palaeogene along the African coasts and dispersed via marine pathways to South America and the Caribbean (Buffetaut 1982; Brochu & Rincón 2004; Vélez-Juarbe *et al.* 2007; Jouve *et al.* 2008; Salas-Gismondi *et al.* 2016). In South America, several species displaying extensive morphological disparity have been recorded in Miocene deposits depicting coastal marine, estuarine, lacustrine and riverine palaeoenvironments (e.g. Langston & Gasparini 1997; Kraus 1998; Salas-Gismondi *et al.* 2016). Part of this disparity resulted from the evolution of highly homoplastic cranial traits that are thought to reflect habitat specialization within the longirostrine condition. As such, gryposuchines found in coastal marine and riverine deposits possess contrasting orbital anatomies, in which riverine-associated traits (e.g. widely separated and protruding eyes or telescoped orbits, clear demarcation of the snout in front of the orbits) occur in late-diverging species (Salas-Gismondi *et al.* 2016). In contrast, presumed coastal marine gryposuchines (e.g. *Piscogavialis*, *Ikanogavialis*) are characterized by a relatively longer rostrum and less marked rostro-cranial transition, although the functional significance of these distinct attributes is unknown. Gryposuchine diversity in the Americas peaked during the Miocene, while the extinction of its last representative occurred at some point during the Pliocene (Buffetaut 1982). Although this extinction is roughly coeval with environmental changes (Jaramillo *et al.* 2017a) and with the arrival to the Caribbean of extant neotropical *Crocodylus* (Hekkala *et al.* 2011; Meredith *et al.* 2011; Scheyer *et al.* 2013), the potential causal connection of these events has barely been explored.

Here, we describe two new Miocene gryposuchines from circum-Caribbean localities, Panama and Venezuela. The fossils from Panama were discovered during excavations in early Miocene rocks of the Cucaracha Formation (*c.* 19 Ma; MacFadden *et al.* 2014) for the Panama Canal Project (PCP-PIRE). They constitute the first unambiguous record of a gryposuchine in the southernmost tip of North America, providing additional evidence on marine dispersals between South and North America before the closing of the Central American Seaway (CAS; Hastings *et al.* 2013; Bloch *et al.* 2016; Jaramillo 2018). The specimen from Venezuela (a skull and fragmentary jaw) was discovered in 1972 during the expedition of the Harvard Museum of Comparative Zoology to the late Miocene deposits of

the Urumaco Formation, northernmost South America. Probably because of its small size, this specimen was identified as a juvenile of a gavialoid species already identified in the area (e.g. unpublished field notes: Patterson *et al.* 1972; Langston & Gasparini 1997; Aguilera 2004). Contrary to previous interpretations, we consider this fossil an adult individual of a new species of *Aktiogavialis*, a taxon previously restricted to the Oligocene of the Caribbean island of Puerto Rico (Vélez-Juarbe *et al.* 2007). Based on phylogenetic and geometric morphometric analyses of the extensive diversification of gryposuchines, we explore the shape variation of the snout and orbits to distinguish patterns of longirostry in gavialoids and other crocodylians. We characterize the gavialoid snout morphotype and investigate how its unique combination of features defines the distinct feeding ecology of the clade. Finally, an assessment on the decline of gryposuchines in the Neotropics is provided.

Material and methods

Institutional abbreviations

MBLUZ: Museo de Biología de la Universidad del Zulia, Maracaibo, Venezuela; **MCNC** (or **MCN**): Museo de Ciencias Naturales de Caracas, Caracas, Venezuela; **MUSM:** Museo de Historia Natural, Lima, Peru; **OCP:** Office Chérifien de Phosphates, Khouribga, Morocco; **PIMUZ:** Paläontologisches Institut und Museum, Universität Zürich; **RC:** Rhinopolis Collections, Gannat, France; **SMNK:** Staatliches Museum für Naturkunde Karlsruhe, Germany; **STRI:** Smithsonian Tropical Research Institute, Panama, Panama; **UF:** University of Florida, Gainesville Florida, USA; **UPRMP:** University of Puerto Rico Department of Geology Palaeontology Collection, Mayagüez, Puerto Rico; **VF:** Universidad Central de Caracas, Caracas, Venezuela.

Phylogenetic analyses

The phylogenetic relationships of the two new neotropical gavialoid taxa were evaluated using a revised version of the data matrix of morphological characters from Salas-Gismondi *et al.* (2016; see Supplemental material). This new updated matrix includes four new characters and contains 209 characters scored for 63 eusuchian taxa, with *Bernissartia fagesii* (Dollo 1883) as an outgroup (see Supplemental material). A maximum parsimony analysis was conducted using 'New Technology' in TNT 1.1 (Goloboff *et al.* 2008). The analyses were run with 1000 replications per hit and random, consensus and exclusive sectorial searches in

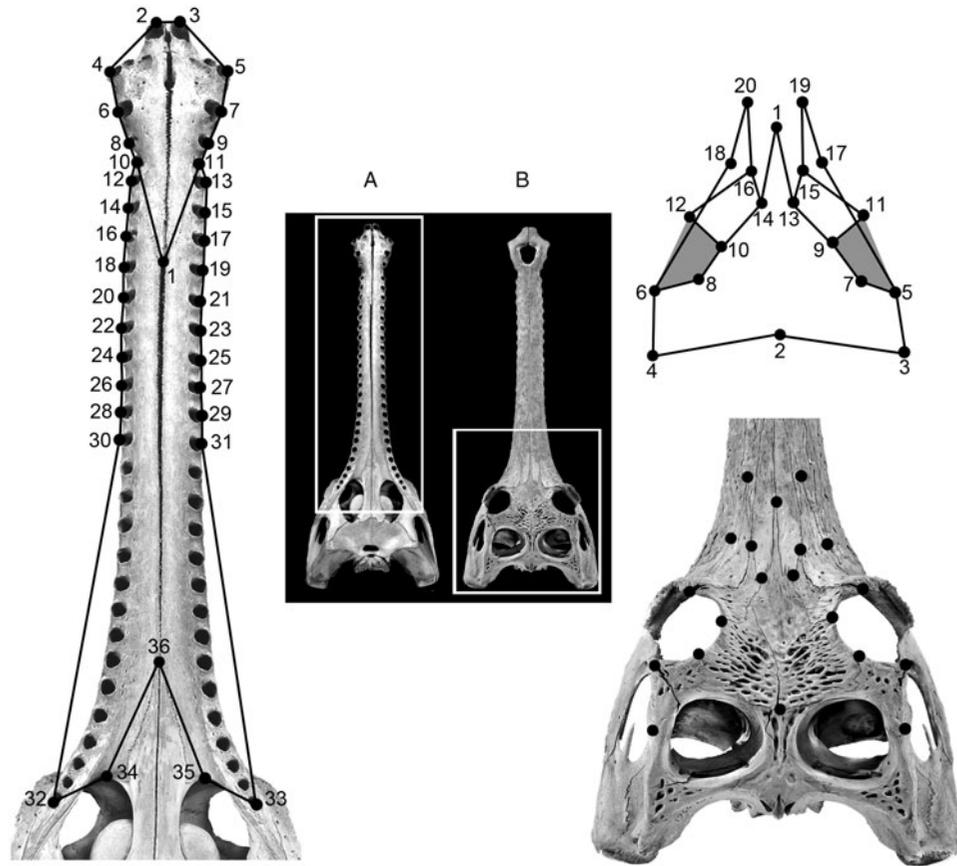


Figure 1. Landmarks selected for the two-dimensional geometric morphometric analyses. The landmark configurations are shown in the snout (A) and circumorbital region (B) of *Gavialis gangeticus*. A complete description of the landmark loci is provided in the Supplemental material.

activated mode. Additionally, we used 10 rounds of tree-fusing, 10 cycles of drift, and 200 iterations of ratchet. For branch-swapping, we applied Tree Bisection Reconnection (TBR) and performed two analyses: the first including the complete set of characters (i.e. characters 1–209) and the second with character 138 collapsed. Character 138 (i.e. ventral margin of the orbit gently circular [0] or with a prominent notch [1]) was excluded from this second analysis because it has been shown to be highly homoplastic within gavialoids (Salas-Gismondi *et al.* 2016). Characters were treated as unordered and non-additive, and had equal weighting. Bremer values were calculated to assess nodal support and are shown in the strict consensus phylogenies (Supplemental material).

Snout and circumorbital morphospace analyses and phylogenetic mapping

Two-dimensional landmark-based geometric morphometric analyses of both snout proportions and circumorbital anatomy were performed. These two anatomical regions show high morphological disparity within

crocodylian clades, likely in association with diet, feeding behaviour or habitat preferences (McHenry *et al.* 2006; Pierce *et al.* 2008; Piras *et al.* 2014; Salas-Gismondi *et al.* 2016). For the first analysis, we selected 36 discrete landmark loci on the palate of 34 crocodylians of longirostrine and non-longirostrine extant and extinct species (Supplemental material). The landmarks correspond to distinct alveolar/interalveolar positions in the maxilla and premaxilla (i.e. large teeth, loci associated to the reception of the fourth dentary tooth, first and last alveoli in a series), and to the relative dimensions of the maxillae and premaxillae (Fig. 1A). We selected these alveolar/interalveolar loci because they accurately capture the shape of the snout in addition to inform about the relative position of teeth with greatest size disparity. In *Brevirostres* (crocodyloids and alligatoroids), the largest teeth (i.e. caniniforms) are associated with deep convexities of the premaxilla and maxilla (Iordansky 1974). Most taxa belonging to the ‘generalized’ and ‘blunt’ snout morphotypes (e.g. *Crocodylus* and *Alligator*; Busbey 1995; Brochu 2001) have robust snouts and relatively large ‘caniniforms’,

probably useful to seize preys at either the tip or mid-length of the snout (Grigg & Kirshner 2015). Gavialoids, in contrast, have tooth size disparity only in the premaxillae (Iordansky 1974). Since both snout shape and caniniforms play the main roles during food acquisition, this landmark configuration would be recovering a functional feeding morphospace. Extant and extinct species are represented by fully adult individuals. The two new Caribbean taxa were not included in this analysis because the snouts of the type specimens were only partially preserved.

For the circumorbital region, we used the set of 20 landmarks of Salas-Gismondi *et al.* (2016). These landmark loci were recovered from 40 crocodylian taxa (Fig. 1B; Supplemental material). All specimens but MCNC 143-72V are considered to represent adult individuals. MCNC 143-72V is presumed to be a juvenile of the gryposuchine *Ikanogavialis gameroi* (Sill 1970) (Aguilera 2004). UF312850 was partially reconstructed from the morphology of the complete right side via geometric reflection (Claude 2008).

Landmark digitalization, Procrustes superimposition, principal component analysis (PCA) and phylogenetic mapping were performed using the R package Geomorph (Adams & Otárola-Castillo 2013) and MorphoJ (Klingenberg 2011). We centred the landmark configurations to the origin and superimposed them to unit centroid size following the generalized Procrustes method (Rohlf 1999). The coordinates of the superimposed configurations were translated to the Euclidean space. We analysed the components of shape variation by performing a PCA. Although Procrustes superimposition minimizes any size-related effect, it is possible that some relationship between size and PC scores remains due to allometry. To test for a possible relationship between size and PC scores due to allometry, we performed a regression of PC1 and PC2 on centroid size (Klingenberg 2011). The null hypothesis of no allometric effect was discarded if 5% or fewer of the permutations use size to explain the PC scores. A simplified version of our phylogenetic topology unweighted for branch length was mapped onto the morphospace of PC axes 1 and 2 to visualize trends of shape evolution. Additional analyses were done in MorphoJ to evaluate the existence of phylogenetic and allometric signals in the results. Canonical variate (CV) and discriminant function analyses were performed to test whether habitat preferences (i.e. pre-defined groups) of extinct and extant crocodylians can be statistically distinguished based on the circumorbital shape. We grouped crocodylians in three habitat preferences: (1) marine-estuarine, (2) generalized (i.e. freshwater settings), and (3) strictly riverine. Among extant crocodylians, the Indian gharial *Gavialis gangeticus* is the sole strictly riverine species (Whitaker & Basu 1983), whereas others are basically

freshwater forms (Grigg & Kirshner 2015). Considering extant and extinct representatives, the ‘strictly riverine’ grouping is composed of five taxa. The habitat assigned to extinct taxa is based on the depositional setting of fossil specimens (Supplemental material), assuming that these specimens were buried and preserved within their real habitat. Although the ‘marine-estuarine’ category probably represents two different habitats (i.e. marine and estuarine), we grouped them together because of the lack of sufficient depositional data.

Geological context, palaeoenvironment and age

Early Miocene Cucaracha Formation, Panama

Fossils of the new gavialoid from Panama were found in two localities of the Cucaracha Formation along the Gaillard (Culebra) Cut of the Panama Canal, north of the Pedro Miguel Locks (Fig. 2A, B). The skull (UF312850) was found in Locality 630059 (9°3'2.88"N, 79°38'58.56"W), a basal conglomerate marking the contact with the underlying Culebra Formation. The portion of the mandible (UF280096) was recovered from Locality 630023 (9°1'51.24"N, 79°38'12.12"W), a channel lag conglomerate close to the contact with the overlying Pedro Miguel Formation (MacFadden *et al.* 2014). The Cucaracha Formation represents a progradational sequence, with deltaic and nearshore wetland deposits in the lower part of the unit, whereas the upper part consists of fluvial and floodplain deposits (Retallack & Kirby 2007; Kirby *et al.* 2008; Montes *et al.* 2012; MacFadden *et al.* 2014). The Cucaracha Formation comprises mainly red, green and purple mudstones and palaeosols with intercalations of lithic sandstones, conglomerates and lignites. Carbonized wood fragments from the lower conglomerate (Locality 630059) lack the terenidid mollusc borings found in fossilized wood from the underlying Culebra Formation, which is indicative that the lower Cucaracha Formation was deposited above sea level (Kirby *et al.* 2008). Magnetostratigraphical and radiometric dating of a marker tuff bed of the Cucaracha Formation indicate an age between 19.05 and 18.78 Ma (early Miocene) for both the uppermost Culebra and Cucaracha formations (MacFadden *et al.* 2014).

