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New cranial and postcranial elements of *Mourasuchus* (Alligatoroidea: Caimaninae) from the late Miocene of Venezuela and their palaeobiological implications

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ABSTRACT

A partial skeleton of *Mourasuchus*, one of the most peculiar crocodylians of all time, that includes cranial and postcranial elements recovered from the late Miocene bone-beds of the Urumaco Formation (northwestern Venezuela) is herein described. Based on the presence of tall squamosal eminences, we assigned it to *Mourasuchus arendsi*. To provide an empirical assessment of the palaeobiological affinities of *Mourasuchus*, we performed estimations of the body mass and body length based on several *Mourasuchus* skull measurements, and an analysis of death roll capability. Our results indicate that *Mourasuchus* was indeed a large crocodylian, with a body length bigger than 9 m and weighed more than 4 tons. We find that *Mourasuchus arendsi* was incapable of executing the ‘death roll’ as a feeding behaviour and as such was unable to predate giant mammals, which are relatively common in the Urumaco Formation. Finally, the specimen includes a slender humerus, which may indicate that *Mourasuchus* had weak forelimbs and would spend more time in the water.

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Introduction

The Venezuelan Neogene geological units contain a significant diversity of crocodyliforms (Aguilera 2004; Sánchez-Villagra and Aguilera 2006; Riff et al. 2010; Scheyer et al. 2013; Solórzano et al. 2018, 2019). This is especially true for the Urumaco Formation (northwestern Venezuela), which exhibits a unique and unusual diversity peak of sympatric crocodylians with distinctive skull morphotypes (Scheyer et al. 2013; Scheyer and Delfino 2016).

A remarkable example of an uncommon skull morphotype is *Mourasuchus*, a genus of caimanine crocodylian exclusive to the Miocene of South America (Bona et al. 2013; Cidade et al. 2017, 2019a) that is one of the most peculiar crocodylians of all time (Brochu 1999; Cidade et al. 2019b). *Mourasuchus* is characterised by a long, broad, duckbill-like preorbital snout, with a thin lower jaw and a relatively small postorbital skull table (Langston 1965; Brochu 1999; Bona et al. 2012, 2013; Cidade et al. 2017). Four species of *Mourasuchus* have been recognised: *Mourasuchus amazonensis* Price (1964), from the late Miocene of Brazil (Price 1964; Cidade et al. 2019c); *Mourasuchus atopus* (Langston 1965) from the middle Miocene of Colombia (Langston 1965; Langston and Gasparini 1997) and Peru (Salas-Gismondi et al. 2015); *Mourasuchus arendsi* Bocquentin-Villanueva (1984) from the late Miocene of Venezuela, Brazil, Argentina and Bolivia (Bocquentin-Villanueva 1984; Souza-Filho and Guilherme 2011; Scheyer and Delfino 2016; Cidade et al. 2018, 2019b); and *Mourasuchus pattersoni* Cidade et al. (2017) from the late Miocene of Venezuela (Cidade et al. 2017). Additionally, records of *Mourasuchus* sp. come from the early–middle Miocene Castilletes Formation, Colombia (Moreno-Bernal et al. 2016), middle Miocene Fitzcarrald Local Fauna, Peru (Salas-Gismondi et al. 2007), Pebas

Formation, Peru (Salas-Gismondi et al. 2015), Socorro Formation of Venezuela (Scheyer et al. 2013), the late Miocene Yecua Formation, Bolivia (Tineo et al. 2014), Solimões Formation, Brazil (Souza et al. 2016; Cidade et al. 2019a) and Urumaco Formation, Venezuela (Scheyer and Delfino 2016). This reflects how biogeographically widespread *Mourasuchus* was in South America, especially during the middle and the late Miocene.

In recent years, intensive palaeontological fieldwork has been carried out in unexplored areas of the Urumaco Formation (Venezuela), resulting in the discovery of some associated cranial and postcranial elements belonging to *Mourasuchus arendsi*. Therefore, the main goal of this paper is to describe these new elements of *M. arendsi* in order to improve the knowledge of the anatomy of the species and the genus. From the information obtained through this description and a survey of the literature, our study also has another objective: to reassess the palaeoecology and feeding habits of *Mourasuchus* through the performing of analyses regarding these issues that had not yet been made for this taxon.

Although studies on the phylogenetics and taxonomy of *Mourasuchus* have increased in recent years (Cidade et al. 2017, 2018, 2019b, 2019c), the lifestyle of this bizarre caimanine is not completely understood. Recently, Cidade et al. (2019d) reviewed hypotheses on the feeding habits and palaeoecology of *Mourasuchus*, proposing that it was a ‘gulp-feeder’ animal that fed on preferably small animals (fish and arthropods) that inhabited preferentially shallow, lentic waters. However, mechanical studies on issues relating to the feeding habits of *Mourasuchus* are still lacking. As such, in this study we performed estimations of total body length, total body mass and an analysis of the ‘‘death roll’’ capability indicator (DRCI) – see Blanco et al. (2015) – to provide,

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 Supplementary data for this article can be accessed [here](#).

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for the first time, empirically-based information on the palaeoecology and feeding habits of *Mourasuchus*.

