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Received 8 Nov 2012 | Accepted 26 Apr 2013 | Published 21 May 2013

DOI: 10.1038/ncomms2940

Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics

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Northern South America and South East Asia are today's hotspots of crocodylian diversity with up to six (mainly alligatorid) and four (mainly crocodylid) living species respectively, of which usually no more than two or three occur sympatrically. In contrast, during the late Miocene, 14 species existed in South America. Here we show a diversity peak in sympatric occurrence of at least seven species, based on detailed stratigraphic sequence sampling and correlation, involving four geological formations from the middle Miocene to the Pliocene, and on the discovery of two new species and a new occurrence. This degree of crocodylian sympatry is unique in the world and shows that at least several members of Alligatoroidea and Gavialoidea coexisted. By the Pliocene, all these species became extinct, and their extinction was probably related to hydrographic changes linked to the Andean uplift. The extant fauna is first recorded with the oldest *Crocodylus* species from South America.

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The late Cenozoic of South America included a singular array of animals that lived in isolation from other continents until the formation of the Panamanian Isthmus. This fauna included endemic forms resulting from either vicariance or dispersal events from other continents, such as gavialoid crocodylians now found only in South East Asia¹. From the Paleogene and Neogene, 26 crocodyliform species are recorded¹. The high diversity of species in the Miocene of the Amazon region^{1,2}, the origins of which are yet poorly understood³⁻⁵, is documented largely in sedimentary basins in Colombia (La Venta), Brazil and Peru (Acre) and Venezuela (Urumaco). In contrast, in modern day ecosystems, overall crocodylian diversity is generally declining and no more than two or three species occur sympatrically^{6,7}.

To be able to ascertain the nature of the crocodylian communities that actually existed requires revisionary taxonomic and stratigraphic work, which has been conducted for the Urumaco sequence^{8,9}. But how many species lived together and how did these species differ ecologically?

Here, we document > 50 records of crocodylian remains from 14 localities and show a diversity peak in sympatric occurrence of at least seven species. This degree of crocodylian sympatry is unique in the world and shows that at least several members of Alligatoroidea and Gavialoidea coexisted.

Results

Geological context. The 50 records of crocodylian remains from 14 localities (Supplementary Tables S1, S2), include two new species, ranging from the middle Miocene Socorro Formation to the early Pliocene¹⁰ San Gregorio Formation (Supplementary Notes 1 and 2). The identification of samples is based solely on cranial material preserving diagnostic features. The stratigraphic sequence correlation of the geological formations (Fig. 1, Supplementary Fig. S1–S4 (ref. 10)) serves to place the localities into a geographic and temporal context.

Systematic section. *Crocodylia* Gmelin, 1789
Crocodylidae Cuvier, 1807
Crocodylinae Cuvier, 1807
Crocodylus falconensis sp. nov.

Etymology. After Falcón State, northwestern Venezuela, in which the town Urumaco is situated.

Holotype. AMU-CURS-300, an almost complete skull with mandibles (Fig. 2a–e, Supplementary Fig. S5).

Locality and horizon. Northeastern part of Urumaco, from the early Pliocene San Gregorio Formation (Vergel Member; Norte Casa Chiguaje, locality ‘No. 8’ in Fig. 1, Supplementary Fig. S2), Falcón State.

Diagnosis. Medium-sized *Crocodylus* species with a flattened, broad and robust skull and dentition differing from all other crocodylids in the supraoccipital reaching or almost reaching

foramen magnum; orbits and supratemporal fenestrae smaller than in other *Crocodylus* species at the same ontogenetic stage; premaxillary rostrum expanded, with relatively small external naris, but larger comparatively; premaxillae meet posterior to

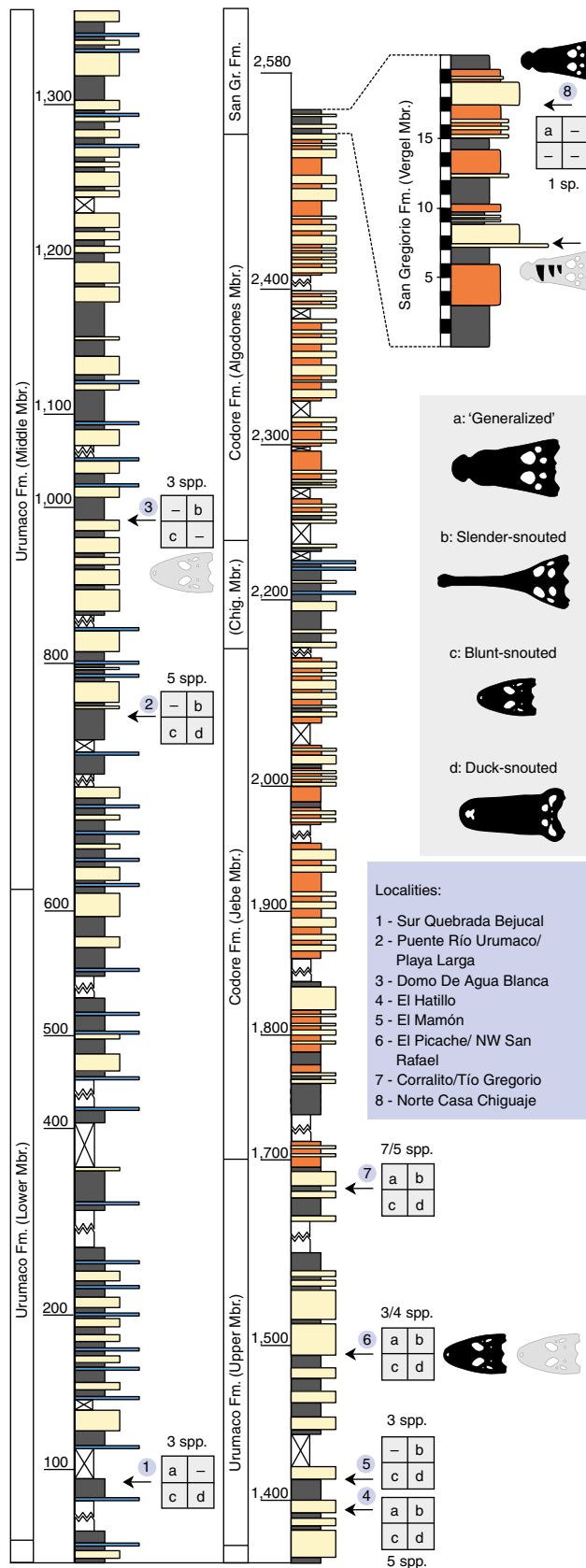


Figure 1 | Simplified stratigraphic profile of the Miocene and Pliocene of Urumaco. Profile is modified from¹⁰, with new data added on San Gregorio Formation. Faunal ecomorphotypes⁴ and number of species are presented for each locality (number above or below gray boxes; note that for locality numbers 6 and 7, two species counts are given; see also Supplementary Figs 1–4). Type localities, as well as sites of recovery of referred material, are indicated by black and gray skull outlines respectively. Isolated teeth collected 1km from type locality (AMU-CURS-302; Supplementary Fig. S10) of *C. falconensis* mark the earliest re-occurrence of crocodylians in the early Pliocene of Falcón State so far. Gray, mudstone/siltstone/shale; blue, coquinoid limestone; yellow, sandstone; orange, mottled mudstone; white, non-exposure/cover interval.

external naris; nasals excluded from external naris, at least externally; orbits circular and slightly larger than external naris; skull table with shallow depression, extending to the frontal; concave posterior margin of skull roof, no posterior convexity; dorsal surface of rostrum bearing medial dorsal boss; rostrum with dorsoventral constriction posterior to external naris; lateral edges of the palatines between the suborbital fenestrae nearly parallel; anterior-most width of intersuborbital bar wider than posterior-most width.

The skull shows obliterated sutures (Supplementary Fig. S5). Size and mass in life was estimated as 4.12 m and 307 kg respectively (Supplementary Tables S3–S5). A medial dorsal boss, a feature shared with other Neotropical *Crocodylus* species, is well developed.

Alligatoridae Gray, 1844

Caimaninae Brochu, 2003 (following Norell, 1988)

Globidentosuchus brachyrostris gen. et sp. nov.

Etymology. Generic name referring to spherical teeth in posterior part of skull ('globi' from Latin *globus* for sphere; 'dento' from Latin *dens* for tooth; 'suchus' after Greek *Suchos*, in reference to the Egyptian crocodile-headed God *Sobek*). Specific name referring to short and wide snout ('brachy' from Greek *brachys* for short; 'rostris' from Latin *rostrum* for snout, in reference to beak-shaped curved prows of Roman ships).

Holotype. AMU-CURS-222, an almost complete skull with associated mandibles (Fig. 2f–n).

Paratype. AMU-CURS-224, fragmentary skull remains associated with mandibles (Supplementary Fig. S6).

Referred material. AMU-CURS-223, associated fragmentary cranial and mandibular remains; AMU-CURS-301, posterior part of right mandible with four crushing teeth preserved; AMU-CURS-383 cranium; AMU-CURS-450 isolated mandibular remains (See also Supplementary Fig. S7–S9).

Locality and horizon. The holotype was collected from El Picache locality ('No. 6' in Fig. 1, Supplementary Fig. S2), Cerro José la Paz site, Urumaco Formation (Upper Member), the paratype from Sorongo site at El Picache, the referred material AMU-CURS-223 from an unnamed site at El Picache, AMU-CURS-301 and AMU-CURS-450 from the Domo de Agua Blanca locality ('No. 3'), Urumaco Formation (Middle Member), and AMU-CURS-383 northwest of San Rafael ('No. 6'), Urumaco Formation (Upper Member).

Diagnosis. Small caimanine species differing from all other crocodylians in having a U-shaped, short and wide skull and deep, robust mandibles; external naris not bisected by nasals; smooth skull surface with weak preorbital ridges but lacking rostral or interorbital ridges; frontal lacks anterior processes and articulates in V-shaped suture with prefrontals rostrally; prefrontals rectangular-shaped, meeting in midline; supraoccipital excludes parietal from posterior skull table edge; dentary and splenial participate in symphysis, which reaches back caudally until seventh mandibular alveolus. Each mandible with 18 teeth; short conical teeth but posterior eight teeth complanate, subspherical and tightly spaced, forming crushing unit; fourth mandibular alveolus is largest, with the largest following dentary alveoli immediately caudal being the whole series from thirteenth alveolus onward; mandible with foramen aërum set in from margin of retroarticular process; articular with laminae both above and below lingual foramen; lingual foramen for articular artery and alveolar nerve perforates surangular/angular suture; surangular pinched off anterior to tip of retroarticular process; surangular–articular suture bowed strongly laterally within glenoid fossa; superior edge of coronoid slopes almost horizontally; splenial forming massive shelf lingual to tooth row; mandibular fenestra large; medial jugal foramen large; margin of orbit flush with skull surface. A strong crushing dentition is developed in a variety of fossil and extant crocodylians, including *Caiman brevirostris*,

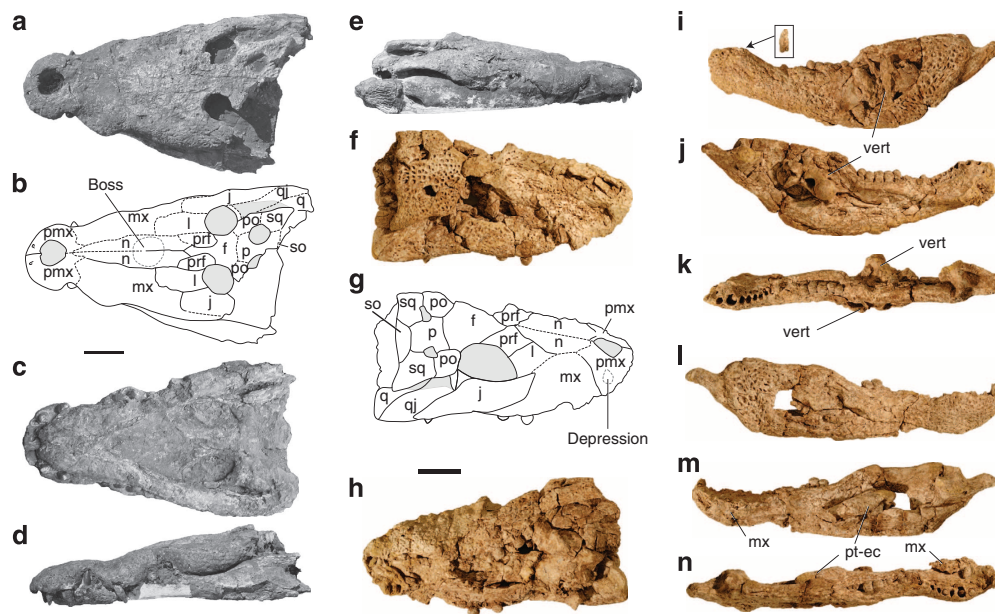


Figure 2 | Holotypes of new species. (a–e) *C. falconensis* sp. nov. (AMU-CURS-300). **(f–n)** *G. brachyrostris* gen. et sp. nov. (AMU-CURS-222).

(b, g) Interpretative drawings of skulls. **(i–k)** Left mandible. Note inset of fourth dentary tooth in **(i)**. **(l–n)** Right mandible, initially attached to skull.

Note that two vertebrae (vert) are fused to the left mandible, and parts of the skull (mx, pt-ec) are fused to the right one. **(a, f, k, n)** Dorsal, **(c, h)** ventral, **(d)** left lateral, **(e)** right lateral, **(i, l)** lateral, **(j, m)** medial views; **(f)** and **(g)** were mirror-imaged for clarity. f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; po, postorbital; prf, prefrontal; pt-ec, pterygoid and ectopterygoid, q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; vert, vertebral remains. Scale bar = 10.0 cm in **(a–e)** and 5.0 cm in **(f–n)**.

Allognathosuchus spp. and *Caiman latirostris*. None of those taxa, however, develops a crushing unit of the eight posterior-most teeth as is found in *G. brachyrostris*. The whole series from the thirteenth alveolus (or fourteenth) onward being the largest immediately caudal to the fourth (character 51-1) is unknown in other caimanines, but a feature that *G. brachyrostris* shares with some globidontan and non-globidontan alligatoroids. *G. brachyrostris* also shares an angular not extending dorsally beyond the anterior end of foramen intermandibularis caudalis (character 65-1) and the surangular–angular suture lingually meeting the articular dorsal to tip (character 66-1) with most derived caimanines; however, the former occurs independently also in the globidontan *Stangerochampsia mccabei*. *G. brachyrostris* shares with *Thecachampsia antiqua* only an articular bone in which laminae are present both above and below the lingual foramen (character 68-3). A foramen aërum being set in from the margin of retroarticular process (character 70-1) is shared by all Alligatoroidea for which this character is known, but is also present in the crocodyloid *Voay robustus*. The maxilla broadly separating the ectopterygoid from the maxillary tooth row (character 103-1) is a typical feature of Alligatoroidea (including the new caimanine taxon), but is also found in the outgroup *Bernissartia fagesii*. Posteriorly flaring lateral edges of the palatine bones that produce a shelf (character 119-1) was found to be shared by most Alligatoroidea with the exception of the basal-most alligatoroid *Leidyosuchus canadensis* and the globidontan *Ceratosuchus burdoshi*. A large exposure of the supraoccipital on the dorsal skull table which excludes the parietal from reaching the posterior edge of the table (character 158-3) appears to be plesiomorphic for Caimaninae. Among caimanines, the absence of an anterior process of the frontal, prefrontals contacting medially and a V-shaped frontal–prefrontal suture are features seen also in the fossil and extant *Melanosuchus* spp. and in the extant *Caiman crocodylus*. *G. brachyrostris* differs from *Culebrasuchus mesoamericanus* in having a curved instead of a linear dentary from d4 to the posterior-most alveolus, a splenial participating in the symphysis, narrower and smaller supra-temporal fenestrae with a more pronounced overhang along the medial wall, and a wider more crescent-shaped supraoccipital exposure in dorsal view. It further differs from *Centenariosuchus gilmorei* in lacking upturned medial orbital margins and in having a larger external mandibular foramen (a smaller foramen is indicated in an angular referred to cf. *C. gilmorei*). *Caiman brevirostris*, another caimanine with crushing dentition¹¹, is superficially similar to *G. brachyrostris*. However, the sutural configuration and shape of the frontals and prefrontals, and the symphyseal participation of the splenial separate both species. The splenial symphysis might be shared with *Tsoabichi greenriverensis*¹². The cranial proportions of *G. brachyrostris* indicate a mean overall size of 1.72 m and body mass of 16.7 kg (Supplementary Tables S3–S5).