Late Miocene Urumaco Formation, Venezuela

Fossil material of the new gavialoid from Venezuela (MCNC 95-72V) was found in the Pipeline Locality (c. 11°12'N, 70°16'W; unpublished Patterson Field Notes, 1972) of the Urumaco Formation, Falcon State (Fig. 2A, C). We identified this locality as pertaining to the middle member of this unit and stratigraphically close to

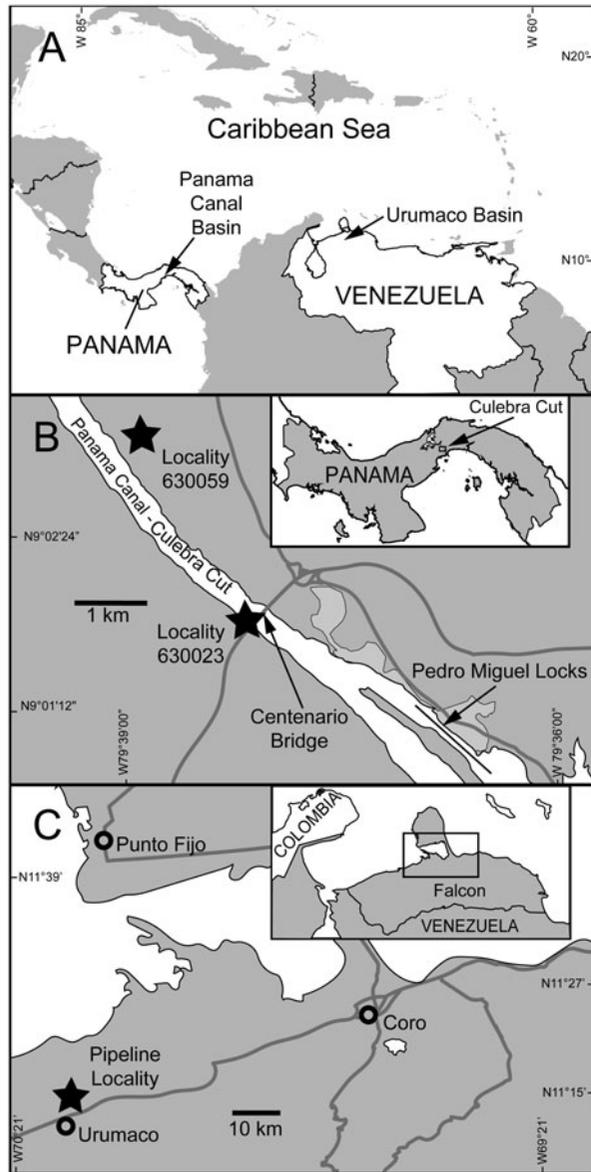


Figure 2. Miocene localities of the new gavialoids. **A**, map of the Caribbean region showing the Panama Canal and Urumaco basins in Panama and Venezuela, respectively; **B**, early Miocene localities 630059 and 630023 in the Panama Canal basin, Cucaracha Formation (c. 19.05–18.78 Ma); **C**, late Miocene locality Pipeline in the Urumaco basin, Urumaco Formation (c. 10–9 Ma).

Bejucal, Puente del Río Urumaco, Playa Larga, Domo de Agua Blanca localities (late Miocene, c. 10–9 Ma; see Scheyer *et al.* 2013 and Carrillo *et al.* 2018). The Urumaco Formation represents a transgressive event and a subsequent establishment of a wetland-deltaic plain (Quiroz & Jaramillo 2010). The unit is characterized by a complex intercalation of fine-grained sandstone, organic-rich mudstone, coal and coquinoidal limestone beds. The middle member comprises mainly channelized

sandstones, which represent deposition in terminal distributary channels (Quiroz & Jaramillo 2010). Trace fossils of *Ophiomorpha* provide evidence of marine influence in this member whereas the organic-rich sandstones represent periods of freshwater discharges.

Systematic palaeontology

Crocodyliformes Hay, 1930

Crocodylia Gmelin, 1789

Gavialoidea Hay, 1930

Gryposuchinae Vélez-Juarbe, Brochu & Santos, 2007

***Dadagavialis* gen. nov.**

Diagnosis. *Dadagavialis gunai* is a relatively small, long-snouted gavialoid crocodylian diagnosed by the following unique combination of characters: more than 22 maxillary alveoli; large process of the palatines projected into the anteromedial suborbital fenestrae, resembling a bulla; ventral margin of the orbit strongly everted laterally; maxilla with sinuate lateral edges only anteriorly; orbits wider than long to rounded; nasals in contact with premaxillae. It differs from all other gavialoids by possessing an anterior process of the frontal wider than the prefrontal at the level of the anterior orbital margin.

Etymology. *Dada*, from Guna (indigenous language in Panama) for ‘ancient’, Greek ‘gavialis’; ‘*gunai*’ to honour the Guna people, known as keen navigators of the Caribbean.

***Dadagavialis gunai* sp. nov.**

(Fig. 3A–C)

Holotype. UF312850, partial snout and rostral skull.

Locality and horizon. Locality 630059, basal levels of the Cucaracha Formation, east margin of the Panama Canal north of the Pedro Miguel locks, Panama, Central America. Early Miocene, c. 19 Ma; Centenario Fauna levels of MacFadden *et al.* (2014).

Description. The holotype of *Dadagavialis gunai* (UF312850; Table 1) is a partial skull that preserves a section of the snout and a portion of the rostrum, skull table, and partial braincase. The snout includes pieces of the right premaxilla, right maxilla, and both nasals; posteriorly the rostrum and skull table preserve additional portions of the maxillae and nasals, as well as the right lacrimal, right jugal, right postorbital, both prefrontals, frontal and parietal. Ventrally, the right palatine, right ectopterygoid and both laterosphenoids are preserved.

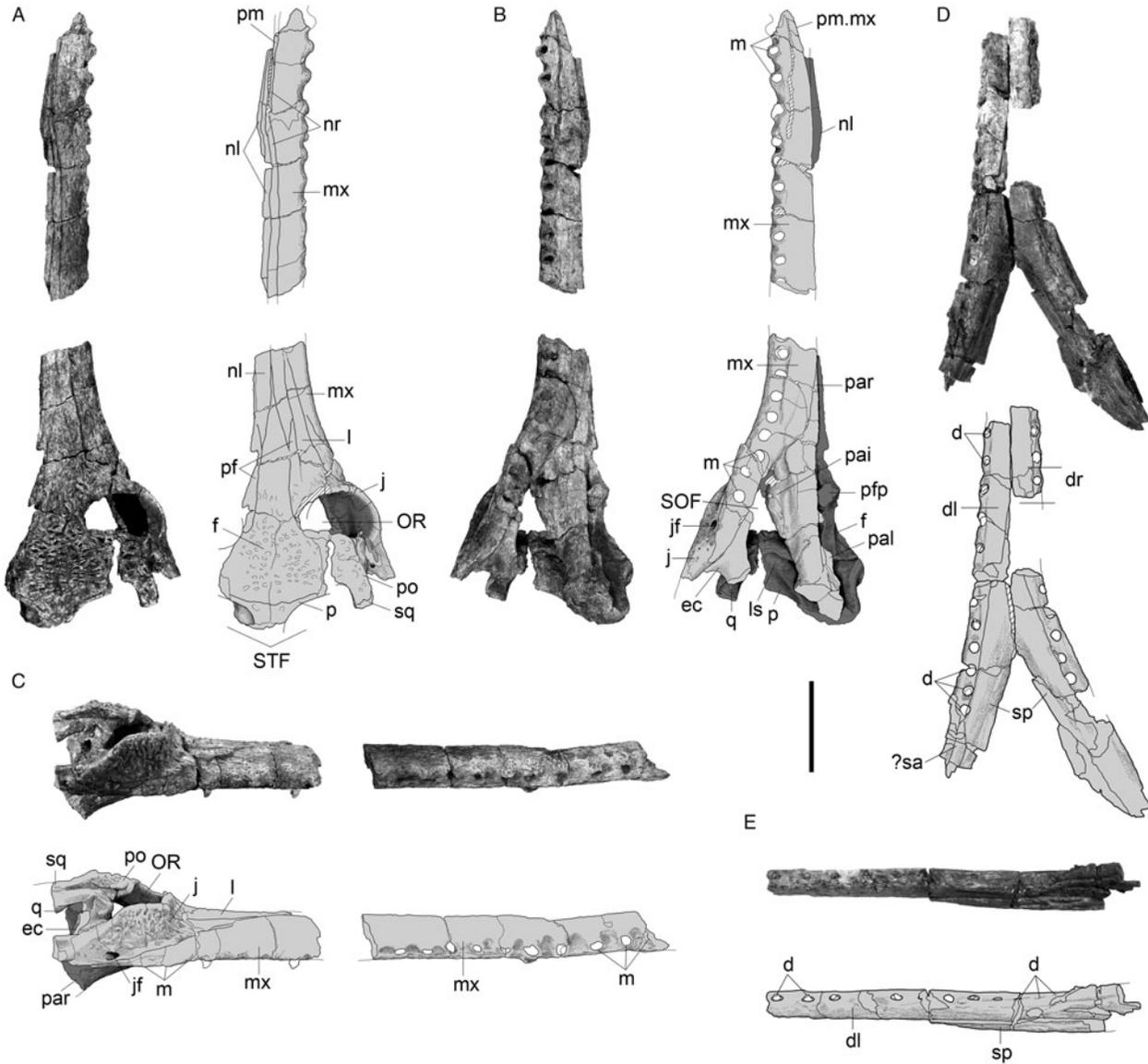


Figure 3. Photograph and schematic drawing of the skull of *Dadagavialis gunai* gen. et sp. nov. (holotype, UF312850) in dorsal (A), ventral (B), and right lateral (C) view. Photograph of the mandible and schematic drawing of cf. *Dadagavialis gunai* (UF 280096) in dorsal (D) and left lateral (E) view. Abbreviations: d, dentary tooth positions; dl, left dentary; dr, right dentary; ec, ectopterygoid; f, frontal; j, jugal; jf, external jugal foramen; l, lacrimal; ls, laterosphenoid; m, maxillary tooth positions; mx, maxilla; nl, left nasal; OR, orbit; p, parietal; pai, inflated palatine; pal, left palatine; par, right palatine; pf, prefrontal; pfp, prefrontal pillar; pm, premaxilla; pm.mx, maxilla surface for the premaxilla; po, postorbital; q, quadrate; sp, splenial; sa, presumed surangular; sq, squamosal; SOF, suborbital fenestra; STF, supratemporal fenestra. Scale bar: 5 cm.

The preserved pieces of the skull indicate that the snout was long and slender and the skull table was relatively wide, as in most gavialoids. The snout is tall and dorsally convex in cross section. In dorsal view, the transition between the snout and orbital region is more marked than in other gavialoids, such as *Ikanogavialis* and *Piscogavialis* (Fig. 3A; Sill 1970; Kraus 1998), but not as much as in *Gavialis* and advanced species of *Gryposuchus* (Mansharamani 1966; Langston &

Gasparini 1997). The right anterolateral portion of the skull table is crushed and anteriorly displaced. Therefore, the precise proportions of the right orbit are distorted, yet the orbit is clearly wider than long to circular in dorsal view. Only the anterior margin of the supratemporal fenestrae is preserved. It lacks the shallow fossae anterior to the supratemporal fenestra typical of *Aktiogavialis* (Vélez-Juarbe *et al.* 2007). The frontal and postorbital bones on the skull table and the external

Table 1. Measurements (mm; after Langston & Gasparini 1997) of the holotype (UF312850) of *Dadagavialis gunai* gen. et sp. nov. and UF 280096. Asterisk indicates doubling of measurement from one side. Measurements with missing data are omitted. Abbreviation: e, estimate.

Measurement	UF312850	UF 280096
Length of preserved snout (anterior piece)	153	–
Length of preserved rostrum-skull table (posterior piece)	145	–
Interorbital distance	31e	–
Orbit length	27e	–
Orbit width	39e	–
Skull table width, anterior	93*	–
Skull width across postorbital pillars	116*	–
Palatal fenestra width	30	–
Length of preserved mandible	–	197
Length of preserved mandibular symphysis	–	126

surface of the jugal are deeply sculptured with large pits and furrows. The skull preserves evidence of 20 maxillary alveoli, yet the total count would be much larger. All the preserved alveoli are round, equal in size and elevated relative to the palatal surface of the maxilla. The six anterior alveoli are implanted within alveolar ‘collars’ that give this region a sinuate profile in dorsal view (Fig. 3A).

The snout preserves a minute fragment of the posterior premaxillary process between the maxilla and the anteriormost tip of the right nasal, indicating that the nasals and the premaxillae were in contact as in most gryposuchines, exclusive of *Hesperogavialis cruxenti* (Bocquentin-Villanueva & Buffetaut 1981). The posterior premaxillary process is positioned just behind the level of the first alveolus preserved in the section of the snout, which might correspond to the fourth to sixth maxillary alveoli of other gryposuchines. In ventral view, no portions of the palatine processes of the premaxillae are preserved. However, the preserved sutural contact for this process in the left maxilla indicates that the posterior premaxillary process was triangular and extended to the level of the third preserved maxillary alveolus (Fig. 3A). Posteriorly, both maxillae were in contact in the sagittal plane along most of the snout.

