

A NEW LONGIROSTRINE DYROSAURID (CROCODYLOMORPHA, MESOEUCROCODYLIA) FROM THE PALEOCENE OF NORTH-EASTERN COLOMBIA: BIOGEOGRAPHIC AND BEHAVIOURAL IMPLICATIONS FOR NEW-WORLD DYROSAURIDAE

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Abstract: Fossils of dyrosaurid crocodyliforms are limited in South America, with only three previously diagnosed taxa including the short-snouted *Cerrejonisuchus improcerus* from the Paleocene Cerrejón Formation of north-eastern Colombia. Here we describe a second dyrosaurid from the Cerrejón Formation, *Acherontisuchus guajiraensis* gen. et sp. nov., based on three partial mandibles, maxillary fragments, teeth, and referred postcrania. The mandible has a reduced seventh alveolus and laterally depressed retroarticular process, both diagnostic characteristics of Dyrosauridae. *Acherontisuchus guajiraensis* is distinct among known dyrosaurids in having a unique combination of craniomandibular characteristics, and postcranial morphology that suggests it may have occupied a more placid, fluvial habitat than most known Old-World dy-

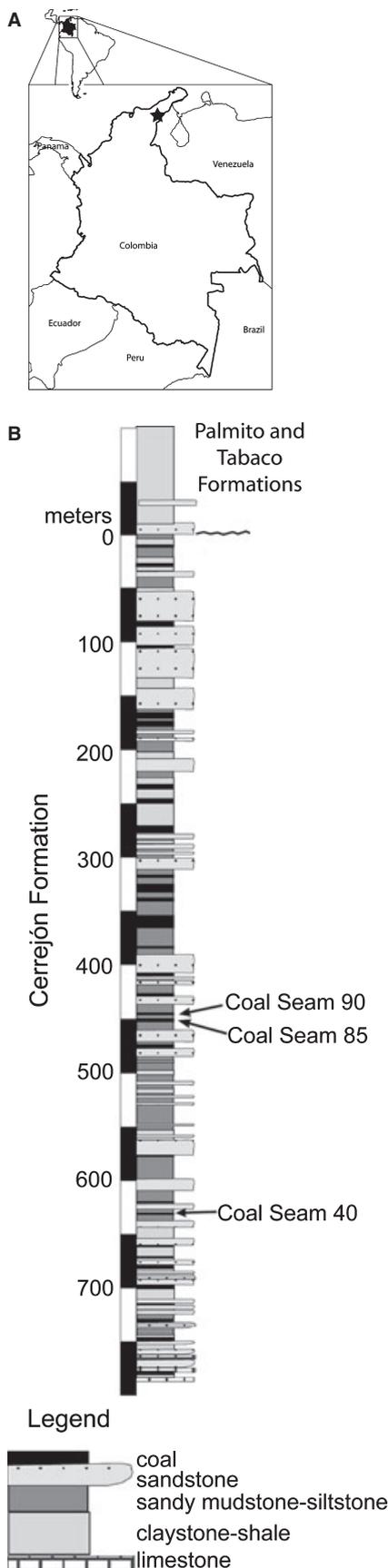
rosaurids. Results from a cladistic analysis of Dyrosauridae, using 82 primarily cranial and mandibular characters, support an unresolved relationship between *A. guajiraensis* and a combination of New- and Old-World dyrosaurids including *Hyposaurus rogersii*, *Congosaurus bequaerti*, *Atlantosuchus coupatezi*, *Guarinisuchus munizi*, *Rhabdognathus keiniensis* and *Rhabdognathus aslerensis*. Our results are consistent with an African origin for Dyrosauridae with multiple dispersals into the New World during the Late Cretaceous and a transition from marine habitats in ancestral taxa to more fluvial habitats in more derived taxa.

Key words: Cerrejón, Colombia, Crocodylomorpha, Dyrosauridae, *Acherontisuchus*, Paleocene, South America.

THE Cerrejón Formation in north-eastern Colombia (Text-fig. 1) has been estimated to be middle–late Paleocene based on carbon isotopes, pollen and spores (Jaramillo *et al.* 2007) and has yielded the first good evidence of tropical terrestrial ecosystems of that age in South America. Recent discoveries, all from exposures in the Cerrejón coal mine, include the oldest megafossil evidence of neotropical rainforests (Doria *et al.* 2008; Herrera *et al.* 2008; Gomez-Navarro *et al.* 2009; Wing *et al.* 2009), many vertebrae and ribs of the largest known snake *Titanoboa cerrejonensis* (Head *et al.* 2009), large pleurodire turtles (Cadena *et al.* 2010), multiple species of undescribed dipnoan and elopomorph fishes (Bloch *et al.* 2005), and a new short-snouted dyrosaurid crocodyliform *Cerrejonisuchus improcerus* (Hastings and Bloch 2007; Hastings *et al.* 2010).

The first vertebrate fossils to be recovered from the Cerrejón Formation, a partial mandible and associated

postcrania, were discovered and collected in 1994 by Mr Henry Garcia, a coal geologist working in the Cerrejón coal mine who was monitoring field operations on the south face of the ‘Expanded West Pit.’ Mr Garcia retrieved the fossils from just below Coal Seam 40 (Text-fig. 1) after seeing them exposed by one of the large earth movers. The fossils were subsequently deposited in a display case at the mine geology offices until they were identified as a dyrosaurid a decade later. Based on these specimens and others recovered by Florida Museum of Natural History-Smithsonian Tropical Research Institute (FLMNH-STRI) collecting expeditions from 2004 through 2007, we describe a second new species of dyrosaurid from the Cerrejón Formation. To date, fossils attributed to the new species have been recovered from underclays below three distinct coal seams within the Cerrejón Formation (Text-fig. 1). As such, it is the only crocodyliform



taxon yet discovered to transcend more than one horizon within the Cerrejón Formation. The fossils were recovered from sediments that were deposited prior to the warming trend of the Paleocene–Eocene Thermal Maximum (Jaramillo *et al.* 2010), although temperatures were still much warmer than today (Head *et al.* 2009).

Dyrosauridae is a diverse family of mesoeucrocodylians that likely had its origins in the Late Cretaceous, survived the K–P boundary extinction event, and is last known from the Late Eocene (Brochu *et al.* 2002). Dyrosaurid fossils have been recovered from transitional freshwater-marine sediments through this interval in Africa, Asia, Europe, North America and South America. The published South American record of dyrosaurids is restricted to six localities, all Late Cretaceous or Paleocene in age (Cope 1886; Langston 1965; Argollo *et al.* 1987; Marshall and de Muizon 1988; Gasparini 1996; de Carvalho and de Azevedo 1997; Gallo *et al.* 2001; Barbosa *et al.* 2008; Hastings *et al.* 2010), and is very fragmentary. The best-known taxa are both from the Paleocene: *Guarinisuchus munizi* from Brazil (Barbosa *et al.* 2008) and *Cerrejonisuchus improcerus* (Hastings *et al.* 2010) from the Cerrejón Formation. These taxa are distinctly different from one another, with *G. munizi* having a substantially longer snout than that of *C. improcerus*. While shorter than that of Old-World dyrosaurids, the longirostrine condition of *G. munizi* seems to be shared with *Hyposaurus derbianus* from the Paleocene of Brazil, known from a nearly complete dentary, and likely represents the primitive condition for New-World Dyrosauridae.

The new species described here represents the third named longirostrine dyrosaurid from the Paleocene of South America. Fossils of the new taxon (Hastings and Bloch 2008) are catalogued at both the Museo Geológico, at the Instituto Nacional de Investigaciones en Geociencias, Minería y Química (IGM) in Bogotá, Colombia and the Florida Museum of Natural History (FLMNH), and are currently housed at the FLMNH. Fossils of the new taxon were recovered from sediments deposited in a large fluvial depositional setting, pertaining to the ancient Amazonian basin (Hoorn *et al.* 2010). The postcrania indicate that while the new taxon was generally similar to Old-World *Dyrosaurus* in its swimming mode, it is

TEXT-FIG. 1. Geographic and stratigraphic position for the localities of all known fossils of *Acherontisuchus guajiraensis*. A, map of Colombia, star marks location of the Cerrejón coal mine, the locality from which all *A. guajiraensis* fossils were recovered. B, stratigraphic column of the Cerrejón Formation; fossils of *A. guajiraensis* were recovered from underclays immediately below the coal seams marked by arrows. All fossils discovered thus far of *Cerrejonisuchus improcerus* have been from the underclay of Coal Seam 90. Stratigraphic column from Jaramillo *et al.* 2007.

distinctly different in ways that likely reflect a difference in habitat utilization in this new dyrosaurid.

Institutional abbreviations. AMNH, American Museum of Natural History; GSP, Geological Survey of Pakistan; IGM, Museo Geológico, at the Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Bogotá, Colombia; OCP DEK-GE, Office Chérifien des Phosphates, Direction de l'Exploitation de Khouribga, Geologie-Exploitation, Khouribga, Morocco; SMNK-PAL, Staatliches Museum für Naturkunde Karlsruhe; STRI, Smithsonian Tropical Research Institute; UF, Florida Museum of Natural History (FLMNH), University of Florida; USGS SAP, United States Geological Survey-Saudi Arabian collection; YPM, Yale Peabody Museum.

Terminology and anatomical abbreviations. Following the study by Hastings *et al.* (2010), teeth and alveoli of the dentary (d) are referred to by a sequential numbering system, with 'd1' being the most anterior.

SYSTEMATIC PALAEOONTOLOGY

CROCODYLIFORMES Walker, 1970

CROCODYLIFORMES Hay, 1930

MESOEUCROCODYLIA Whetstone and Wybrow, 1983

DYROSAURIDAE de Stefano, 1903

ACHERONTISUCHUS gen. nov.

Derivation of name. *Acheron*, from ancient Greek mythology, the river Acheron ('the river of woe') a branch of the underworld river Styx over which Charon ferried the dead across into Hades; *suchus*, Greek for crocodile.

Type species. *Acherontisuchus guajiraensis*.

Range. Middle-Late Paleocene, Colombia.

Diagnosis. As for the type species.

Acherontisuchus guajiraensis, sp. nov.

Derivation of name. Named for the Guajira Peninsula in north-eastern Colombia, the location of the Cerrejón Coal mine from which all specimens described here were recovered.

Holotype. UF/IGM 34, a mostly complete mandible including left and right dentaries, splenials, 14 partial mandibular teeth, right surangular, and four maxillary fragments, four partial teeth, and two partial ribs.

Type locality. All known specimens are from the Cerrejón Formation within the Cerrejón Coal Mine (11°08.944'N, 72°32.891'W) in north-eastern Colombia. Middle to late Paleocene in age.

Type stratum. The type stratum is below Coal Seam 85 within the La Puente Pit.

Referred specimens. UF/IGM 35, mandible including left and right dentaries and splenials, the left surangular, angular and articular, and a total of three partial teeth. Associated postcrania include two ribs, one sacral vertebra with partial sacral ribs and one metatarsal. These fossils were recovered from the underclay of Coal Seam 90 within the La Puente Pit (11°09'03.70"N, 72°33'18.98"W). UF/IGM 36, edentulous mandible including partial left and right dentaries, recovered from the underclay of Coal Seam 40 within the West Extension Pit. Also recovered were a dorsal vertebra (UF/IGM 37), a nearly complete ilium and ischium (UF/IGM 38), and a femur (UF/IGM 39) from the same locality, all of which might be associated and are here referred to one or more individuals of *A. guajiraensis*.

Diagnosis. A longirostrine dyrosaurid that differs from all other dyrosaurids by the following unique combination of characteristics: (1) 19–22 mandibular teeth; (2) a symphysis that ends between 17th and 19th alveoli; (3) splenials that end anteriorly between 10th and 13th alveoli; and (4) maxillae that have straight lateral margins and are weakly ornamented.

Remarks. It differs from: (1) *Dyrosaurus*, *Atlantosuchus*, *Rhabdognathus* and *Congosaurus* in having a shorter snout; (2) *Arambourgisuchus* in having strongly striated lingual and buccal surfaces of teeth; (3) *Chenanisuchus* in possessing teeth that are not strongly laterally compressed, some of which possess striations; (4) *Rhabdognathus* in having a mandible that is much wider than high and a mandibular symphysis which ends prior to 19th mandibular alveolus; (5) *Congosaurus* in having a shorter snout that is wider than high; (6) *Guarinisuchus* in having a much larger inferred total body length; (7) *Sokotosuchus* and *Phosphatosaurus* in having smooth-margined maxillae; (8) *Hyposaurus* in having a mandibular symphysis that is much wider than tall; and (9) *Cerrejonisuchus* in having greater body size, a greater overall number of mandibular teeth, and a proportionally greater number of symphyseal teeth.