Alligatoridae Gray, 1844

Caimaninae Brochu⁴ (following Norell, 1988)

Mourasuchus nativus (Gasparini, 1985)

Referred material. AMU-CURS-212, a posterior skull roof and braincase (Fig. 3); AMU-CURS-218, additional cranial material.

Locality and horizon. AMU-CURS-212 was collected from El Mamón locality, Upper Member of the Urumaco Formation ('No. 5' in Fig. 1, Supplementary Fig. S2) and AMU-CURS-218 from Puente Río Urumaco locality, Middle Member of the Urumaco Formation ('No. 2' in Fig. 1, Supplementary Fig. S2).

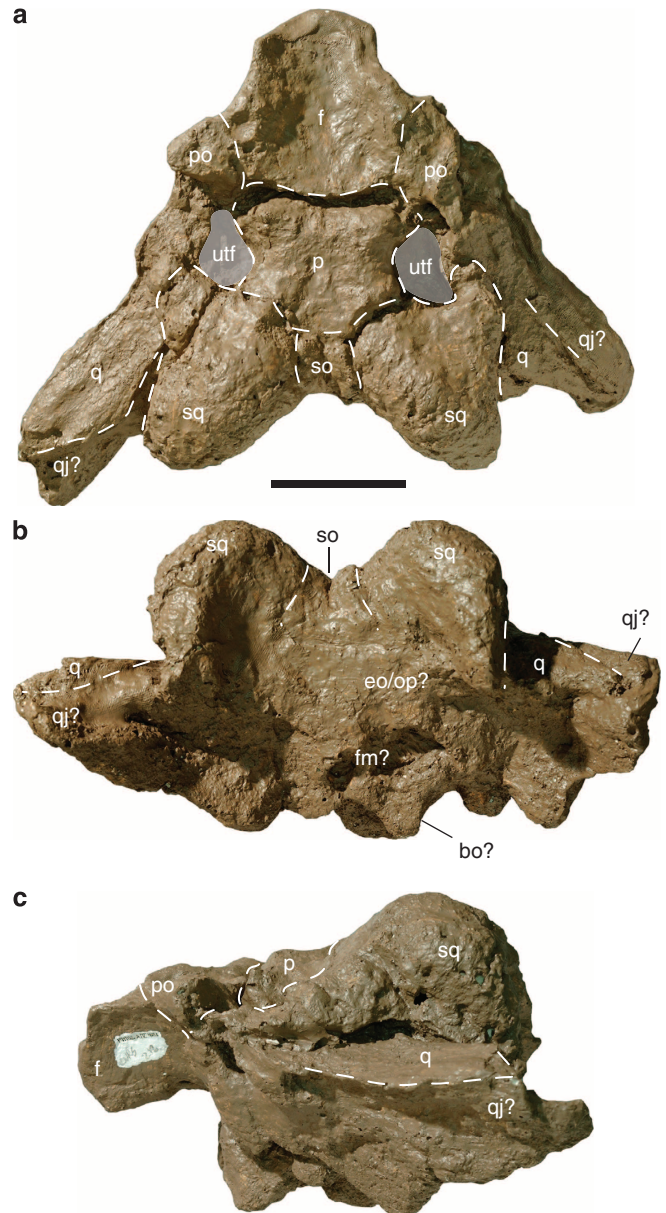


Figure 3 | Posterior skull roof and braincase of *M. nativus*. Specimen (AMU-CURS-212) in (a) dorsal view, (b) occipital view and (c) left lateral view. Note that sutures are generally difficult to trace in occipital and lateral views and that the elements of the braincase floor (for example, basioccipital) shifted laterally towards right. bo, basioccipital; eo/op, exoccipital/opisthotic; f, frontal; fm, foramen magnum; j, jugal; l, lacrimal; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; po, postorbital; prf, prefrontal; pt-ec, pterygoid and ectopterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; vert, vertebral remains. utf, upper temporal fenestra. Scale bar = 5.0 cm.

Diagnosis. *M. nativus* is the second species of duck-snouted ('nettosuchid') caimanines, besides *M. arendsi*¹³, and is the fourteenth crocodylian recognized from the Neogene (that is, Urumaco Formation) of Urumaco (Fig. 4). Especially AMU-CURS-212 preserves enough of the diagnostic features (that is, small crest in midline of parietal; entire posterior part of skull table raised; squamosals particularly high and strongly developed forming transverse ridge) for species recognition^{14,15}. Previously recognized from the Ituzaingó fauna in Argentina, and Acre in Brazil^{1,15,16}, the palaeogeographic occurrence of the species was thus

Formation (FM.)	Socorro	Urumaco							Codore	S. Gregorio
Member (Mbr.)		Lower	Middle		Upper				Vergel	
Locality (Loc.)	Pooled	1	2	3	4	5	6	7	8	
Alligatoroidea (Caimaninae)										
<i>Purussaurus</i> sp.	x	x					x	x	x	
<i>Purussaurus mirandai</i>					x					
<i>Mourasuchus</i> sp.	x	x					x		x	
<i>Mourasuchus arendsi</i>					x	-	-	-	x	
<i>Mourasuchus nativus</i>			x	-	-	x				
<i>Caiman</i> sp.	x	x	x						x	
<i>Caiman brevirostris</i>						x	x	-	-	
<i>Caiman lutescens</i>									x	
<i>Melanosuchus fisheri</i>			x	-	x	-	-	-	x	
<i>Globidentosuchus brachyrostris*</i>			x	-	-	x	x			
Gavialoidea										
<i>Gryposuchus</i> sp.							x			
<i>Gryposuchus croizati</i>					x	-	-	x	x	
<i>Gryposuchus jessei</i>								x		
<i>Hesperogavialis cruxenti</i>			x	x	-	x				
<i>Ikanogavialis gameroi</i>	x	-	x	-	-	-	-	-	x	
Crocodyloidea										
? <i>Thecachamps</i> a sp. 1 (Tomistominae)	x									
? <i>Thecachamps</i> a sp. 2 (Tomistominae)				x						
<i>Crocodylus falconensis*</i>									x	
Crocodylians (uncertain affinities)										
<i>Charactosuchus mendesi</i>					x					
No. of species per LOC./MBR.	5	3	5	3	5	3	3	4	7	

Figure 4 | Taxic crocodylian diversity and locality data. New described taxa are indicated by asterisk and images scaled to same size. Locality numbers in circles correspond to locality names given in Fig. 1. Notice that the total number of species does not count reconstructed records in the middle of stratigraphic extremes of distribution.

spanning >4000 km from the Buenos Aires region in the South to the Caribbean Sea in the North, which is more than any of the living crocodylians does in South America today.

Phylogenetic analysis. The phylogenetic analysis including the new *Crocodylus* species recovered only one most parsimonious tree (MPT; length = 59, CI = 0.6 and RI = 0.7; see Fig. 5a). As in previous analyses^{17,18}, the crown *Crocodylus* was monophyletic. *C. palaeindicus* is sister taxon of the crown clade, but support is weak. The New World assemblage represents a monophyletic and well-supported clade, having *C. falconensis* sp. nov. as the basal-most representative species and the sister group of a clade comprising the extant species (see also Supplementary Fig. S10 for additional crocodylian teeth from the San Gregorio Formation). The New World crocodiles are supported by two unambiguous synapomorphies: the dorsal surface of rostrum bears medial dorsal boss (15-1) and the palatine-ptyergoid suture lies nearly at the posterior angle of suborbital fenestra (20-0). These characters seem to have evolved shortly after the dispersion event from the Old World to the New World¹⁹, as they are present in *C. falconensis* sp. nov. already early in the Pliocene. Some features are present in all extant species of the clade, but due to the incompleteness of *C. falconensis* sp. nov., they could not be traced back to the early evolution of the group: ventral tubercle of proatlas more than one-half the width of the dorsal crest (1-0), and the pterygoid surface lateral and anterior to internal choana is pushed inward around choana to form the “neck” surrounding aperture (22-2). These are unknown in *C. falconensis* sp. nov., and may represent synapomorphies of the New World crocodiles or only of the extant species. Nevertheless, some features were recovered as unambiguous synapomorphies of the extant group: the posterior margin of the skull roof with a posterior process, forming a distinct convexity (30-1), and the

posterior process of palatines have nearly parallel sides (31-1). *C. acutus* and *C. intermedius* share an anterior process of palatines wider than the posterior process (32-2). Although only one feature groups them together, the sister-group relationship between *C. acutus* and *C. intermedius* has been already proposed by molecular phylogenies^{7,19-21}. The New World clade is a well-supported group and has accumulated distinctive differences from its sister taxon, *C. niloticus*, and other extant and extinct crocodile species (Fig. 5a).

The phylogenetic analysis including *G. brachyrostris* gen. et sp. nov. resulted in a total of 20,160 most parsimonious trees (minimum length = 650; Fig. 5b). The computed strict consensus was overall in accordance with the one recovered by Brochu *et al.*²², including all major monophyletic groups, but differing slightly in relationships among highly nested gavialids and tomistomine crocodyloids (Supplementary Fig. S11, S12). Relationships within Caimaninae are also as in Brochu *et al.*²², with *G. brachyrostris* gen. et sp. nov. being sister to all remaining caimanine species. Character (66-1; surangular-angular suture lingually meets articular dorsal to tip) was revealed as a potential unambiguous and unequivocal synapomorphy of Caimaninae.

Discussion

The phylogenetic analysis recovered *C. falconensis* sp. nov. as sister taxon to all remaining New World *Crocodylus* species (Fig. 5a), suggesting that tropical South America was probably the center of origin of the *Crocodylus* neotropical radiation, after transatlantic dispersal either across the Atlantic from Africa or across the Pacific from Asia²³. All living species of *Crocodylus* last shared a common ancestor within the past 15 million years, with the group first appearing in the Old World¹⁷. The monophyly of the New World clade (*C. falconensis* + extant neotropical species) and its minimal early Pliocene age is supported, which has been

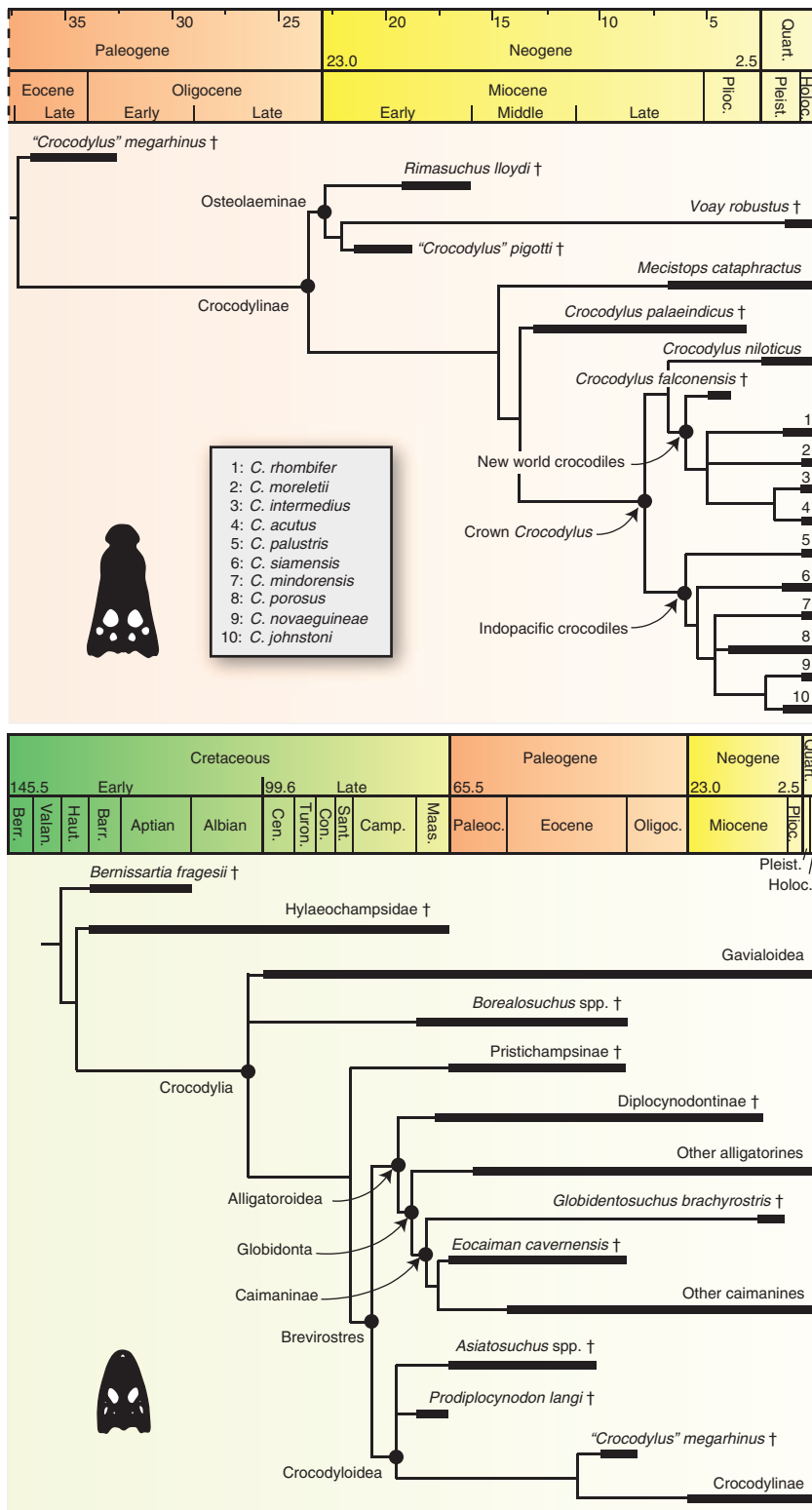


Figure 5 | Simplified phylogenetic hypotheses and stratigraphic occurrences of new taxa. The occurrence and placement^{22,24} of the two new species is indicated based on analyses outlined in Supplementary notes.

estimated from both the fossil record and molecular markers^{7,17,24}.

The analysis with *G. brachyrostris* gen. et sp. nov. supports the monophyly of Caimaninae¹² (Fig. 5b) and a close relation between *Tsoabichi greenriverensis* and extant dwarf caimans (Supplementary Fig. S11). *Globidentosuchus* is at the stem of the

caiman lineage, representing the sister taxon to all remaining caimanines, including the hitherto basal-most *Eocaiman cavernensis* (Paleogene, South America)¹². Adding one of the oldest caimanines known, *Necrosuchus ionensis* (early Paleocene, Argentina), did not change the basal-most position of *Globidentosuchus*, but reduced overall resolution among basal

caimanines (Supplementary Fig. S12). As such, *Globidentosuchus* provides insights into character evolution and polarity (for example, symphyseal shortening that led to exclusion of splenial; large exposure of supraoccipital on skull table), and represents an example of the preservation of basal species in the tropics²⁵.

Recently, a report of two new caimanines, one basal form from the early Miocene Culebra Formation (*C. mesoamericanus*) and a more highly nested form from the early or middle Miocene Cucaracha Formation (*Centenariosuchus gilmorei*) of Panama was presented²⁵. *C. mesoamericanus* shares with *Globidentosuchus*, for example, a large exposure of the supraoccipital on the posterior skull roof, but differs in the anterior extent of the splenial, with a termination before the symphysis and larger supratemporal fenestrae without a large overhang being present in the Panamanian taxon. The presence of yet another basal form greatly underscores the importance of the Central American and Northern South American region for the evolution of the whole clade.