Geological setting

Three successive geological units are exposed as outcrops in the Urumaco area (northern Falcón State, northwestern Venezuela; Figure 1), the Socorro, Urumaco and Codore formations. They are middle Miocene to early Pliocene in age (Díaz de Gamero 1989; Linares 2004; Carlini et al. 2006a, 2006b; Quiroz and Jaramillo 2010; Smith et al. 2010), and mostly represent a complex of marginal and near-shore coastal environments, including nearshore marine, deltaic systems and continental settings (Díaz de Gamero and Linares 1989; Hambalek et al. 1994; Quiroz and Jaramillo 2010; Smith et al. 2010).

The specimen here described was collected in the Urumaco Formation, which consists of complex intercalations of medium to fine-grained sandstone, organic-rich mudstone, coal, shale, and thick-bedded coquinooidal limestones with abundant mollusc fragments (Quiroz and Jaramillo 2010). The predominant paleoenvironment during the sedimentation of the Urumaco Formation is still unclear. According to Díaz de Gamero and Linares (1989) and Hambalek et al. (1994), the sedimentation of the formation occurred in a complex of marginal and near-coastal environments. Quiroz and Jaramillo (2010) suggested that the formation was probably deposited in a prograding strand plain-deltaic complex, while Smith et al. (2010) alternatively suggested brackish inner shelf settings. Díaz de Gamero and Linares (1989) proposed a late Miocene age for the Urumaco Formation based on foraminifera content, whereas Linares (2004) assigned it to the middle-late Miocene based on several terrestrial mammals found in the unit. The vertebrate assemblage of the Urumaco Formation includes fishes, birds, mammals and reptiles (see Sánchez-Villagra et al. 2010 for details). However, work on fossil vertebrates from the

Urumaco Formation has been mostly taxonomic and in a few cases phylogenetic, whereas little has been discussed specifically on the adaptations or palaeoecology of these animals (Aguilera 2004; Scheyer and Sánchez-Villagra 2007; Sánchez-Villagra et al. 2010).

Lithologically, the Urumaco Formation can be informally divided into three members: lower, middle, and upper. The lower member is dominated by mudstone, with coarsening-upward sandstone beds, whereas the middle member is characterised by a similar coarsening-upward sandstone beds but also present limestone and channelled sandstone up 20 metres thick, and the upper member lithologically broadly resembles the lower member with the predominance of mudstone (see more details in Quiroz and Jaramillo 2010). The specimen here described was collected in a mudstone of the lower member of the Urumaco Formation, Buchivacoa Municipality, Falcón State, Venezuela (Figure 1). This member has very few localities and levels with vertebrate fossils (Rincón et al. 2015; Cáceres et al. 2016). The described specimen is poorly preserved and covered by a thin gypsum crust, with all elements having suffered physical and chemical weathering during diagenesis and surface exposure. In some areas, the bones are partly replaced by gypsum as typically occurs in Urumaco Formation vertebrate fossils (Bocquentin-Villanueva 1984; Langston 2008).

Materials and methods

The specimen reported here is housed at the Instituto Venezolano de Investigaciones Científicas (IVIC), San Antonio de Los Altos, Miranda state, Venezuela. All measurements are in millimetres and were taken with a caliper. The specimen was anatomically and taxonomically compared with the available specialised literature about *Mourasuchus* (Price 1964; Langston 1965, 2008; Bocquentin-Villanueva 1984; Gasparini 1985; Bocquentin and Souza-Filho