Description

General. While a complete skull of *Acherontisuchus guajiraensis* has not been recovered, we estimate its total length to have been 72–86 cm, based on the morphology and measurements of the mandible. The skull length estimate, from the presumed tip of the snout to the occipital condyle, includes a range of possibilities for the extent of the occipital condyle and the premaxilla. The quadrate-articular/surangular articulation corresponds to the approximate position along the skull length of the occipital condyle in *Dyrosaurus maghribensis* (Jouve *et al.* 2006), and is

TABLE 1. Snout proportions of all members of Dyrosauridae with material complete enough for skull length estimation.

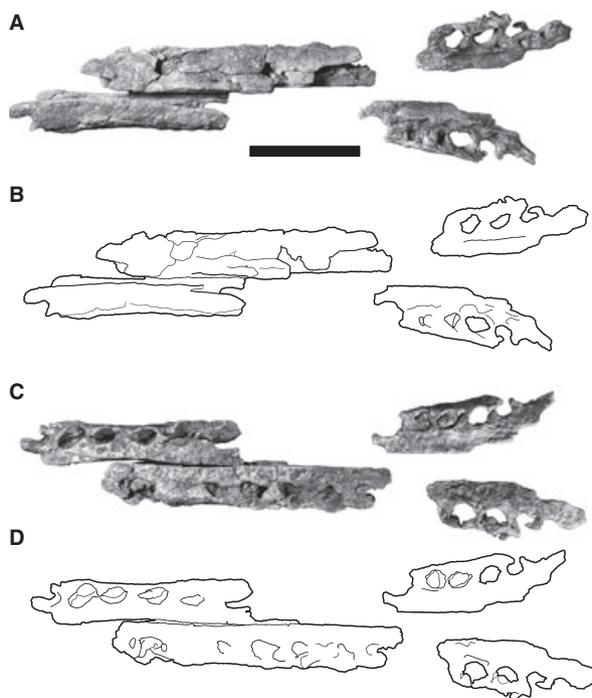
	DL (cm)	PreoL (cm)	R (PreoL/DL) × 100	TBL (m)
<i>Cerrejonisuchus improcerus</i> (UF/IGM 31) ¹	31.4	17.2	54.78	1.72–2.22
<i>Cerrejonisuchus improcerus</i> (UF/IGM 29) ¹	25.8	15.3	59.30	1.22–1.79
<i>Chenanisuchus lateroculi</i> ²	57.6	36.5	63.37	3.57–4.24
<i>Acherontisuchus guajiraensis</i> (UF/IGM 35)	77.5–86.3	43.2/52.1	55.74–60.37	5.04–6.46
<i>Acherontisuchus guajiraensis</i> (UF/IGM 34)	72.4–78.7	41.9/50.8	57.87–64.52	4.66–5.87
<i>Congosaurus bequaerti</i> ³	63	41	65.08	3.97–4.66
<i>Guarinisuchus munizi</i> ⁴	47.1	30.8	65.41	2.79–3.43
<i>Hyposaurus rogersii</i> ²	42.9	28.2	65.73	2.48–3.11
<i>Sokotosuchus ianwilsoni</i> ²	60.1	39.7	66.06	3.75–4.44
<i>Phosphatosaurus gavioloides</i> ²	107	72	67.29	7.22–8.05
<i>Arambourgisuchus khouribgaensis</i> ⁵	100	71.5	71.50	6.71–7.51
<i>Dyrosaurus phosphaticus</i> ²	104	75	72.12	7.00–7.82
<i>Dyrosaurus maghribensis</i> ⁶	89–97	–	73.00	5.89–7.28
<i>Rhabdognathus keiniensis</i> ²	73.1	53.4	73.05	4.72–5.44
<i>Atlantosuchus coupatezi</i> ⁷	104.5	83	79.43	7.04–7.86

Owing to the incomplete nature of *Acherontisuchus guajiraensis*, skull lengths of the two mostly complete specimens (UF/IGM 34 and 35) were estimated from the preserved mandibles, resulting in possible ranges of size and proportion, based on longest and shortest reasonable dorsal skull lengths. The preorbital skull lengths of these two specimens represent the shortest possible snout for the minimum dorsal skull length and longest possible for the maximum length, resulting in a minimum and maximum ratio of preorbital skull length to dorsal skull length. DL, dorsal skull length; PreoL, preorbital skull length; R, ratio of preorbital skull length to dorsal skull length; TBL, estimated total body length using method described by Sereno *et al.* (2001). Citations are marked by numbered superscripts: ¹Hastings *et al.* (2010); ²Jouve *et al.* (2005a); ³an estimation from the study by Jouve *et al.* (2008b); ⁴an estimation from figure 2 in the study by Barbosa *et al.* (2008); ⁵Jouve *et al.* (2005b); ⁶Jouve *et al.* (2006); ⁷Jouve *et al.* (2008a).

used here as a reference for estimating skull length in *A. guajiraensis*. The anterior extent of the skull was further estimated based on alveolar size and spacing of the anterior mandibular symphysis. All three fossils (UF/IGM 34–36) preserve morphology consistent with the interpretation that *A. guajiraensis* had a long and narrow snout that would have represented 56–65 per cent of the estimated total skull length (see Table 1). As the estimate incorporates large allowances for variation, we are very confident that this species had snout proportions within this range.

Maxilla. The holotype of *A. guajiraensis* includes four associated fragments of the right and left maxilla (Text-fig. 2). The preserved mediadorsal margin of these fragments suggests that the maxillae would have been separated by the nasals, which were not recovered in this specimen. While the recovered sections of the maxillae contain no less than four partial teeth, relative tooth positions are not preserved and cannot be estimated with confidence. Based on comparison to the mandible, most of the maxillae must be present, with only the portions connecting the different sections missing. The more complete right side possesses a total of 11 preserved alveoli (Text-fig. 2). As portions are missing, this implies that the maxillary tooth count for *A. guajiraensis* is greater than 11. The maxilla is very weakly ornamented dorsally and has a smooth, straight lateral margin (Text-fig. 2).

Mandible. Despite imperfect preservation, the fossils lack visible signs of significant deformation and likely represent similar pro-



TEXT-FIG. 2. UF/IGM 34, holotype of *Acherontisuchus guajiraensis*. A–B, UF/IGM 34 maxillary fragments in dorsal view. C–D, UF/IGM 34 maxillary fragments in ventral view. Scale bar represents 10 cm.

portions as found in life, particularly for the holotype (Text-fig. 3). The width of the symphyseal region of the dentaries/splenials is wider than its height throughout its length. UF/IGM 34 possesses 19 alveoli (Text-fig. 3), while UF/IGM 35 possesses 22 (Text-fig. 4). UF/IGM 36 is incomplete, but possesses 8 alveoli (Text-fig. 5). The seventh alveolus is reduced relative to the eighth and is placed notably closer to the eighth than the sixth in both UF/IGM 34 and 35. The symphysis ends posteriorly at the 17th alveolus in UF/IGM 34 and between the 18th and 19th alveoli in UF/IGM 35. The alveoli of the symphysis are wider and rounder than those posterior to the symphysis. The postsymphyseal alveoli are reduced in size, and their medial borders are formed by the splenial. A series of depressions adjacent to the alveoli is evident on the left side of the mandible of UF/IGM 35. These depressions are likely for occlusion with maxillary teeth, and are smaller and shallower than the alveoli that house the mandibular teeth. A prong of the dentary extends posteriorly into the surangular, dorsal to the mandibular fenestra.

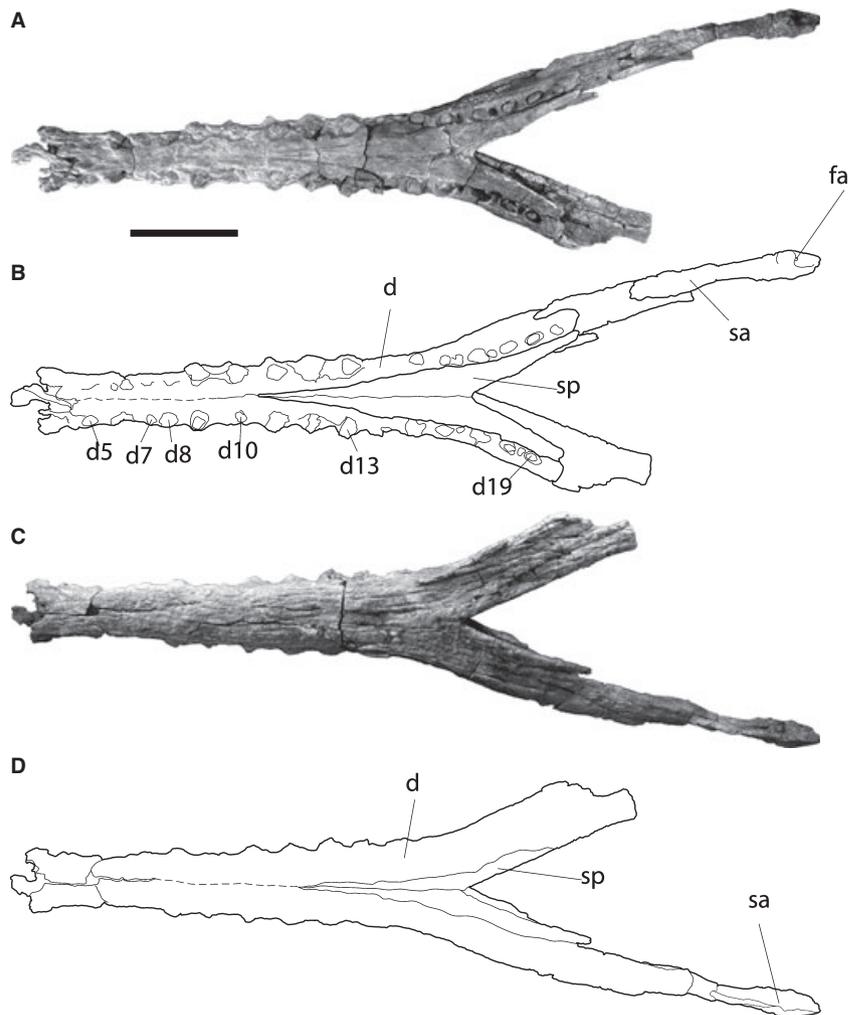
The splenials in both UF/IGM 34 and 35 form sharp wedges that participate broadly in the symphysis. The splenials end anteriorly between the 10th and 11th alveoli in UF/IGM 34 on the dorsal surface and even with the 13th alveolus on the ventral

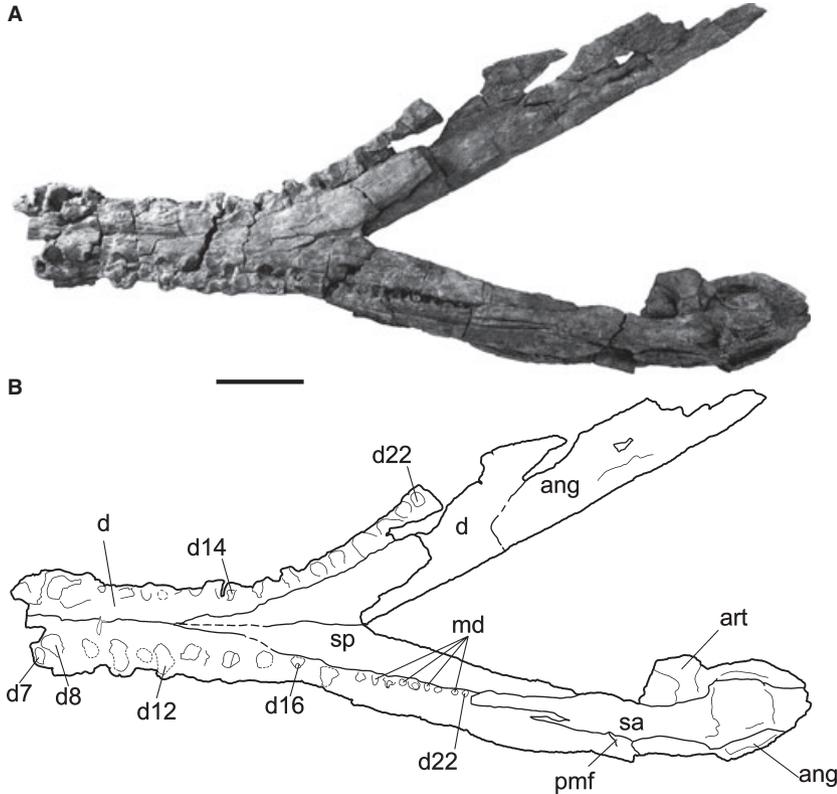
surface (Text-fig. 3). The splenials in UF/IGM 35 end anteriorly between the 12th and 13th alveoli on the dorsal surface (Text-fig. 4) and their anterior extent cannot be discerned on the ventral surface. The spreading angle of the splenials, as measured from the anterior point along the left and right dentary-splenial sutures, is 17.5 degrees in UF/IGM 34 and 33.5 degrees in UF/IGM 35. However, when measured from the posterior symphysis of the splenials along the medial dorsal surface, the angle is 57.9 degrees for UF/IGM 34 and 58.5 degrees in UF/IGM 35. The splenials cannot be discerned in either dorsal or ventral views of UF/IGM 36 (Text-fig. 5).