The extreme ecomorphological breadth among the Urumaco crocodylians with at least seven sympatric species (Fig. 4), ranging from small, blunt-snouted ‘crushers’ with body sizes and masses ranging from 1.5–2 m and 10–820 kg (for example, *Globidentosuchus*, Supplementary Tables S3–S5) to several giant-sized forms, clearly suggests niche partitioning^{5,26}. The duck-snouted *Mourasuchus* is represented by two species, with our discovery of *M. nativus* for Urumaco. The gavialoid *Gryposuchus* and the ‘generalist’ *Purussaurus* reached 8–11.5 m and 1.7–3.5 t^{8,9} and overlap with or exceed some of the other largest crocodyliforms known, such as the pholidosaurid *Sarcosuchus* (Cretaceous, Africa) and alligatoroid *Deinosuchus* (Cretaceous, North America), the tomistomine *Rhamphosuchus* (Miocene, Indian subcontinent), and *C. thorbjarnarsoni* (Plio–Pleistocene, Kenya)^{24,27,28}. The crocodylian disparity is indicative also of food web complexity, with the smaller to medium size species acting as meso-predators and the giant *Gryposuchus* and *Purussaurus* as apex predators in the system²⁹. In modern South American assemblages the lower size spectrum is covered by dwarf caimans (*Paleosuchus*), whereas the upper end remains devoid, with the largest living South American crocodylian, the black caiman (*Melanosuchus niger*), reaching usually no more than 4.5 m (ref. 6).

The disparity encountered among Urumaco crocodylians appears to be rivaled by fossil crocodylomorph faunas from Eocene localities (for example, middle Eocene Bridger and lower Eocene Green River Formations in Wyoming; the World Heritage site of Messel, a Konservatlagertstätte near Darmstadt, Germany) and the Late Cretaceous crocodyliform assemblage from the Maevarano Formation of Madagascar²⁹. The North American formations however crop out over huge areas and although morphological and dietary disparity is apparently high³⁰, the actual level of sympatry of taxa, was not^{31,32}. In the Maevarano Formation, which crops out in northern Madagascar yielding an astounding array of vertebrates including dinosaurs, levels of sympatry are also high, although including largely crocodylomorph taxa²⁶ rather than members of crown Crocodylia. In contrast, the European Messel locality is fairly restricted in exposure. Of the seven taxa currently recognized in Messel only *Asiatosuchus* and *Diplocynodon* species are common, indicating that they were true lake inhabitants—the other taxa were washed in only occasionally from adjacent habitats³³. In general, the size and mass spectrum of the Eocene taxa from Messel is also more restricted compared with that of the Urumaco fauna, ranging between 0.8 and 5.0 m in length.

In contrast, the sampling of the Miocene crocodylians in Urumaco was done mainly by surface collecting in relatively restricted localities (Supplementary Fig. S1). The lithology and depositional environment of the fossil-bearing sediments in each

locality is interpreted as preserving fossils *in situ* or with very little transport. It is thus reasonable to assume sympatry of the species, which were recovered in each of the localities.

The new stratigraphical and geographical information presented, together with specific references to numerous specimens in collections and their identifications, leaves no doubt about the sympatry of species reported in this paper. The disarticulated nature of the fossils we find in the field in Urumaco, does not preclude the same stratigraphical origin and contemporaneity, from strata well documented in the new or synthesized geological information presented in this paper. Furthermore, in most cases, many skeletal materials of the same individual are found in association, and never together with remains of other individuals, showing thus that post-mortem transport does not result in spurious associations of species in a site.

Representatives of Alligatoroidea, especially Caimaninae, and Gavialoidea, constitute the highest percentage of species in the Urumaco Formation (and the underlying Socorro Formation; Fig. 4). In the case of the material tentatively referred to *Thecachampsa* and *Charactosuchus* (*‘Brasilosuchus’ mendesi*), a systematic assignment is less clear. Previous works have identified the former pertaining to Crocodylidae^{34,35} or Crocodyloidea², and the latter to either Crocodylidae¹, Gavialoidea² or Gavialidae^{34–36}. In the case of *C. mendesi*, although no ‘non-crocodylian’ taxa have been so far recovered from post-Middle Miocene rocks, incompleteness of the fossil material currently restricts an assignment beyond Crocodyliformes *incertae sedis*³⁷. On the other hand the *Thecachampsa* material is regarded as belonging to Tomistominae, which according to anatomical, fossil and developmental data (but contra molecular data) are within Crocodylidae³⁸ (see Supplementary Note 3). Our results further revealed that disparity is high (for example, indicated by the presence of ecomorphotypes, Fig. 1) throughout most localities studied and at least in three out of the seven localities within the Urumaco Formation (nos. 4, 6 and 7), all four ecomorphotypes are present prior to the drastic faunal turnover.

Palaeoenvironmental reconstructions based on palynofloras from the Urumaco Formation suggest a continuation of the Amazonian forest into northwestern Venezuela during the Miocene³⁹, with the faunal context including marginal marine, freshwater and continental vertebrates⁴⁰. The latest Miocene-early Pliocene Codore Formation flora replaced the Amazonian palynoflora with xerophyte-dominated vegetations during the major environmental change related to the collapse of the Urumaco delta in the late Miocene, which correlates with a major uplift of the northern Andes⁴¹ and the eastward changing hydrograph course of a paleo-Orinoco River^{10,42}. From the El Jebe Member, Codore Formation, faunal elements such as glyptodontids⁴³ and grassy wetlands ciconiid birds⁴⁴ were recovered. These discoveries suggest that the absence of crocodylians from the Codore Formation (Fig. 4) is not a sampling bias. Temperature is usually one of the main parameters limiting crocodylian distribution patterns³. The overlying Pliocene San Gregorio Formation, however, represents sedimentary accumulation in alluvial fans (Fig. 1 and Supplementary Fig. S4)¹⁰, and the aquatic palaeoenvironment is reconstructed as a tropical wetland with meandering channels and inundate savanna²⁵. Therefore, the turnover was clearly not driven by temperature changes, as the mean annual range values in the Caribbean did not vary significantly until the upper Pliocene⁴⁵. Instead, the lack of the diverse crocodylian fauna previously present in the region during the Miocene clearly shows the turnover to a new community was most likely coupled with the documented climatic and hydrographic changes linked to the Andean uplift^{10,41,42}.

Methods

Phylogenetic framework. To elucidate the phylogenetic position of the new described species within Crocodylia, two separate maximum parsimony analyses were performed using TNT v. 1.1 (ref. 46) (see Supplementary Fig. S11 and S12; Supplementary Note 3). The first analysis including *C. falconensis* sp. nov. is based on a matrix of 32 morphological characters, coding 29 characters that vary inside Crocodylinae, and adding two new characters. An exhaustive branch-and-bound search strategy was conducted performing the “implicit enumeration” option. For the second analysis *G. brachyrostris* gen. et sp. nov. and *Necrosuchus ionensis* were added to the 179-characters matrix of Brochu *et al.*²², which included 95 ingroup taxa and *Bernissartia fagesii* as outgroup. For these analyses, a heuristic search (traditional search; space for 50,000 trees in memory, random seed = 1) with 1,000 random additional sequence replicates with 100 trees saved per replication and tree-bisection reconnection option was performed. In all analyses, characters were set as non-additive.

Length and mass estimation. Estimating the length and mass of the newly described taxa (Supplementary Tables S3–S5) followed previously published linear regression formulas of Webb and Messel⁴⁷, which have been used also on fossil taxa^{27,48}, as well as those used by Hurlburt *et al.*⁴⁹ and Platt *et al.*^{50,51}. Hall *et al.*⁵² indicated that there is a discrepancy of 4% among dorsal cranial length measurements between freshly killed animals and dried and cleaned skulls of *C. novaeguineae*⁵³. As such, the size and mass estimates herein are treated as conservative underestimates of real size. In the case of applying the regressions of Hurlburt *et al.*⁴⁹ to *Globidentosuchus*, the orbito-cranial length-based value led to an estimated total length of more than 3 m, which we treat here as a strong overestimation. We nevertheless kept the values in addition to the other results in Supplementary Table S3 and the body mass estimates in Supplementary Table S5, but marked them with an asterisk and put them in square brackets. Note that in-depth osteological description of both new species is in preparation elsewhere.

Nomenclatural acts. This published work and the nomenclatural act it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘http://zoobank.org’. The LSID for this publication is: urn:lsid:zoobank.org:pub:E4D47A14-9D74-40B9-8B19-ABA141C8AE1E.

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Acknowledgements

Specimens are deposited at The Alcaldía del Municipio Urumaco (AMU), Falcón, Venezuela. J. Hernández provided access to the specimens. We thank the authorities at the Instituto del Patrimonio Cultural of the República Bolivariana de Venezuela for generous support to conduct this research. M. Reisser (ETHZ) and C. Colucci (UZH) are thanked for preparation and discussions. This work was funded by the Swiss National Science Foundation (grant 31003 A 127053 and 146440 to TMS; and Sinergia CRSII3-136293 to MRS-V) and Spanish Ministerio de Economía y Competitividad (CGL2011-28681 to MD). Collections visits to DCF funded by The Florida Museum of the Natural History and Brazilian agencies CAPES and CNPq.

Author contributions

T.M.S., M.R.S.-V. and O.A.A. wrote the manuscript and devised the study. M.D., D.C.F., and T.M.S. conducted the morphological descriptions and performed the phylogenetic analyses. L.Q., J.C.-B., R.S., and A.A.C. provided stratigraphic and GIS-data.

Additional information

Supplementary Information accompanies this paper at <http://www.nature.com/naturecommunications>

Competing financial interests: The authors declare no competing financial interests.

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How to cite this article: Scheyer, T. M. *et al.* Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nat. Commun.* 4:1907 doi: 10.1038/ncomms2940 (2013).

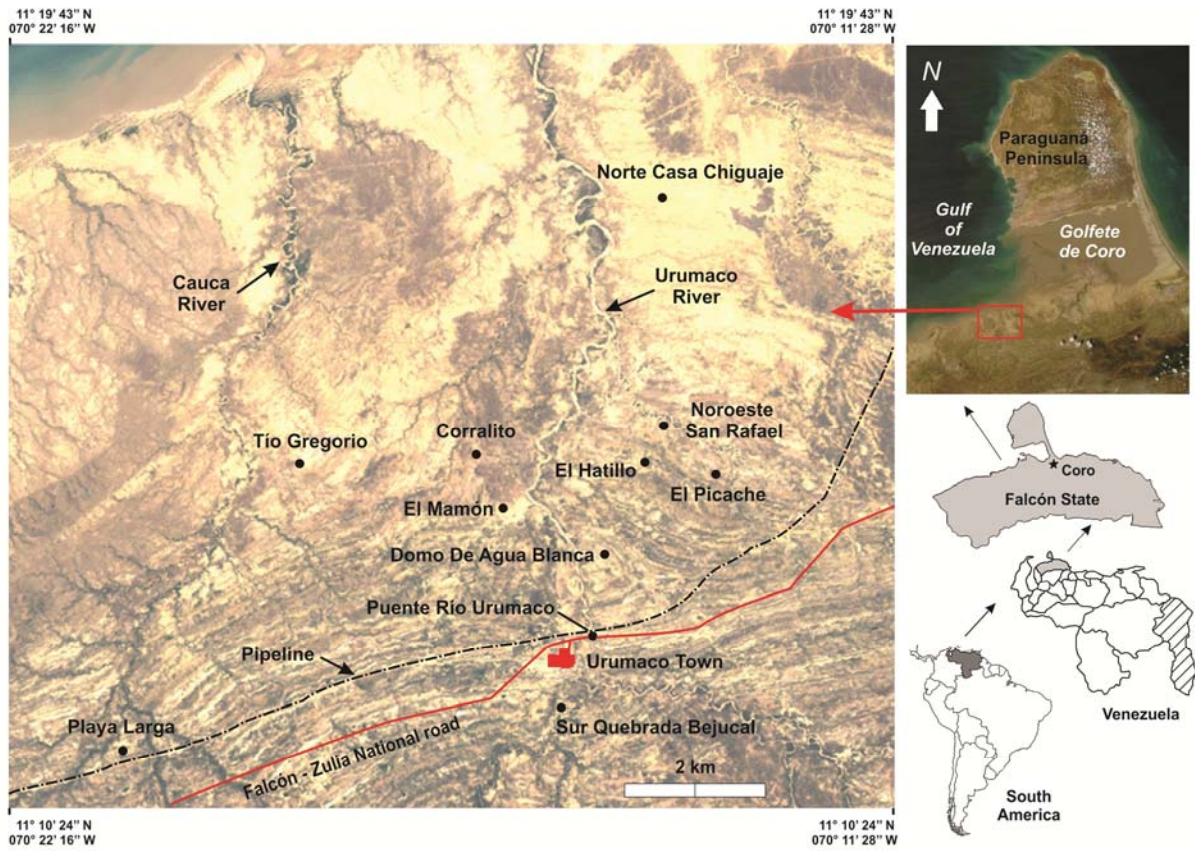
Supplementary Information for:

**Crocodylian diversity peak and extinction in the late Cenozoic of the northern
Neotropics**

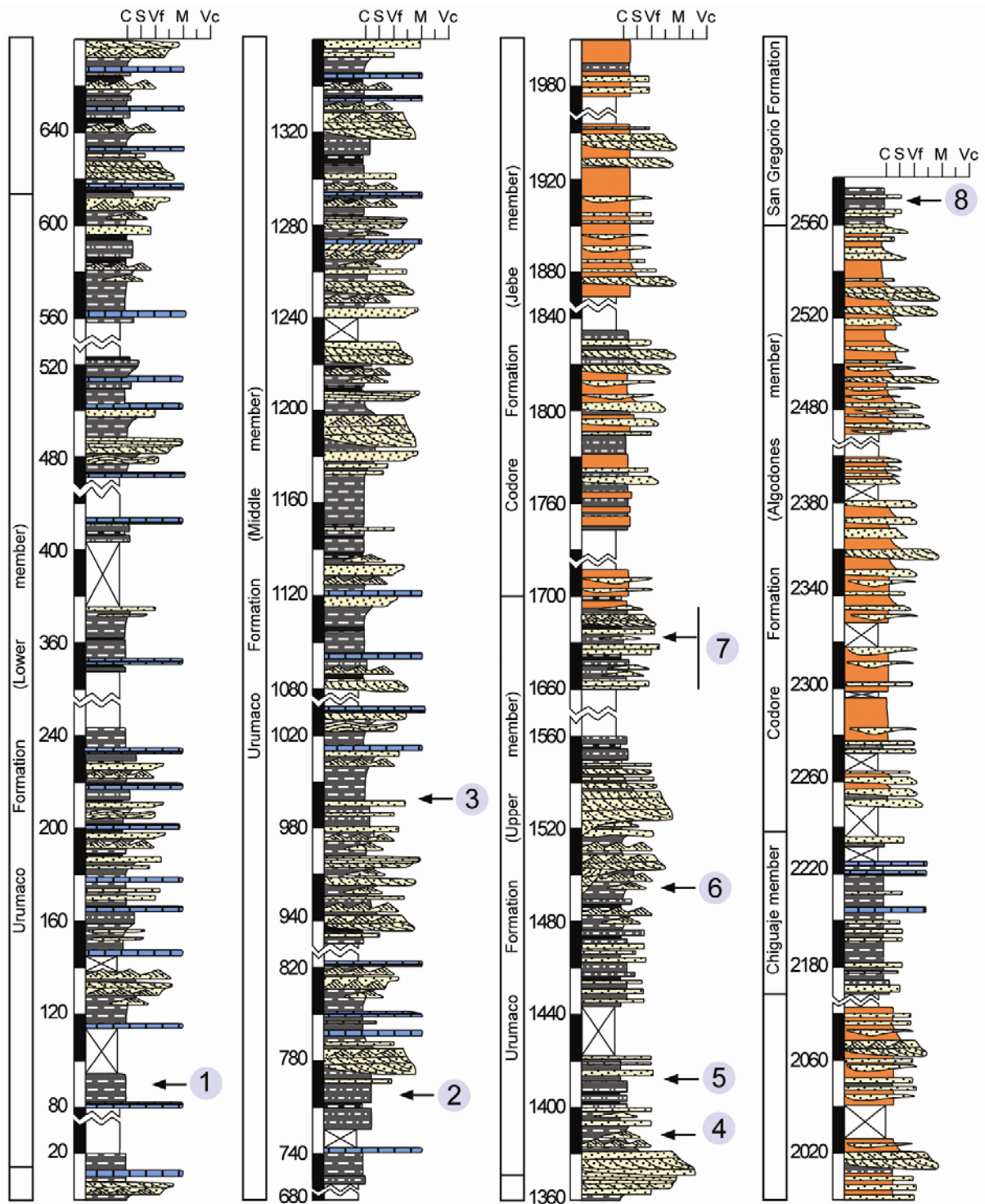
Scheyer, T. M., Aguilera, O. A., Delfino, M., Fortier, D. C., Carlini, A. A., Sánchez, R.,
Carrillo-Briceño, J. D., Quiroz, L. & Sánchez-Villagra, M. R.