The nasals are long and slender. The posterior ends of the nasals are triangular and do not reach posteriorly the level of the anterior margin of the orbits, as in *Piscogavialis jugaliperforatus* (Kraus 1998), *Ikanogavialis* and *Argochampsia krebsi* (Hua & Jouve 2004). In the rostrum, the lacrimal is a long, roughly triangular bone that bears a medial contact with the prefrontals and nasals. The prefrontals are slender as well and anteriorly reach the level of the rostral tip of the jugal. Dorsal to the edentulous posterior process of the

maxilla, the jugal bears a discrete, large foramen on its lateral surface, probably homologous to that of *Piscogavialis*, *Gryposuchus* and *Eogavialis africanus* (Andrews 1901). The rostral process of the frontal is notably broad and parallel sided at the level of the prefrontals, and wedges out between the nasals almost to the level of the anterior tip of the lacrimal (Fig. 3A). The frontal plate is wide and slightly concave. The frontoparietal suture is roughly linear between the supratemporal fenestrae and lies entirely on the skull table. The parietal embraces anteromedially the supratemporal fenestra.

Anterior to the suborbital fenestra, the palatine bone contacts laterally with the maxilla by means of a rostral tapering process that reaches the level of the eighth maxillary alveolus (counting from behind; Fig. 3B). Posteriorly, the palatine comprises the entire length of the palatine bridge and bears an inflated, anterolateral bulla-like process on the anterior half of the suborbital fenestra (Fig. 4B). The walls of this hollowed structure are thick and compact, and may include portions of the anterodorsal process of the pterygoid. A similar anatomical feature is only seen otherwise in the type of *Ikanogavialis* (Fig. 4C). Posteriorly, a slightly concave, smooth surface on the dorsolateral palatine bridge might have served to receive the pterygoid bulla (Fig. 4B).

The maxillary ramus of the ectopterygoid is long and robust whereas the infratemporal process is relatively longer than in *Gavialis*. An ascending process of the ectopterygoid contributes to the posteromedial surface of the postorbital pillar. The capitate process of the latrospenoids is oriented laterally.

Circumorbital anatomy. The anterior margin of the orbit is thick, raised and comprised entirely of the lacrimal. On the ventral margin, the jugal is robust, bowed medially and dorsolaterally projected. The orbital margin of the jugal surpasses laterally the external profile of the maxillo-jugal horizontal bar. This raised orbital margin progressively descends at the level of the postorbital pillar (Fig. 3A, C). Although the frontal and prefrontal at the dorsal edges of the orbits are damaged, it is clear that the margins at this position were upturned, yet not as elevated as in *Gavialis* and *Gryposuchus colombianus* (Langston 1965). The interorbital bridge seems to be narrower to equivalent to the width of the orbit. The right postorbital is robust and relatively flat at the orbital margin. The postorbital pillar is thick, bears a prominent anterolateral process, and lies dorsal to the horizontal bar of the jugal, as in *Gavialis*, *Gr. colombianus* and *Ikanogavialis* (Fig. 3C).

Based on regressions for *Gavialis gangeticus* (Serenio et al. 2001), we estimate the body length of *Dadagavialis* to be 226 cm (Supplemental material).

cf. *Dadagavialis gunai*

(Fig. 3D, E)

Referred material. UF 280096, partial mandible.

Locality and horizon. Locality 630023, Centenario Bridge, upper levels of the Cucaracha Formation, west margin of the Panama Canal near Centenario Bridge, Panama. Early Miocene, *c.* 18.8 Ma; Centenario Fauna levels of MacFadden *et al.* (2014).

Description. UF 280096 is preliminarily referred to cf. *Dadagavialis gunai* because this partial mandible and the type specimen of *Dadagavialis gunai* (UF312850) are roughly coeval and consistent in size, and there is currently no evidence of any other gavialoid in the Cucaracha Formation. UF 280096 is a small partial jaw comprising portions of the mandibular symphysis and posterior adjacent divergent rami (Table 1). It includes sections of both dentaries and splenials, and the anterior medial process of the left surangular. The right ramus is represented by two disconnected pieces. There are 12 alveoli preserved on the left ramus and seven on the right ramus. The preserved mandibular symphysis extends for about the length of nine alveoli. It is not clear whether the last alveolus preserved in the left ramus is actually the last alveolus of the series.

In dorsal view, the jaw fragment is elongated and Y-shaped (Fig. 3D). The dentaries and splenials participate in the mandibular symphysis. The long dentary symphysis possesses parallel sides with modest sinuate lateral profiles. Both mandibular rami gradually diverge backwards throughout the length of the splenials. The angle of divergence of the posterior mandibular rami is similar to that of *Ikanogavialis* and *Gryposuchus* (see Sill 1970; Langston & Gasparini 1997). The splenial participates in the symphysis for about the distance of six alveoli, as in *Gr. colombianus*. The dorsal surface of the dentary symphysis between the alveolar rows is transversally convex and the alveoli are underlined relative to this surface (Fig. 3E), as in other gavialoids. Ventrally, the surface of the dentaries is rounded, but posteriorly this surface becomes flatter and inclined from the ventral border of the ramus to the alveolar margin. The alveoli are rounded, equivalent in size and oriented dorsolaterally. In the left ramus, some basal portions of tooth crowns are preserved in their alveoli. These tooth fragments bear sharp carinae with smooth surfaces and fluted enamel.

The tips of the splenials are lacking but it is possible to determine their anteriormost extension from the sutural contact for the splenial on the left dentary. The rostral tip of the splenial reaches the level between the ninth and tenth alveoli (counting forward from the last

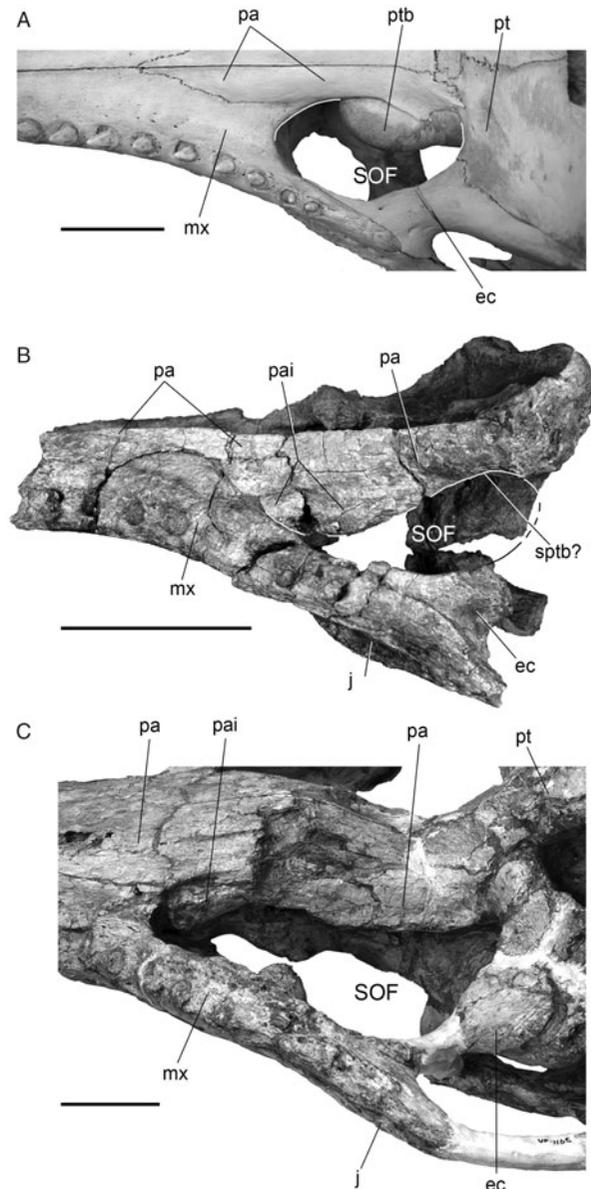


Figure 4. Palatine anatomy in selected gharials. **A**, *Gavialis gangeticus* (PIMUZ A/III752) in ventral view; **B**, *Dadagavialis gunai* (UF312850) in ventrolateral view; **C**, *Ikanogavialis gameroi* (holotype, VF 1165) in ventrolateral view. Abbreviations: ec, ectopterygoid; j, jugal; mx, maxilla; pa, palatine; pai, inflated palatine; pt, pterygoid; ptb, pterygoid bulla; sptb, presumed surface for the pterygoid bulla; SOF, suborbital fenestra. Scale bars: 5cm.

preserved alveolus). The dentary-splenial sutures are straight and not bowed medially as in tomistomines and *Gryposuchus pachakamue* (Salas-Gismondi *et al.* 2016) (Brochu & Rincón 2004). The lateral extent of the splenials contributes to the medial margin of the last two preserved alveoli. In ventral view the rostral end of the left splenial is pointed and extends anteriorly to the

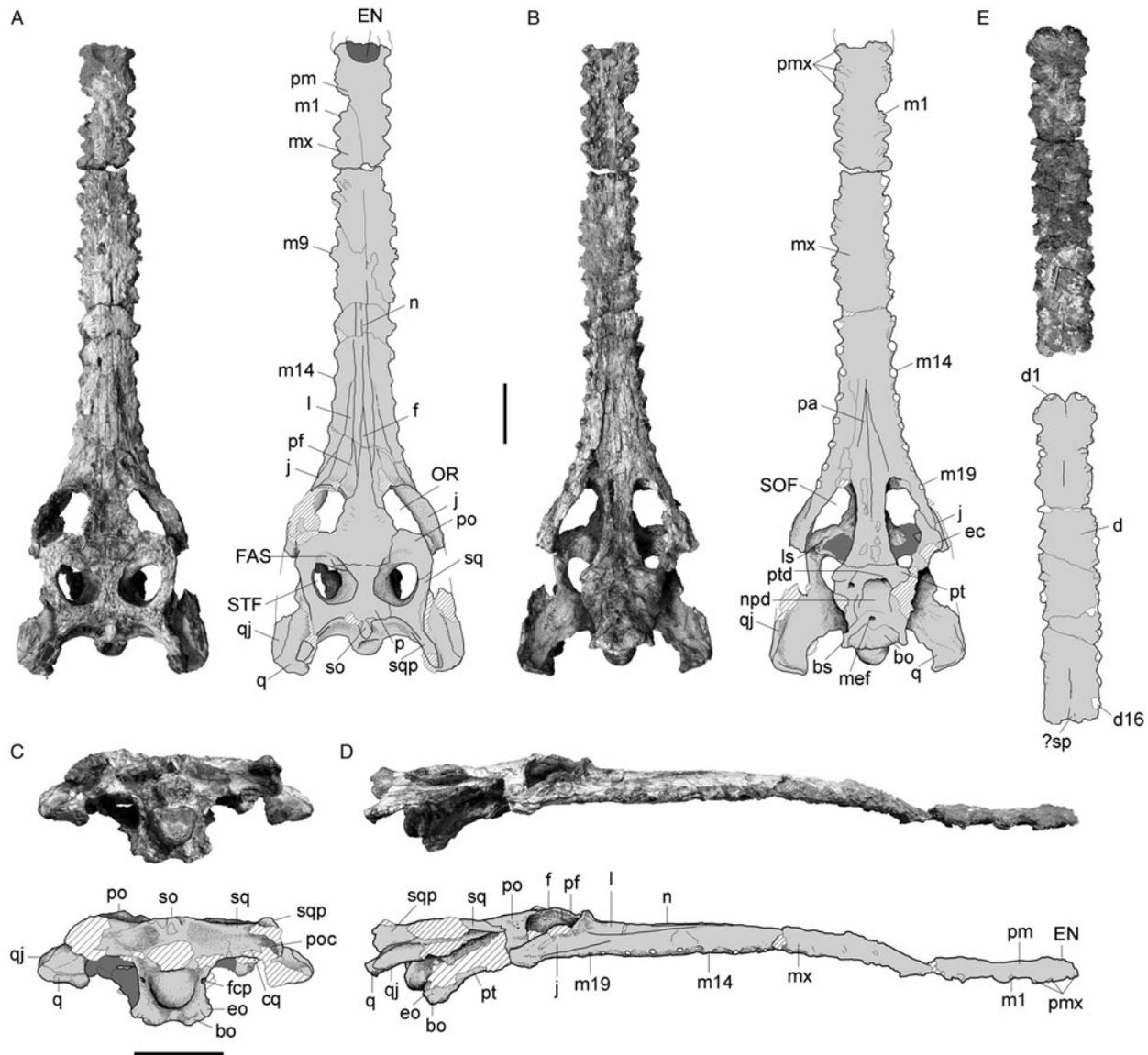


Figure 5. *Aktiogavialis caribesi* sp. nov. (holotype, MCNC 95-72V). Photograph and schematic drawing of the skull in dorsal (A), ventral (B), occipital (C), and right lateral (D) view. Photograph and schematic drawing of the symphyseal mandible in dorsal (E) view. Abbreviations: bo, basioccipital; bs, basisphenoid; cq, cranioquadrate foramen; d1, d16, dentary tooth positions; d, dentary; ec, ectopterygoid; EN, external nares; eo, exoccipital; f, frontal; fcp, foramen carotideum posterior; FAS, fossa anterior to supratemporal fenestra; j, jugal; l, lacrimal; ls, laterosphenoid; m1, m9, m14, m19, maxillary tooth positions; mef, medial Eustachian foramen; mx, maxilla; n, nasal; npd, nasopharyngeal duct; OR, orbit; p, parietal; pa, palatine; pf, prefrontal; pm, premaxilla; pmx, premaxillary tooth positions; po, postorbital; poc, paraccipital process; pt, pterygoid; ptd, pterygoid ducts; q, quadrate; qj, quadratojugal; so, supraoccipital; SOF, suborbital fenestra; sp, presumed splenial; sq, squamosal; sqp, squamosal prongs; STF, supratemporal fenestra. Scale bars: 5 cm.

level of the ninth alveolus (counting forward from the last preserved alveolus). Both rami are damaged posterior to the dental series; thus, anatomical details or sutures are not discernible.