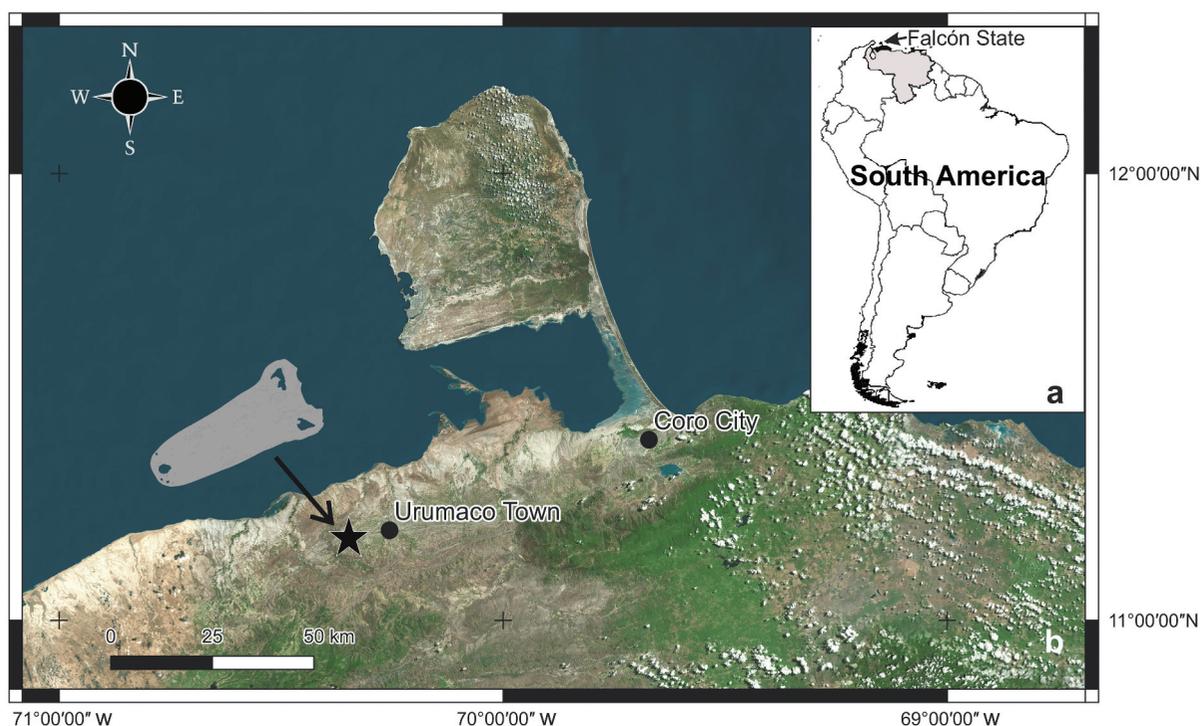


Figure 1. The geographic location of Venezuela within South America, and Falcón state within Venezuela (a), and satellite view of the area surrounding the Urumaco town (Venezuela) (b). The black star indicates the locality in which the fossil described here was collected.

1990; Brochu 1999; Riff et al. 2010; Bona et al. 2013; Cidade et al. 2017, 2018, 2019b, 2019c).

'Death roll' capability

The 'death roll' capability indicator (DRCI) was developed by Blanco et al. (2015) as a biomechanical model to estimate the capability of living and fossil crocodyliforms to execute a 'death roll', an iconic crocodylian behaviour. This is a spinning manoeuvre used by certain modern crocodylians to subdue and dismember large prey, but is also utilised during inter- and intra-specific conflict as a means to escape or injure an opponent (Blanco et al. 2015; Drumheller et al. 2019). As the DRCI index is heavily based on skull measurements (see details below), they are necessary to provide a way to explore crocodylian feeding behaviour (Blanco et al. 2015). We investigated the DRCI using the holotype of *M. arendsi* (CIAAP-1297), as it contains the skeletal elements necessary for calculation: skull length (HI), skull half-diameter (a), and skull half-height at the upper caniniform tooth level (b). The half width (a) and half height (b) were measured, with a digital caliper, in dorsal and lateral skull views, respectively, at the level of the fifth maxillary tooth (ninth upper tooth). Blanco et al. (2015) proposed two well-defined groups of living crocodylians, based on their DRCI: 1) values of DRCI close to or greater than 1 are related to species that perform or that have the potential to perform the 'death roll' (DRCI>1), and 2) values of DRCI below 1 includes species that do not perform the 'death roll' (DRCI<1).

Body mass estimations

Estimations of body size for extinct taxa could provide an important line of evidence for understanding their role in ancient ecosystems (e.g. Aureliano et al. 2015; Solórzano et al. 2019, 2020). Consequently, we use the dorsal cranial length (DCL = skull length) to predict the total length (TL in mm) and the body mass (BM in kg) of several specimens of *Mourasuchus*. Although several equations have been proposed in the literature, we use those from Aureliano et al. (2015), which is based on *Caiman latirostris* (Daudin 1802), Hurlburt et al. (2003), which is based on *Alligator mississippiensis* (Daudin 1802), and Grigg (2015), which is also based on *A. mississippiensis*. Besides, given the fragmentary nature of the *Mourasuchus* specimen here described, we also used for its calculations the equations proposed by Solórzano et al. (2019),

which related the anteroposterior length of the skull table in relation with DCL in modern caimanines. All the allometric equations previously mentioned are shown in the Supplemental Online Material (Table S1). For each of the *Mourasuchus* species, we estimated the mean TL and BM giving the results of the distinct equations employed.

Institutional abbreviations

IVIC-P, Colección de Paleontología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; MCNC, Museo de Ciencias Naturales de Caracas, Caracas, Venezuela; CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro, Venezuela.

Results

SYSTEMATIC PALAEOLOGY

CROCODYLIA Gmelin 1789 (sensu Benton and Clark 1988)
ALLIGATOROIDEA Gray 1844 (sensu Norell et al. 1994)
CAIMANINAE Brochu 1999 (following Norell 1988)

Mourasuchus Price 1964
Mourasuchus arendsi Bocquentin-Villanueva 1984
(Figure 2–10)

Material

IVIC-P-2907 (collected at 11°11'3.29"N; 70°20'49.54"W), associated cranial and postcranial remains from the same individual consisting of a fragmented posterior portion of the skull (including the postorbital, supraoccipital, frontal, squamosal, parietal, quadrate, and quadratojugal), fragments of the dentary, nine vertebrae (three cervical, four thoracic, one lumbar, and one sacral), and a right humerus.

Descriptions and comparisons

Skull. The skull table is slightly deformed and mostly covered by gypsum, thus not exhibiting any distinctive ornamentation (Figure 2). In occipital view, the skull table surface is significantly tall due to the abrupt elevation of the parietal, the squamosals and the supraoccipital (Figure 3). The supratemporal fenestrae are significantly reduced in size, as typical of caimanine crocodylians,