Supplementary Figures

Supplementary Figure S1. Satellite image of Urumaco region with localities.

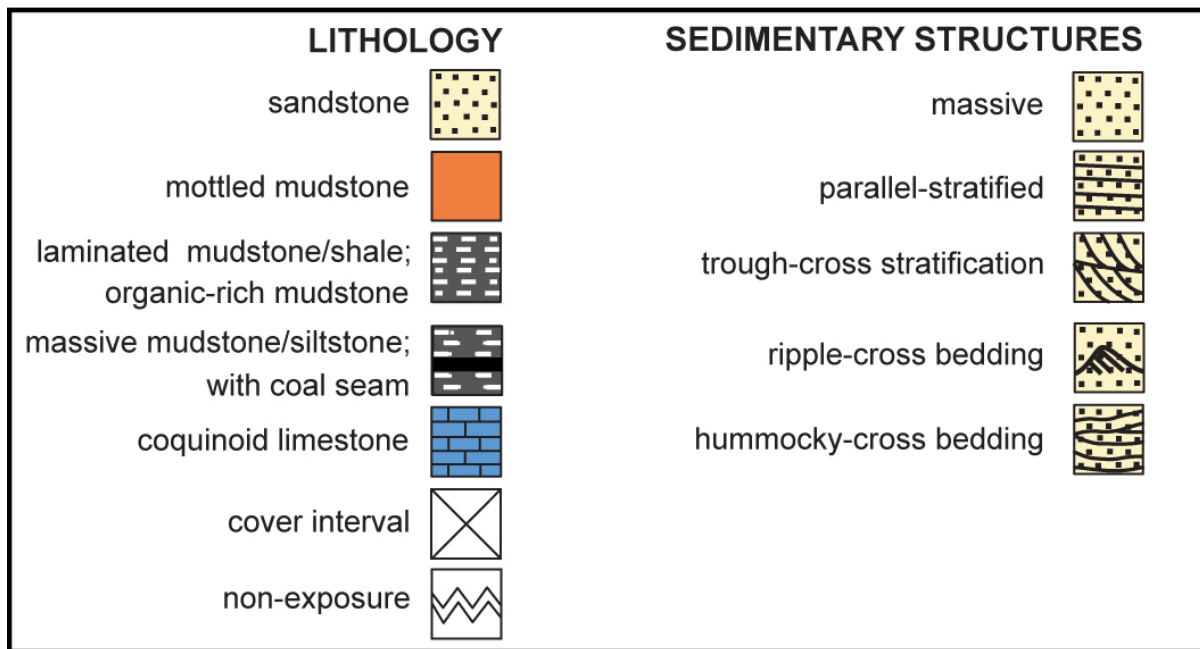


Supplementary Figure S2. Detailed stratigraphic log showing the localities in the Urumaco and San Gregorio Formations used herein.



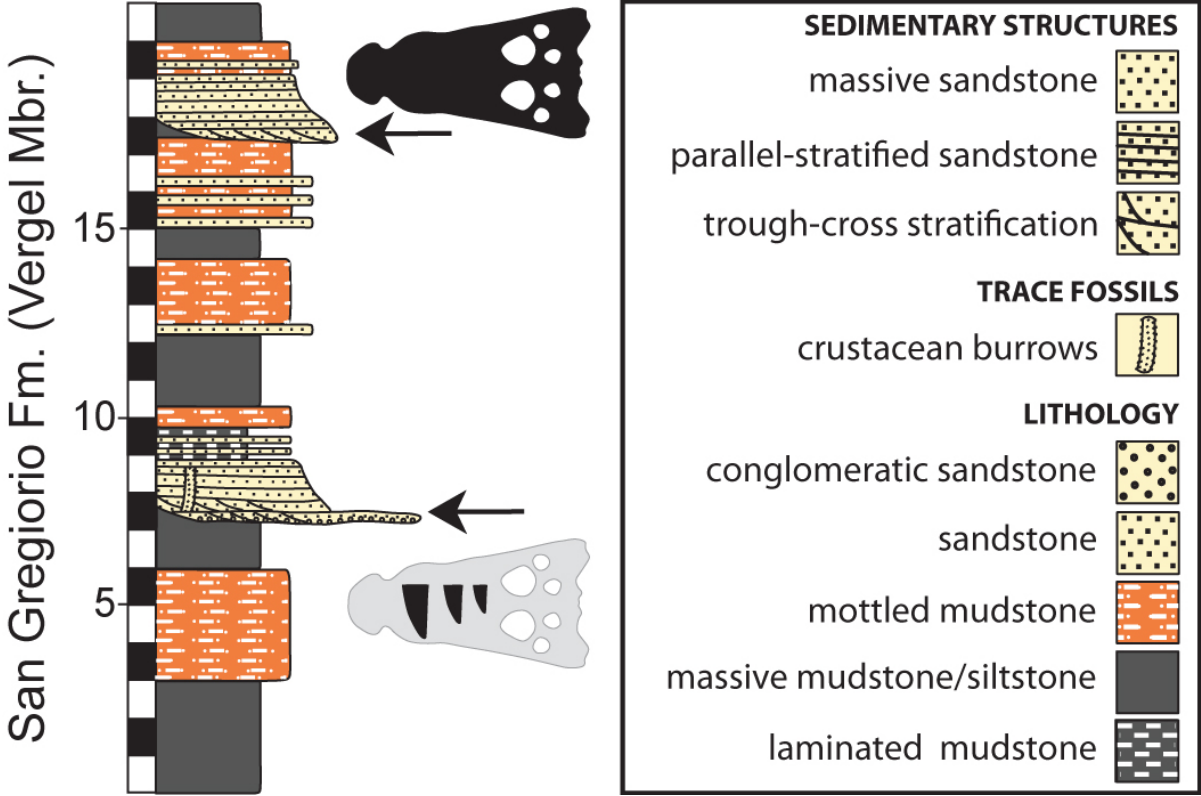
Modified from Quiroz and Jaramillo⁵⁴. Locality names and coordinates are compiled in Supplementary Table 1. For legend see Supplementary Figure 2.

Supplementary Figure S3. Legend accompanying stratigraphic log in Figure S2.



Modified from Quiroz and Jaramillo⁵⁴.

Supplementary Figure S4. Detailed stratigraphic log of the Vergel Member of the San Gregorio Formation and its accompanying legend.



Note that the horizons where the holotype (black skull outline, adapted from Brochu⁵⁵) and referred material (teeth in grey skull outline) were found in, are marked by black arrows.

Supplementary Figure S5. Series of isolated teeth from the early Pliocene Vergel Member of the San Gregorio Formation.



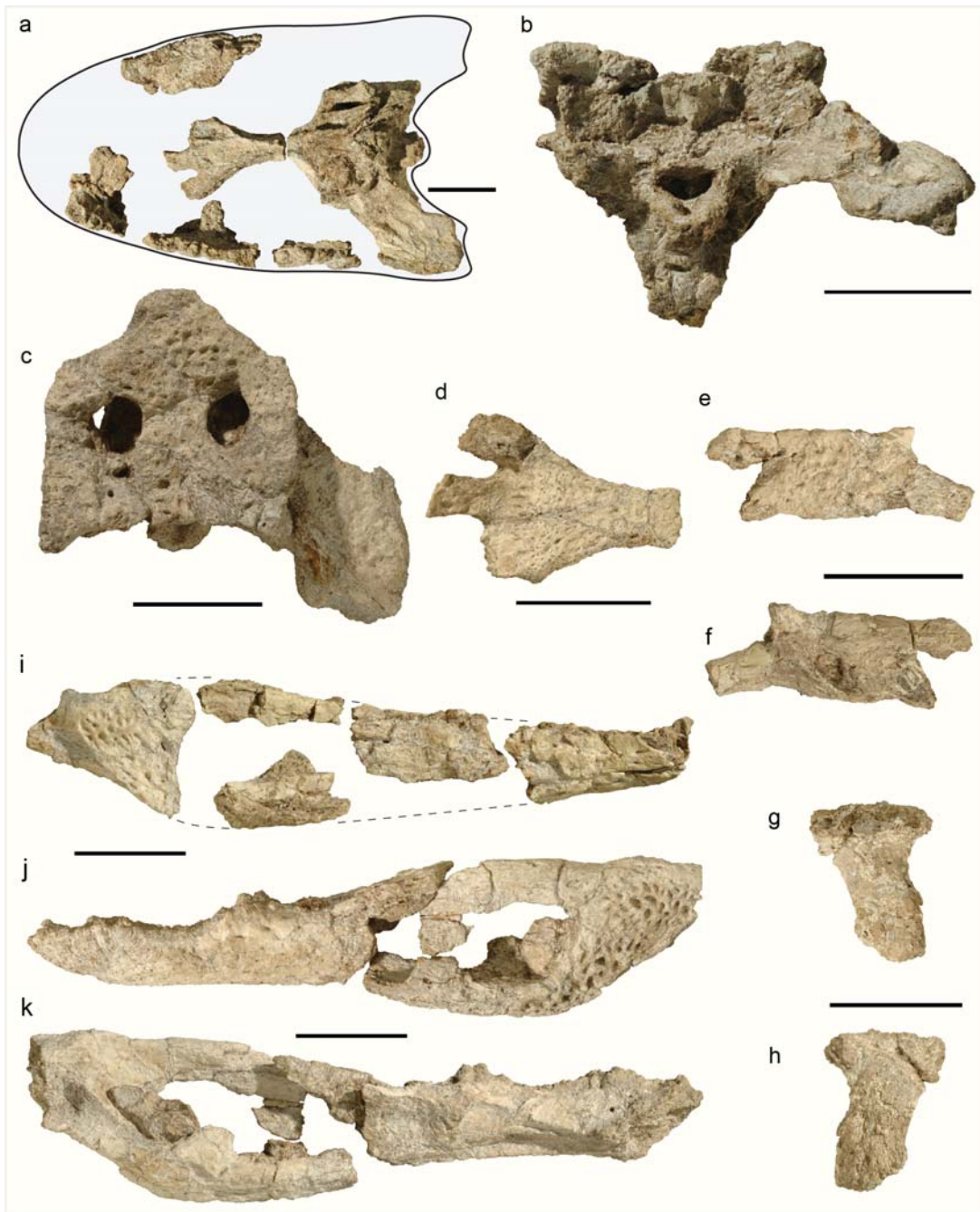
The specimens (AMU-CURS-302) were collected 1 km from the holotype ($11^{\circ} 17' 56.4''$ N, $70^{\circ} 13' 52.8''$ W) of *Crocodylus falconensis* sp. nov. Scale bar = 1.0 cm.

Supplementary Figure S6. Holotype skull AMU-CURS-300 of *Crocodylus falconensis* sp. nov.



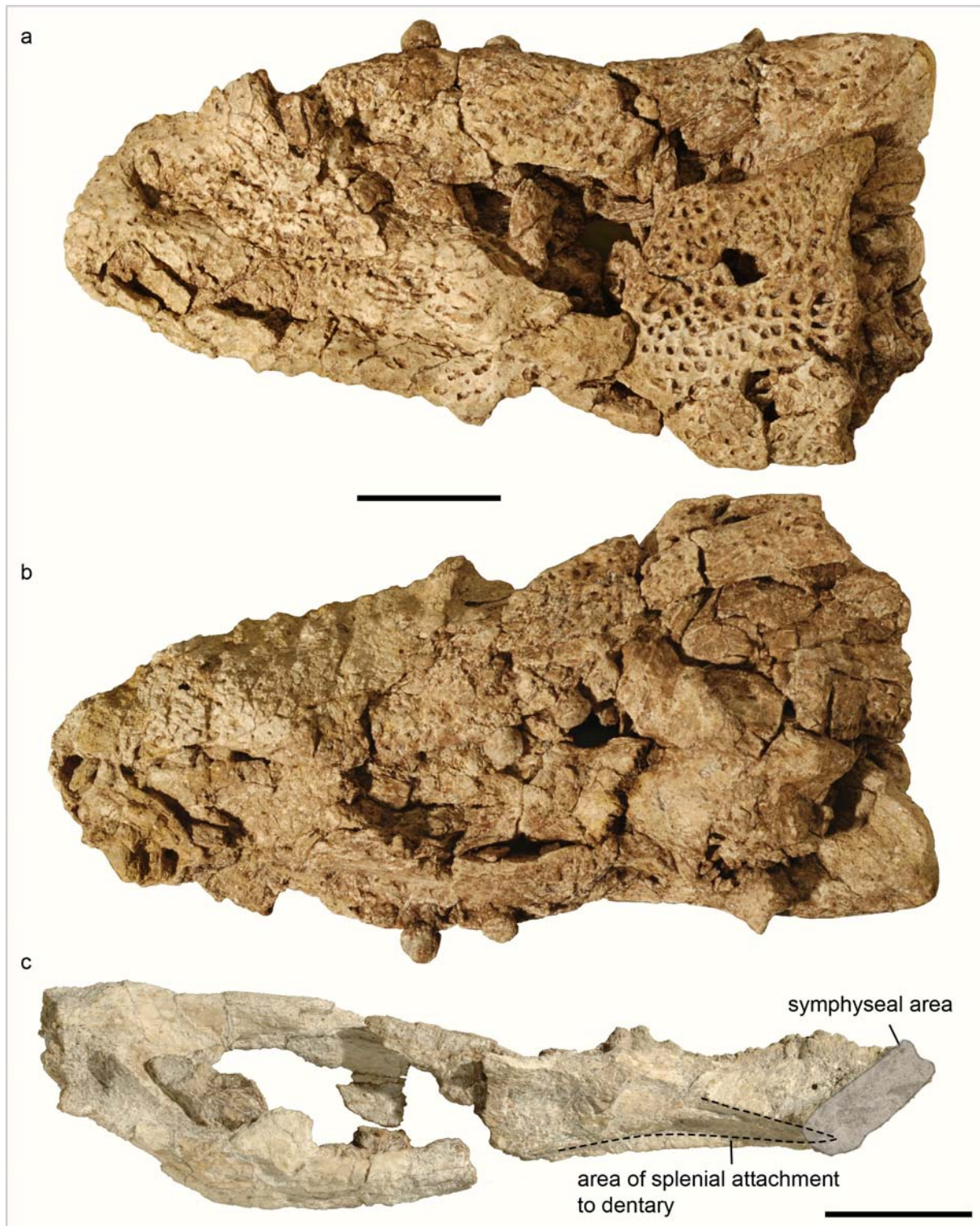
(a) Rostral view of skull. **(b)** Left lateral view of rostrum. **(c)** Occipital view of skull. Note that even though the skull is damaged, the ventral extension of the supraoccipital (so) is visible, reaching or almost reaching the foramen magnum (fm). Scale bars = 5.0 cm.

Supplementary Figure S7. Paratype material AMU-CURS-224 of *Globidentosuchus brachyrostris* gen. et sp. nov.