Aktiogavialis (Vélez-Juarbe, Brochu & Santos 2007)

Emended diagnosis. Posterior skull table transversally constricted; wide posttemporal bar; supratemporal

fenestrae longer than wide; shallow fossa anterior to the supratemporal fenestrae.

Type species. *Aktiogavialis puertoricensis* (Vélez-Juarbe, Brochu & Santos 2007).

Aktiogavialis caribesi sp. nov.
(Fig. 5A–E)

Diagnosis. *Aktiogavialis caribesi* is a relatively small long-snouted gavialoid crocodylian diagnosed by the following unique combination of characters: 19 maxillary teeth separated by long gaps and implanted along salients of the maxillary lateral edge; ventral margin of the post-orbital pillar inset from the lateral jugal surface; orbits longer than wide. Differs from *Aktiogavialis puertoricensis* in having a posterior orbital margin not upturned and a comparatively wider and less concave interorbital bridge. Lacks the prominent process of the postorbital pillar that is observed in other gryposuchines. Unlike any other gavialoid, the dorsal portion of the snout is vaulted, forming a uniform, curved profile in cross section.

Etymology. The Urumacan *Aktiogavialis* species is named after the ‘Caribes’, a native ethnic group of northern Venezuela who fished across the Caribbean Sea.

Holotype. MCNC 95-72V, skull and partial mandible.

Locality and horizon. Pipeline Locality of Patterson Field Notes, 350 m N from kilometre 157 of the Pipeline, Urumaco area, Venezuela; middle member of the Urumaco Formation; late Miocene, *c.* 10–9 Ma.

Description. The type of *Aktiogavialis caribesi* (MCNC 95-72V; Table 2) comprises an almost complete skull and a symphyseal mandible, the former element being partially weathered in the rostrum and palatal region. The skull lacks both jugals, the right ectopterygoid, part of the pterygoids and the tip of the premaxillae. The symphyseal mandible is preserved from the tip of the snout to the level of the sixteenth alveoli and is strongly encrusted with a gypsum matrix.

The skull is long, slender and lightly constructed. The snout is also relatively low, vaulted dorsally and flattened ventrally, with markedly sinuate lateral margins. The snout was probably slightly wider at the distal end than at the mid-length (Fig. 5A). The rostral length/skull length index is 77, similar to the proportions of *Gr. pachakamue* and *G. gangeticus*. In dorsal view, the transition between the snout and the orbital region is less marked than in *Gr. colombianus* but more so than in *Ikanogavialis* (see Langston & Gasparini 1997). Only the posterior half of the narial opening is discernible; it seems to be roughly semi-circular. The orbits are longer than wide and slightly larger than the supratemporal fenestrae. The skull table has an unusual inverted trapezoid shape, anteriorly wide and constricted at the level of the posttemporal bar (Figs 5A, 6A). The supratemporal fenestrae are ovoid in shape. The anterolateral corner of the skull table is more rounded than usually in Crocodylia (Clark & Norell 1992). As in *Ak. puertoricensis*, the

Table 2. Measurements (mm; after Langston & Gasparini 1997) of the holotype (MCNC 95-72V) of *Aktiogavialis caribesi* sp. nov. Measurements with missing data are omitted. Abbreviation: e, estimate.

Measurement	MCNC 95-72V
Preserved basal length of the skull	510
Greatest width	155
Width of the rostrum, posterior	85
Length of the snout, medial axe	373e
Length of skull, dorsal	489e
Interorbital distance	30
Orbit length	32
Skull table width, anterior	105
Skull table length, lateral	106
Skull table width, posterior	83
Skull width across postorbital pillars	131
Occipital condyle width	25
Occipital condyle height	19
Orbit width	40
Nares width	27e
Skull table length, medial	80
Snout length, to posterior nares	353
Quadrate condyle width	27e
Supratemporal fenestra width	35
Supratemporal fenestra length	35
Palatal fenestra length	70
Palatal fenestra width	26e
Rostrum width at fourth maxillary alveoli	48e
Maxillary tooth row length	314
Palatine bar width	22e
Preserved skull length	518
Skull height	31
Preserved mandible length	262

skull table bears a shallow fossa extending anteriorly from the supratemporal fenestrae. The posterior corners of the skull table project long posterolateral squamosal ‘prongs’ to laterally embrace the occiput (Fig. 6A). The occipital plate is posteriorly inclined. The dorsal portion of the paraoccipital processes is concave. The suborbital fenestrae are long and ellipse shaped. The incisive foramen and the infratemporal fenestrae are not preserved.

The limits between the premaxillae and maxillae are hardly recognizable. However, a hint of the left dorsal premaxillary-maxillary suture reveals a long and slender posterior premaxillary process, yet it is not possible to determine its caudal end. The premaxillae encircle posteriorly the narial opening. The preserved portion of the narial opening is flush with the premaxillary dorsal surface. In ventral view, the premaxillae preserve three tooth positions, with the most posterior of these three being apparently the smallest in diameter. Gaps between these alveoli seem to be roughly equivalent in length and larger than the alveoli diameter. The maxillae bear 19 alveoli (Fig. 5B). The first thirteen alveoli are implanted within strong maxillary alveolar ‘collars’; posteriorly, the maxillae still have lateral undulations along their alveolar extent, but the alveolar ‘collars’ are

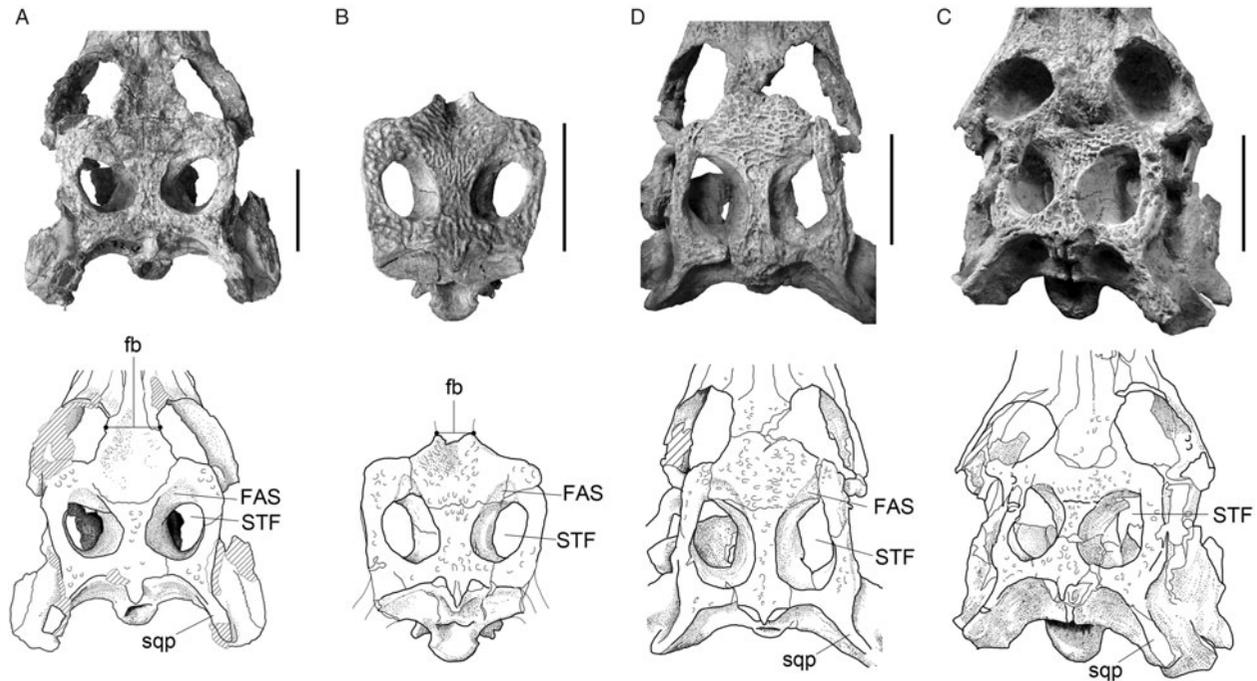


Figure 6. Photograph and schematic drawing of the skull table of *Aktiogavialis* (A, B) and *Argochampsia* (C, D) in dorsal view. A, *Aktiogavialis caribesi*, holotype, MCNC 95-72V; B, *Aktiogavialis puertoricensis*, holotype, UPRMP 3094; C, *Argochampsia krebsi*, holotype, OCP DEK-GE 1201; D, *Argochampsia krebsi*, RC Phosphate 1. Abbreviations: FAS, fossa anterior to supratemporal fenestra; fb, frontal bridge; sqp, squamosal prong; STF, supratemporal fenestra. Scale bars: 5 cm.

less prominent. The maxillary alveoli are relatively small and widely separated by long diastemata. The edge of the maxillary alveoli is higher than the maxillary palate between the tooth series. The premaxillary alveoli and the anterior maxillary alveoli open more rostrad and lateral than the posterior maxillary alveoli, which essentially face ventrad. The nasals are long and slender. The anterior portion of the nasals is not preserved; thus, the relation between nasals and premaxillae is uncertain. Posteriorly, the pointed rostral process of the frontal wedges out between the left and right nasal bones at the level of the fifteenth maxillary alveolus (Fig. 5A). The caudal extension of the nasals fails to reach the level of the anterior margin of the orbits, as in *Piscogavialis*, *Ikanogavialis* and *Argochampsia*. The lacrimals are large, elongated bones; they reach anteriorly to about the level of the twelfth maxillary alveolus, far beyond the frontal and prefrontal distal ends. The prefrontals are long as well and restricted to the anteromedial margin of the orbit. Apparently, the frontoparietal suture intersects the anteromedial rim of the supratemporal fenestrae, as in *Ak. puertoricensis* (Fig. 6B; Vélez-Juarbe *et al.* 2007). The squamosals are long, Y-shaped bones in dorsal view and low in lateral view. The squamosal ‘prongs’ are proportionally longer than those of the *Gryposuchus* species and comparable to the lengthened ‘prongs’ of *Argochampsia*, *Siquisiquesuchus*

venezuelensis (Brochu & Rincón 2004) and *Piscogavialis*. Together with the parietal, the squamosals form a wide, flat posttemporal bar that slopes ventrally from the medial axis (Fig. 5C). The squamosals share with the postorbital bones an oblique contact on the skull table surface. This squamosal-postorbital contact continues anteriorly, on the lateral flank of the skull table, to reach the posterodorsal end of the postorbital pillar. The preserved portion of the quadratojugal plates gives no evidence on the characteristics of the infratemporal fenestrae. On the dorsal surface, the quadrate-quadratojugal suture meanders anteriorly without approaching medially the squamosals, as in *Gavialis*. The quadrates are badly damaged and encrusted with matrix, particularly on the lateral surface of the braincase. The base of the posterolateral prongs comprises the squamosals and paraoccipital processes. In the occipital region, several areas are badly preserved or covered with matrix. Apparently, the exoccipital ventral extension does not cover posteriorly the cranioquadrate foramen. The dorsal surface of the supraoccipital is not preserved, but a relatively large rhomboid supraoccipital bone projects posteriorly from the occipital plate, as in *Ak. puertoricensis* (Fig. 6A, B). The limits of the supraoccipital in the occipital plate are not visible. The basioccipital and the long ventral processes of the exoccipitals form two pendulous tubera (Fig. 5C). As in

gharials (*sensu* Salas-Gismondi *et al.* 2016), the lateral margins of the basioccipital tubera bear ventrally divergent sides. The basioccipital plate bears a medial vertical bump-like crest. The ventral margin of the tubera is anteroposteriorly expanded and depressed posterior to the medial Eustachian foramen. The foramen carotideum posterior is placed lateral to the occipital condyle and faces posteriorly. No other foramina in this region are preserved. In ventral view, the medial Eustachian foramen is probably encircled by the basisphenoid and the roof of the nasopharyngeal duct denotes a posteroventrally oriented choanal opening, similarly to what was established for *Ak. puertoricensis* (Vélez-Juarbe *et al.* 2007). Lateral to the nasopharyngeal duct, relatively large passages filled with matrix might correspond to the paths connecting the nasal duct with the pterygoid bullae, as in *Gavialis* (Fig. 5B; B. G. H. Martin & Bellairs 1977), yet there are no traces of these latter structures in the Venezuelan specimen. The pterygoids form the posterior border of the suborbital fenestrae, precluding contact between the palatines and the ectopterygoids in this region. The ectopterygoids have no posterior process along the infratemporal bar. Details of the anatomy of the anterior processes of the ectopterygoids are missing. The palatines are long and relatively flat, and comprise entirely the palatal bridge. The rostral processes of the palatines converge to a point at the level of the gap between the fifteenth and sixteenth maxillary alveoli (Fig. 5B).

The dentaries are relatively flat and slightly expanded laterally at the anterior tip (Fig. 5E). The maximum lateral expansion occurs at the level of the second and third dentary alveoli. Apparently, the second and third alveoli are similar in diameter whereas the first is slightly larger. The lateral margins of the dentary and the alveolar borders are badly damaged. However, it is possible to confidently recognize the position of 16 alveolar loci in the right dentary. The alveoli are probably located in alveolar ‘collars’ along the paralleled-sided, lateral border of the dentaries. A wedge-like bone, probably corresponding to the rostral tip of the splenials, is observed at the level of the sixteenth dentary alveolus.