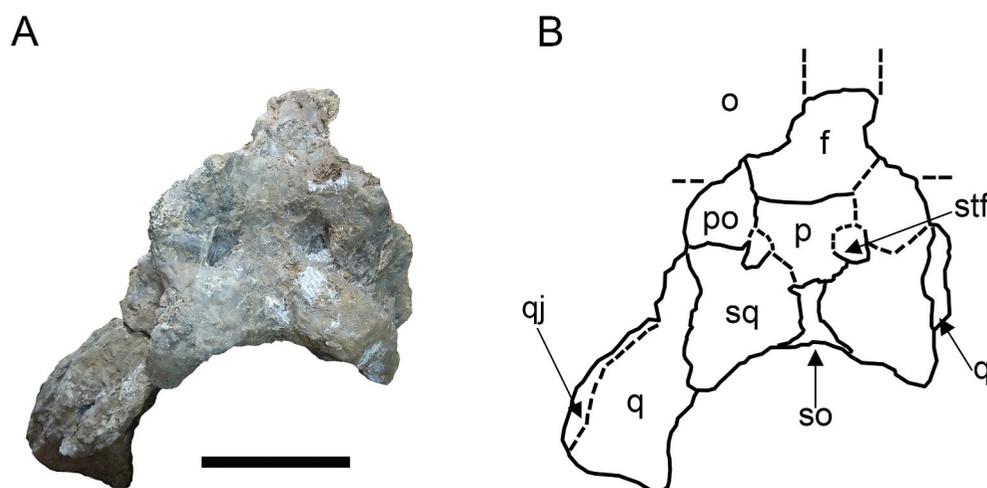


Figure 2. *Mourasuchus arendsi* (IVIC-P-2907): skull in dorsal view, including the left quadrate ramus. Picture of the specimen (a) and interpretative drawing (b). Dotted lines outside of the specimen itself in the interpretative drawing represent part of orbital margins. Abbreviations: f = frontal; o = orbit; p = parietal; po = postorbital; q = quadrate; qj = quadratojugal; so = supraoccipital; sq = squamosal; stf = supratemporal fenestra. Scale bar = 5 cm.

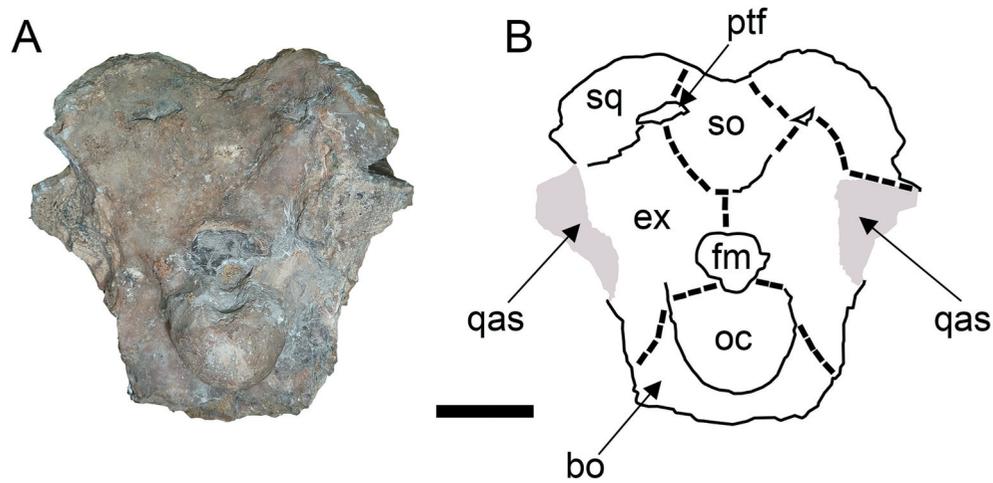


Figure 3. *Mourasuchus arendsi* (IVIC-P-2907): skull in occipital view, without the left quadrate ramus. Picture of the specimen (a) and interpretative drawing (b). Abbreviations: bo = basioccipital; ex = exoccipital; fm = foramen magnum; oc = occipital condyle; ptf = posttemporal fenestra; qas = quadrate articular surface; so = supraoccipital; sq = squamosal. Scale bar = 5 cm.

including *Mourasuchus* (Brochu 2011, Character 152–1; Cidade et al. 2017, Character 151–1, 2019b). Both supratemporal fenestrae are roughly sub-triangular in shape; the anterior margin of the left fenestra is eroded, whereas in the right fenestra the anterior and the medial margins are eroded.

The incomplete frontal bone is narrow, and its dorsal surface is generally flat. It contacts the parietal bone and the rostral-most portion of the postorbitals (Figure 2). The parietal is narrow and convex; the highly elevated parietal crest seen in other specimens of *Mourasuchus arendsi* (Gasparini 1985; Bona et al. 2013; Cidade et al. 2018, 2019b) is not preserved in this specimen. Nevertheless, the specimen can be assigned to *M. arendsi* due to the presence of tall squamosal eminences, as detailed below. The parietal contacts the squamosal at the posterior-most edge of the supratemporal fenestrae. The suture between the frontal and parietal bones is not well preserved; it is only slightly convex, entirely placed on the surface of the skull table and does not reach the supratemporal fenestrae (Figure 2). The postorbitals are incomplete. The dorsal surface of the left postorbital is very eroded in its anterolateral portion, and both postorbital bars are not preserved (Figure 4).