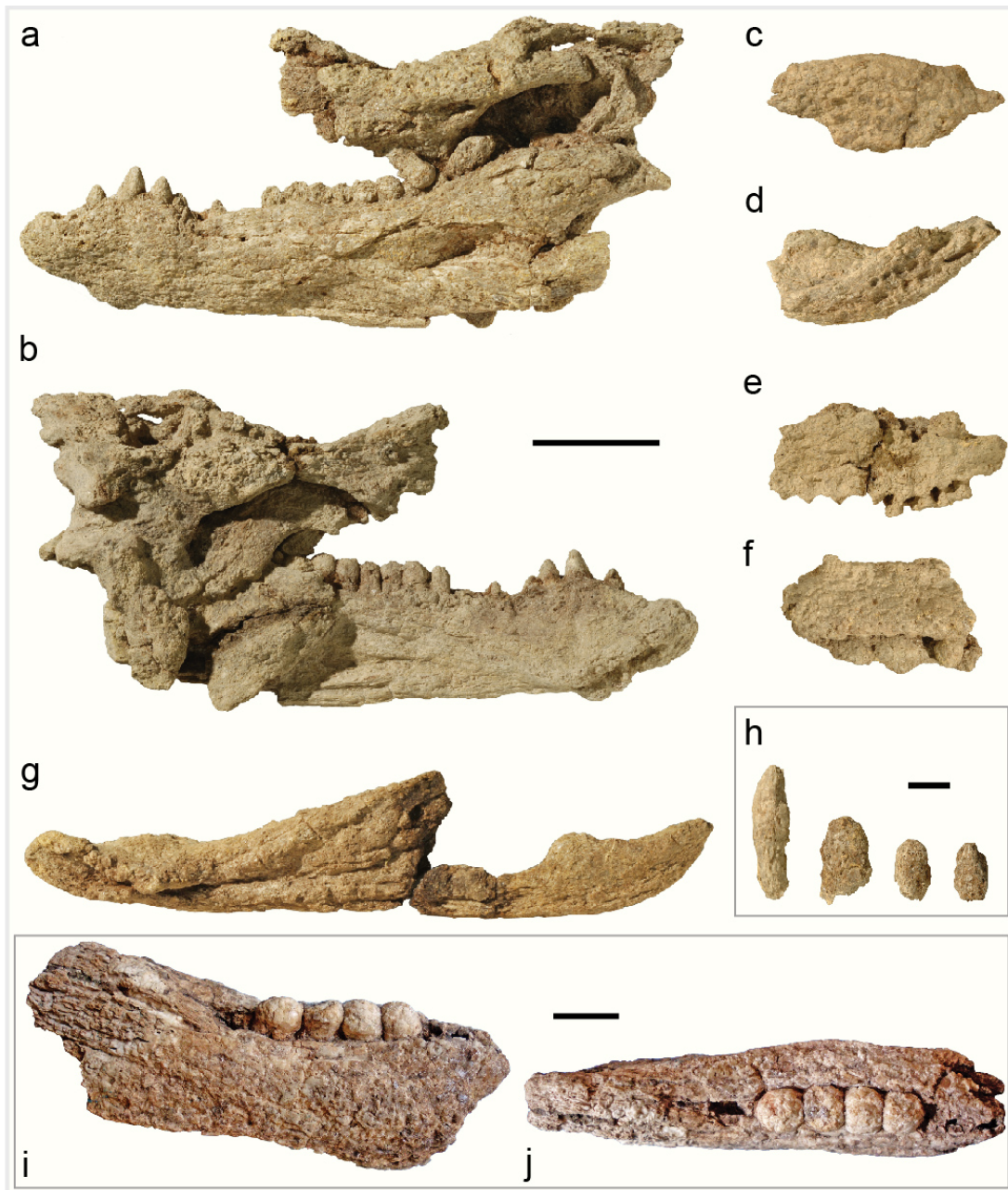
(a) Skull table/braincase, frontals and tooth-bearing elements and their assumed position in palatal view. (b) Skull table and braincase in occipital view. (c) Skull table and braincase in dorsal view. (d) Frontals in dorsal view. (e) Left jugal in lateral view. (f) Left jugal in medial view. (g) Left ectopterygoid in lateral view. (h) Left ectopterygoid in medial view. (i) Assembled right mandible in lateral view. (j) Assembled left mandible in lateral view. (k) Assembled left mandible in medial view. Scale bars = 5.0 cm.

Supplementary Figure S8. Selected holotype and paratype material of *Globidentosuchus brachyrostris* gen. et sp. nov.



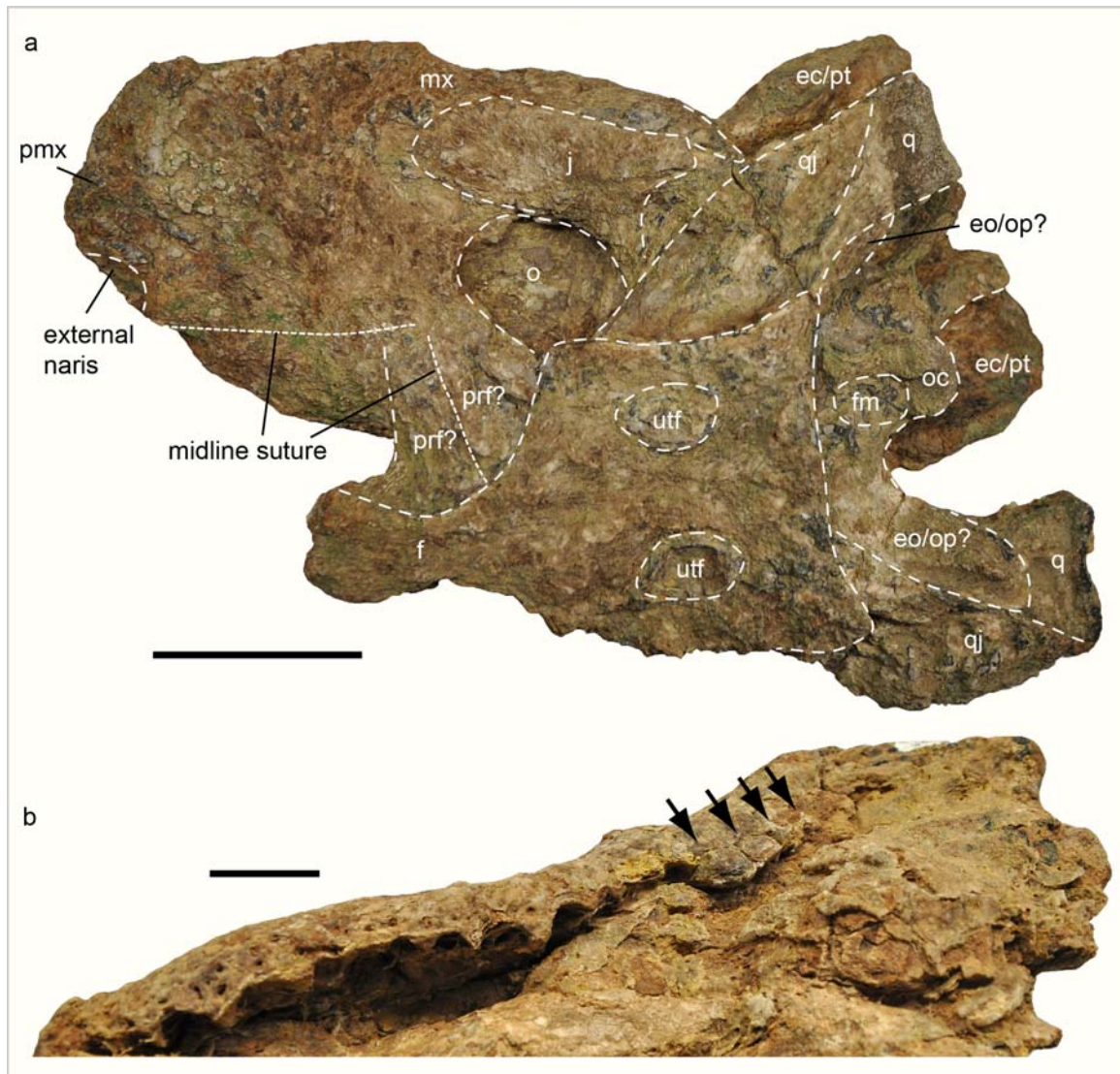
(a) Holotype skull (AMU-CURS-222, not mirror-imaged) in dorsal view. **(b)** Holotype skull in ventral view. **(c)** Left mandible of paratype (AMU-CURS-224) in which the extension of the splenial scar and the symphyseal area is indicated (compare to Supplementary Figure S7k). Scale bars = 5.0 cm.

Supplementary Figure S9. Referred material of *Globidentosuchus brachyrostris* gen. et sp. nov.



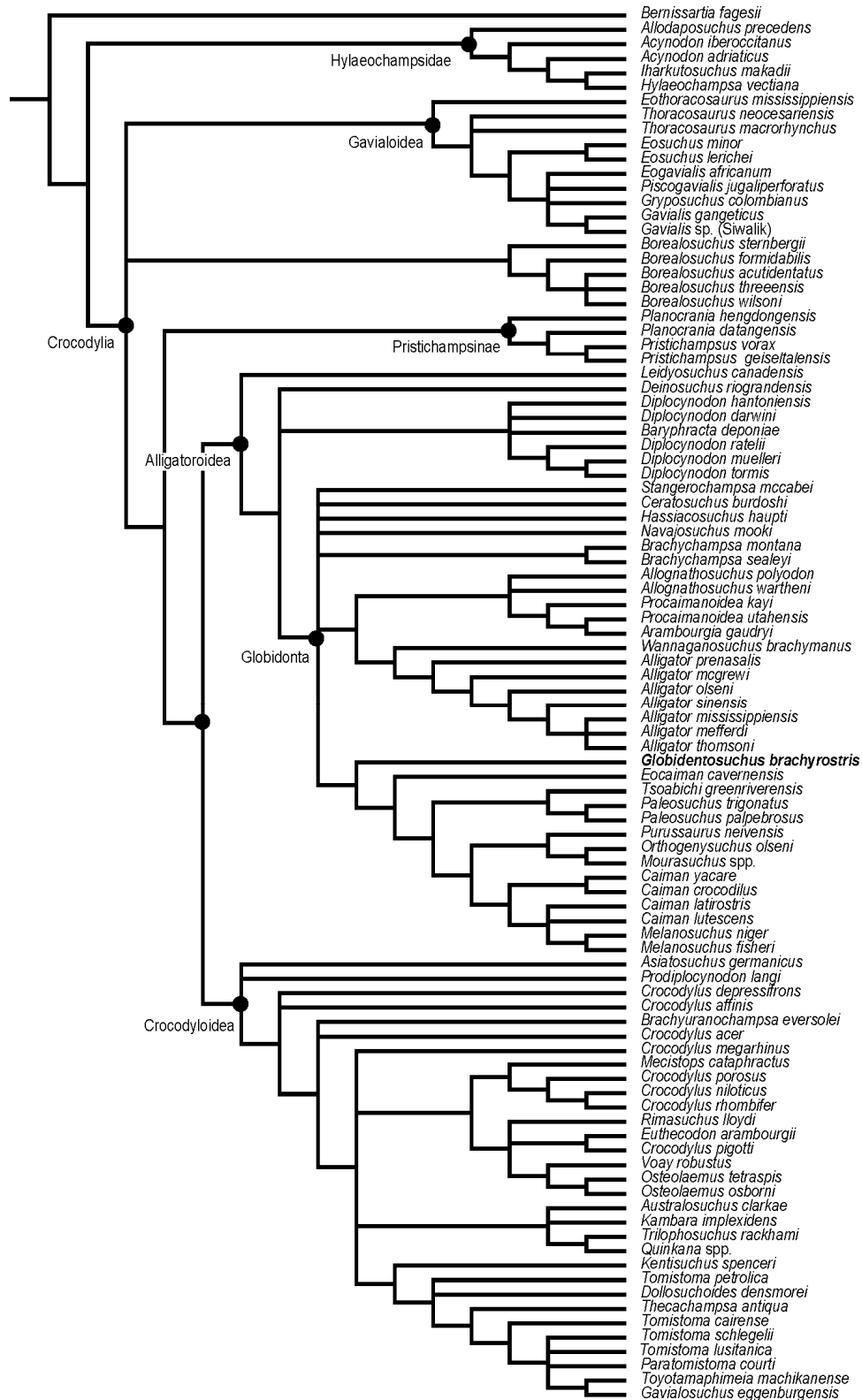
(a-h) Associated fragmentary cranial and mandibular remains (AMU-CURS-223). **(i, j)** Posterior part of right mandible showing four bulbous crushing teeth (AMU-CURS-301) in **(i)** lateral and **(j)** dorsal view. Part of skull roof and anterior part of left mandible in **(a)** lateral view and **(b)** medial view. **(c)** Left surangular in lateral view. **(d)** Left angular in lateral view. **(e)** Maxillary fragment showing alveoli in palatal view. **(f)** Maxillary fragment with bulbous tooth in lateral view. **(g)** Assembled right mandible fragment in medial view. **(h)** Series of teeth associated with the cranial remains. Scale bars = 5.0 cm in **(a-f)**, 1.0 cm in **(h)** and 2.0 cm in **(i, j)**.

Supplementary Figure S10. Referred material of *Globidentosuchus brachyrostris* gen. et sp. nov.



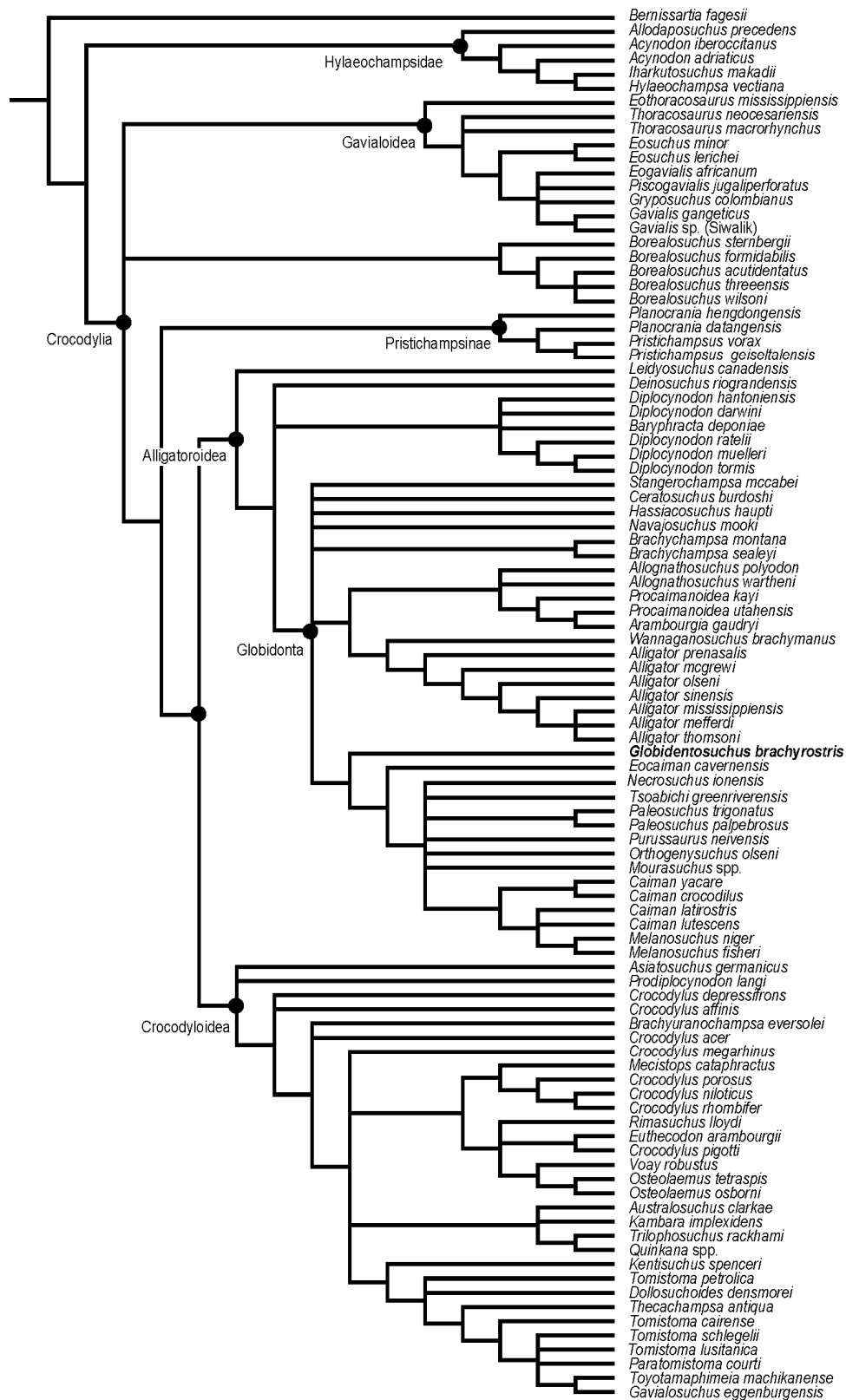
(a) Distorted skull (AMU-CURS-383) in dorsal view. Note that size of specimen is comparable to paratype specimen AMU-CURS 224 (based on skull table proportions). The rostrum is dislocated from the skull table and most of the tip of the snout and left side of rostrum has been folded and displaced ventrally. Due to strong weathering of the skull, most sutures are not traceable. **(b)** Left side of skull in oblique ventral view. The lateral walls of 13 alveoli of the anterior part of the left maxilla (maybe including also posterior end of premaxilla?) are visible. In the posterior part of the maxilla four closely spaced crushing teeth are still partly preserved (black arrows). Abbreviations: eo/op: exoccipital/opisthotic; f, frontal; fm, foramen magnum; j, jugal; mx, maxilla; o, orbit; oc, occipital condyle; pmx, premaxilla; prf, prefrontal; ec/pt, ectopterygoid and pterygoid; q, quadrate; qj, quadratojugal. Scale bars = 5.0 cm in **(a)** and 2.0 cm in **(b)**.