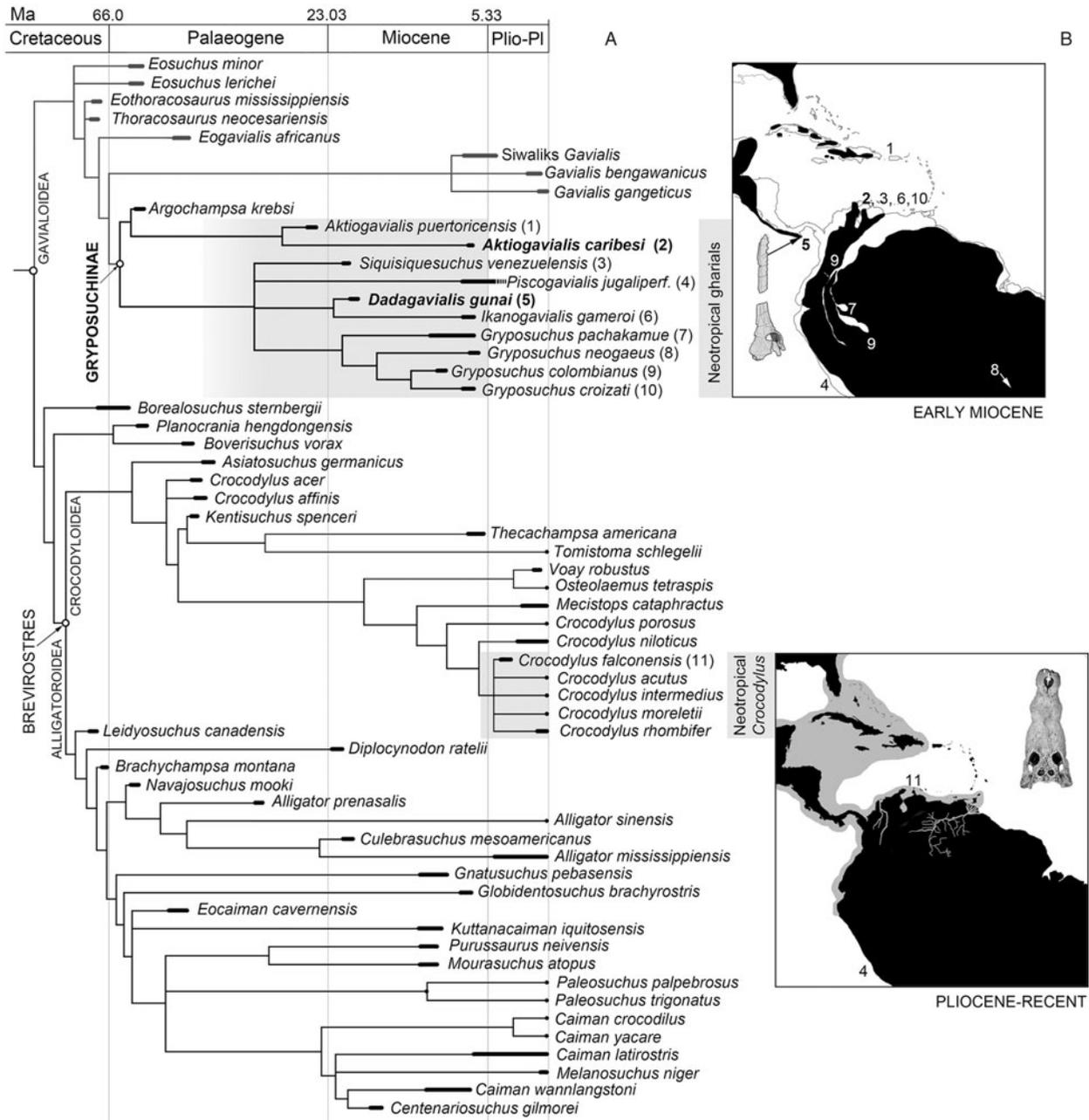
Circumorbital anatomy. The lacrimals, prefrontals and jugals are strongly everted along the orbital margin; therefore, the orbits are raised relative to the snout dorsal surface (Figs 5D, 6A). Conversely, the frontal is only moderately concave within the interorbital bridge, as in most Brevirostres and some gavialoids, such as *Piscogavialis* and *Ikanogavialis* (Salas-Gismondi *et al.* 2016), and differing from *Gavialis* species, *Gr. colombianus* and *Ak. puertoricensis* in which the dorsal (i.e. frontal) and posterior (i.e. postorbital) margins are sharp, elevated and projected towards the orbits. The frontal width

between the orbits is slightly narrower than the transversal diameter of the orbits, but comparatively wider than the slender, strongly concave interorbital bridge of *Ak. puertoricensis* (Fig. 6B). The postorbitals are large and slightly upturned along the orbital margin. They form the strong, rounded anterolateral borders of the skull table. The postorbital pillar is massive and anteroposteriorly elongated. In cross section, the posterior margin of the postorbital pillar presents a sharp angle, contrasting with the typical smooth rounded margin of *Gavialis* and other crocodylians. The postorbital pillar lacks the prominent process of other gryposuchines (see Langston & Gasparini 1997). This pillar is only moderately inset from the edge of the skull table but clearly rooted on the medial wall of the horizontal bar of the jugal, forming a longitudinal sulcus between both structures, as in *Piscogavialis*, *Ikanogavialis* and *Gr. pachakamue*. Lateral to this sulcus, the jugal orbital margin is gently circular (Fig. 5D).

Based on regressions for *Gavialis gangeticus* (Sereno *et al.* 2001), we estimate the body length of *Aktiogavialis caribesi* to be 301 cm (Supplemental material).

Phylogenetic analysis

Our first analysis recovered 162 most parsimonious trees (MPTs) with a minimum length of 623 steps (ensemble consistency index (CI)=0.429; ensemble retention index (RI)=0.817; Supplemental material). The second analysis (i.e. with character 138 set as inactive) recovered 81 MPTs with a maximum length of 619 steps (CI=0.43; RI=0.82). Results of both analyses are consistent with previous morphologically based phylogenies for major clade relationships within the Crocodylia (Brochu & Rincón 2004; Vélez-Juarbe *et al.* 2007; Jouve *et al.* 2008; Salas-Gismondi *et al.* 2016). In contrast to molecular approaches (Hass *et al.* 1992; Gatesy *et al.* 2003; Harshman *et al.* 2003; Oaks 2011), the monophyly of the Gavialoidea clade, including *Gavialis* and *Eosuchus* but not *Tomistoma*, received strong Bremer support (≥ 3). Brevirostres includes *Crocodylus*, *Tomistoma* and *Alligator* and all other taxa closer to them than to *Gavialis*. Within the alligatoroids, the early Miocene Panamanian *Culebrasuchus mesoamericanus* (Hastings *et al.* 2013) is within the *Alligator* clade as the sister taxon of *A. mississippiensis*. These results contrast with the original phylogenetic proposal for *Culebrasuchus*, in which this taxon was nested basal to all remaining caimanines (Hastings *et al.* 2013). The position of *Cu. mesoamericanus* within the *Alligator* clade was also recovered by a study exploring character evolution of the caimanines (Hastings *et al.* 2016). Our analyses confirm that the neotropical



Crocodylus, which includes the four extant New World species (*Cr. acutus* (Cuvier 1807), *Cr. moreletii* (Duméril & Duméril 1851), *Cr. intermedius*, *Cr. rhombifer* (Cuvier 1807)) and the extinct *Crocodylus falconensis* (Scheyer *et al.* 2013) from the Pliocene of Venezuela is a monophyletic group, closer to *Cr. niloticus* (Laurenti 1768) than to *Cr. porosus* (Schneider

1801). However, we recovered no resolution within the neotropical *Crocodylus* clade.

Compared with the strict consensus cladogram of the first approach in which relationships of *Gavialis* and neotropical gavialoids are not resolved, the second one (with character 138 collapsed; Fig. 7) gained better resolution within gharial relationships and is used here for

discussion and conclusions. The new Caribbean gavialoids herein described are identified as members of the Gryposuchinae, a clade including all known neotropical gavialoids and *Argochampsia* from the Palaeocene of Africa (Fig. 7A). The gryposuchine clade is supported by the presence of long posterolateral squamosal ‘prongs’ (character 158-2) and a retroarticular longitudinal crest (character 203-1). The lack of a broad prootic exposure on the braincase (character 164-1) might also diagnose gryposuchines, as suggested by Vélez-Juarbe *et al.* (2007), but this condition is only unambiguously known from *Piscogavialis* and *Gr. colombianus*. Within the gryposuchines, we recovered two sister clades: (1) a large group of South American species, including the new Panamanian taxon *Dadagavialis gunai*, and (2) a smaller group in which the new Venezuelan species, *Aktiogavialis caribesi*, and *Ak. puertoricensis* are sister taxa, and both are closely related to *Argochampsia* (*Aktiogavialis* + *Argochampsia* clade). *Aktiogavialis* is diagnosed by the presence of a fossa anterior to the supratemporal fenestrae (character 153-0), 18 to 22 maxillary teeth (character 186-1), and the posterior skull table transversally constricted (Fig. 6; character 207-1). The placement of *Aktiogavialis* within the gryposuchines agrees with the original proposal of Vélez-Juarbe *et al.* (2007) and differs from Salas-Gismondi *et al.* (2016), in which *Aktiogavialis* was positioned outside the Gryposuchinae + *Gavialis* clade. The *Aktiogavialis* + *Argochampsia* clade is supported by the presence of long supratemporal fenestrae (character 191-0) and a thick posterior bar of these fenestrae (character 205-0). If *Argochampsia* is a gryposuchine, then the neotropical forms would have derived from two different ancestors, one giving rise to the large clade of South American-Panamanian species and another to *Argochampsia* and *Aktiogavialis*.

Dadagavialis gunai is regarded as the sister taxon of the Venezuelan species *Ikanogavialis gameroi*, sharing a lateral palatine process projecting anteriorly into the sub-orbital fenestrae (character 117-1) and a postorbital pillar flushing with the lateral jugal surface (character 135-0). The acquisition of a laterally displaced postorbital pillar in (1) the *Gavialis* clade, (2) the *Gryposuchus croizati* (Riff & Aguilera 2008) + *Gr. colombianus* clade, and (3) the *Dadagavialis* + *Ikanogavialis* clade, is identified as occurring in three independent evolutionary events by our phylogenetic analysis, likely as part of the highly homoplastic rearrangement occurring in the orbital region in association with the longirostry and ecology (Salas-Gismondi *et al.* 2016). The *Dadagavialis* + *Ikanogavialis* clade lies in a polytomy with *Piscogavialis*, *Siquisiquesuchus* and *Gryposuchus*. A frontoparietal suture entirely on the skull table (character 150-2) is observed in *Dadagavialis*, *Ikanogavialis* and *Piscogavialis*, but is

currently unknown in *Siquisiquesuchus*. The lacustrine-riverine *Gryposuchus* species share 18 to 22 maxillary teeth (character 186-1), a lateral extension of the skull table reaching the level of the lateral margin of the quadrate condyle (character 187-0), orbits wider than long to rounded (character 200-1), the largest premaxillary alveolus being the second (third of crocodylians with five premaxillary alveoli; character 201-2), and a barely sculpted frontal plate surface (character 202-1). This latter character is shown to be polymorphic.

Other characters previously diagnosing gryposuchines (e.g. four premaxillary teeth (character 87-1) and a quadrate with a detached medial hemicondyle (character 181-4); Salas-Gismondi *et al.* 2016), are unknown in *Aktiogavialis* and they currently ambiguously support the South American-Panamanian association. The gharials (*sensu* Salas-Gismondi *et al.* 2016), a subset of late-diverging gavialoids closer to *Gavialis* and *Eogavialis* than to the ‘thoracosaur’, receives strong character support. The ‘thoracosaur’ are drawn as the first offshoots of the gavialoids.