The angular joints with the dentary ventral to the external mandibular fenestra and contributes broadly to the ventral portion of the back of the mandible. While the preservation of the retroarticular process is incomplete, the angular clearly participates in at least the ventral portion of its base (Text-fig. 6).

The surangular reaches anteriorly nearly to the level of the posteriormost alveolus (Text-fig. 6). The retroarticular processes of both UF/IGM 34 and 35 are incomplete, but clearly are formed in large part by the surangular. The surangular contributes to the lateral portion of the glenoid fossa. The surangular of the holotype, UF/IGM 34, bears a foramen aerum on the lateral side (Text-fig. 3). The foramen is fully contained within this

TEXT-FIG. 3. UF/IGM 34, holotype of *Acherontisuchus guajiraensis*, from the Cerrejón coal mine of north-eastern Colombia, middle-late Paleocene. A–B, UF/IGM 34 mandible in dorsal view; C–D, UF/IGM 34 mandible in ventral view. Abbreviations: fa, foramen aerum; d, dentary; d7–d8, seventh and eighth dentary alveoli; sa, surangular; sp, splenial. Dotted lines are used to indicate sutures that were unclear. Scale bar represents 10 cm.





TEXT-FIG. 4. Referred mandible in dorsal view of *Acherontisuchus guajiraensis*, UF/IGM 35, from the Cerrejón coal mine of north-eastern Colombia, middle–late Paleocene. Abbreviations: ang, angular; art, articular; d, dentary; d7, 8, 12, 14, 16, 22, see Terms and Anatomical Abbreviations section; md, maxillary depressions; pmf, partial mandibular fenestra; sa, surangular; sp, splenial. Dotted lines indicate sutures which were unclear. Scale bar represents 10 cm.



TEXT-FIG. 5. Partial mandibular symphysis (UF/IGM 36) referred to *Acherontisuchus guajiraensis* from the West Extension pit of the Cerrejón coal mine in north-eastern Colombia, middle–late Paleocene. A, dorsal view; B, ventral view. Scale bar represents 10 cm.

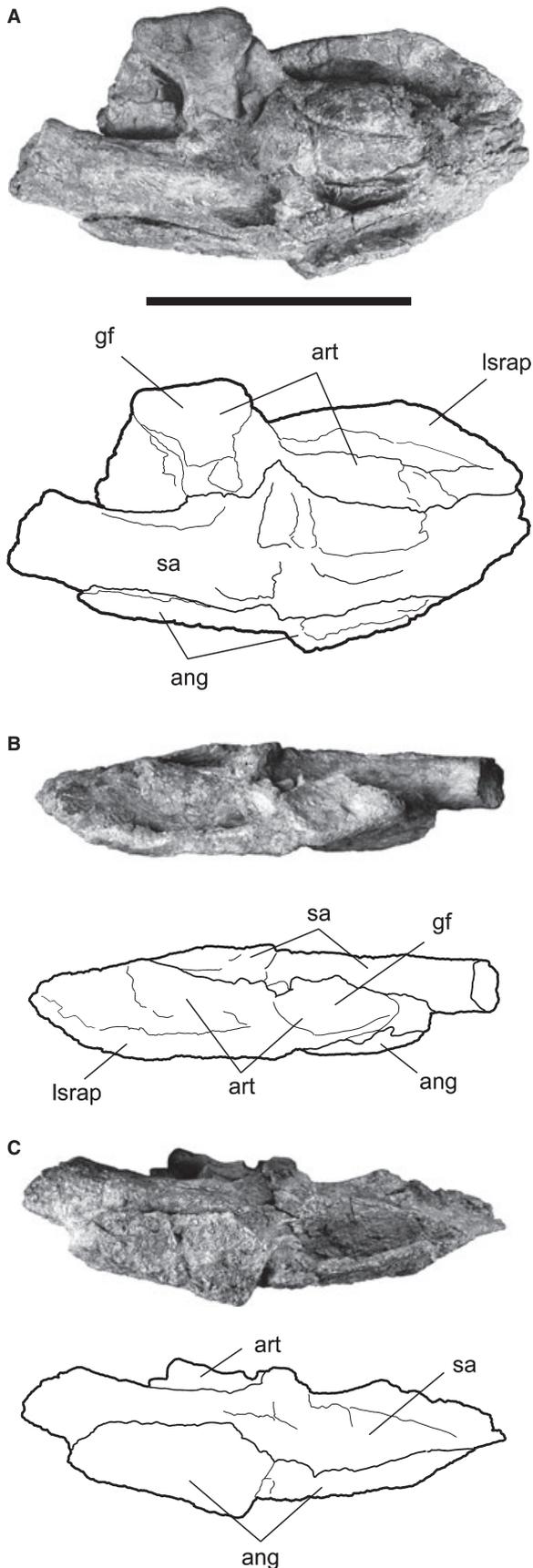
bone and is just caudal to a transversely oriented rugosity. A small, narrow shelf arises from this rugosity and extends anteroposteriorly along the lateral surface of the surangular and narrows posteriorly, forming part of the base of the retroarticular process. The surangular of UF/IGM 35 bears a ridge that extends anteroposteriorly and defines the boundary between the dorsal and lateral surfaces of the bone (Text-fig. 6).

The articular forms the medial portion of the glenoid fossa. Posterior to the fossa is a depression, forming a shelf that extends anteroposteriorly along the preserved retroarticular process (Text-fig. 6). If undistorted, this shelf gives the cross-section of the retroarticular process an L-shape. The articular forms the medial portion of the retroarticular process.

Only the anterior portion of the left external mandibular fenestra is preserved in UF/IGM 35. The fenestra appears small and is bordered anteriorly and ventrally by the dentary, dorsally by the surangular, and posteriorly by the angular (Text-fig. 4).

Dentition. The symphyseal teeth have wide bases that narrow towards their apex. A distinct carina is present on the preserved teeth, and most have preserved striations along both lingual and labial surfaces (Text-fig. 7). The carinae are well developed and define the labial and lingual surfaces of the tooth. The anterior carina is not fully preserved on any tooth, but the preserved portion does not indicate any twisting. Postsymphyseal alveoli are only slightly lateromedially compressed, but are notably smaller in all dimensions than the symphyseal alveoli (Text-figs 3, 4).

Dorsal vertebra. A single dorsal vertebra (UF/IGM 37) was found near UF/IGM 36 and is here referred to *A. guajiraensis*. The anterior articular facet of the centrum bears a circular tubercle at its lower right centre (Text-fig. 8). The vertebra is a posterior dorsal, based on its lack of any hint of hypapophysis and its square-shaped anterior/posterior articular facets, most likely between positions 8 and 13 (Text-fig. 8). However, as only partial transverse processes were preserved, it is difficult to assign an exact position within the vertebral column. In ventral and dorsal views, the centrum of the vertebra is distinctly hour-glass-shaped. In ventral view, the width of the central constriction (32 mm) is 64 per cent of the caudal margin (50 mm). In lateral view, the centrum height (41 mm) is 71 per cent of the



centrum length (58 mm). Also in lateral view, the centrum length at the ventral margin (56 mm) is 3 per cent shorter than at the level of the neurocentral suture (58 mm).

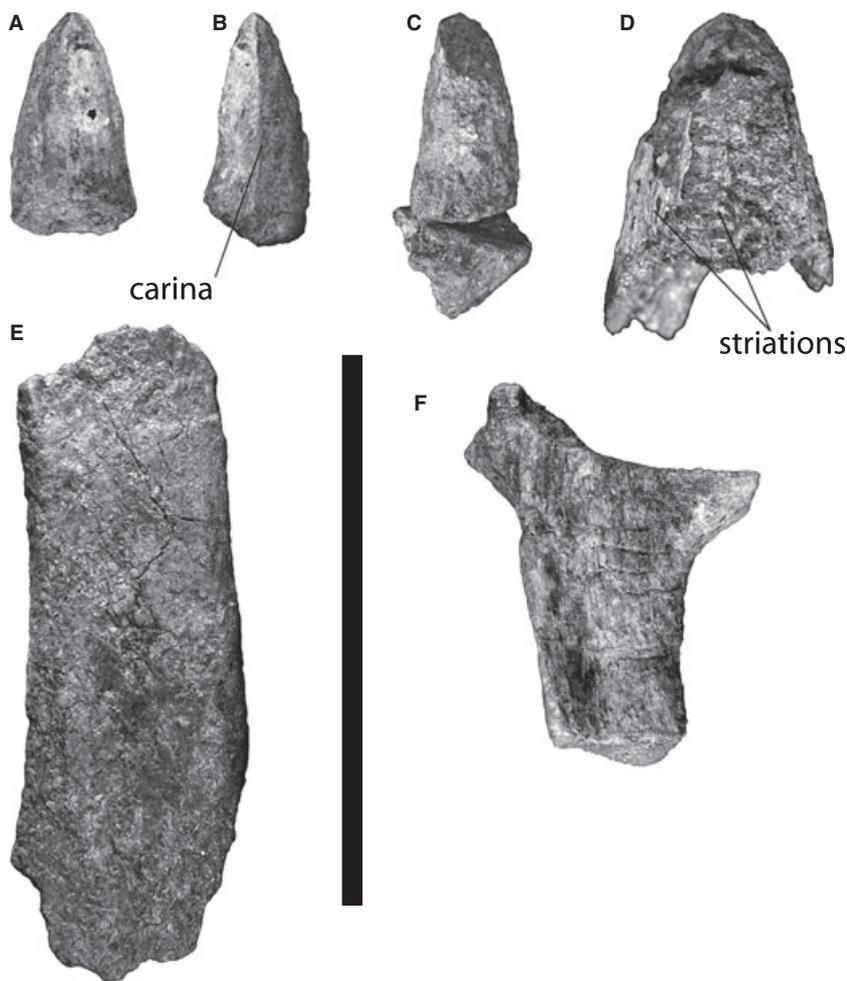
Sacrum. A second sacral vertebra with partial left and right second sacral ribs was found associated with UF/IGM 35 (Text-fig. 9). The vertebra can be identified as the second sacral based on the lack of a tuber on the anterior surface of the centrum as well as the articulation of the sacral rib exclusively with the centrum with no facet for additional articulation with a more anterior vertebra. The second sacral ribs were identified as such based on the identification of the vertebra as well as their complete lateral circumferential suture with the lateral vertebral surface. The second sacral rib's insertion onto the second sacral vertebra occupies nearly the entire lateral surface, very different from the transverse process of a dorsal vertebra, which is more limited.

Ilium. A pelvis, UF/IGM 38, was collected with UF/IGM 36 and is thus attributed to *A. guajiraensis*. The iliac blade is large, with a convex dorsal margin, rounded posterior margin and a strongly concave anterior margin (Text-fig. 10). The iliac craniodorsal tubercle is very pointed and projects strongly anterodorsally. The ventral margin bears peduncles anteriorly and ventrally for articulation with the ischium. The anterior peduncle is incomplete. The acetabular foramen created by the ilium and ischium is small and longer dorsoventrally than it is antero-posteriorly. The supracetabular crest extends along the lateral surface from the iliac craniodorsal tubercle ventrally three-fourths of the distance to the ventral margin of the ilium. Articular surfaces for the first and second sacral ribs are preserved on the medial surface, but their overall shapes cannot be reliably discerned (Text-fig. 10).

Ischium. The ischium of UF/IGM 38 is long and notably curved posteriorly with a straight shaft (Text-fig. 10). The connection between the ischium and ilium is complete posteriorly and incomplete anteriorly. Although the articular surface for the pubis is not completely preserved, it appears to have been oriented at c. 90 degrees from the shaft of the ischium. What is preserved of the ventral surface of the ischium shows no indication of expansion and instead smooths to a point. The preserved portion of the anterior surface thins significantly indicating termination near the antermost preserved surface. The anterior surface is complete up until a severe restriction (see Text-fig. 10) at which point there is minimal missing material as the bone thins significantly. The ischiac blade is long, smooth, thin and lacks any notable rugosities.