The supraoccipital bone is on the dorsal and the occipital surfaces of the skull table and it contacts the parietal bone anteriorly, the squamosal bones laterally – excluding the parietal from the posterior margin of the skull table, as in all caimanines except

Paleosuchus, *Purussaurus mirandai* Aguilera et al. (2006) and *Tsoabichi* (Souza-Filho et al. 2018) – and the exoccipital bone ventro-laterally (Figures 2 and 3). The occipital surface of the supraoccipital is concave, while the median crest of the bone is not visible. In occipital view (Figure 3), the supraoccipital is as long as wide. The left posttemporal fenestra is roughly elliptical, whereas the right one is severely eroded (Figure 3); both are surrounded dorsolaterally by the squamosals, ventro-medially by the supraoccipital and ventrally by the exoccipital. The foramen magnum is wider than long, and the occipital region dorsal to the foramen magnum is tall (Figure 3). Each exoccipital has a slender ventral process lateral to the basioccipital, which seems to participate in the basioccipital tubera. This feature is present in most caimanines (see Brochu 2011, Character 176–2; Cidade et al. 2018, 2019b; Figure 3). In occipital view, the basioccipital bone is wide and quadrangular in shape, and it contacts the exoccipitals dorsally and laterally (Figure 3).

Significantly, the squamosals are deeply convex in occipital view (Figure 3), a consequence of the presence of tall eminences of the dorsal surface of the bones. This condition also occurs in all specimens currently assigned to *Mourasuchus arendsi* (see Cidade et al. 2018, 2019b, 2019c), and different squamosal eminences are also present in some crocodyloids and alligatoroids (see Bona et al. 2013; Souza-Filho et al. 2018 for details). However, in these last ones these

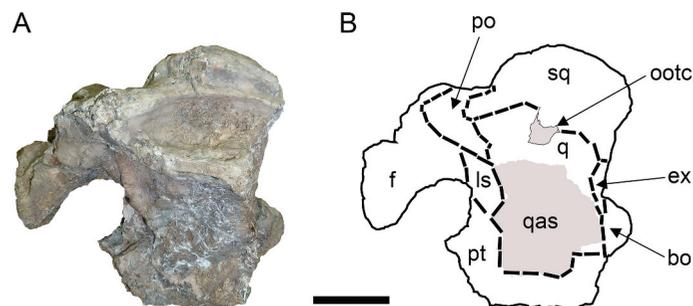


Figure 4. *Mourasuchus arendsi* (IVIC-P-2907): skull in left lateral view. Picture of the specimen (a) and interpretative drawing (b). Abbreviations: bo = basioccipital; ex = exoccipital; f = frontal; ls = laterosphenoid; ootc = otic opening of the tympanic cavity; po = postorbital; pt = pterygoid; q = quadrate; qas = quadrate articular surface; sq = squamosal. Scale bar = 5 cm.

eminences are usually placed mostly or exclusively parallel to the sagittal plane and not situated entirely on the dorsal surface of the squamosal bone as in *Mourasuchus arendsi* (see Cidade et al. 2017, 2018, 2019b). In IVIC-P-2907, the squamosal eminences form an angle of 40 degrees with the sagittal plane. The sizes of the squamosal eminences vary among *Mourasuchus arendsi* specimens, and it has been suggested that this is either due to individual variation, ontogenetic variation or sexual dimorphism (Gasparini 1985; Bona et al. 2013; Cidade et al. 2019b), but a larger sample and more detailed studies are needed to corroborate these hypotheses. The posterolateral margin of the squamosal is sub-horizontal. The parietal and the squamosal bones apparently meet along the posterior wall of the supratemporal fenestrae, but this feature must be seen with caution.

Only the left quadrate (that is not articulated with the skull, but was placed in its original position for Figure 2) is significantly preserved, exhibiting the typical morphology of *Mourasuchus* (see Cidade et al. 2017, 2018, 2019b), with a relatively long ramus (Figure 2). Only a small part of the medial portion of the left quadratojugal seems to be preserved anterior to the quadrate (Figure 2).

Dentary. One fragment of the right dentary is preserved (Figure 5). The dentary has a slender morphology, as is typical in *Mourasuchus* (Langston 1965; Bocquentin-Villanueva 1984; Bona et al. 2012, 2013; Cidade et al. 2017; Figure 5). It has 12 alveoli, with seven broken teeth preserved (Figure 5). The dentary of IVIC-P-2907 is linear between the fourth and tenth alveoli (Figure 5), which is a synapomorphy of *Mourasuchus* (Bona et al. 2012, 2013; Cidade et al. 2017). In the dentary of IVIC-P-2907, the first tooth is the largest of the dentition and the fourth is the next largest, with the second and the third being intermediate between these. A long diastema occurs between the second and third anterior teeth. In the dentary of *M. atopus*, 44 teeth have been reported (Langston 1965) while 'more than 40' mandibular teeth are reported for *M. amazonensis* (Price 1964), but due to the incompleteness we are unable to observe the total number of dentary teeth of IVIC-P-2907.

Humerus. The right humerus of IVIC-P-2907 is long, narrow, and sigmoid in lateral view (Figure 6). The ratios between the proximal and distal expansions with respect to humerus length are 0.24 and 0.24 respectively, in contrast to the 0.40 and 0.42 observed in *Crocodylus* (Mook 1921). The ratio of the circumference of the diaphysis (30 mm) over the total length of the humerus (340 mm) is 0.088 in IVIC-P-2907, whereas in *Crocodylus* it is 0.410 (Mook 1921). These ratios indicate a significantly slenderer humerus in *Mourasuchus arendsi* than in *Crocodylus* (Mook 1921).