Morphospace analyses and phylogenetic mapping

Snout shape analysis

The PCA based on the landmark data set of the snout of 34 crocodylians shows that the first two axes capture 92.1% of the total variance. The morphospace defined by PC1 (79.2%) and PC2 (12.9%) with the phylogeny mapped on it is shown in Figure 8A. This shape variation is independent of size (regression of PC1 and PC2 on centroid size: $p = 0.32$; Supplemental material). PC1 correlates mainly with the width and length of the snout, and the length of the dental series posterior to the eighth maxillary alveolus loci. Species on the negative extreme of PC1 present long and slender snouts, the premaxillae wider than the distal maxillae (i.e. at the level of the 3rd–6th tooth positions), the proximal maxillae extremely elongated, and the anterior margin of the sub-orbital fenestrae located at the level of the most proximal maxillary tooth loci. Those on the positive extreme of PC1 bear a short, broad rostrum notably expanded at the level of the 3rd–6th tooth positions (i.e. large ‘caniniforms’ at the maxillary largest convexity), short posterior maxilla, and anterior margin of the sub-orbital fenestrae positioned at the level of the eighth maxillary tooth loci. PC2 describes variation in the length of the premaxillae and the relative position of the 4th–8th maxillary tooth positions. Species with lower scores possess long premaxillae and the 4th–8th maxillary alveoli lie at mid-length of the maxillae, whereas taxa with higher PC2 scores have comparatively short

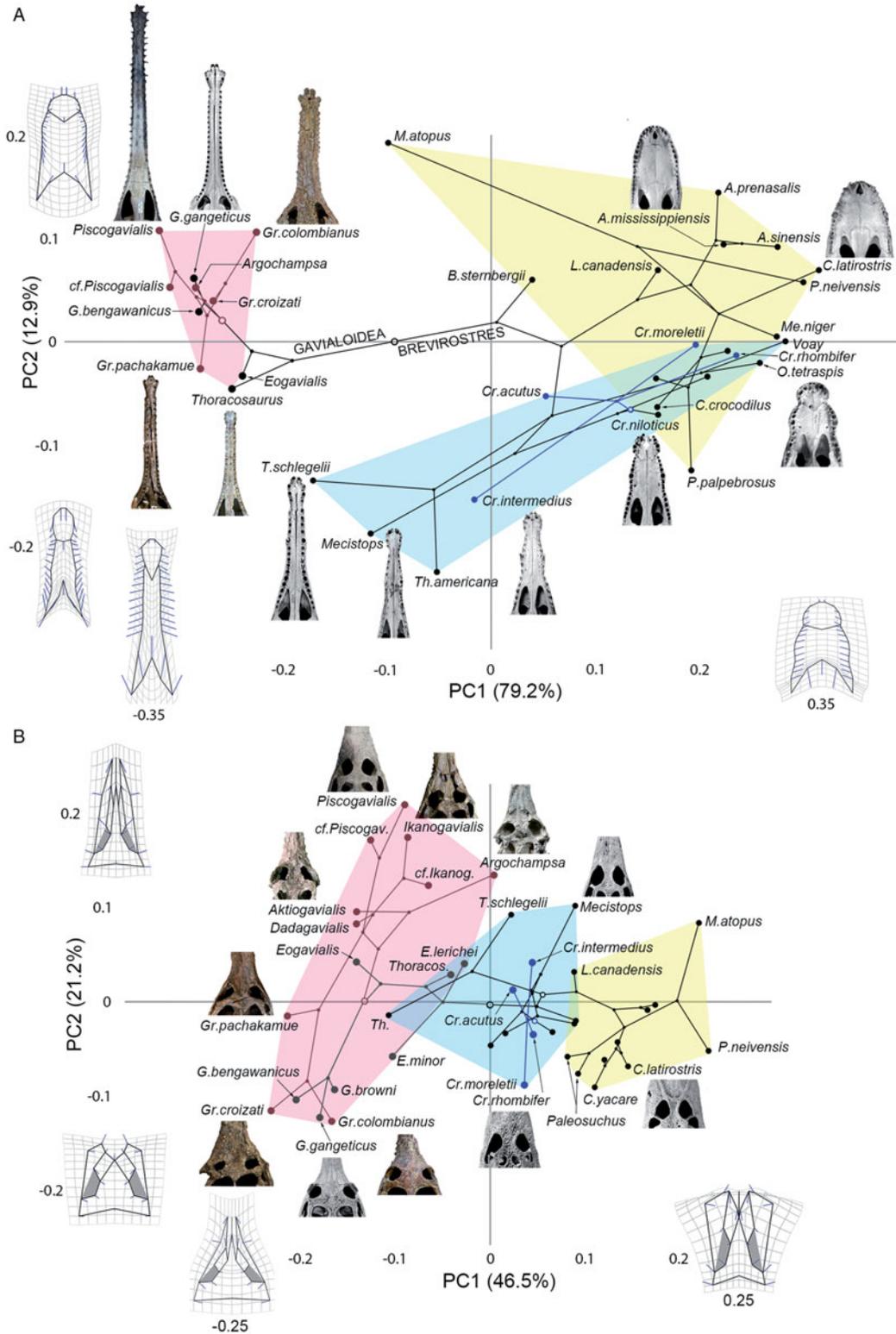


Figure 8. Phylogenetic relationships of the Crocodylia mapped onto the snout (**A**) and circumorbital (**B**) morphospaces defined by PC1 and PC2 (PC, principal component). Deformation grids depict extreme values along each axis. Blue vectors represent the mean value relative to the landmark variation. Relevant anatomical region of selected taxa of Brevirostres and Gavialoidea is shown for best visualization of shape variation. Convex polygons encircle the morphospace of Gavialoidea (pink), Alligatoroidea (yellow) and Crocodyloidea (blue). Phylogeny of gryposuchines and neotropical *Crocodylus* is in red and blue, respectively. Abbreviations: *Ikanog.*, *Ikanogavialis*; *Th.*, *Thecachamps*; *Thoracos.*, *Thoracosaurus*.

premaxillae and those tooth alveoli are located in the distal half of the maxillae. The scatter plot shows that the Brevirostres (i.e. alligatoroids and crocodyloids) and gavialoid clades occupy distinct, separated areas of the morphospace, resembling general results obtained by Pierce *et al.* (2008) for extant crocodylians using landmarks of the whole skull. The exclusive morphospace of gavialoids is notably smaller compared to the areas occupied by either crocodyloids or alligatoroids (Fig. 8A). The overlap between the morphospaces of crocodyloids and alligatoroids is limited to the higher scores of PC1 and is essentially discriminated by their PC2 scores (higher in alligatoroids and lower in crocodyloids). These crocodylian sub-clades mostly occupy different regions of the snout morphospace, in contrast with the extensive overlap proposed by previous contributions based on landmark configurations of the whole skull (Pierce *et al.* 2008; Piras *et al.* 2014). Longirostrine crocodyloids are represented by *Tomistoma*, *Thecachampsa*, *Mecistops* and, to a lesser degree, *Cr. intermedius*. Higher scores for PC1 and lower scores for PC2 separate these from gavialoids and reflect typical features of crocodyloids, such as relatively long premaxillae and transversally expanded maxillae with enlarged teeth at mid-length.

Mapping the phylogeny over the morphospace revealed convergent evolution of snout shape by extensive intersection of branches and parallel-trending radiations, notably between long-snouted crocodyloid sub-clades (tomistomines, *Mecistops*, *Cr. intermedius*) and within the region of crocodyloid-alligatoroid overlap. Some extant caimanines (*Caiman crocodilus* (Linnaeus 1758), *Caiman yacare* (Daudin 1802), *P. trigonatus*) and neotropical *Crocodylus* (*Cr. moreletii*, *Cr. rhombifer*) show no distinction in their snout morphospace occupation. The morphospace occupation of neotropical *Crocodylus* represents about half of the area of crocodyloids (Fig. 8A). Our permutation test indicates that the crocodylian snout is significantly correlated with phylogeny (tree length = 0.40, $p < 0.0001$).

Circumorbital shape analysis

The first two axes of the PCA analysis of the orbital region explain 67.7% of the variation. The morphospace defined by PC1 (46.5%) and PC2 (21.2%) of the 40-taxon data set with the phylogeny mapped on it is shown in Figure 8B. Regression of PC1 and PC2 on centroid size indicates that PC1 is independent of size ($p = 0.06$) whereas PC2 is not ($p = 0.31$). To evaluate the effect of this allometric signal in our results, we used the residuals of the regression scores to generate a new covariance matrix. Since the residual component of variation is uncorrelated with size, we conducted a new PCA analysis based on these values to produce a non-allometric morphospace

(i.e. R PCA; Klingenberg 2011). The morphospace of R PC1 and R PC2 generates essentially the same results as those based on the original shape data set (Supplemental material) and confirms that allometry is not significant for the shape variation described by these axes. Changes along PC1 reflect mainly the width of the pre- and post-orbital regions. PC2 describes variation of length of the pre-orbital bones, the separation between the orbits, and level of demarcation of the snout in front of the orbits. Our permutation test discards the null hypothesis of no phylogenetic signal and indicates that the crocodylian orbital region is significantly correlated with the phylogeny (tree length = 0.40, $p < 0.0001$). Accordingly, PC1 scores (from positive to negative) discriminate the morphospace of alligatoroids, crocodyloids and gavialoids, and reflect the increasing slenderness of the snout relative to the widening of the skull table, an important feature concerning the evolution of longirostry in crocodylians. PC2 scores reveal high orbital shape plasticity throughout the evolution of longirostrine crocodylians that clearly contrasts with the conservative morphology of clades with moderate snout length. *Dadagavialis* and *Aktiogavialis* are positioned close to each other within the gavialoid morphospace defined by low positive PC2 values. This intermediate gavialoid morphospace also includes the African taxon *Eogavialis* and is relatively close to taxa (with higher PC2 values) recovered from deposits representing estuarine/transitional palaeoenvironments (Salas-Gismondi *et al.* 2016).

Within the CV results, the first canonical axis explains 74.5% of the total variation and we find strong support to discriminate the riverine habitat grouping from the coastal-estuarine and generalized ones. Scores of the second axis are less conclusive on differences among habitat categories, yet are sufficient to distinguish the coastal-estuarine grouping from the two others. The unique morphology of the riverine habitat grouping was further recognized by each of the pairwise comparisons (i.e. riverine versus coastal-estuarine and generalized) of the discriminant and crossed validation analyses. The shape deformation grids of riverine versus coastal-estuarine habitat grouping show that riverine crocodylians (i.e. gavialoids) typically possess broader skull tables, widely separated orbits, and shorter lacrimals and prefrontals (Supplemental material).

Discussion

Phylogenetic relationships and biogeography

The new taxa *Dadagavialis gunai* and *Aktiogavialis caribesi* indicate that two sub-clades of gryposuchine gavialoids occupied the Caribbean region during the Miocene (Fig. 7). Prior to these discoveries, the only unambiguous Caribbean gryposuchine from a non-South

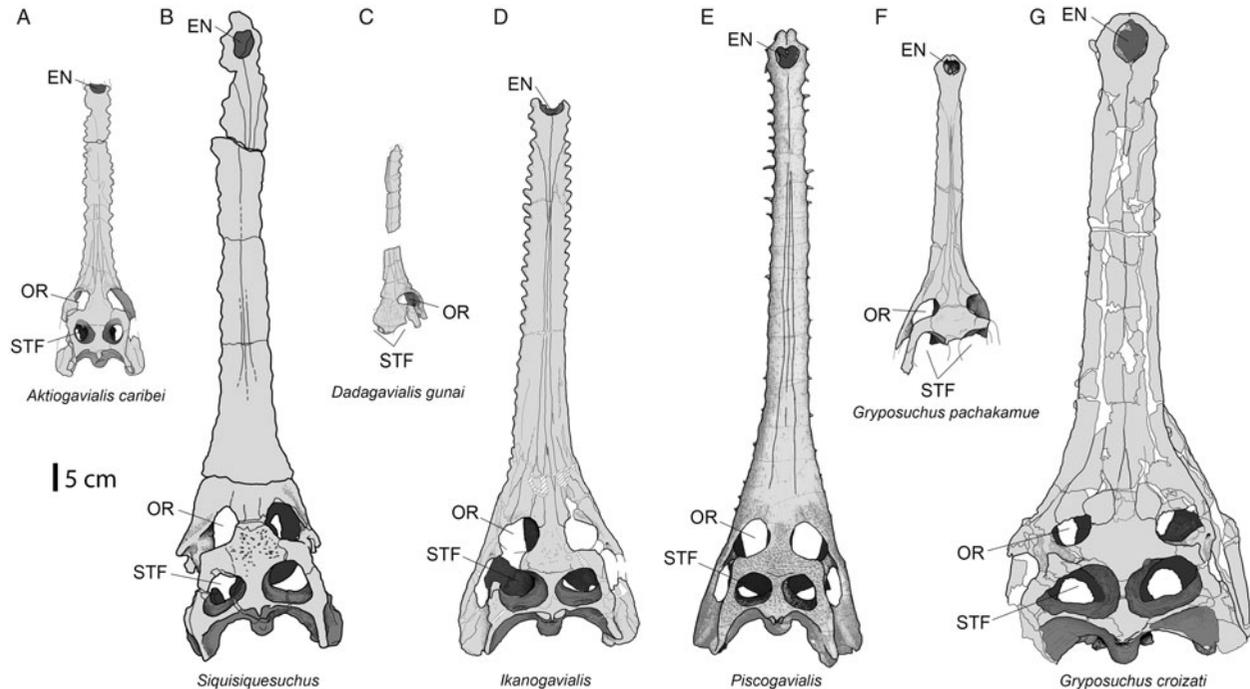


Figure 9. Gryposuchine diversity. **A**, *Aktiogavialis caribesi* (holotype, MCNC 95-72V), late Miocene, Venezuela. **B**, *Siquisiquesuchus venezuelensis* (holotype, MBLUZ 5054), early Miocene, Venezuela. **C**, *Dadagavialis gunai* (holotype, UF312850), early Miocene; Panama. **D**, *Ikanogavialis gameroi* (holotype, VF 1165), late Miocene, Venezuela. **E**, *Piscogavialis jugaliperforatus* (holotype, SMNK 1282 PAL), late Miocene–Pliocene, Peru. **F**, *Gryposuchus pachakamue* (holotype, MUSM 1981); middle Miocene, Peru. **G**, *Gryposuchus croizati* (holotype, MCN-URU-2002-77), late Miocene, Venezuela. Abbreviations: EN, external nares; OR, orbits; STF, supratemporal fenestra.

American locality was *Aktiogavialis puertoricensis*, a relatively small species known by a skull table and braincase from the late Oligocene of Puerto Rico (Vélez-Juarbe *et al.* 2007). Although incomplete, this cranial material bears several characters typical of gharials, such as a posteriorly pointing supraoccipital (character 160-1), anteroposteriorly wide basisphenoid (character 172-1), robust exoccipital ventral process extending to basioccipital tubera (character 176-1), and basioccipital plate with ventrally divergent sides (character 196-1). Its precise identity, however, was problematic because the specimen could belong to a juvenile, not only based on its small size but also because of the presence of features usually observed at very early ontogenetic stages, such as elongated supratemporal fenestrae and convex lateral margins of the skull table (Mook 1921). The skull of the new *Aktiogavialis* species, *Ak. caribesi*, has a total preserved length of 51 cm, which is small when compared with other South American gryposuchines (Fig. 9), but ~40% bigger than *Ak. puertoricensis*. *Aktiogavialis caribesi* possesses the same allegedly juvenile features observed in the skull table of the Puerto Rican form, suggesting that they are not inherent to immaturity but instead typify the adult morphology of *Aktiogavialis*.