Ribs. Two rib fragments were associated with UF/IGM 34 (Text-fig. 7), and two fairly complete ribs were associated with UF/IGM 35 (Text-fig. 9). The most complete rib from UF/IGM 35, a

TEXT-FIG. 6. Referred mandible of *Acherontisuchus guajiraensis*, UF/IGM 35, left articular region only. A, in dorsal view; B, in medial view; C, in lateral view. Abbreviations: ang, angular; art, articular; gf, glenoid fossa; lsrap, lateral shelf of the retroarticular process; sa, surangular. Scale bar represents 10 cm.



TEXT-FIG. 7. UF/IGM 34, holotype of *Acherontisuchus guajiraensis*. A, associated tooth in lingual view; B, same associated tooth from A in posterior view, with its carina labelled; C, associated tooth in lingual view; D, associated tooth in labial view with striations labelled; E, associated rib fragment; F, associated rib fragment. Scale bar represents 5 cm.

mid-thoracic, clearly shows the vertical orientation typical of dyrosaurids (Schwarz-Wings *et al.* 2009) and bears a median crest along its lateral surface. The ribs are otherwise flat and smooth.

Femur. A femur (UF/IGM 39) was collected with UF/IGM 36 and is assigned to *A. guajiraensis*. The femur is sigmoidally curved with a straight shaft (Text-fig. 11). Relative to the midline of the shaft, the proximal end is angled medially 52 degrees and the distal end is angled laterally 51 degrees. The fourth trochanter is enlarged and clearly visible in cranial view, despite flattening, and is located along the border of the cranial and lateral surface. A shallow oval depression forms the paratrochanteric fossa, anterior to the fourth trochanter. The lateral and medial condyles of the distal extremity are separated by an intercondylar fossa (Text-fig. 11).

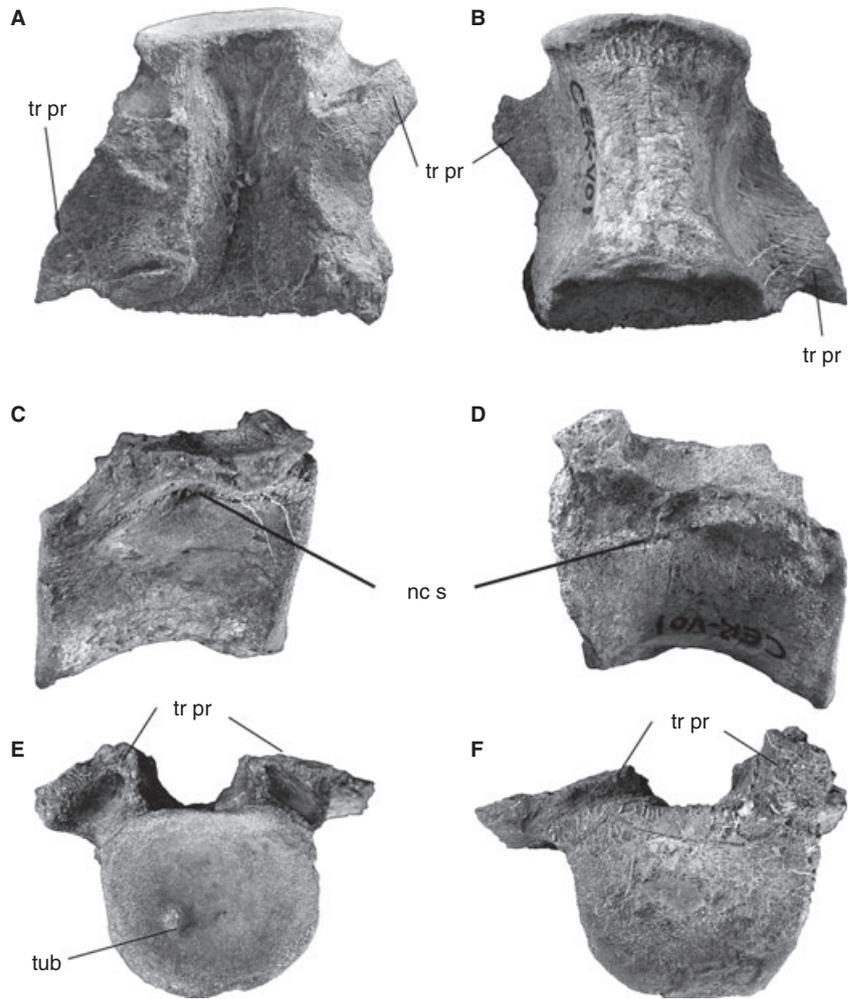
Metatarsal. A single metatarsal was associated with UF/IGM 35 (Text-fig. 9). The metatarsal is lacking its distal end, but possesses the midshaft and proximal portions. The proximal surface is spatulate and becomes progressively thinner towards the proximal-most edge. The proximal articular surface is largely worn away, but still preserves an elongate form (Text-fig. 9). There is

a strong proximodistal groove along the dorsal surface, to one side of the midline. A strong crest forms near the proximal end of the metatarsal, which flares along the edge towards the proximal-most edge of the bone. Towards the distal end, a slight constriction occurs for the distal head of the metatarsal, which has been collapsed atop the plantar surface.

Comparison

General. The snout proportions for UF/IGM 34 and 35 were estimated based on minimum and maximum likely skull lengths, resulting in a range of 56–65 per cent for the proportion of the skull composed of the snout (Table 1). The estimated snout proportions of *Acherontisuchus guajiraensis* imply a longirostrine form, unlike the relatively short-snouted condition seen in the other dyrosaurid from this locality, *Cerrejonisuchus improcerus* (Hastings *et al.* 2010). Nevertheless, the snout of *A. guajiraensis* is shorter than such long-snouted dyrosaurids as *Dyrosaurus* (Jouve *et al.* 2006), *Rhabdognathus* (Jouve 2007) and *Atlantosuchus* (Jouve *et al.* 2008a). The snout shape of *Acherontisuchus* is similar in basic structure to dyrosaurids included in the skull shape study conducted by Pierce *et al.* (2009).

TEXT-FIG. 8. Referred dorsal vertebra, UF/IGM 37, of *Acherontisuchus guajiraensis* from the West Extension pit of the Cerrejón coal mine in north-eastern Colombia. This specimen was likely associated with UF/IGM 36 and as such is referred to *A. guajiraensis*. A, dorsal view; B, ventral view; C, left lateral view; D, right lateral view; E, anterior view; F, posterior view. Abbreviations: nc s, neurocentral suture; tub, tuberosity; tr pr, transverse process. Scale bar represents 10 cm.

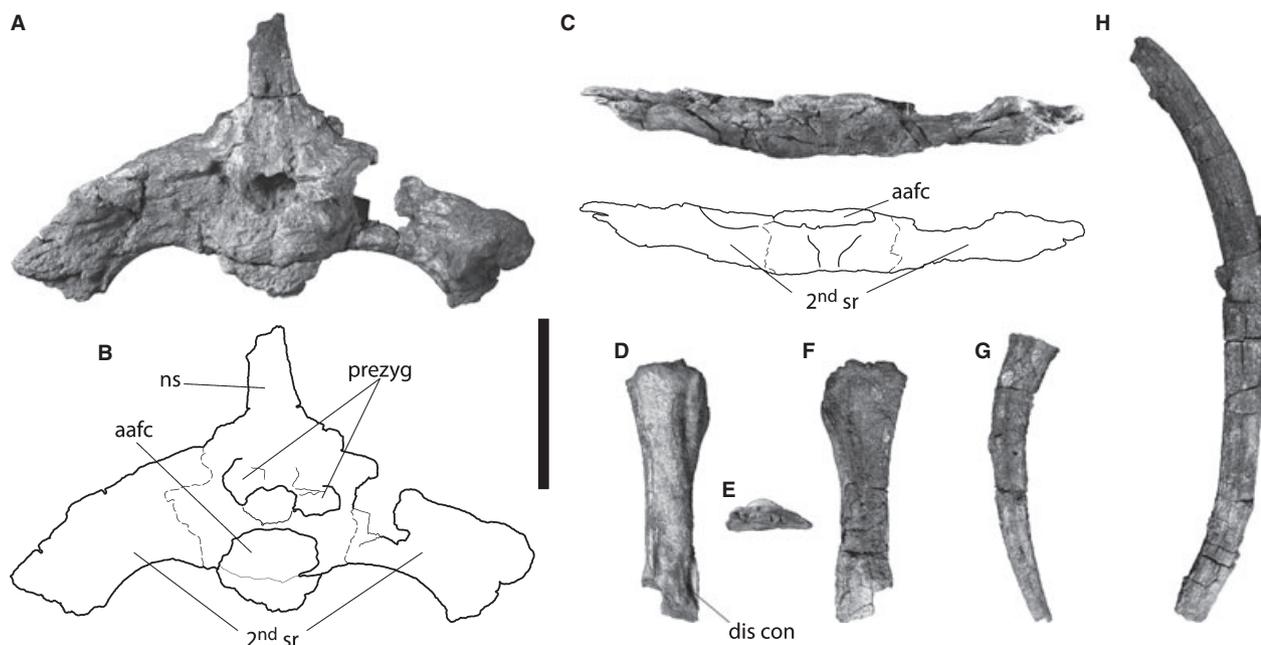


Maxilla. The maxilla of *A. guajiraensis* is straight and not 'festooned' as it is in *Phosphatosaurus* (Buffetaut 1978a) and *Sokotosuchus* (Buffetaut 1979a). The dorsal surface of the maxilla of *A. guajiraensis* is very weakly ornamented, in contrast to that of the shallow longitudinal and spaced furrows of *Dyrosaurus* *maghribensis* (Jouve et al. 2006) or the dorsal and lateral ornamentation of *C. improcerus* (Hastings et al. 2010). The maxillary tooth count (greater than 11) of *A. guajiraensis* is greater than the total tooth count (11) known for skulls of *C. improcerus* (Hastings et al. 2010).

Mandible. The total number of mandibular teeth for *A. guajiraensis* (19–22) is much higher than that of *C. improcerus* (13; Hastings et al. 2010). The number of symphyseal teeth for *A. guajiraensis* (17–19) is similar to that of *D. maghribensis* (17–21; Jouve et al. 2006) but greater than that of *C. improcerus* (9; Hastings et al. 2010) and that of *Hyposaurus derbianus* (12; AH, pers. obs.). The disparity of alveolar size between d7 and d8 of *A. guajiraensis* is much greater than that of *C. improcerus* (Hastings et al. 2010). The anterior extent of the splenials of

A. guajiraensis ranges from between d10 and d11 and between d12 and d13, which is more posterior than the condition seen in *C. improcerus* (between d6 and d7; Hastings et al. 2010), *Hyposaurus rogersii* (d7; Jouve 2007), or *H. derbianus* (d9; AH, pers. obs.). *A. guajiraensis* is instead more similar in this respect to *Arambourgisuchus khouribgaensis* (between d10 and d11; Jouve et al. 2005b) and *D. maghribensis* (d11–d14; Jouve et al. 2006). The symphysis is much wider than high, as measured from the uncompressed holotype (UF/IGM 34), wider than in *Hyposaurus*, *Congosaurus* or *Rhabdognathus* (Text-fig. 12).

The lateral placement of the foramen aereum seen in *A. guajiraensis* has been noted in *Congosaurus bequaerti* (Jouve and Schwarz 2004) and *D. maghribensis* (Jouve et al. 2006), but differs from the foramen's medial placement in extant crocodylians (Iordansky 1973). In extant crocodylians, the foramen allows for a siphonium to connect the internal cavity of the quadrate to the cavity of the articular (Iordansky 1973). Therefore, in dyrosaurids, this cavity in the mandible must instead be located within the surangular. The external mandibular fenestra of *A. guajiraensis* differs from that of *D. maghribensis* in being bound ventrally by the dentary,



TEXT-FIG. 9. Postcranial fossils associated with referred mandible, UF/IGM 35, of *Acherontisuchus guajiraensis*. A–C, second sacral vertebra with sacral ribs in: A, anterior view; B, anterior view, interpretive drawing; C, ventral view and interpretive drawing; D–F, metatarsal (III?) in: D, dorsal view; E, view of proximal articular surface; F, plantar view; G, associated rib; H, associated rib. Abbreviations: 2nd sr, second sacral ribs; aafc, anterior articular facet of the centrum; dis con, distal constriction; ns, neural spine; prezyg, prezygapophyses. Dotted lines indicate sutures between sacral vertebra and sacral ribs. Scale bar represents 10 cm.

not the angular and dentary (Jouve *et al.* 2006), or angular only as it is in *C. bequaerti* (Jouve and Schwarz 2004).