Supplementary Figure S11. Phylogenetic analysis including the new caimanine taxon.



Strict consensus tree of 20160 most parsimonious trees (tree length=650 steps) recovered by TNT analysis. The new taxon is marked in bold.

Supplementary Figure S12. Phylogenetic analysis including the new caimanine taxon and *Necrosuchus ionensis*.



Strict consensus tree of 24100 most parsimonious trees (tree length=650 steps) recovered by TNT analysis. The new taxon is marked in bold. Note loss of resolution within Caimaninae.

Supplementary Table S1. Locality coordinates.

Socorro Formation localities

Quebrada Honda (Llano Largo)	11° 11' 35.00" N; 70° 10' 49.00" W
Quebrada Honda (Cerro Maniaero)	11° 11' 00.90" N; 70° 09' 44.00" W
Quebrada Honda (Cerro Alto)	11° 12' 30.00" N; 70° 08' 12.00" W

Urumaco Formation localities

Sur Quebrada Bejucal (1)	11° 11' 18.46" N; 70° 15' 03.00" W
Puente Río Urumaco (2)	11° 12' 24.66" N; 70° 14' 59.27" W
Playa Larga (2)	11° 10' 58.00" N; 70° 20' 50.00" W
Domo de Agua Blanca (3)	11° 13' 25.00" N; 70° 14' 50.00" W
El Hatillo (4)	11° 14' 34.00" N; 70° 14' 20.00" W
El Mamón (5)	11° 13' 60.00" N; 70° 16' 06.00" W
El Picache (6)	11° 14' 25.00" N; 70° 13' 27.00" W
Noroeste (NW) San Rafael (6)	11° 14' 52.00" N; 70° 14' 06.00" W
Corralito (7)	11° 14' 40.00" N; 70° 16' 26.00" W
Tío Gregorio (7)	11° 14' 33.13" N; 70° 18' 38.00" W

San Gregorio Formation localities

Norte Casa Chiguaje (8)	11° 17' 52.00" N; 70° 14' 07.80" W
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Numbers in brackets behind location names correspond to the number system used for the study (see locality numbers in Supplementary Figure 2). In the case of Puente Río Urumaco/Playa Larga, El Picache/ Noroeste (NW) San Rafael and Tío Gregorio/Corralito, the localities have been combined under numbers (2), (6) and (7) respectively, because of their close proximity in the stratigraphic column. Coordinates of Urumaco town for reference: 11° 17' 53.9" N, 70° 14' 33.7" W.

Supplementary Table S2. List of fossil material examined.

Formation/Locality	Specimen Number	Taxon	Material present
Socorro Formation (pooled localities)			
	AMU-CURS-031	<i>Purussaurus</i> sp.	Right mandible
	AMU-CURS-034	?cf. <i>Thecachampsa</i> sp. 1	Cranium and rostrum
	AMU-CURS-095	<i>Mourasuchus</i> sp.	Partial rostrum
	AMU-CURS-141	<i>Mourasuchus</i> sp.	Mandible
	AMU-CURS-151	<i>Caiman</i> sp.	Cranium
	AMU-CURS-433	<i>Ikanogavialis gameroi</i>	Rostrum
Urumaco Formation			
Sur Quebrada Bejucal (1)			
	AMU-CURS-018	<i>Caiman</i> sp.	Mandible
	AMU-CURS-020	<i>Purussaurus</i> sp.	Cranial and postcranial remains
	AMU-CURS- unnumbered	<i>Mourasuchus</i> sp.	Partial cranial remains
Puente Río Urumaco/ Playa Larga (2)			
	AMU-CURS-001	<i>Hesperogavialis cruxenti</i>	Cranium and rostrum
	AMU-CURS-113	<i>Caiman</i> sp.	Cranium
	AMU-CURS-217	<i>Melanosuchus fisheri</i>	Cranium
	AMU-CURS-218	<i>Mourasuchus nativus</i>	Cranium
	MCN-URU-2002- unnumbered	<i>Ikanogavialis gameroi</i>	Cranium and rostrum
Domo de Agua Blanca (3)			
	AMU-CURS-012	?cf. <i>Thecachampsa</i> sp. 2	Cranium and mandible
	AMU-CURS-132	<i>Hesperogavialis cruxenti</i>	Rostrum
	AMU-CURS-301	<i>Globidentosuchus brachyrostris</i> (referred material)	Posterior part of right mandible with four crushing teeth
	AMU-CURS-450	<i>Globidentosuchus brachyrostris</i> (referred material)	partial mandibular remains
El Hatillo (4)			
	AMU-CURS-134	<i>Gryposuchus croizati</i>	Rostrum
	AMU-CURS-135	<i>Purussaurus mirandai</i> (paratype)	Cranium with associated mandibles
	AMU-CURS-234	<i>Melanosuchus fisheri</i>	Cranium and mandibles (also postcranium)
	AMU-CURS- unnumbered	<i>Charactosuchus mendesi</i>	partial cranial remains

El Mamón (5)	AMU-CURS- unnumbered	<i>Mourasuchus arendsi</i>	partial cranial remains
	AMU-CURS-212	<i>Mourasuchus nativus</i>	Cranial fragment
	AMU-CURS-429	<i>Caiman brevirostris</i>	Cranial/mandibular fragments
	UNEFM-CIAPP-319	<i>Hesperogavialis cruxenti</i>	Rostrum
El Picache (6)	UNEFM-CIAPP-320	<i>Hesperogavialis cruxenti</i> (holotype)	Partial cranium and rostrum
	AMU-CURS-222	<i>Globidentosuchus brachyrostris</i> (holotype)	Cranium and mandibles
	AMU-CURS-223	<i>Globidentosuchus brachyrostris</i> (referred material)	Associated fragmentary cranial and mandibular remains
	AMU-CURS-224	<i>Globidentosuchus brachyrostris</i> (paratype)	Fragmentary cranial remains associated with mandibles
NW San Rafael (6)	AMU-CURS- unnumbered	<i>Purussaurus</i> sp.	Cranium and mandibular remains
	MCN- unnumbered	<i>Caiman brevirostris</i>	Cranium with associated mandibles
	AMU-CURS-383	<i>Globidentosuchus brachyrostris</i> (referred material)	Cranium and mandibles
	AMU-CURS-384	<i>Purussaurus</i> sp.	Left mandible
Corralito (7)	AMU-CURS-390	<i>Mourasuchus</i> sp.	Mandibular fragment
	AMU-CURS-395	<i>Mourasuchus</i> sp.	Cranial fragments
	AMU-CURS-396	<i>Mourasuchus</i> sp.	Cranial fragments
	AMU-CURS-399	<i>Gryposuchus</i> sp.	Cranial fragments
	AMU-CURS-049	<i>Caiman lutescens</i>	Partial rostrum
	AMU-CURS-090	<i>Caiman</i> sp.	Cranium and rostrum
Tío Gregorio (7)	AMU-CURS- unnumbered	<i>Purussaurus</i> sp.	Cranial remains
	MCN-243	<i>Melanosuchus fisheri</i> (holotype)	Cranium and rostrum
	UNEFM-CIAPP-617	<i>Gryposuchus jessei</i>	Rostrum
	UNEFM-CIAPP-1297	<i>Mourasuchus arendsi</i> (holotype)	Skull and mandible
	UNEFM-CIAAP-1440	<i>Gryposuchus croizati</i> (paratype)	Mandible
	AMU-CURS-057	<i>Purussaurus</i> sp.	Mandible
AMU-CURS-058	<i>Gryposuchus croizati</i> (paratype)	Cranium and rostrum and postcranial material	
AMU-CURS-073	<i>Mourasuchus</i> sp.	Right mandible and incomplete rostrum and	

AMU-CURS-105	<i>Caiman brevirostris</i>	postcranial material
AMU-CURS-106	<i>Caiman brevirostris</i>	Cranium
AMU-CURS- unnumbered	<i>Purussaurus</i> sp.	Mandible
MCN-URU-2002-143	<i>Ikanogavialis gameroi</i>	partial cranial remains
UCV-VF-1165	<i>Ikanogavialis gameroi</i> (holotype)	Cranium and rostrum
UCV-VF-1166	<i>Ikanogavialis gameroi</i> (holotype)	Cranium
		Mandible

San Gregorio Formation locality

Norte Casa Chiguaje (8)

AMU-CURS-300	<i>Crocodylus falconensis</i> (holotype)	Almost complete skull with mandibles
AMU-CURS-302	<i>Crocodylia</i> indet.	Series of isolated teeth

Abbreviations: UNEFM-CIAAP, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; MCN, Museo de Ciencias Naturales de Caracas, Venezuela; AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; UCV, Universidad Central de Venezuela, Maracay, Venezuela.

Supplementary Table S3. Length estimations I.

New <i>Crocodylus</i> species	DCL = 59.0 [cm], SL = 42.5 [cm], ODCL = 165.0 [mm]	
<i>Gavialis gangeticus</i> formula	(modif. from Sereno et al. ⁵⁶)	
TL = (7.4 * DCL) – 69.369	TL = (7.4 * 59.0) – 69.369	TL = 367.23
<i>Crocodylus porosus</i> formula	(modif. from Sereno et al. ⁵⁶)	
TL = (7.717 * DCL) – 20.224	TL = (7.717 * 59.0) – 20.224	TL = 435.08
<i>Crocodylus moreletii</i> formula	(modif. from Platt et al. ⁵⁷)	
TL = (10.48 * SL) + 6.20	TL = (10.48 * 42.5) + 6.20	TL = 451.60
<i>Crocodylus acutus</i> formula	(modif. from Platt et al. ⁵⁸)	
TL = (9.01 * SL) + 10.80	TL = (9.01 * 42.5) + 10.80	TL = 393.73
<i>Alligator mississippiensis</i> formula	(modif. from Hurlburt et al. ⁵⁹)	
Log TL = (log ODCL * 1.259) + 0.793	Log TL = (log 165.0 * 1.259) + 0.793	TL = 384.43
Log TL = (log DCL * 0.970) + 0.954	Log TL = (log 590.0 * 0.970) + 0.954	TL = 438.25
		Mean = 411.72
New caimanine species	DCL = 29.0 [cm], SL = 14.0 [cm] ODCL = 150.0 [mm]	
<i>Gavialis gangeticus</i> formula	(modif. from Sereno et al. ⁵⁶)	
TL = (7.4 * DCL) – 69.369	TL = (7.4 * 29.0) – 69.369	TL = 145.23
<i>Crocodylus porosus</i> formula	(modif. from Sereno et al. ⁵⁶)	
TL = (7.717 * DCL) – 20.224	TL = (7.717 * 29.0) – 20.224	TL = 203.57
<i>Crocodylus moreletii</i> formula	(modif. from Platt et al. ⁵⁷)	
TL = (10.48 * SL) + 6.20	TL = (10.48 * 14.0) + 6.20	TL = 152.92
<i>Crocodylus acutus</i> formula	(modif. from Platt et al. ⁵⁸)	
TL = (9.01 * SL) + 10.80	TL = (9.01 * 14.0) + 10.80	TL = 136.94
<i>Alligator mississippiensis</i> formula	(modif. from Hurlburt et al. ⁵⁹)	
Log TL = (log ODCL * 1.259) + 0.793	Log TL = (log 150.0 * 1.259) + 0.793	[TL = 340.96*]
Log TL = (log DCL * 0.970) + 0.954	Log TL = (log 290.0 * 0.970) + 0.954	TL = 220.05
		Mean = 171.74 [199.95*]

Total body length (TL) estimations in [cm] using dorsal cranial length (DCL), snout length (SL) and orbito-cranial length (ODCL). Note that for the *Alligator*-based formula⁵⁹, values have to be entered in millimeters. Results are rounded to the nearest [mm].

Supplementary Table S4. Length estimations II.

New <i>Crocodylus</i> species	DCL = 59.0, SL = 42.5	
<i>Crocodylus porosus</i> formula	(modif. from Webb and Messel ⁶⁰)	
SVL = (3.60 * DCL) - 4.30	SVL = (3.60 * 59.0) - 4.30	SVL = 208.10
<i>Crocodylus moreletii</i> formula	(modif. from Platt et al. ⁵⁷)	
SVL = (5.32 * SL) + 1.61	SVL = (5.32 * 42.5) + 1.61	SVL = 227.71
<i>Crocodylus acutus</i> formula	(modif. from Platt et al. ⁵⁸)	
SVL = (4.68 * SL) + 4.57	SVL = (4.68 * 42.5) + 4.57	SVL = 203.47
		Mean = 213.09
New caimanine species	DCL = 29.0, SL = 14.0	
<i>Crocodylus porosus</i> formula	(modif. from Webb and Messel ⁶⁰)	
SVL = (3.60 * DCL) - 4.30	SVL = (3.60 * 29.0) - 4.30	SVL = 100.10
<i>Crocodylus moreletii</i> formula	(modif. from Platt et al. ⁵⁷)	
SVL = (5.32 * SL) + 1.61	SVL = (5.32 * 14.0) + 1.61	SVL = 76.09
<i>Crocodylus acutus</i> formula	(modif. from Platt et al. ⁵⁸)	
SVL = (4.68 * SL) + 4.57	SVL = (4.68 * 14.0) + 4.57	SVL = 70.09
		Mean = 82.09

Snout-vent length (SVL) estimations in [cm] using dorsal cranial length (CL) and snout length (SL); results are rounded to the nearest [mm].

Supplementary Table S5. Mass estimations.

New <i>Crocodylus</i> species	mean SVL = 213.09, mean TL= 411.72	
<i>Crocodylus porosus</i> formula	(modif. from Webb and Messel ⁶⁰)	
log BM = (3.2613 * log SVL) - 2.0894	log BM = (3.2613 * log 213.09) - 2.0894	BM = 319.70
<i>Crocodylus moreletii</i> formula	(modif. from Platt et al. ⁵⁷)	
ln BM = (ln TL - 2.05) / 0.32	ln BM = (ln 411.72 - 2.05) / 0.32	BM = 244.58
ln BM = (ln SVL - 1.25) / 0.33	ln BM = (ln 213.09 - 1.25) / 0.33	BM = 257.75
<i>Crocodylus acutus</i> formula	(modif. from Platt et al. ⁵⁸)	
ln BM = (ln TL - 2.06) / 0.31	ln BM = (ln 411.72 - 2.06) / 0.31	BM = 353.38
ln BM = (ln SVL - 1.27) / 0.32	ln BM = (ln 213.09 - 1.27) / 0.32	BM = 357.40
		Mean = 306.56
New caimanine species	mean SVL = 82.09, mean TL = 171.74 [mean TL = 199.95*]	
<i>Crocodylus porosus</i> formula	(modif. from Webb and Messel ⁶⁰)	
log BM = (3.2613 * log SVL) - 2.0894	log BM = (3.2613 * log 82.09) - 2.0894	BM = 14.25
<i>Crocodylus moreletii</i> formula	(modif. from Platt et al. ⁵⁷)	
ln BM = (ln TL - 2.05) / 0.32	ln BM = (ln 171.74 - 2.05) / 0.32	BM = 15.91 [25.59*]
ln BM = (ln SVL - 1.25) / 0.33	ln BM = (ln 82.09 - 1.25) / 0.33	BM = 14.32
<i>Crocodylus acutus</i> formula	(modif. from Platt et al. ⁵⁸)	
ln BM = (ln TL - 2.06) / 0.31	ln BM = (ln 171.74 - 2.06) / 0.31	BM = 21.05 [34.39*]
ln BM = (ln SVL - 1.27) / 0.32	ln BM = (ln 82.09 - 1.27) / 0.32	BM = 18.14
		Mean = 16.73 [21.34*]

Body Mass (BM) estimations in [kg] using total length (TL) and snout-vent length (SVL) in [cm]; results are rounded to the nearest [mm].