Comparisons between *Aktiogavialis* species are limited by the fragmentary condition of the Puerto Rican type specimen, but some differences exclusive of size are recognized. In *Ak. puertoricensis*, the frontal bridge between the orbits is extremely slender and deeply concave (Fig. 6B). The orbital margins are incomplete in this fossil, but the preserved anatomy indicates that the orbits were strongly procumbent and very close together. This combination of features is unique among gavialoids, as procumbent orbits are usually associated with an expanded interorbital bridge (i.e. the fully telescoped orbits of *Gr. colombianus* and *G. gangeticus*). Because procumbent orbits are typically circular in gavialoids, we would expect this morphology in *Ak. puertoricensis*. In contrast, the orbital anatomy of *Ak. caribesi* is closer to that of *Argochampsia* and *Piscogavialis*, with no procumbent orbits and a comparatively wider interorbital bridge.

Remarkable features of *Aktiogavialis caribesi* are also observed in the snout. Although badly preserved, it is possible to recognize that the dorsal surface of the maxilla forms a low dome in cross section. This morphology contrasts with the relatively flattened dorsal surface recorded in gavialoid snouts known so far. Probably in association with the dome-shaped surface of

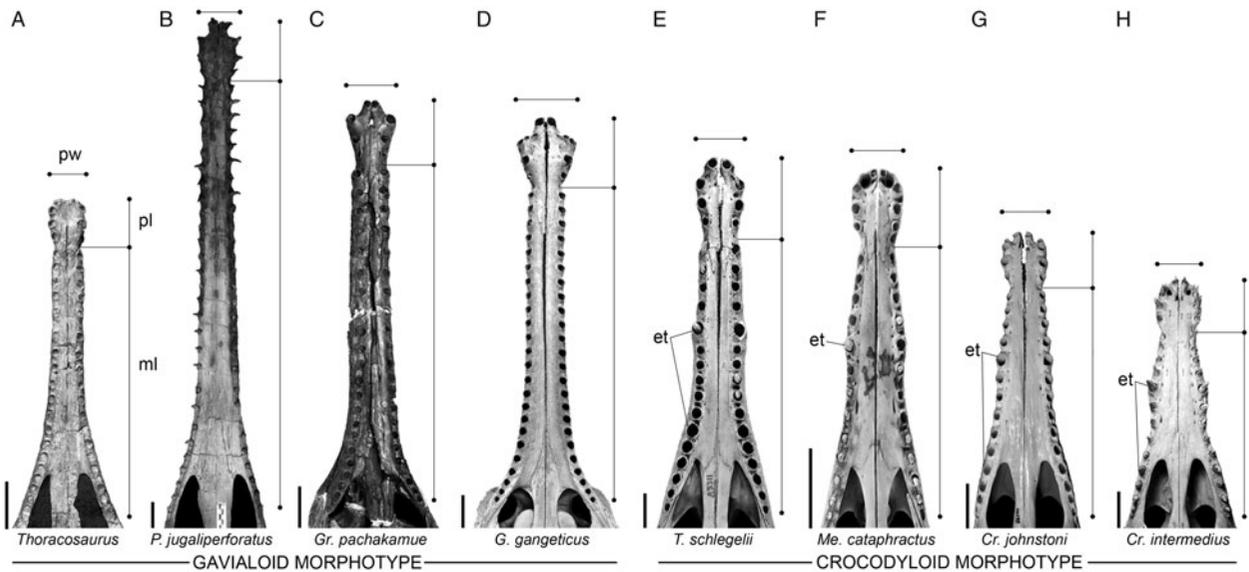


Figure 10. Longirostrine morphotypes in crocodylians. Ventral view of the snout of the gavialoid (A–D) and crocodyloid morphotypes (E–H). **A**, *Thoracosaurus macrorhynchus* (MNHN1902-22). **B**, *Piscogavialis jugaliperforatus* (holotype, SMK 1282 PAL). **C**, *Gryposuchus pachakamue* (holotype, MUSM 1981). **D**, *Gavialis gangeticus* (MNHN A5321). **E**, *Tomistoma schlegelii* (MNHN A5311). **F**, *Mecistops cataphractus* (MNHN NN). **G**, *Crocodylus johnstoni* (AMNH 86540). **H**, *Crocodylus intermedius* (UF 211281). In the gavialoid morphotype, the tip of the snout is wider than the maxillae at mid-length. The crocodyloid morphotype retains relatively long premaxillae and enlarged teeth in the maxilla. All specimens reduced to the same snout width measured at the end of the maxillary tooth series. Abbreviations: et, enlarged maxillary teeth; ml, maxillary length; pl, premaxillary length; pw, premaxillary width. Scale bars: 5 cm.

Aktiogavialis, maxillary (and presumably premaxillary) alveoli were implanted anterolaterally and constituted strong lateral salients particularly along the distal half of the snout length, resembling the sinuate profile of *Ikanogavialis* (Fig. 9D; Sill 1970) and the long-snouted crocodyloid *Charactosuchus* (Langston 1965).

The early Miocene *Dadagavialis gunai* from the Cucaracha Formation is the first gryposuchine gharial from North America (Fig. 7B). This formation had already yielded remains of putative gavialoids, but they were too fragmentary to distinguish them from any other longirostrine crocodylian, such as the North American tomistomine *Thecachampsia* (Hastings *et al.* 2013). These previous findings (UF 280096, UF 259875, UF 24435, UF 280669) and the new cranial material herein used to describe *Dadagavialis* likely represent the same single taxon because they were recovered from roughly coeval levels and possess comparable small size. Like most gavialoids, *Dadagavialis* bears a maxillary tooth row underlined relative to the palatal surface (character 182-1) and a long posterior process of the maxillae without teeth (character 189-1). When complete, the skull of *Dadagavialis* would have reached a total length of *c.* 40 cm and it would have had a total body length of 227 cm, and therefore represents a smaller animal than *Ak. caribesi* (skull length = 51.0 cm; total body length = 301 cm; Fig. 9).

Phylogenetic relationships of *Dadagavialis* are problematic. The material is incomplete and diagnostic characters for the gryposuchine clade are not preserved. However, *Dadagavialis* has characters only recorded among non-*Gryposuchus* gryposuchines. For example, the frontoparietal suture lies entirely on the skull table in *Dadagavialis*, *Ikanogavialis* and *Piscogavialis*. In all other gharials in which this feature is known, including *Gavialis* and *Gryposuchus*, this suture makes a modest entry into the supratemporal fenestrae (See Langston & Gasparini 1997). Additionally, *Dadagavialis* possesses a conspicuous, inflated process of the palatine bone projected into the anterolateral suborbital fenestrae, resembling a bulla. Although this inflated structure might comprise portions of the pterygoid, we consider that it does not correspond to the pterygoid bulla, a thin-walled dilatation of the pterygoid bone consistently documented dorsal to the posterior palatine bridge in *Gavialis* (Fig. 4A; see B. G. H. Martin & Bellairs 1977) and some fossil gharials (e.g. *Eogavialis*, *Gryposuchus*; Langston 1965; Salas-Gismondi *et al.* 2016). After detailed revision of gryposuchine material, we recognized an inflated palatine bone as that of *Dadagavialis* in the type specimen of *Ikanogavialis gameroi* (Fig. 4C). Although we interpret this structure in *Ikanogavialis* to be homologous to that of *Dadagavialis*, more fossil material is required to test its phylogenetic value in diagnosing this

gryposuchine sub-clade. The functional significance of this inflated palatine structure is unknown but a connection with the nasopharyngeal duct is expected.

These new fossils highlight the role of northernmost South America as a pivotal area for the biogeographical interchange of South America with North America and the Caribbean islands prior the rise of the Panama Isthmus, and involving oversea dispersals. *Dadagavialis* inhabited fluvio-deltaic areas of Panama *c.* 20 Ma. Although geological and palaeontological data on the timing and mode of the formation of the isthmus are highly debated, several studies have proposed an almost continuous emerged land from central Panama (via Central America) to the rest of North America since the early Miocene (*c.* 20 Ma; Kirby *et al.* 2008; Farris *et al.* 2011; Montes *et al.* 2012; Bacon *et al.* 2015; Jaramillo *et al.* 2017a; Jaramillo 2018). This southernmost North American land was separated from South America by deep sea waters – the CAS – for most of the Cenozoic until *c.* 10 Ma, yet shallow-marine water exchange between the Caribbean and Pacific might have persisted up to the beginning of the Pliocene (*c.* 3.5–4.2 Ma; Lear *et al.* 2003; Lunt *et al.* 2008; Osborne *et al.* 2014; Jaramillo *et al.* 2017a; Jaramillo 2018). Early gavialoids (i.e. ‘thoracosaurus’) are reported from the Cretaceous to the Eocene of the Atlantic coast of North America (Brochu 2004) and could explain the presence of early Miocene *Dadagavialis* in the southern peninsula of North America (Panama). However, our phylogenetic analysis indicates that the archaic ‘thoracosaurus’ are only distantly related to *Dadagavialis*, which is instead nested within the derived South American gryposuchines, as the sister taxon of *Ikanogavialis gameroi* (Fig. 7). Therefore, the occurrence of *Dadagavialis* in tropical North America is best explained by a spreading event from South America during the early Miocene, when a large uplift event generated extensive terrestrial landscapes in Panama (Farris *et al.* 2011; MacFadden *et al.* 2014), and there was a narrow CAS separating it from South America (~200 km; Montes *et al.* 2012). This time interval seems to be critical for understanding the initial stages of the Great American Biotic Interchange (Bacon *et al.* 2015) because it documents the earliest South American-derived vertebrates in Panama, including a platyrrhine primate (Bloch *et al.* 2016), a caiman (*Centenariosuchus gilmorei* Hastings *et al.* 2013) and terrestrial reptiles (Cadena *et al.* 2012; Head *et al.* 2012).

Aktiogavialis probably dispersed across marine barriers as well. This taxon is known from the late Oligocene of Puerto Rico and the late Miocene of Venezuela, which provides a temporal range of about 20 million years throughout the Caribbean region. Given

these fragmented geographical distributions and the recurrent findings of fossil gavialoids in marine deposits, it is probable that early members of the clade had osmoregulatory adaptations to thrive in marine-associated ecosystems, and crossed marine barriers (Vélez-Juarbe *et al.* 2007; Salas-Gismondi *et al.* 2016). Alternatively, the distribution of *Aktiogavialis* could be explained by a coastal dispersal mechanism if an Eocene–Oligocene land bridge (GAARlandia = Greater Antilles - Aves Ridge) would have connected the Greater Caribbean Islands and northernmost South America, as proposed by Iturralde-Vinent and MacPhee (1999). However, the GAARlandia hypothesis is still widely debated and challenged by molecular analyses that proposed diachronous events of colonization throughout the Cenozoic when there were no presumed land connections (Hedges 2001; Concheiro-Pérez *et al.* 2007; Kay 2015; Fabre *et al.* 2014).

Morphospace occupation and longirostry in gavialoids

The morphological disparity reached by Miocene gavialoids in the Neotropics is incontestable and borne out by simple observation of species currently known from well-preserved skulls (Fig. 9). However, our morphometric analysis of the snout shape demonstrates that, despite the extensive diversification of the neotropical forms, the variation of the gavialoid snout proportions is extremely reduced when compared to that of *Brevirostres* sub-clades (Fig. 8A). In other words, whereas the snout shape was liable to change throughout alligatoroid and crocodyloid evolution, the gavialoid snout shape remained comparatively stable since the Cretaceous. An invariable feature encapsulated by PC1 in gavialoids involves having the premaxillae wider than the distal maxillae. This condition is defined by the presence of enlarged teeth exclusively at the tip of the snout (i.e. premaxillae and matching region of the dentary), a feature previously referred to as the ‘Greifapparat’ *sensu* Kälin (1933). The higher degree of elongation of the maxillae (encapsulated by PC1 and PC2; Fig. 8A) and the shorter premaxillae (encapsulated by PC2; Fig. 8B) relative to *Brevirostres* also pertain to the gavialoid snout shape (Fig. 10A–D). The evolution of this snout shape might have required the acquisition of slender and long maxillae concomitant with enlarged teeth exclusively at the tip of the snout. Tomistomines, *Mecistops*, *Cr. johnstoni* and *Cr. intermedius* are also longirostrine crocodylians, but their morphotype comprises relatively long premaxillae and the retention of two additional regions of enlarged teeth in the maxillae (Fig. 10E–H).

The large range of snout shapes and the independent evolution of similar morphologies across crocodylians are strongly indicative of ecological adaptation (e.g. Busbey 1995; McHenry *et al.* 2006). However, dietary studies suggest that extant Brevirostres are generalist feeders with snout proportions not correlating with diets (Magnusson *et al.* 1987; Pooley 1989; Thorbjarnarson 1993; Tucker *et al.* 1996). In fact, the aforementioned studies and recent isotopic analyses revealed distinct shifts in diets throughout the ontogeny of most species (Radloff *et al.* 2012). Accordingly, the positive allometry of adductor muscles during the ontogeny of *Alligator* and comparable powerful bite forces in similar-sized taxa with contrasting snout shapes (e.g. *Cr. johnstoni*, *C. latirostris* (Daudin 1802)) suggest that dietary preferences in crocodylians are mainly driven by body size (Erickson *et al.* 2003, 2012; Gignac & Erickson 2016). Although most longirostrine species possess powerful bite forces, distal jaw loci are subject to higher stress and bending moments than blunt-snouted forms (McHenry *et al.* 2006; Pierce *et al.* 2008; Erickson *et al.* 2012; Walmsley *et al.* 2013). Therefore, we would expect the snout proportions positioned towards the positive PC1 values (relatively slender, long and tubular snouts; Fig. 8A) to better suit the capture and feeding of comparatively smaller prey, than forms defined by negative PC1 values.