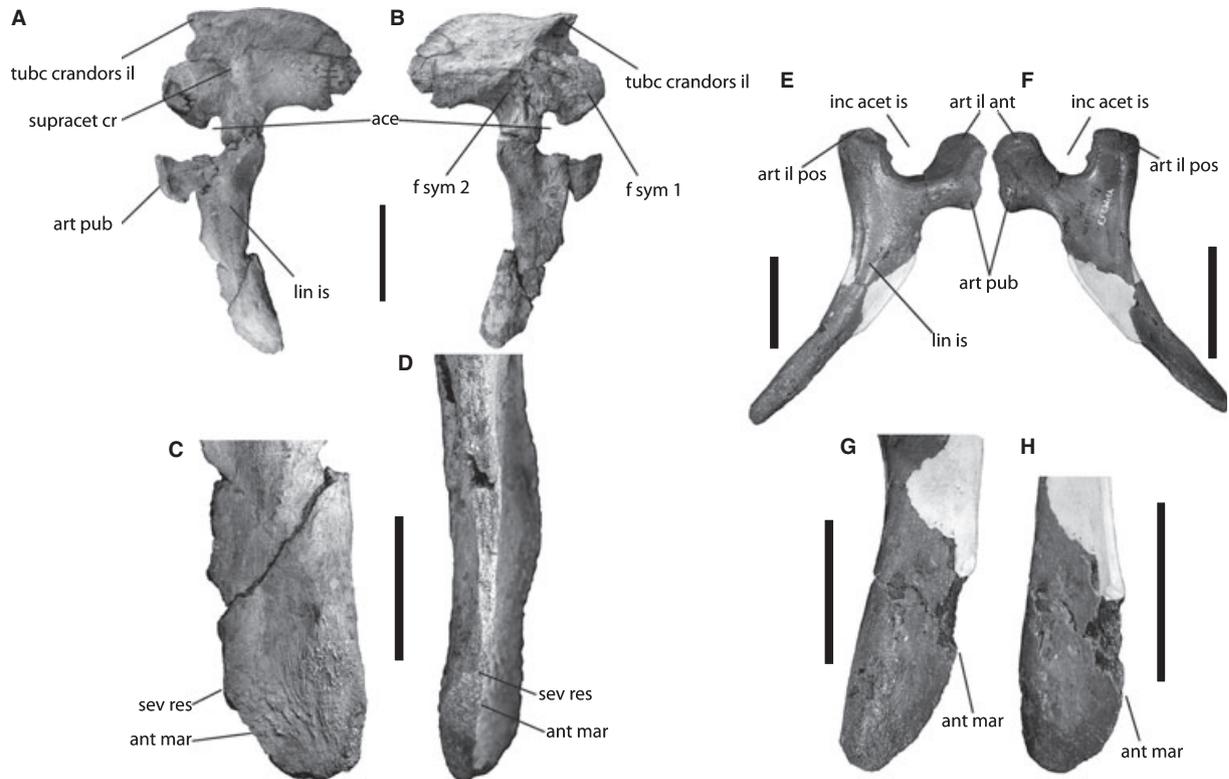
Dentition. The rounded apices of the teeth of *A. guajiraensis* are comparable to those of *C. improcerus* (Hastings *et al.* 2010) and *C. bequaerti* (Jouve and Schwarz 2004). As in *C. bequaerti* (Jouve and Schwarz 2004), *Dyrosaurus phosphaticus* (Jouve 2005), *D. maghribensis* (Jouve *et al.* 2006), *C. improcerus* (Hastings *et al.* 2010) and *H. derbianus* (Cope 1886), the carinae of *A. guajiraensis* are well developed and define the lingual and labial surfaces of the teeth. Like *C. bequaerti* (Jouve and Schwarz 2004), *Dyrosaurus* (Jouve *et al.* 2006) and *Atlantosuchus coupatezi* (Jouve *et al.* 2008a), *A. guajiraensis* possesses striations on at least some of its teeth, unlike the smooth surfaces of the teeth of *C. improcerus* (Hastings *et al.* 2010) or described for *Chenanisuchus lateroculi* (Jouve *et al.* 2005a). Teeth of *A. guajiraensis* are only weakly laterally compressed at certain portions of the jaw (see Text-fig. 7), not strongly laterally compressed as described for *C. lateroculi* (Jouve *et al.* 2005a).

Dorsal Vertebra. In ventral view, the centrum of UF/IGM 37 exhibits the hourglass shape typical of Dyrosauridae (Schwarz *et al.* 2006). For *A. guajiraensis*, the ventral width at the central constriction is 64 per cent shorter than at the caudal margin, very similar to that described for Hyposaurinae (2/3 or 67 per cent). In lateral view, UF/IGM 37 has a centrum with a height/length ratio of 71 per cent, which makes it more similar to the 2/3 ratio of the post-eighth dorsal verte-

brae of Hyposaurinae, as opposed to 1/3 for the first through eighth (Schwarz *et al.* 2006). Also in lateral view, the length of the centrum when measured along the ventral margin is 3 per cent shorter than when measured at the neurocentral suture, similar to the 5 per cent stated for Hyposaurinae (Schwarz *et al.* 2006).

The placement of the small rounded tubercle on the anterior surface of UF/IGM 37 at the lower right centre of the anterior articular facet is unique among described dyrosaurid taxa (Text-fig. 8). Tubercles have only been mentioned once before for dorsal vertebrae: a dorsal vertebra of *Congosaurus* was described as having a circular dorsomedially positioned tubercle (Schwarz *et al.* 2006). However, tubercles have been mentioned for other segments of the vertebral column. Schwarz *et al.* (2006) mention a very dorsally placed tubercle on the anterior articular surface of a cervical vertebra of *Dyrosaurus* sp., SMNK-PAL 3826 55/94. Tubercles have also been described on the sacral vertebrae of *Dyrosaurus* sp., SMNK-PAL 3826 69/94, and *Hyposaurus*, YPM 753 (Schwarz *et al.* 2006).

Sacrum. Schwarz *et al.* (2006) mention two parallel, dorsoventrally oriented sulci present on the caudal surface of the second sacral vertebrae that appear not to be present in UF/IGM 35. As in *Dyrosaurus* sp. (SMNK-Pal 3826 69/94), the second sacral rib of UF/IGM 35 is hourglass-shaped in ventral view (Text-fig. 9). As in *D. maghribensis*, the second sacral rib of UF/IGM 35 covers nearly the entire lateral surface of the second sacral vertebra (Jouve *et al.* 2006).

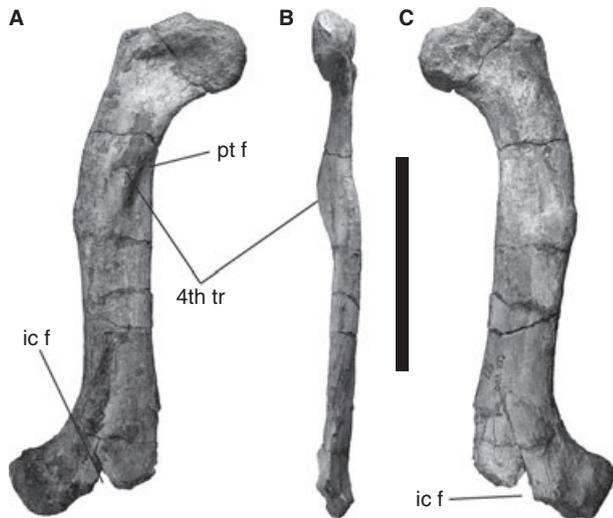


TEXT-FIG. 10. New-World dyrosaurid pelvis fossils. A–D, referred left ilium and ischium, UF/IGM 38, of *Acherontisuchus guajiraensis* from the West Extension pit of the Cerrejón coal mine in north-eastern Colombia. This specimen was likely associated with UF/IGM 36 and as such is referred to *A. guajiraensis*. A, lateral view; B, medial view; C, lateral view of distal ischiac blade; D, anterior view of distal ischiac blade. E–G, right ischium of *Hyposaurus natator oweni* (YPM 753), referred to *Hyposaurus rogersii* in Denton *et al.* (1997). E, lateral view; F, medial view; G, lateral view of distal ischiac blade; H, anterior view of distal ischiac blade. Abbreviations: ace, acetabulum; ant mar, anterior ischiac margin; art il ant, anterior articular surface for the ilium; art il pos, posterior articular surface for the ilium; art pub, articular surface for the pubis; f sym 1, articular surface for the first sacral rib (*facies symphyialis costa sacralis* 1); f sym 2, articular surface for the second sacral rib (*facies symphyialis costa sacralis* 2); inc acet is, incision of acetabular foramen; lin is, ischiac crest separating cranio-lateral and caudolateral margins of lateral surface (*linea arcuata ischii*); sev res, severe restriction of anterior ischiac margin; supracet cr, supracetabular crest; tubc crandors il, iliac craniodorsal tubercle. Scale bar for A–B represents 10 cm, scale bar for C–H equals 5 cm. Images of YPM 753 are copyright of the Division of Vertebrate Paleontology, YPM 753. © 2010 Peabody Museum of Natural History, Yale University, New Haven, CT, USA. All rights reserved.

Ilium. The ilium of UF/IGM 38 possesses a dorsal iliac wing similar to *Congosaurus* (Schwarz *et al.* 2006) and cf. *Hyposaurus* (Storrs 1986), in that the indentation caudal to the craniodorsal tubercle is very slight, with the rest of the margin being smooth and shallowly convex. In *Hyposaurus natator* (Troxell 1925), there is a broad concavity caudal to the craniodorsal tubercle. However, the concavity cranial to the craniodorsal tubercle is much stronger in UF/IGM 38 than it is in either *Congosaurus* or cf. *Hyposaurus*, and is more similar to the concavity seen in *Hyposaurus natator*.

Ischium. The ischium of UF/IGM 38 is also more similar to that of *Hyposaurus natator* (Troxell 1925, fig. 11; YPM 753) than that of other known dyrosaurids. Neither UF/IGM 38 nor YPM 753 is completely preserved, but the preservation of UF/IGM 38 suggests the same thin recurved, narrow shaft interpreted for *H. natator* (Text-fig. 10), not the robust thick, vertically oriented column seen in *Dyrosaurus* sp. (SMNK 3826

73/94; Schwarz *et al.* 2006) or *D. maghribensis* (OCP DEK-GE 252 and 254; Jouve *et al.* 2006). The ischium of *Acherontisuchus* has a more slender shaft than *D. maghribensis*, as measured by the ratio of the minimum anteroposterior width of the ischial shaft to the proximodistal shaft length from the level of the cranio-lateral depression, below the articulation for the pubis, to its distal-most extent (*A. guajiraensis*, 0.31 for UF/IGM 38; *D. maghribensis*, 0.45 for OCP DEK-GE 254 and 0.57 for OCP DEK-GE 254, as determined from fig. 17 in the study by Jouve *et al.* 2006). In addition, the ischial shaft of *A. guajiraensis* is more slender relative to the ilium than in *D. maghribensis*, as measured by the ratio of minimum anteroposterior width of the ischial shaft to anteroposterior length of the ilium (*A. guajiraensis*, 0.25 for UF/IGM 38; *D. maghribensis*, 0.36 for OCP DEK-GE 254 and 0.35 for OCP DEK-GE 252, as determined from fig. 17 in the study by Jouve *et al.* 2006). Preservation of *Dyrosaurus* sp. (SMNK 3826 73/94) is too incomplete for these ratios to be measured. Were the unpreserved portion to flare

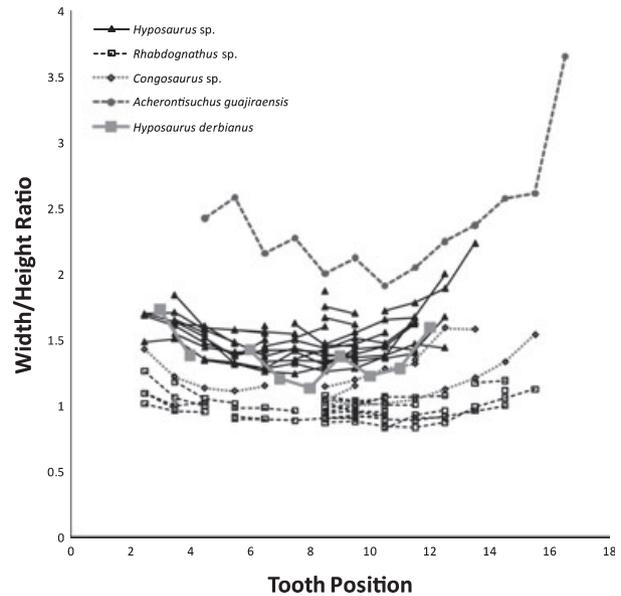


TEXT-FIG. 11. Referred femur, UF/IGM 39, of *Acherontisuchus guajiraensis* from the West Extension pit of the Cerrejón coal mine in north-eastern Colombia. This specimen was likely associated with UF/IGM 36 and as such is referred to *A. guajiraensis*. A, lateral view; B, anterior view; C, medial view. Abbreviations: 4th tr, fourth trochanter; ic f, intercondylar fossa; pt f, paratrochanteric fossa. Scale bar represents 10 cm.

out (unexpectedly), the shape would still be much narrower than that seen in *Dyrosaurus*. The angle between the articulation points of the ischium and pubis for *A. guajiraensis* is around 90 degrees, very similar to that figured in Troxell (1925) for *H. natator* (YPM 753). These are both very different from the c. 30 degree separation reconstructed for Hyposaurinae (Schwarz-Wings *et al.* 2009). Both *Dyrosaurus* and *Congosaurus* are known exclusively from Africa and have been discussed as having robust ischia (Swinton 1950; Schwarz *et al.* 2006). Both known ischia of the New World, *H. natator* and *A. guajiraensis*, are associated with ilia that have prominent iliac craniodorsal tubercles.