The humerus of IVIC-P-2907 has, as is typical in Alligatoridae, distal and proximal epiphyses that are

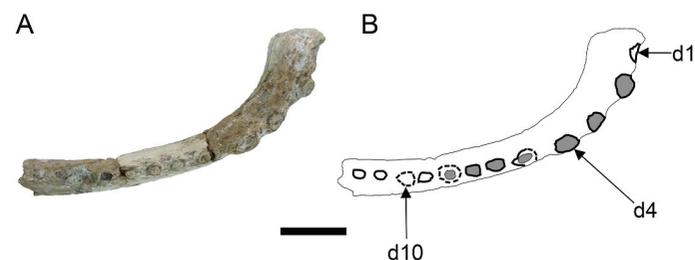


Figure 5. *Mourasuchus arendsi* (IVIC-P-2907): partial right dentary in occlusal view. Picture of the specimen (a) and interpretative drawing (b). Abbreviations: d1 = first dentary alveolus; d4 = fourth dentary alveolus; d10 = tenth dentary alveolus. Scale bar = 5 cm.

lateromedially wider (Chamero et al. 2013). The proximal and distal epiphyses have almost the same width (~83 mm). Proximally, the humerus is expanded transversely, flattened dorsoventrally, and dorsally projected (Figure 6). The dorsal depression between the lateral humeral process and the glenohumeral condyle (humeral head) is well-marked. In lateral view, near to the proximal margin, a large, prominent, sharp deltopectoral crest is present, which occurs at approximately one-quarter of the total length of the humerus (Figure 6). The deltopectoral crest is 95.5 mm long.

In ventral and dorsal views, there is an angle of about 160° formed by the lateral humeral process and the glenohumeral condyle (humeral head) with respect to the position of the medial humeral process and the glenohumeral condyle (humeral head). This angle is similar to *Crocodylus* (Mook 1921), smaller than *Alligator* (Snyder 2007; Maidment and Barrett 2011) and bigger than observed in *M. atopus*, which has a more closed angle (around 150°; based on Langston 1965, p. 64, Figure 25).

Distally, the humerus is expanded transversely. Both the ulnar and the radial condyles are rounded. The ulnar condyle is significantly smaller than the radial condyle. Additionally, the radial condyle is more ventrally projected than the ulnar condyle. Proximally, a significant plane surface occurs in the medial side of the deltopectoral crest, which possesses a subtriangular shape in cross-section.

Cervical vertebrae. IVIC-P-2907 preserves three cervical vertebrae (likely the third, fifth and sixth; Figure 7). The sizes of the centra of the cervical vertebrae are shown in Table 1. Following Langston (2008), the measurement of the length of the vertebral centra excludes the condyles, the measurement of height excludes the hypapophyses and the measurement of the width was taken behind the parapophyses.

The cervical vertebrae are generally poorly preserved (Figure 7). None of the cervical vertebrae has the neural spine preserved. Cervical hypapophyses span between 30% and 40% of the vertebral centrum body and are usually blunt. The length of the hypapophyses slightly increases posteriorly. As observed by Langston (2008) for the holotype of *Mourasuchus pattersoni*, the largest preserved hypapophysis occurs on the sixth cervical vertebra. The diapophyses are ventrolaterally short and project strongly downwards. In the cervical vertebrae, the capitular facet is oval, flat, and diagonally oriented, while the tubercular facet is roughly oval in shape and (at least in the possible fifth and sixth vertebrae) longer than the capitular facet. In lateral view, the parapophyses of the third cervical vertebra are shorter and more ventrolaterally compressed than those of the fifth and the sixth, which are subtriangular in shape (Figure 7). The diapophyses of the third cervical vertebra are eroded, but smaller than those of the fourth and the sixth cervical vertebrae. Only the sixth cervical vertebra preserves a complete right prezygapophysis and left postzygapophysis. In this vertebra, the articular facets of the prezygapophysis and the postzygapophysis slant towards the sagittal plane at an angle of 45°.

Measurements of IVIC-P-2907 indicate that the ratio of the width of the centrum in comparison with the length of the centrum in the cervical vertebrae (excluding the condyle; Table 1) are between 0.93 and 0.95. These values are similar to the observations of Langston (2008) of a maximum vertebrae ratio value of 0.98 in the holotype of *Mourasuchus pattersoni*. These ratios are significantly shorter than those of some extant taxa such as *Alligator mississippiensis* (1.29), *Melanosuchus niger* (Spix 1825) (1.49), *Tomistoma schlegelii* (Müller 1838) (1.31), and *Crocodylus acutus* (Cuvier 1807) (1.28) (Langston 2008).