Gavialis gangeticus is the sole outlier in most morphometric and biomechanical analyses (Pierce *et al.* 2008; Erickson *et al.* 2012). Relative to crocodyloids and alligatoroids, *Gavialis* shows substantial divergence in snout shape, adductor chamber anatomy and posterior pterygoideus muscle histology that resulted in a unique morphotype with low bite force but rapid closure of the jaws (Endo *et al.* 2002; Pierce *et al.* 2008; Erickson *et al.* 2012; Piras *et al.* 2014). Because this snout shape (Fig. 8A) and adductor-related anatomy are both retained within the adaptive radiation of the neotropical gavialoids (Fig. 9; Brochu 2004; Salas-Gismondi *et al.* 2016), these extinct forms would have shared equivalent jaw-closing capabilities to *G. gangeticus*. Enlarged teeth only in the premaxillae (i.e. Greiffapparat) might have been a key evolutionary feature used to (1) seize prey with the tip of the snout and (2) feed on agile, small targets. Although other longirostrine forms (e.g. *Tomistoma*, *Mecistops*) also prey on small targets, having powerful bite forces and prominent teeth in the maxilla (Fig. 10E–H), relatively close to the quadrate-articular joint, might give these crocodyloids access to prey of a comparatively larger size range. The fluctuating and labile snout shape typical of crocodylian evolution might be explained by this prey-size flexibility, prevailing even in non-gavialoid longirostrine forms.

In turn, the circumorbital anatomy of gavialoids shows high disparity, expressed in a much larger morphospace occupation than that of crocodyloids or alligatoroids (Fig. 8B). This large disparity has been attributed to the evolutionary enhancement of visual foraging strategies in longirostrine crocodylians (Salas-Gismondi *et al.* 2016). Based on the riverine habitat of *Gavialis* and the depositional setting documented for its fossil relatives, divergent values of gavialoids along PC2 were proposed to represent the morphospace of riverine (negative PC2 values) and coastal marine taxa (positive PC2 values; Salas-Gismondi *et al.* 2016). The Indian *Gavialis* and advanced species of the South American *Gryposuchus* converge on the same riverine region of the morphospace through independent, parallel acquisition of the fully ‘telescoped’ orbits condition. Our CV and discriminant analyses indicate that this circumorbital morphology is strongly correlated with riverine habitat preferences. We presume that procumbent and more separated eyes of riverine gavialoids improve binocular vision and distance estimation of a selected target prior to seizing with the tip of the snout. Although experimental studies suggest that crocodylians are not able to focus underwater (Fleishman *et al.* 1988), differential visual properties across extant crocodylian species are poorly known.

Dadagavialis and *Ak. caribesi* emphasize the homoplastic evolution of characters associated with the orbital region in gavialoids. Both taxa are closely related to forms occupying the coastal marine morphospace (i.e. *Ikanogavialis*, *Argochampsia*). However, because *Dadagavialis* and *Ak. caribesi* possess some traits linked with the ‘telescoped’ orbit condition of taxa prevailing in the riverine morphospace, they are set apart from the marine forms and positioned in a roughly intermediate region defined by low positive PC2 values (Fig. 8B). Consistently, the new Caribbean forms were recovered from deposits representing transitional palaeoenvironments, such as deltaic or nearshore wetland areas (Quiroz & Jaramillo 2010; MacFadden *et al.* 2014). These results suggest that habitat shifts occurred extensively within gharial subclades, producing iterative restructuring of the orbital anatomy without notable correction of the snout shape. If the snout and orbital region are functional modules (e.g. Piras *et al.* 2014), then these are poorly integrated with each other in gavialoids. Within the gavialoid orbital module, the level of integration of traits (i.e. morphology of the orbital margins, separation of the orbits, and position of the post-orbital pillar) is still unclear.

With estimated total lengths of about 226–301 cm, *Dadagavialis* and *Ak. caribesi* are the smallest neotropical gharials (Fig. 9). As longirostrine representatives of the gavialoid morphotype, a diet based on small fishes

or amphibians would be expected. In semi-natural conditions, sub-adult gharials (200–240 cm of total length) were successfully fed on trout individuals (*Salvelinus*, *Oncorhynchus*; Thorbjarnarson 1990), whose fork lengths ranges from 20 to 30 cm (Fausch & White 1981; Naiman *et al.* 1987). The fossil record of the type locality of *Dadagavialis* (Locality 630059) shows that small fishes (vertebrae diameter of ≤ 10 mm; JM-B, pers. obs.) were relatively common, whereas larger fishes have not been recorded so far.

The decline of the gryposuchines

Fossil evidence suggests that the decline of gryposuchines occurred soon after their late Miocene diversity peak. During the late Miocene interval, *Gryposuchus* species inhabited major South American fluvial basins (Amazonia, Orinoco and Paraná; Gasparini 1968; Buffetaut 1982; Cozzuol 2006; Riff & Aguilera 2008; Souza *et al.* 2016; Bona *et al.* 2017) and *Piscogavialis* was distributed along the Pacific coasts of Peru and northern Chile (Kraus 1998; Walsh & Suárez 2005). The largest gharial diversity might have been concentrated in the highly dynamic Caribbean coastal wetlands of northernmost South America because four (i.e. *Ikanogavialis*, *Gryposuchus*, *Hesperogavialis*, *Aktiogavialis*) out of the six late Miocene taxa were recovered from the Urumaco Formation (Venezuela; Sill 1970; Bocquentin-Villanueva & Buffetaut 1981; Riff & Aguilera 2006; Scheyer *et al.* 2013).

The uppermost levels of the Urumaco Formation (*c.* latest Miocene) also document the youngest gryposuchines from the Caribbean, just prior to a drastic environmental and faunal turnover that marked the end of the whole hyperdiverse, coastal wetland ecosystem (Scheyer *et al.* 2013). Overlying beds of the latest Miocene–Pliocene Codore Formation suggest the onset of a drier fluvial plain, with no crocodylians recovered so far (Quiroz & Jaramillo 2010). As part of this turnover, the Amazonian palynoflora documented in the Urumaco Formation was replaced by the Codore xerophyte vegetation (Díaz de Gamero 1996; Quiroz & Jaramillo 2010). Whether this environmental change is coeval with the complete establishment of a terrestrial landscape across the Isthmus of Panama, *c.* 4.2–3.5 Ma, is a matter currently unknown (see Jaramillo 2018). Likewise, the lack of a better resolved chronology precludes precise correlations with other South American localities with gryposuchines of putative late Miocene–Pliocene ages, such as Acre and Paraná (Cione *et al.* 2000; Cozzuol 2006; Souza *et al.* 2016).

Although local gryposuchine extirpations presumably coincide with environmental changes (Gasparini 1968; Buffetaut 1982; Scheyer *et al.* 2013), we cannot ignore that their demise and the arrival of *Crocodylus* to the

Americas are roughly coeval. Combined molecular and palaeontological data are consistent with a late Miocene–Pliocene age for divergence between ancestral eastern African populations of *Cr. niloticus* and the neotropical *Crocodylus* (Oaks 2011; Hekkala *et al.* 2011; Meredith *et al.* 2011). Earliest neotropical fossil *Crocodylus* have been recorded in Pliocene deposits of northernmost South America, in the same areas where gryposuchines were reported in lower levels (Scheyer *et al.* 2013; Moreno-Bernal *et al.* 2016). In fact, the distribution of modern species of *Crocodylus* and Miocene gryposuchines comprises about the same Caribbean coasts and rivers, including the Orinoco and Magdalena drainages (Fig. 7B; Thorbjarnarson & Hernández 1992; Thorbjarnarson *et al.* 2006; Grigg & Kirshner 2015). Although they inhabited the same coastal areas, biomechanical models and our morphometric analyses suggest that gryposuchines and neotropical *Crocodylus* – even the long-snouted *Cr. intermedius* – have largely distinct feeding ecologies and morphospace occupations (Fig. 8; Pierce *et al.* 2008; Erickson *et al.* 2012). In the hypothetical scenario of a gryposuchine–*Crocodylus* sympatry, extirpation by competition appears to be quite unlikely (but see Oaks 2011).

The Pisco Formation, in the Pacific coast area of South America (Southern Peru), presumably records the last gryposuchine in the continent. In association with finely preserved skeletons of cetaceans, pinnipeds, birds, fishes, and even the aquatic sloth *Thalassocnus*, remains of *Piscogavialis jugaliperforatus* are ubiquitous across the vertebrate-bearing horizons identified in the Sacaco area, ranging from about 9 to 5.75–3.9 Ma (Muizon & Bellon 1980; Muizon & DeVries 1985; Kraus 1998; Brand *et al.* 2011; Ehret *et al.* 2012; Lambert & Muizon 2013). Yauca is a new younger locality in the Sacaco area that has yielded remains of the most derived species of *Thalassocnus* (i.e. *T. yaucensis* Muizon *et al.* 2004) and large individuals of *Piscogavialis* (MUSM specimens). If this locality truly corresponds to the late Pliocene as has been proposed (3–1.5 Ma; Muizon *et al.* 2004), then gryposuchine survival in the Pacific largely surpassed that of the Caribbean and its final demise might have occurred at or after the Pliocene faunal turnover of marine vertebrates of the Southern Hemisphere (Olson 1983; Valenzuela-Toro *et al.* 2013).

Conclusions

Dadagavialis gunai and *Aktiogavialis caribesi* are Caribbean representatives of the gryposuchine gavialoids and indicative of the extensive Miocene diversification and distribution of the clade across the circum-Caribbean coasts. The Panamanian *Dadagavialis* is the

sister taxon of the South American *Ikanogavialis game-roi* by possessing a distinct, inflated palatine process projected into the anterolateral suborbital fenestrae. Although *Dadagavialis* presumably was not a coastal marine inhabitant, ancestral South American relatives might have crossed the CAS to reach the southernmost tip of North America at the beginning of the Neogene, as part of pre-isthmus dispersal events among the Americas.

The lifespan of *Aktiogavialis* comprises about 20 million years, from the late Oligocene to the late Miocene, probably confined to the Caribbean region. *Aktiogavialis* is found as most closely related to the African *Argochampsia*. This is consistent with notable shared features in the skull table (Fig. 6), but implies a Cretaceous–Palaeocene separation between gryposuchines and the *Gavialis* clade, which is contradicted by the fossil record of *Gavialis* and molecular data. New anatomical studies on African Palaeogene *Argochampsia* and *Eogavialis* will be crucial to test phylogenetic relationships of *Gavialis* based on morphology.

Although phylogenetic relationships of *Gavialis* are far from resolved, the osmoregulatory capabilities of extinct gavialoids that allowed them to thrive through a wide range of salinities and cross sea barriers are supported by current evidence. In fact, the fossil record suggests that predominantly slender and elongate-snouted crocodyliforms acquired different sorts of marine specializations (e.g. dyrosaurids, teleosaurids, metriorhynchids, crocodylids; see Buffetaut 1982; Busbey 1995; Hua & Buffrenil 1996; Leslie & Taplin 2000; Jouve *et al.* 2005; Young *et al.* 2010; Meredith *et al.* 2011; Grigg & Kirshner 2015). These snout morphotypes could have been favoured when venturing into the sea because of their suitability for capturing relatively small prey in coastal or pelagic waters (Hua 1994; Hua & Buffrenil 1996; Pierce *et al.* 2009; Erickson *et al.* 2012). Conversely, short- and wide-snouted forms apparently never prospered in marine palaeoenvironments, probably because these morphotypes were originally associated with terrestrial and freshwater benthic feeding (Buckley *et al.* 2000; Salas-Gismondi *et al.* 2015). Consistently, extant taxa with relatively wide snouts, such as *Alligator* and *Caiman*, show distinctly less saltwater tolerance (e.g. lacking salt glands) than those taxa bearing a comparatively longer rostrum, such as *Crocodylus* species, owing to a potential ancestral marine stage in these latter forms (Taplin *et al.* 1985; Vélez-Juarbe *et al.* 2007).

Long-snouted crocodyloids and gavialoids exhibit different patterns of longirostry. Whereas crocodyloids bear caniniforms in both the maxillae and premaxillae, gavialoids possess these enlarged teeth exclusively in

the premaxillae, and, as a consequence, the tip of the snout in gavialoids is wider than the maxillae at mid-length. This distinct anatomical configuration for small prey capture, ‘the Greifapparat’ (Kälin 1933), has remained stable since the Cretaceous period, in contrast to the extremely variable snout shape depicted by crocodyloid and alligatoroid evolution. This labile snout shape, however, requires the conservation of maxillary caniniforms and powerful bite forces, which together allow the foraging of a wide range of prey sizes, even in longirostrine forms. Thus, the snout of non-gavialoid crocodylians is continuously re-shaped based on prey size availability.

Concerning the orbital region, there is little variation in non-gavialoid crocodylians. Conversely, this region in gavialoids became highly plastic due to new habitats and more visual foraging strategies, yet the latter is still contentious (see Fleishman *et al.* 1988). Gryposuchine gavialoids were able to explore and conquer multiple aquatic environments for millions of years in the Neotropics with a relative stable snout morphology but evolving different degrees and patterns of protruding eyes by conspicuous rearrangements of the circumorbital bones.

The initial decline of gryposuchines might have occurred in the Caribbean region, in association with drastic environmental changes that affected the area at the Miocene–Pliocene boundary. *Crocodylus* arrival to the Caribbean occurred in the Pliocene, when apparently gryposuchines were already extirpated from the region. Given their different eco-morphospace occupation, gryposuchines and *Crocodylus* species could have potentially coexisted without competing for the same resources. Gryposuchines survived in the southern Pacific coasts of Peru through the Pliocene, where there are no palaeontological or historical records of *Crocodylus*.

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Supplemental material

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