Ribs. A nearly complete rib associated with UF/IGM 35 (Text-fig. 9) shows the clear vertical orientation, typical of Dyrosauridae, but not seen in eusuchians (Schwarz-Wings *et al.* 2009). As in *Congosaurus*, it bears a median crest on its lateral surface (Schwarz *et al.* 2006). The rib fragments are also flat and blade like, as was described for cf. *Rhabdognathus* (Langston 1995). The capitular and tubercular processes are missing in all specimens, preventing further comparison.

Femur. A femur, UF/IGM 39, is similar to other dyrosaurid femora in its overall sigmoidal shape and longitudinal shaft (Text-fig. 11). Despite flattening, the fourth trochanter is especially large for the family and the paratrochanteric fossa is deeper than the shallow pit seen in *Congosaurus bequaerti* (Schwarz *et al.* 2006). The angle of the proximal head relative to the midline of the shaft is 52 degrees in *A. guajiraensis*, comparable to the angle of c. 45 degrees reported for Hyposaurinae (Schwarz *et al.* 2006).



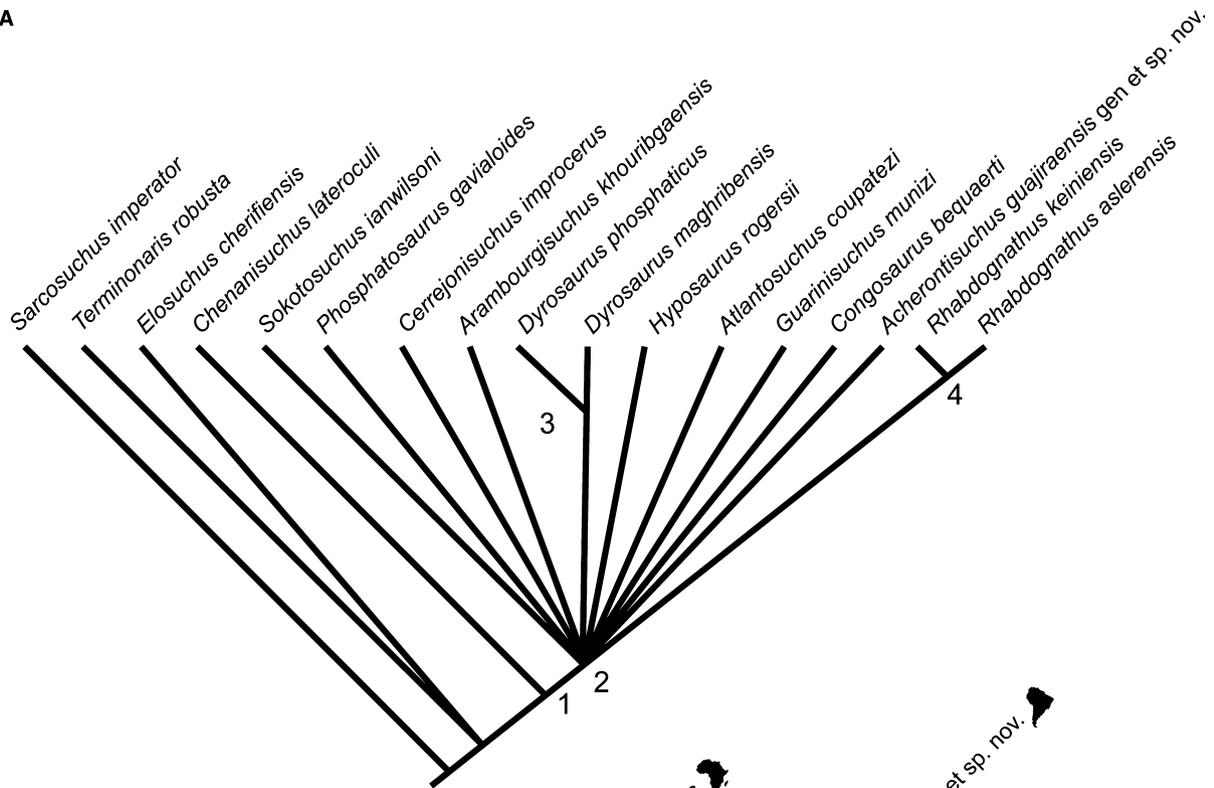
TEXT-FIG. 12. X–Y scatter plot depicting width/height ratios along the mandible, 1 being the most anterior tooth alveolus, for several genera of Dyrosauridae. The new taxon described herein (*Acherontisuchus guajiraensis*) has a wider snout in relation to the height as compared to other similar dyrosaurids. Width was measured from left to right external alveolar walls. Height was measured dorsoventrally at the midpoint of the mandible. Data for all taxa except *A. guajiraensis* and *Hyposaurus derbianus* are from the study by Jouve (2007). Measurements for *A. guajiraensis* were taken from the holotype as compression of UF/IGM 35 made it impractical to include. UF/IGM 36 was not included as tooth position could not be reliably ascertained from the fossil.

Metatarsal. Metatarsals are known for cf. *Rhabdognathus* (Langston 1995), *Congosaurus* (Jouve and Schwarz, 2004), *D. maghribensis* (Jouve *et al.* 2006) and *Hyposaurus* sp. (Schwarz *et al.* 2006), but little about their individual morphology has been published. Based on comparison to modern *Alligator* and cf. *Rhabdognathus* (Langston 1995, fig. 29), the metatarsal of UF/IGM 35 seems most similar to metatarsal III, using overall shape in dorsal/plantar views and the articular surface (Text-fig. 9).

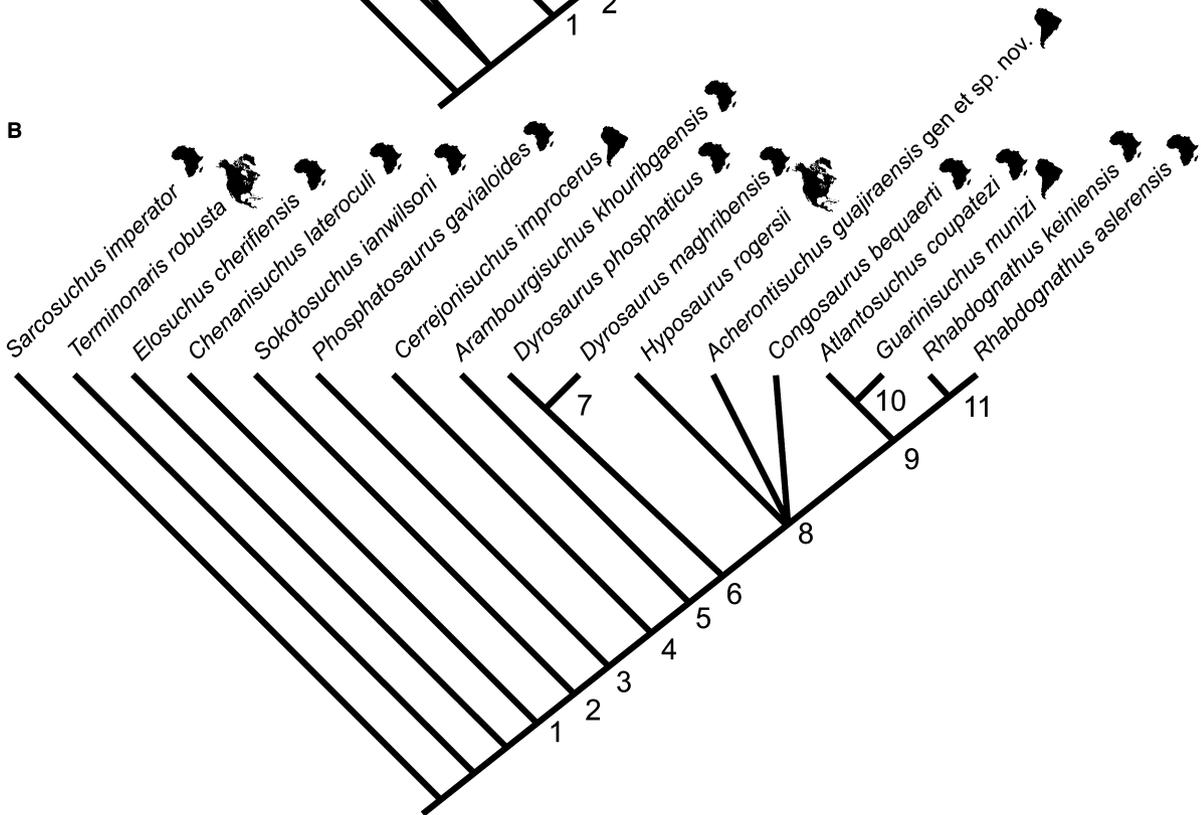
PHYLOGENETIC RELATIONSHIPS

A matrix of 82 morphological characters (including cranial, mandibular and one postcranial character) was used to assess the ingroup relationships of Dyrosauridae by Hastings *et al.* (2010). That study included all species known from skulls and/or nearly complete mandibles, for a total of 16 taxa, including 3 outgroups. The only known dyrosaurid fossil from Europe, a mandibular symphysis fragment from Portugal, was not included in that analysis as it could not be identified beyond family (Buffetaut and

A

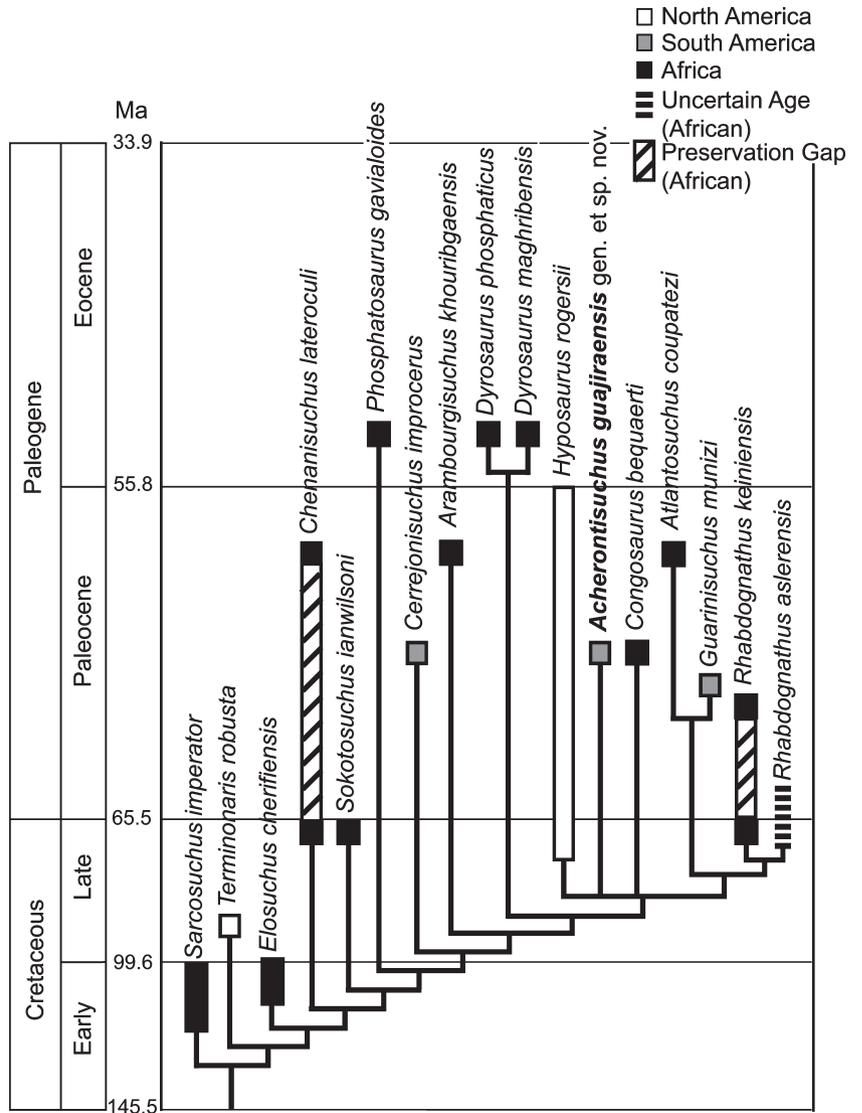


B



TEXT-FIG. 13. Strict consensus cladograms from phylogenetic analyses of Dyrosauridae. Character matrix contained 82 characters and 17 taxa, including 3 outgroup (see the study by Hastings *et al.* 2010 and Table 2). A, Strict consensus of 15 equally parsimonious cladograms from a branch and bound search using both ordered and unordered characters. Tree lengths: 172 each; C.I.: 0.541; R.I.:0.639; R.C.:0.346; H.I.: 0.459. B, 50 per cent majority rule consensus of the same analysis; support at nodes are 1, 100 per cent; 2, 100 per cent; 3, 73 per cent; 4, 73 per cent; 5, 73 per cent; 6, 73 per cent; 7, 100 per cent; 8, 73 per cent; 9, 87 per cent; 10, 87 per cent; 11, 100 per cent.