Supplementary Notes

Supplementary Note 1: Stratigraphic and Palaeoenvironmental Context of New Taxa New *Crocodylus* species

The new *Crocodylus* species comes from outcrops that have only recently been discovered to be fossiliferous and described, so we provide here a context for future reference in explorations, or in stratigraphical, taphonomical or palaeoecological studies. The San Gregorio Formation is the upper-most part of the large Urumaco sequence⁵⁴. The contact between the Codore and San Gregorio Formations is transitional near the Urumaco River area, and the age is early Pliocene. It is exposed in the north-central area of the Falcon State coastal plain, 10 km north of the Urumaco Town. The fossiliferous outcrops are of the lower part of the Vergel Member of the San Gregorio Formation (Supplementary Figure 4), consisting of brown to dark gray, massive mudstone and mottled muddy sandstone, interbedded with massive to cross-bedded conglomeratic sandstone with lenticular geometry and erosive base, grading to parallel-stratified, fine to medium grained sandstone. This succession represents flood plain deposits and associated crevasse splays, with low sinuosity ephemeral channels mostly filled during river flooding, in an alluvial fan setting. The lateral outflow of the channels during inundate events form a sub-aerial savannas, such as, wetlands. The results of these inundate soils are palaeosols over sandy deposits, characterized by the presence of a terrestrial and semi-aquatic fossil assemblage, including mammals⁶¹. The faunal assemblage represents the last testimonies of the hydrographic and climate change around the Miocene/Pliocene boundary.

New caimanine species

The type and most of the referred material of the new caimanine come from the El Picache locality, Upper Member of the Urumaco Formation, whereas the isolated mandible (AMU-CURS-223) was recovered from the Middle Member of the Urumaco Formation. The sedimentary environments of the Urumaco Formation have been described in Quiroz and Jaramillo⁵⁴ (see stratigraphic logs in Fig. 1 and Supplementary Figures 2-4). According to the authors, both the Middle and Upper Member are composed of siliciclastic sequences and intercalated limestone beds deposited in a prograding delta and strand plain environment.

Supplementary Note 2: Major Expeditions to the Fossiliferous Outcrops around Urumaco

Expeditions to the Urumaco region were conducted by Royo y Gómez from Universidad Central de Venezuela in Caracas (1958-1959), C. González de Juana at Universidad Central de Venezuela together with Bryan Patterson from Harvard University (1972), Jean Bocquentin-Villanueva (1982 and following years in the 1980s) and by Orangel Aguilera (1992-2012) at the Universidad Francisco de Miranda in Coro, R. Sánchez at Alcaldía de Urumaco and Smithsonian Tropical Research Institute (1990-2012), M. Sánchez-Villagra from University of Tübingen (2002-2004), The Natural History Museum in London (2004-2006), and from University of Zürich (2007-2012).

Supplementary Note 3: Phylogenetic Analyses

New *Crocodylus* species

The dataset for the testing the position of the new *Crocodylus* species comprised 32 characters in total (coding 29 characters that vary inside Crocodylinae⁶² plus two new characters), 14 ingroup taxa and the outgroup consisting of the basal crocodyline “*Crocodylus*” *megarhinus* and the three osteolaemines “*Crocodylus*” *pigotti*, *Rimasuchus lloydi* and *Voay robustus*.

Character description

1. Ventral tubercle of proatlas more than one-half (0) or no more than one half (1) the width of the dorsal crest. (Brochu et al.⁶², character 1)
2. Fused proatlas boomerang-shaped (0), strap-shaped (1), or massive and block-shaped (2). (Brochu et al.⁶², character 2)
3. Anterior half of axis neural spine oriented horizontally (0) or slopes anteriorly (1). (Brochu et al.⁶², character 6)
4. Axis neural spine crested (0) or not crested (1). (Brochu et al.⁶², character 7)
5. Posterior half of axis neural spine wide (0) or narrow (1). (Brochu et al.⁶², character 8)
6. Hypapophyseal keels present on eleventh vertebra behind atlas (0), twelfth vertebra behind atlas (1), or tenth vertebra behind atlas (2). (Brochu et al.⁶², character 9)
7. Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1). (Brochu et al.⁶², character 10)
8. Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0) or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1). (Brochu et al.⁶², character 11)
9. Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1). (Brochu et al.⁶², character 14)
10. Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1). (Brochu et al.⁶², character 15)
11. Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation (“wasp-waisted;” 2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4). (Brochu et al.⁶², character 19)
12. Supraacetabular crest narrow (0) or broad (1). (Brochu et al.⁶², character 20)

13. Dentary symphysis extends to fourth or fifth alveolus (0) or sixth through eighth alveolus (1) or behind eighth alveolus (2.) (Brochu et al.⁶², character 28)
14. Angular-surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1). (Brochu et al.⁶², character 34)
15. Dorsal surface of rostrum curves smoothly (0) or bears medial dorsal boss (1). (Brochu et al.⁶², character 52)
16. Preorbital ridges absent or very modest (0) or very prominent (1) at maturity. (Brochu et al.⁶², character 53)
17. Surface of maxilla within narial canal imperforate (0) or with a linear array of pits (1.) (Brochu et al.⁶², character 55)
18. Anterior ectopterygoid process tapers to a point (0) or forked (1). (Brochu et al.⁶², character 63)
19. Palatine process generally broad anteriorly (0) or in form of thin wedge (1). (Brochu et al.⁶², character 65)
20. Palatine-pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra. (Brochu et al.⁶², character 67)
21. Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form “neck” surrounding aperture (2) or everted from flat surface to form “neck” surrounding aperture (3). (Brochu et al.⁶², character 69)
22. Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) or maxilla with posterior process between lacrimal and prefrontal (2). (Brochu et al.⁶², character 71)
23. Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra; quadrate participates in fenestra (1). (Brochu et al.⁶², character 80; adapted from Buscalioni et al.⁶³ according to Brochu et al.⁶⁴)
24. Posterolateral margin of squamosal horizontal or nearly so (0) or upturned to form a discrete “horn” (1.) (Brochu et al.⁶², character 86)
25. Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paraoccipital process. (Brochu et al.⁶², character 87)
26. Supraoccipital exposure on dorsal skull table small (0), absent (1), large (2), or large such that parietal is excluded from posterior edge of table (3). (Brochu et al.⁶², character 88)

27. Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1). (Brochu et al.⁶², character 89)
28. Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1). (Brochu et al.⁶², character 91; adapted from Norell⁶⁵ according to Brochu et al.⁶⁴)
29. Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal. (Brochu et al.⁶², character 96; adapted from Norell⁶⁶ according to Brochu et al.⁶⁴)
30. Posterior process of palatines with nearly parallel sides (0) or expands posteriorly (1). (This character was not used by Brochu et al.⁶², it is adapted, however, from character 2 of Norell⁶⁶ according to Brochu⁶⁷)
31. Posterior margin of skull roof concave (0) or with a developed medial convexity (1) late in ontogeny. (NEW)
32. Anteriormost width of the intersuborbital bar wider than (0) or as wide as (1) the posteriormost width. (NEW)

Character codings

Unknown or non-applicable characters were coded as question marks. Polymorphisms are noted in brackets.

<i>"Crocodylus" megarhinus</i>	????? ??0?? ??100 00001 02100 ?100? 00
<i>"Crocodylus" pigotti</i>	??00? ?0011 ??1?0 10111 1??01 0?100 11
<i>Rimasuchus lloydi</i>	????? ?????? ?????0 1?00? ?1101 0110? 00
<i>Voay robustus</i>	????? ?????? 11100 10001 10111 1?100 01
<i>Mecistops cataphractus</i>	10000 00011 20110 00011 00100 01100 10
<i>Crocodylus palaeindicus</i>	????? ?????? ??010 00100 00100 1011? 1?
<i>Crocodylus porosus</i>	11001 10101 20010 11(01)01 00100 01111 01
<i>Crocodylus palustris</i>	10001 01111 21010 11(01)01 00100 01111 01
<i>Crocodylus siamensis</i>	11111 00010 20010 11(01)01 00110 01111 00
<i>Crocodylus johnstoni</i>	11001 10101 20?10 11(01)11 00100 01110 00
<i>Crocodylus mindorensis</i>	11001 10101 20010 11(01)01 00100 01111 10
<i>Crocodylus novaeguineae</i>	11001 10101 20010 11(01)01 00000 01010 00
<i>Crocodylus niloticus</i>	10101 00111 20010 01(01)01 01100 01110 00
<i>Crocodylus falconensis</i> sp. nov.	????? ?????? ??011 01000 ?1?00 ?????0 00
<i>Crocodylus acutus</i>	00101 00111 20011 01(01)00 21100 01111 11
<i>Crocodylus intermedius</i>	00101 00111 20111 01(01)00 20100 01111 11

<i>Crocodylus moreletii</i>	00101 00111 20011 01(01)00 21100 01111 10
<i>Crocodylus rhombifer</i>	00101 00111 10011 01(01)00 21110 01111 10

Apomorphy List

The apomorphy list was constructed based on the tree shown in Figure 5a. ACCTRAN optimization in bold and DELTRAN optimization underlined.

Osteolaeminae: 12(1), 16(1), 22(1), 26(1)

Rimasuchus lloydi: 23(1)

“*Crocodylus*” *pigotti* + *Voay robustus*: 21(1), 32(1)

“*C*”. *pigotti*: 18(1), 19(1), 30(1)

Voay robustus: 12(1), 24(1), 26(1)

Mecistops cataphractus + *Crocodylus*: 11(2), 14(1), 30(1)

Mecistops cataphractus: 19(1), 30(1)

C. palaeindicus + Crown *Crocodylus*: 5(1), 8(1), 13(0), 29(1)

C. palaeindicus: 18(1), 20(0), 26(1), 26(0), 30(1)

Crown *Crocodylus*: 5(1), 8(1), 17(1), 30(0)

Indopacific *Crocodylus*: 16(1), 31(1)

C. palustris: 7(1), 12(1), 30(1), 32(1)

C. siamensis + *C. porosus* + *C. mindorensis* + *C. johnstoni* + *C. novaeguineae*: 2(1)

C. siamensis: 3(1), 4(1), 8(0), 10(0), 24(1)

C. porosus + *C. mindorensis* + *C. johnstoni* + *C. novaeguineae*: 6(1), 9(0)

C. porosus: 32(1)

C. mindorensis: 30(1)

C. johnstoni + *C. novaeguineae*: 31(0)

C. johnstoni: 19(1)

C. novaeguineae: 23(0), 28(0)

C. niloticus + New World *Crocodylus*: 3(1), 22(1)

C. niloticus: no autapomorphies

New world *Crocodylus*: 1(0), 15(1), 20(0), 21(2)

C. falconensis: no autapomorphies

C. moreletii + *C. rhombifer* + *C. acutus* + *C. intermedius*: 1(0), 21(2), 30(1), 31(1)

C. moreletii: no autapomorphies

C. rhombifer: 11(1), 24(1)

C. acutus + *C. intermedius*: 32(1)

C. acutus: no autapomorphies

C. intermedius: 13(1), 22(0)

New caimanine species

The phylogenetic analysis including *Globidentosuchus brachyrostris* gen. et sp. nov. resulted in a total of 20160 most parsimonious trees (minimum length=650; Fig. 5b; Supplementary Figure S11). Note that character (97) for *Alligator thomsoni* (=althom in matrix file) in the original matrix of Brochu et al.⁶⁴ was incorrectly scored with "9" instead of "0" and character (156) was scored with (2) in *Piscogavialis jugaliperforatus* and *Gryposuchus colombianus*, although (0) or (1) should have been the only possible character states following the character description. Both taxa are scored with (1) herein based on personal observation of holotypes by one of us (DCF). The original score (0) for character (150) and (3) for character (158) in *Eocaiman cavernensis* (=eocai in matrix file) by Brochu et al.⁶⁴ were changed to (?), based on the poor preservation of that region of the skull in the holotype specimen.

The results of the TNT analysis could be verified by a second analysis using the heuristic search option in PAUP v. 4.0b10 for Microsoft Windows⁶⁸. For the latter, a setting of MaxTrees=15000 was enforced as previous tries with an open, step-wise automated increase of the number of trees retained led to a critical termination of the analysis. The statistics of this analysis were: tree length = 650; consistency index (CI) = 0.3477; homoplasy index (HI) = 0.6523; CI excluding uninformative characters = 0.3426; HI excluding uninformative characters = 0.6574; retention index (RI) = 0.8110; rescaled consistency index (RC) = 0.2820. The strict consensus of the first 1000 MPTs shows exactly the same topology and tree length (650 steps) as in the TNT analysis.

Re-running the analysis after incorporating *Necrosuchus ionensis*⁶⁹ in the matrix basically recovered the same results as the previous analysis (tree length remained at 650; total number of MPTs = 24100), but with less resolution among basal caimanines (see Supplementary Figure S12). The previous sister group relationship between *Tsoabichi* and *Paleosuchus* was not recovered in this second run and the tree configuration with the polytomy among caimanines resembles that of the strict consensus shown in figure 9B in Brochu⁷⁰. Following that previous work, we thus tentatively treat *Tsoabichi* as a caimanine herein as well.

Note that fundamental differences exist between the morphology-based matrices like the one from Brochu et al.⁶⁴ used herein and molecular analyses⁷¹⁻⁷⁴, especially pertaining to the hotly debated relationship between true and false gharials and crocodylines. However, assuming that tomistomines (the material tentatively assigned to *?Thecachampsa*) are included in the

Crocodylidae as suggested by anatomy and the palaeontological record⁶², as well as developmental data⁷⁵, it is possible to include the latter clade in the crocodylian fauna of Urumaco as well.