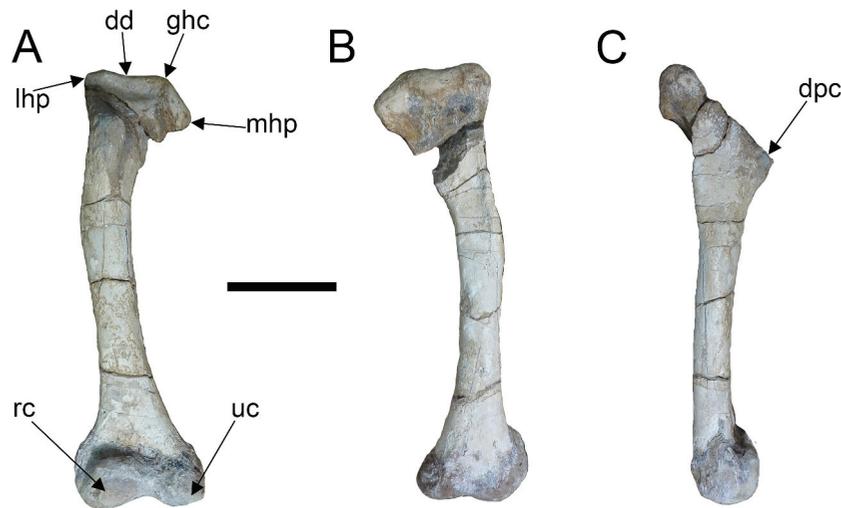


Figure 6. *Mourasuchus arendsi* (IVIC-P-2907): right humerus in: ventral (a), dorsal (b) and lateral (c) views. Abbreviations: dd = dorsal depression; dpc = deltopectoral crest; ghc = glenohumeral condyle; lhp = lateral humeral process; mhp = medial humeral process; rc = radial condyle; uc = ulnar condyle. Scale bar = 10 cm.

Thoracic vertebrae. Four thoracic vertebrae are preserved, with three from anterior positions (possibly the first, second and third) and one posterior (tentatively referred as the ninth or tenth thoracic vertebra) (Figure 8). The sizes of thoracic vertebral centra are shown in Table 1. Generally, the vertebral centra are wider than high. In lateral view, the parapophyses are high and massive in the first thoracic vertebra, while they are more gracile and smaller in the second and third thoracic vertebrae. Only the third thoracic vertebra preserves a complete right prezygapophysis, whereas the second thoracic preserves the right postzygapophysis. In the thoracic vertebrae (similarly to the cervical vertebrae), the articular facets of the prezygapophysis and postzygapophysis slant towards the sagittal plane at an angle of 55°, quite similar to the 57° reported by Langston (2008). The hypapophyses are eroded but span about 50% of the length of the centrum. The diapophyses are ventrolaterally short and project strongly downwards.

In the posterior thoracic vertebra (tentatively, the ninth or tenth thoracic vertebra), the vertebral centrum is sub-pentagonal in transverse section and wider than high (Figure 8, Table 1). The posterior thoracic vertebra is larger than the anterior ones. The hypapophysis is low and small. The right prezygapophysis is preserved and makes an angle of 60° with the sagittal plane. The postzygapophyses are broken. The neural spine is broken, but the base suggests a length of 423 mm and a maximum width of 127 mm.

Lumbar vertebra. One lumbar vertebra, possibly the third, is preserved (Figure 9). The size of the vertebral centrum is shown in Table 1. As in the posterior thoracic vertebra, the vertebral centrum is wider than high and sub-pentagonal in transverse section (Figure 9-A). The neural spine is eroded, but its base is 430 mm long, with a maximum width of 90 mm. The hypapophysis is eroded. The articular facets of the prezygapophyses slant towards the sagittal plane at an angle of 70°, which is not significantly different from the 79° observed by Langston (2008). In posterior view (Figure 9-B), the articular facets of the prezygapophyses and the postzygapophyses are separated from the neural spine by a relatively wide sulcus of 70 to 130 mm, resembling those mentioned by Langston (2008). Both transverse processes are eroded; the right process, which is more complete, is 355 mm long and 154 mm high.

Sacral vertebra. There is only one sacral vertebra preserved, which is possibly the first one (Figure 10). The vertebral centrum is much wider than high and anteroposteriorly shorter than the centrum of the lumbar vertebra (Table 1). The sacral ribs attached to the vertebra are very stout, but these are unfortunately too poorly preserved to provide additional details.

Body mass estimations

The presence of several vertebral centra without closed sutures suggests that IVIC-P-2907 died as a juvenile, following Brochu (1996). The holotype of *M. pattersoni* (MCNC-PAL-110-72 V) has a skull length (=DCL) of 106 cm, while the type specimen of *M. arendsi* (CIAAP-1297; Bocquentin-Villanueva 1984) has a skull length (=DCL) of 91 cm. The specimen here described is smaller than the holotypes of *M. arendsi* and *M. pattersoni*, because the preserved anteroposterior length of the skull table of IVIC-P-2907 is only 12 cm, and this measurement in the *M. arendsi* holotype (CIAAP 1297) is 16 cm. Using the equation of Solórzano et al. (2019), which related the anteroposterior length of the skull table with the DCL in caimanines (see Table S1), the DCL of IVIC-P-2907 was estimated to be 64 cm.

Using DCL measurements, we estimated the total length (TL) and body mass (BM) for all species of *Mourasuchus* (Table 2). Our results indicated that *Mourasuchus* was a giant crocodylian. The largest species is *M. amazonensis* (late Miocene of Brazil), with a body length that could reach ~9.5 metres and up to four tons in weight. In the lower range of size is *M. atopus* (middle Miocene of Colombia) with a body length around 6.3 metres and up to one ton in weight. The two species of *Mourasuchus* from the Urumaco Formation (late Miocene of Venezuela), could reach 7.7–9 metres and up 3.5 tons in weight. Therefore, *M. arendsi* and *M. pattersoni* were, together with *Gryposuchus croizatzi* Riff and Aguilera (2008) and *Purussaurus mirandai*, the largest crocodylians in this formation (Riff and Aguilera 2008; Scheyer et al. 2013; Aureliano et al. 2015). With an estimated total length of 5.5 m and a mass of ~750 kg, IVIC-P-2907 represents a rather ‘small’ specimen of *M. arendsi*. However, it is necessary to highlight that even when IVIC-P-2907 represents a juvenile individual, it is larger than the adults of the largest modern caimanine in the Neotropics, the black caiman (*Melanosuchus niger*), which usually grow up to 4.5–5 metres (Grigg 2015).