TEXT-FIG. 14. Majority-rule consensus tree of phylogenetic analysis placed in stratigraphic and palaeobiogeographic context. Geologic dates from Gradstein *et al.* (2004).



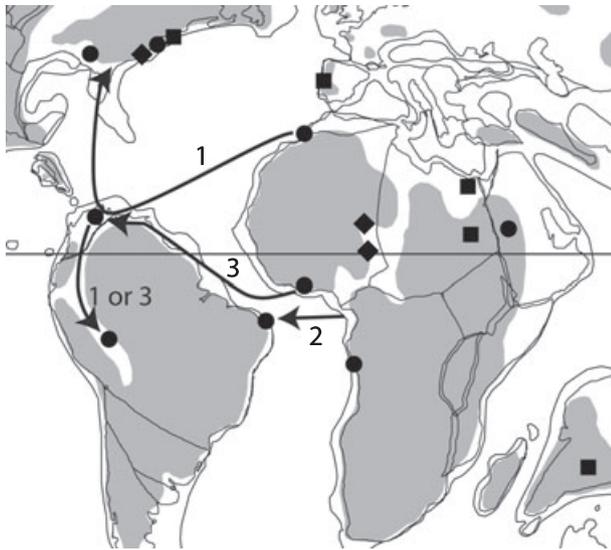
DISCUSSION

Dispersal

The concept of an African origin for Dyrosauridae has existed in the literature for nearly 30 years. Buffetaut (1981) proposed an African origin and argued for a Tethyan dispersal both east and west for the family emanating from Africa. His reasoning for this scenario stemmed from the much higher known diversity of dyrosaurids from Africa than any other area, as well as ancient oceanic currents. Models of the Tethys and proto-Atlantic suggested that an oceanic current flowed from Africa and Europe east to west across the proto-Atlantic, towards South America, then curved towards what is now the Gulf of Mexico, continuing east along the eastern coast of North America (Berggren and Hollister 1974). Furthermore, sea

surface temperatures for the Turonian (93.5–89.3 Ma) were likely very warm, around 32°C (Poulsen *et al.* 2001). Warm temperatures would aid in the long-range dispersal of poikilothermic reptiles such as dyrosaurids. The ancient oceanic current and sea surface temperatures of the proto-Atlantic waters thus explain very well the occurrences of dyrosaurids in the New World (Text-fig. 15). In addition, a study has shown modern crocodylians’ ability to disperse in marine waters using their natural buoyancy to coast along currents (Campbell *et al.* 2010), a trait which may have been present in dyrosaurids as well.

Dyrosaurid biogeography was tested empirically first by Jouve *et al.* (2005b). In this study, eight genera of Dyrosauridae were entered into a phylogenetic analysis, then geographic data were added to elucidate the place of origin of the family. *Hyposaurus rogersii* was the only representative of the family included from the New World. In the



TEXT-FIG. 15. Proposed routes for three independent dyrosaurid dispersal events from Africa to the New World. Numbers correspond to dispersal descriptions provided in text. Symbols: squares, Late Cretaceous dyrosaurids; circles, Paleocene dyrosaurids; diamonds, areas that have both Late Cretaceous and Paleocene dyrosaurids. Map of Late Cretaceous from Scotese (2001).

analysis, this North American taxon fell out as a derived relative to several African taxa, and for this reason, Jouve *et al.* (2005b, 2008a) supported an African origin of the family. Jouve *et al.* (2008a) went on to suggest dispersal from Africa to North America, but no specific dispersal route was proposed. Hill *et al.* (2008) conducted a phylogenetic analysis using an expanded version of the Jouve *et al.*'s (2005b) matrix and also found support for an African origin of Dyrosauridae. Barbosa *et al.* (2008) conducted an analysis using the matrix of Jouve *et al.* (2005b) and proposed that '...before the end of the Cretaceous, dyrosaurids could have crossed the Atlantic Ocean from the western coast of Africa to ... Brazil ... From there they could have dispersed northwards along the coast reaching North America and other areas of the South American continent...' (Barbosa *et al.* 2008, p. 1389). This dispersal hypothesis was further corroborated by Hastings *et al.* (2010), who also found support for multiple dispersals to the New World, based on a new cladistic analysis. Multiple dispersals are supported again by the current analysis, which shows separation of *C. improcerus* from the derived polytomy including all other New-World taxa.

Results from the current analysis, while less resolved than reported by Hastings *et al.* (2010), still support an African origin for Dyrosauridae. Furthermore, while far from definitive, results from the 50 per cent Majority Rule consensus cladogram have *Cerrejonisuchus* and *A. guajiraensis* separated by *Arambourgisuchus* and *Dyrosaurus*, and *Guarinisuchus* is nested within an African

clade that includes *Atlantosuchus* and *Rhabdognathus*. This result suggests the possibility of at least three independent dyrosaurid dispersals to the New World. Moreover, 9 of the 15 MPTs from which the 50 per cent Majority Rule tree was derived support three dispersals, with five others supporting four dispersals. One topology suggested three dispersals with a single back-dispersal from the New World to the Old World. Assuming this is correct, each dispersal would likely have taken place along similar routes from western Africa, along the paleo-current of the proto-Atlantic (Berggren and Hollister 1974) to South America (Text-fig. 15). One dispersal of a marine dyrosaurid from western Africa, during or before the Late Cretaceous (based on the Maastrichtian age of *H. rogersii* see Text-fig. 14) could have given rise to *Acherontisuchus* from the mid-late Paleocene of Colombia and *H. rogersii* from the Late Cretaceous–Paleocene of North America (labelled 1 in Text-fig. 15). The *H. rogersii* lineage could have dispersed northward to the east coast of North America. There is a temporal problem with this hypothesis, though, in that these dyrosaurids are known from the Late Cretaceous of North America, but only the Paleocene of South America. However, this discrepancy is potentially because of sampling bias. A second dispersal following the current of the proto-Atlantic likely gave rise to *Guarinisuchus* from the early Paleocene of Brazil (labelled 2 in Text-fig. 15). A third dispersal would have been of a marine ancestor of *Cerrejonisuchus* that moved across the proto-Atlantic and into Colombia sometime before the mid-late Paleocene (labelled 3 in Text-fig. 15).

Dyrosaurids would then have dispersed from Colombia southward along a paleo-shoreline, accounting for the occurrence of dyrosaurid fossils from the Paleocene of Bolivia (labelled '1 or 3' in Text-fig. 15; Buffetaut 1991). Owing to the fragmentary nature of the Bolivian fossils, it is unclear which ancestral stock would have made the southward expansion, but it likely would have been the first or third because of fossils occurring in Colombia in each of these events. Owing to ocean currents moving in the opposite direction at this time (Berggren and Hollister 1974), dispersal from Europe to North America is unlikely. The dominant direction of current in the central Atlantic is east-to-west, with both the north and south equatorial currents. The equatorial countercurrent flows west-to-east between these two currents, returning water to the eastern Atlantic (Fratantoni 2001). Owing to the older occurrence of dyrosaurids in Africa (Text-fig. 14), and the phylogenetic origin of the family in Africa, we suggest dyrosaurids likely dispersed utilizing the dominant equatorial currents, with a back-dispersal along the equatorial countercurrent being unlikely.

Dispersal from Africa to South America has been proposed for a diversity of vertebrate groups, which may have been assisted by the possible existence of marine

islands in the central Atlantic during ocean spreading. There are a few volcanic islands in the mid-Atlantic today, many of which are part of volcanic lines (e.g. Cameroon volcanic line; Aka *et al.* 2001) and archipelagos (e.g. Fernando de Noronha archipelago; Almeida 2002), forming linear island groupings. As Africa and South America separated, the narrow trough may have had small islands at the mid-ocean spreading ridge, further enabling cross-ocean dispersal (Carr and Coleman 1974). The east-to-west equatorial currents (Poulsen *et al.* 2001) would have assisted travel from the mid-Atlantic towards the South American coast. The possible existence of ancient islands in the central Atlantic has been proposed to explain dispersal in such organisms as the green sea turtle (*Chelonia mydas*; Carr and Coleman 1974).

In addition, platyrrhine monkeys and caviomorph rodents made the transition from Africa to South America postcontinental separation some time prior to their first occurrences in the Oligocene (Houle 1999; Huchon and Douzery 2001; Poux *et al.* 2006). Ancestors of the skink genus *Mabuya* are thought to have immigrated twice from Africa to South America in the last nine million years, long after the two continents separated (Carranza and Arnold 2003). Evidence for tortoise dispersal from Africa to South America postseparation was found by Le *et al.* (2006) using mitochondrial and nuclear genes, and must have occurred before the first fossils in the Miocene (Auffenberg 1971). Perhaps most surprisingly, the burrowing amphisbaenids, or worm lizards, of the New World were found to have dispersed across the Atlantic during the Eocene, again using mitochondrial and nuclear genes (Vidal *et al.* 2007). Late Cretaceous dinoflagellates also show a strong interchange between Africa and tropical America, the 'Malloy suite' (Lentin and Williams 1980). Finally, plants continued to have a strong interchange between Africa and South America during the Late Cretaceous, the 'Palmae province' of Herngreen and Chlonova (1981).

Palaeobiology

While postcrania attributed to Dyrosauridae are known from many localities, most of what has been inferred with regard to positional behaviours has come from well-preserved skeletons of *Dyrosaurus* from the Eocene of Morocco and a nearly complete skeleton of *Congosaurus* from Angola (Schwarz *et al.* 2006). In general, dyrosaurids have been reconstructed as being shallow, near-shore marine animals utilizing axial swimming, typical of extant crocodylia, with perhaps greater tail undulatory frequency and more powerful forward thrust generated by expanded muscles of the tail (Schwarz-Wings *et al.* 2009). The associated postcranial elements of *A. guajiraensis* allow for

some interpretation of its functional morphology. Of particular interest is the morphology of the ribs, femur and pelvis that can reflect aspects of locomotion and respiration in crocodyliforms. As for other known dyrosaurids (e.g. Schwarz-Wings *et al.* 2009), the ribs of *A. guajiraensis* are vertically orientated. This orientation has been interpreted as allowing for expanded *m. iliocostalis*, as well as altering the angle of attachment to the craniodorsal tubercle of the ilium (Schwarz-Wings *et al.* 2009). The *m. iliocostalis* activates during axial swimming and contributes to lateral flexion in *Crocodylus porosus* (Macdonald 2005), and the expanded contact for the *m. iliocostalis* implies its use would have been more extensive in dyrosaurids than in extant crocodylians (Schwarz-Wings *et al.* 2009). Even if muscle force is greater in this region in dyrosaurids, range of flexion/extension may have been comparable to modern crocodylians because of restrictions of the osteodermal shield in this part of the trunk, as determined for other dyrosaurids (Schwarz-Wings *et al.* 2009). The enlarged fourth trochanter of the femur, paired with the adjacent enlarged paratrochanteric fossa, would presumably allow for a more extensive attachment of *m. caudofemoralis longus* that controls hip flexion and retraction of the femur (Schwarz-Wings *et al.* 2009).