Character codings

The following coding based on and modified from the matrix of Brochu et al.⁶⁴ was used (unknown or non-applicable characters were coded as question marks; the coding of *Necrosuchus ionensis* follows Brochu⁶⁹):

Bernissartia fragesii

?????0??011102100?00?0?000??0000?100010??0010?000??????10?0?00?001?1????0
00?0?0000?00030?00????1000????1?0000?000??0100?0??000100?0?0?0?0?0010?0?00??
0????????000?0000?000

Allodaposuchus precedens

??00010?
000000123000000?100000??00000001010300011000101100??0100000001100010000??
??1?01?010001?000

Acynodon iberoccitanus

??10104101??????0??????0?0????00010
?000000106000000??00100??0000000101?00??20000?0100?110?0000??010100000?1??
??????1??0???010

Acynodon adriaticus

????1????????????01?100?1????????010?10????????01??????0??0??100?00??000
10?000?0?1060000?0????110????00?00011010000?1?11?0?0100??0??0??010?0?0010??
??????????1??01?0

Iharkutosuchus makadii

??10124????????110??00??10?1????0001
??0000011061000?0??0110????0000001001100001201001?100?1?0?00?0??12??100?2??
??1??1000000??110

Hylaeochampsia vectiana

??0????0?????
?????0?0?1000?00??0110?0?00000001001000?0?2110000120????1?0?000010100000000??
?1?001001000?0110

Eothoracosaurus mississippiensis

?????0?????????01?0000????????00?00?0?0??122??3?????0????00?011?0????001
20?000??102500000??000000????0000101001000????00?000100??01???10000010?001?00
????????100010000000

Thoracosaurus neocesariensis

?????0??????111?1?010????0011?0?0?00?0?0??1122??3????????10?000?01?0????00
120?0000?1025000000??000000?0?00001010010000?00000000110?00010??1?0000100001
00000000?00100?10000000

Thoracosaurus macrorhynchus

?????0???0?1111?1?01????00????0?0?00?0?0??1?22??3?????0?100000001100????00
120?00?0?1025000000??000000?0?00001010010000110000000110?000100?10001010?001
0000??0?0?0100010000000

Eosuchus minor

?????0???0??111??01?00?0?01??0000?000?0?0??1122??0300?0000?10?000001100????0
0120?0000?1025?00000?000000?00000001010010000?10000000110??0100?10?10010000
1?0100??1??101010101003

Eosuchus lerichei

?????0?????01????01??????1????????0????????1122??3?????????????????0????0012
0?0000?1025000000?0000000??000010100100000100000?0110?000?0??10?2001000010?1
????????10?01?101003

Eogavialis africanum

????????1?????11??010?????????0?????????0??1122??03?????10?100000??1101????001
20?000?01025?00000?000000000000001010010000010000000121?000100?1001001000010
100?000??0101010100000

Piscogavialis jugaliperforatus

????????????????????????????????1?????????????11?2??3?????0001??????10?????00120
?001001025000000?000000????0000101001000000?000000111?1?0001010020010000100?
0?1?0?0?12??1?10?000

Gryposuchus colombianus

????0?0???001?????01??000?????????????????0??11223?030100?000100000001100????00
12010000?1025?00000?0?0000?0?00001010010000011000000121?000100?100110100001
00000100?00121010100000

Gavialis sp. (Siwalik)

?????????????????010????????????????????????????22????3?????0?100000?1?0?????00?3
0?0?????2??0??0?0?0000?0?0000?0?00100?0?1??0000121?000100?100??0?000010000
?????00121010100000

Gavialis gangeticus

020000000?001111011010000000111000000?0000000011223003000000001000000011000
100001301000001025?0000000000000000000101001000001100000012100001000100110
10000100000000000121010100000

Borealosuchus threeensis

????0?????????????01??????0??????1?00??20??01002??1?????10?11?000001000??????
??
??????????????

Borealosuchus formidabilis

000?000?0?11001001001000000101000001?000?20??0110200000?000?110000000100001
??00020?0000?0023100000?0000001000000010100100010100201?11000000?00?00001010
0101000?????00100110000000

Borealosuchus wilsoni

?????0??????????1001000000101??00?1?000?20??01002??100?0?001100000201000????0
0020?0?0??0231000?????00001?0?0?001010010001010020101100?000100??00110100101
0000?00??010011?0?0000

Borealosuchus acutidentatus

?????????????????????????????0????????????????????002?????????????000?????0?????00020
?0?00?0231000?????0000????0?0?0?0??????1?002?1?1100?0?0?0??0?011010?101000??
????010??1?0?0000

Borealosuchus sternbergii

000000000?110010?1001000000101000001?00??0???011020000000?00010000000100000
??00020?00000001310000001000001?0?00000111010001010000111100?000100?00000010
0101000000?1?00100110000000

Pristichampsus vorax

????0?0??01001001?01?00000111??0100?10??1???1110?000?????0??1000001?1?0?????2
1010?0000?0003000100?000000?0?00000010010001010000111110??0100?01000010010
1000??01??1100110000002

Pristichampsus geiselalensis

?????????????0?0??01?000?0??1??0100?1???1????11102000?????0?1????0??1?1?????21?
20?0000000030001???000000??0000001001010??10000111110?0?0?00?0?010010?10100
?????????1??10000002

Planocrania hengdongensis

????????????????????1????????????????????????????1110????1????????1????0?01?0?????20010
?0?????01300?????0?000????0????01001????????0??1?1100?????????0?0?00100?0100?????
1??1??10?10001

Planocrania datangensis

??11?????0????????????????????????20010?
000??1003000000?0?000??????000?01??????0??1?1110?????????0?000010010?0?0?????
????????10??0?0?

Leidyosuchus canadensis

????0?0??????1????010000011?1??10?0?11??11??0110?00000?0?01?100000011101?????
0010?0000000030000000001000100010000111010001010000111100?01010010010001001
0100000001?00100110010001

Deinosuchus riograndensis

?????0????????????01?????????????????00??1??0110??001?0?11?10?0??11?0????00??
1?0?????0?0000??0?000011?00?0?????????????000111120?012210?1110001001?1000??
000?0?????1??100?1

Diplocynodon ratelii

?????0?????000??010?00?1111001400?10??21??01002101?????0111000001?1101?????
0120?0000001230000000101000??0?00000011110001010000111100??10100100000010110
100000001?10100110010001

Diplocynodon hantoniensis

100??1?1?01000010001000011111??1400?101?21??011021010????011100000111101???
?00120?0?000?11300?000?1010001?0?00000010110001010000111100?110100?001010101
101000??0?1??010011?010001

Diplocynodon muelleri

????????????????????1?01??1?????14?0?10??21??01002??2?????01110??10011100????00
120?1000001230000000101000??0000001111000001000?1?1100?110?0?01?010101101
00?????????0100110010001

Diplocynodon tormis

????????????????????1????1????????10??21??01?021?1????01?1?00????11?????0?12
0??00000123000000?1010001??000000111100?0?10000111100?110100000101010110100
?0???1?001?0110010001

Diplocynodon darwini

100001001?010000?00010000?1111??1400?101121??011020010??0?01?10000011110100?
?00020?0000?0103000000?0?000?0?0000001111?00101000?111100?110100?0110101011
01000??????0100110010001

Baryphracta deponiae

100?0?0??????0????01?0???1?????14?0?10??21????1?02??0????01?10??0??1110?????00
1??000??01030000?0????000????0?0001?11000?01000?111100?110100?0??011?0?101?0
0????????1???1??10001

Brachychampsia montana

101011001?1100??0001?0000111100?000?103111??11101101????01110?00001110100?
?00110?0002?1101000000?0010001?0?01000001111001012001111100?110200?011100101
10102000101?00100110010001

Brachychampsia sealeyi

????????????????????????????????????10??1??11101??0??????11?0000111?1????001?
0?0002?110100000??010?????????00????????10?2001101?00??????????100???????2????
?????????1??10??1

Stangerochampsia mccabei

????110??010010?0001000001111001000?01??11??111010100????0111110000?110?????
00110?0002?1102000000?001000????00000001111001012001111100?110200?0?11001021
01000??1?1??0100110010001

Ceratosuchus burdoshi

????????????????????????????????????0?1??????11111??0?????01?10??00?11?01????0001
0?0?01?0102000000??1000?0?0??00??01??1?1??0?111100????????0??010?111?????
?????10??10010001

Hassiacosuchus haupti

001?1?0?1?????0??01?000?1111?????0??11?11??111110?0?????01?10?0?0?11101????00
010?00??010?0000?????0001?0?????0????????1100?111100?1?0200?01120010210101?
??????01??10010001

Navajosuchus mooki

?????0?1?????0??0?00??1111??1??0?111111??11111010?????01?10?00??110?????00
010?0001?01020000??0?1000??0??00?00?111001011001111100??020??0112?01021010
00????1??010??10010001

Allognathosuchus polyodon

??11111010?????01?11??00?111?1????0001
0?000?01020000?0?????00?0?00?00?0?111001?1?01?111100?????????0??20010?101?????
??????1??1??1??1

Allognathosuchus wartheni

????1?0?????????????0?0000?1111??1000?11??1??11111010?100?011110000011101?????0
0010?0000?010200000000010001?0?000000?0111001?11011111100?110200?01120010210
10000?1?1?0010011001?001

Procaimanoidea kayi

????110?1?????0??010?00?1111??10?0?112121?????010?1??100?01?11000001110?????1
0?????0??010?0000??0?1000??0?0000000011100?0110111111000??0200?011200102101
010??????0100110010001

Procaimanoidea utahensis

??110100?00??01011110??0011101????101
10?0100?01020?0000??01000??0000000?11100101101?111100?1?0200?01120010?10100
0??????0100110010001

Arambourgia gaudryi

??11010??0?????01?100?0??1110?????1001
??010?01020000?0??10001000??000????11?0??1101?111100?1102?0?0?1210?0210100??
??????10011?010?01

Wannaganosuchus brachymanus

????1?0??1?00?0??010000?1111001000?11??1??111110?0?????0??100?00?11?0?????0
0110?0000??10200?00??1000??0?100000??1??01?1101?111100?????????0?12001??1010
00??????10011?010001

Alligator sinensis

101011101?110010100010110111110011000112111110110000120?001011200000111101??
11001000010000102000000000100011001000000111100101101111110011020010112001
0210101000111100100110010001

Alligator mississippiensis

101011001?01001000001011011111001100011210110011000112010010112000101111010
011001000010000102000000000100011100000000111100101101111111001102001011210
10210101000111100100110010001

Alligator mefferdi

??
100?0100?0102000000?0?10001?1?0000000?111001011011111110?110200?011210102101
010??1???00100110010001

Alligator thomsoni

????????????????????????01?????????1?????0?1?????????110000?2?????011200010011101????001
00?01000010200000?0010001?1?000000?0001?????1011111110?1?0200101?21010210101
?001?11?0100110010001

Alligator olseni

?????0?1?????10??01?10011111??100?11?????????11010010?????011200000011101????0
0100?01000?10200?00??1000??0?00010111110101101111110?110200?011200102101
010?????00100?1?010001

Alligator mcgrewi

100010001?010010?00010000111?1101??0?11??1??11110010?100?011100000111101???
?00000?0100?0102000000?0010001?00100000011110010110111111000110200?011200102
101010?01??00100110010001

Alligator prenasalis

10001?0?1?????10?0?01000011111??1000?112111??11111010?????01110000011110100??
00000?0100?0102000000?001000110010000001111001011011111100?110200?0112001021
01000001?1?00100110010001

Eocaiman cavernensis

??
?0?????0?????????100??0?1??0000??????0?????1??1?0?????0?????????????1?????????
??0??1?2?????

Tsoabichi greenriverensis

????????????????????01????????????????10??20???1100??2?????????1??????11??01??0001
0?10????10?000????????0????????????????????0000?1111?0?1?0????0?211????101?2?????
????????????100??

Purussaurus neivensis

101?100?1?000010?0??1????011??????0?11????1??1?00??1?1010?111201100011001????0
0110?0001?0102000000?0010001?0?0?000001111012111111111110?110201?0112011?210
102000101??010??10210001

Orthogenysuchus olseni

??00????????????????????????0????00121?
0?01??10?0?0??????000????01?000????????????????1110????????0????11??101??0?????
?????????10001

Mourasuchus spp.

10??100?1?00?010?00?1?10?011????1300?11??1??1102?112?????01110?100011000????0
0121?0000?1105000100?0010001?0?01000001111012?1011?111110?110?00????2111??111
?30????1??100110?10001

Caiman yacare

101111001?10001000001010111111001100011122111011002112101011101011020110010
11100110000000011200000000100011001000000111101211110111111001102011011201
11210103000101100100110210001

Caiman crocodilus

101111001?10001000001010111111001100011122111011002112101011101011020110010
11100110000000011200000000100011001000000111101211100111111001102011011201
11210103000101100100110210001

Caiman latirostris

101110001?10001000001010?111110011000111221210110021121010111?10110201100??
110011000000001020010000001000110010000001111012111001111110011020110112111
1210103000101100100110210001

Caiman lutescens

??0????????????????????????00110?
0000?0102001000?001000????1000000111101211200?1?1?10????0??????1????0??????
????????????100?1

Melanosuchus fisheri

?????0??????0????????????????????????????????????02?????????1?11011????10?1????001?
0?0000??102001010??1000?0??0????11????2?11???11110????????0????11??1010?????
????010??1?2?0001

Melanosuchus niger

101111001?1?0010000010101111100110001112212101100211210101111101102011001??
110011000000001020010100001000110010000001111012111001111110011020110112111
1210103000101100100110210001

Paleosuchus trigonatus

100111111?0100101000100011111121130001113211201100212221111111011000110010
11110110000100010200000000010001100010001011110111100011111011102011011211
1?210102000101100100110210001

Paleosuchus palpebrosus

100111111?010010101010001111112113000111321120110021222111?11?10110001100?01
11101100001000102000000000100011000100010111101111000111110111020110112111
?210102000101100100110210001

Mecistops cataphractus

10?001001?000010000011100111112012000111101101111041010100010010001110101?1
001001200000010021000000010000011010000101101000101000011111000010111001200
10010100011101011110010000003

Crocodylus niloticus

101000001?10101000101110011111201200011120110111002101010001011000111010111
001001100000010021000000110000011010010001101000101100011111000010111001200
10010100011101011110011000003

Crocodylus porosus

111000001?00101010101110001111201200011120110111002101010001011000111010111
001001100000010021000100110000011010010001101000101000011111000010111001200
10010100011101011110011000003

Crocodylus rhombifer

001000001?10101000101110011111201100011120110111002101010001011000111010111
001001100000010021010000110000011010010001101000101100011111000010111001200
10011100011101011110011000003

Euthecodon arambourgi

??
0000?1025000100?1000001101000000??0??0??000111110??11011?001210100101100??
??1??11?0?1000?003

Osteolaemus tetraspis

??1?00001?00101010001110011111201110011111101110021010100010110000110101110
011010000010100210001000100000110110010111010101010000111110100101010012111
0010110011101011110110000003

Osteolaemus osborni

??1?00001?00101010001110011111201110011111101110021010100000110000110101110
011011000010100210001000100000110110010010010101010000111110100101010012111
0010110011101011110110000003

Voay robustus

?????0??????0??011????111??1110?????1???110210101000001100011111011????0
0110?0000?00210001000100000110100010111010101010000111110?00101110012011001
11110?1101?11110010000003

Rimasuchus lloydi

??1????????????????????1?????00110?
0000?0021000100?100000110100000????10??1??100?111110?001011?00120010010110011
1?1??1110?1000?003

Crocodylus pigotti

?????????00?010?00?11??01111????????10??0??11102??1????????1???111??1?????000
10?0100?00210001000100000???0010101101010001?0?0111110???1?1??00121010010110
0??1?1??1100?10000003

Crocodylus megarhinus

?????0??????????001????????????????????????????11102101?????00110000??01011?????001
10?0000?002300000001?0000?0?00000011010001012000111110?002?11?0012?01001010
?01100??1110010000003

Australosuchus clarkae

?????0???????1??0??1?????11??????0?10??1??1110?101?????001100001101011?????00
110?00001102100000001000001?0?000000???????1010000111110?002011?011200100101
00011??1??11?001000?001

Kambara implexidens

?????0?????????????01?????11?????1100?10??1??11102101?????001100001101011?????00
110?00001102100000001000001?0100000010010001010000111110?002011?001200100101
00011101?11110010000001

Trilophosuchus rackhami

??
0??????2?0?0?0?1000?0?1?000001010???01?0?011110??120111011210100001020111
01?111?0?1000?001

Quinkana spp.

??
?0000?10(0,2)(1,5)00(0,1)0000100000????0?0????????????1??1000111?10?002011100121010
010102?11101?11??01?000???

Tomistoma schlegelii

021000001?0010100010110001111110110001013011011122?104000001001000000010100
001001200000011021000001010000011010001001001000101100011111000001101001210
10010100011001011110010000003

Tomistoma lusitanica

??????0????????????01????????????????10???1???1??2??4????00?10000?0101?????0012
0?0000?1021?00001?100000110?00001010010001010000111110?0001?1?10121010010100
011001??1110010000003

Toyotamaphimeia machikanense

00100100??11111100101100011111101100?00??1?????22??04?????10010?0000?101000??
00120?00001100400000??00000??0000?010010000?10000011110??00?1??1??21010?10
10??????????110010?00003

Gavialosuchus eggenburgensis

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Paratomistoma courti

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Tomistoma caireense

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Thecachampsa antiqua

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Tomistoma petrolica

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Dollosuchoides densmorei

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Kentisuchus spenceri

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Brachyuranochampsia eversolei

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Crocodylus acer

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Crocodylus depressifrons

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Crocodylus affinis

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Asiatosuchus germanicus

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Prodiplocynodon langi

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Necrosuchus ionensis

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Globidentosuchus brachyrostris gen. et sp. nov.

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