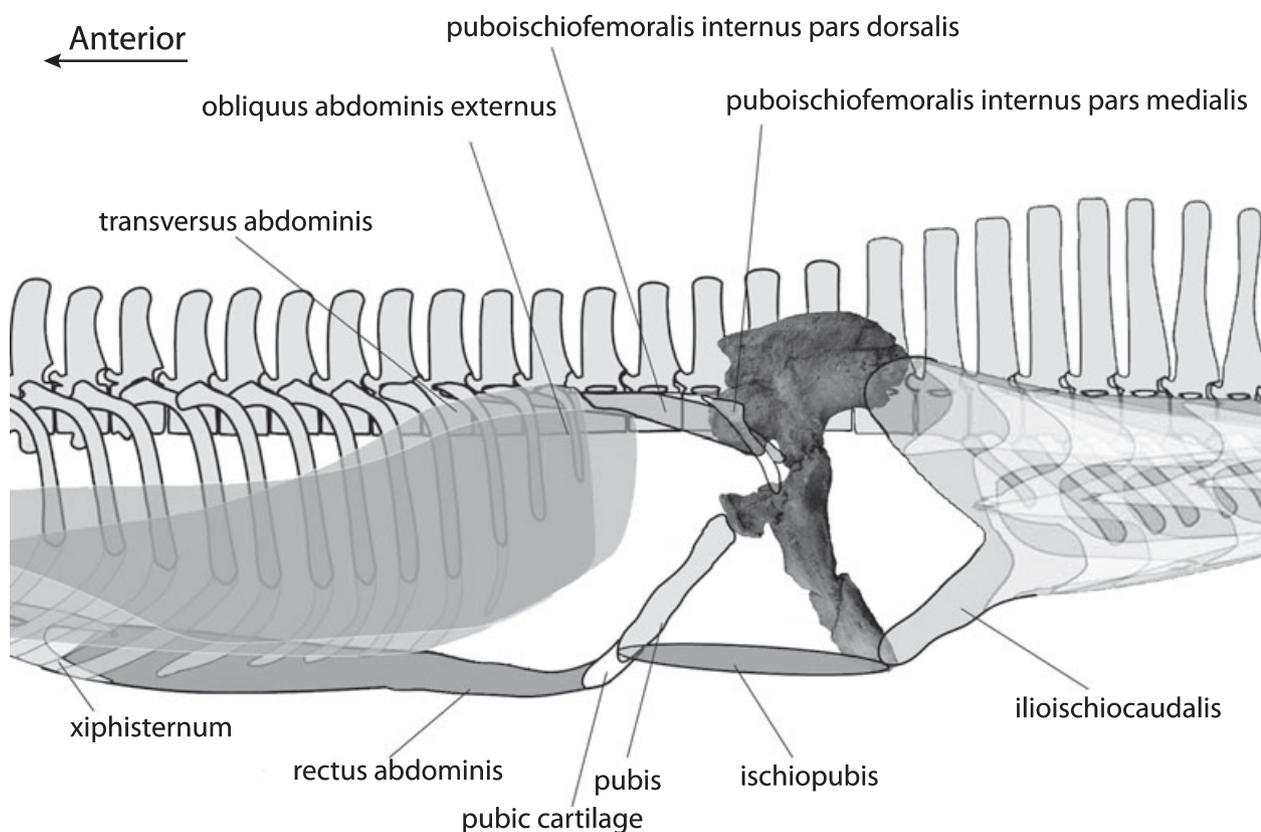
Prior to this study, ischial blades were published for three dyrosaurids from Africa and one from North America. The ilium and ischium of UF/IGM 38 are the first known from South America (Text-fig. 10), and only the second nearly complete ones from the New World. The North American dyrosaurid pelvis, YPM 753, of *Hyposaurus natator* (Troxell 1925; but referred to *Hyposaurus rogersii* by Denton *et al.* 1997) has an elongate posteriorly angled ischium and was found in Late Cretaceous marine deposits of New Jersey (Text-fig. 10). There is another partial pelvis of *Hyposaurus natator*, YPM 985, but the ischial shaft was not preserved. The pelvis of dyrosaurids from the Old World consistently bears a robust, dorsoventrally orientated ischium, seen in *Dyrosaurus maghribensis* (OCP DEK-GE 252 and 254; Jouve *et al.* 2006) and *Dyrosaurus* sp. (SMNK 3826 73/94; Schwarz *et al.* 2006). A nearly complete ilium and partial ischium of an indeterminate dyrosaurid (GSP 1020; Storrs 1986) was recovered from near shore marine deposits of the late Paleocene of Pakistan, but the ischial shaft is not preserved. Another pelvis was found in lagoonal/estuarine sediments from the Paleocene of Saudi Arabia, but only the pubis was figured (Langston 1995), and this specimen (USGS SAP 37-CR-1) does not possess the distal portion of the ischium.

In extant crocodylians, the vertebral column undergoes dorsal extension via contraction of epaxial muscles of the trunk, leading to tension in the *m. ilioischiocaudalis* and *m. rectus abdominis* during locomotion. Dominant load-

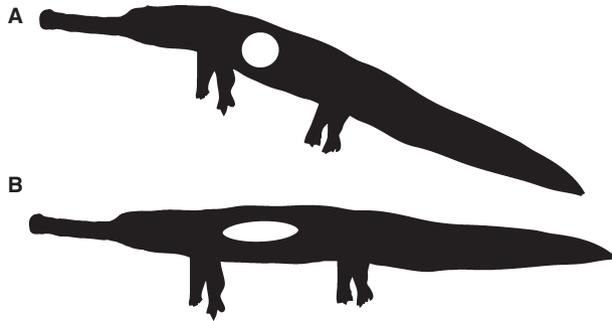
ing in this circumstance occurs during terrestrial movement when the weight of the body is supported only by the limbs (Schwarz-Wings *et al.* 2009). The *m. ilioischio-caudalis* originates dorsally on the caudal tuber of the ilium and originates ventrally on the ventral margin of the ischiac wing (Text-fig. 16; Schwarz-Wings *et al.* 2009). The *m. rectus abdominis* does not attach to the ischium directly, but originates anteriorly at the xiphisternum and postermost sternocostal ribs and inserts posteriorly at the pubic cartilage, which in turn serves as an attachment point for the *m. ischiopubis* (Schwarz-Wings *et al.* 2009). The *m. ischiopubis* muscle connects the pubis with the ischium. Both *m. ischiopubis* and *m. rectus abdominis* are utilized in pitch control during diving, with higher activity when weight is added to the tail (Uriona and Farmer 2008). The relatively large cross-sectional area of the tall tail-base, typical of dyrosaurids (Schwarz-Wings *et al.* 2009), and the weight associated with a larger tail may also be involved in this motion. Alteration of pitch is accomplished in this manner as the muscle pulls the viscera caudally, moving air in the lungs posteriorly. Air positioned more posteriorly increases the buoyancy of the

posterior end of the body while simultaneously decreasing the buoyancy of the cranial end, thus altering pitch within the water column (Text-fig. 17; Uriona and Farmer 2008).

Acherontisuchus guajiraensis likely had reduced surface area on the ischial shaft for muscle attachments relative to known Old-World dyrosaurids, because of its slender shape and narrow proportions (Text-fig. 10). Despite incomplete preservation, the shape and proportions of the ischial shaft are clearly different from those of *Dyrosaurus* from the Eocene of Africa (see Comparison), with a distinctly narrower shaft. The reduced size of the ischial shaft of *A. guajiraensis* in turn would imply reduced size and therefore less application of the *m. rectus abdominis* and *m. ischiopubis* for respiration and pitch control in water. The difference in ischial shaft morphology of *A. guajiraensis* may in fact reflect the freshwater habit for *A. guajiraensis*, as inferred from the sedimentological context and associated faunas and floras, a shallow aquatic environment where these features may have been less necessary than in the deeper water marine habitat typical of dyrosaurids (Denton *et al.* 1997). *Dyrosaurus* is inter-



TEXT-FIG. 16. Reconstruction of skeleton of *Acherontisuchus guajiraensis*, with muscle attachments to pelvic region. Fossil is UF/IGM 38, skeleton and muscle attachments modified by Schwarz-Wings *et al.* (2009). Pubic bone is not preserved, and its girth and length are estimated here based on pubic bones figured by Schwarz-Wings *et al.* (2009). The angle of attachment of the pubis is based on the preserved articulation point of UF/IGM 38.



TEXT-FIG. 17. Pitch regulation in a generalized dyrosaurid crocodyliform. A, lungs are compressed towards the anterior portion of the pleural cavity, resulting in reduced buoyancy of the posterior end of the body and thus a less linear position. B, pleural cavity is pulled posteriorly, resulting in greater buoyancy for the posterior portion of the body and a more linear position.

preted as occupying a marine habitat as an adult (Jouve *et al.* 2008b) and is therefore likely a more aquatic animal than *A. guajiraensis* and/or lived within more turbid waters, requiring greater pitch-correction. *Hyposaurus* in North America may lack the robust ischial shaft because it is the primitive condition, and it is much older (Maastriichtian) than *Dyrosaurus* (Ypresian). *A. guajiraensis* likely would have occupied calmer waters and engaged in shorter dives than *Dyrosaurus*, requiring it to hunt either closer to the surface or in a more fluvial, terrestrial setting. This paleobiological interpretation is further supported by the expansion of muscle attachment in the femur and ribs for the trunk of *A. guajiraensis*. These features combined imply that *A. guajiraensis* possessed a different lifestyle from Old-World hyposaurine dyrosaurids.

Acherontisuchus guajiraensis likely would have been between 4.66 and 6.46 m in adult body length (see Table 1), much larger than the other described dyrosaurid from this locality, *Cerrejonisuchus improcerus* (1.22–2.22 m). Maturity in *C. improcerus* was confirmed using morphological features of associated vertebrae and osteoderms. Based on size, fusion of the bones in the mandible, and fusion of the sacral ribs to the sacral vertebra associated with the jaw of UF/IGM 35, these size values for *A. guajiraensis* likely reflect adult body size. The size of *A. guajiraensis* was therefore comparable to that of *Rhabdognathus keiniensis* (4.72–5.44 m) and *Dyrosaurus maghribensis* (5.89–7.28 m), and the largest predicted values of *Congosaurus bequaerti* (3.97–4.66 m). *A. guajiraensis* was likely larger than *Chenanisuchus lateroculi*, *Guarinisuchus munizi*, *Hyposaurus rogersii* and *Sokotosuchus ianwilsoni*. Even at the largest predicted sizes, it was likely smaller than *Phosphatosaurus gavialoides*, *Arambourgisuchus khouribgaensis*, *Dyrosaurus phosphaticus* and *Atlantosuchus coupatezi*.

Buffetaut (1981) described Dyrosauridae as an extinct family of particularly marine crocodyliform. However, dyrosaurids have been found previously in freshwater and potentially freshwater deposits in Burma (Buffetaut 1978b), Pakistan (Buffetaut 1978c), India (Rana 1987; Prasad and Singh 1991; Khosla *et al.* 2009), Sudan (Buffetaut *et al.* 1990), Kenya (Sertich *et al.* 2006), Bolivia (Buffetaut 1991) and Colombia (Hastings *et al.* 2010). Dyrosaurids have yet to be found in freshwater deposits of North America. Of these records, only the Colombian dyrosaurids are known from fossils preserved well enough for identification beyond the family level.

The sediments of the Cerrejón Formation indicate a coastal influence and may represent a transition between the marine habitat of most dyrosaurids and a more fully fluvial environment. Buffetaut (1978c) proposed the idea that dyrosaurids may lay eggs inland then spend most of their adult life in coastal waters. Thus, the young would live inland until they reached larger size then move coastward. Buffetaut (1978c) proposed this to account for the apparent smaller size of freshwater dyrosaurids found in Pakistan. Jouve *et al.* (2008b) use this same idea to account for the entirely adult fossil record of *Dyrosaurus* in Morocco within marine deposits. However, there does seem to be some variation, and larger dyrosaurid individuals are known from freshwater deposits. In the same publication as the proposed idea, Buffetaut (1978c, p. 17–18) described the freshwater dyrosaurid vertebral fossils as such: ‘Most of those vertebrae are rather small (about 4 cm long) for dyrosaurids, especially Eocene ones. However, a few specimens ... are fairly large ... with centra reaching a length of 7 cm ... and may indicate animals some 5 or 6 m long.’ In addition, the only known dyrosaurid fossil from Burma, found in freshwater deposits, was described as ‘a fairly large dyrosaurid crocodylian’ (Buffetaut, 1978b, p. 275).

Furthermore, all specimens of *Acherontisuchus* and all but one of *Cerrejonisuchus* (Hastings *et al.* 2010) represent mature individuals, and not the expected bias towards immature individuals had the area been a nesting ground. Within this environment, *Cerrejonisuchus* was a more generalized, small-bodied dyrosaurid likely preying upon lizards, snakes and small mammals (Hastings *et al.* 2010). On the other hand, *Acherontisuchus* was a larger, more specialized piscivorous dyrosaurid. So far, dipnoan and elopomorph fossil fishes have been recovered from Cerrejón and were likely prey sources for *Acherontisuchus*. At least in this region of the world, but possibly other regions as well, mature individuals appear to live and specialize within freshwater environments; especially considering the large size of *Acherontisuchus* relative to other dyrosaurids (see Table 1), it seems likely that at least some large dyrosaurids regularly inhabited inland waters.

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