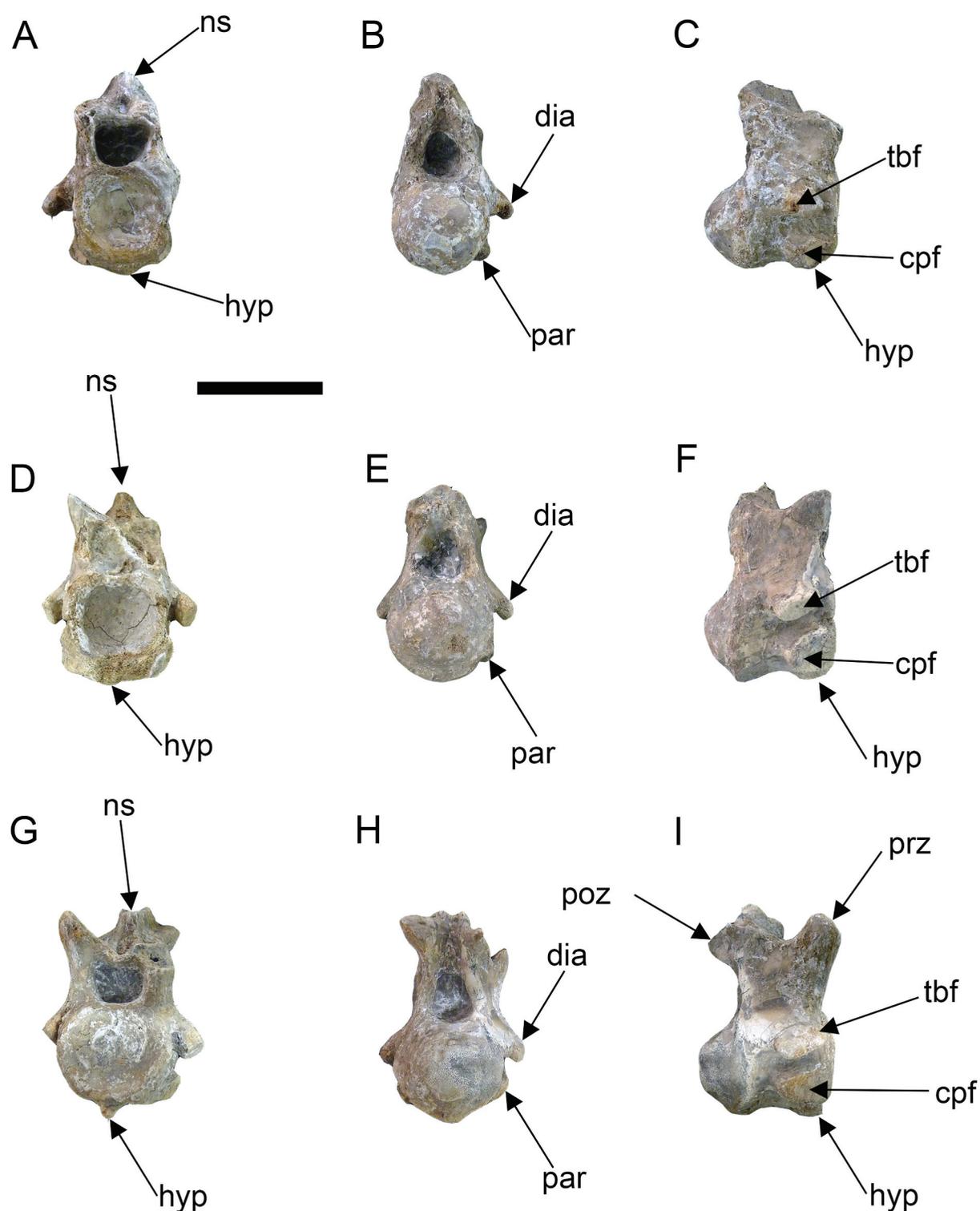


Figure 7. *Mourasuchus arendsi* (IVIC-P-2907): cervical vertebrae in anterior (left row), posterior (middle row) and right lateral (right row) views. Possible third cervical vertebra (a, b and c); possible fifth cervical vertebra (d, e and f); possible sixth cervical vertebra (g, h and i). Abbreviations: cpf = capitular facet; dia = diapophysis; hyp = hypapophysis; ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tbf = tubercular facet. Scale bar = 5 cm.

Palaeoecology and feeding habits of *Mourasuchus*

Here, we use the ‘death roll’ capability indicator (DRCI) to provide new insights into the palaeoecology and feeding habits of *Mourasuchus*, by evaluating this indicator in the species *M. arendsi* (based on its holotype). The results indicate a very low DRCI value (DRCI = 0.14; $\text{DRCI} \ll 1$; Table 3), which is similar to

the values of *Mecistops cataphractus* (Cuvier 1825), *Tomistoma schlegellii* and *Gavialis gangeticus* (Gmelin 1789) (Blanco et al. 2015). This is suggesting that *M. arendsi* was highly unlikely to have been able to execute the ‘death roll’ as a feeding behaviour, though other uses, such as escaping an opponent, cannot be ruled out (see Drumheller et al. 2019, and below).

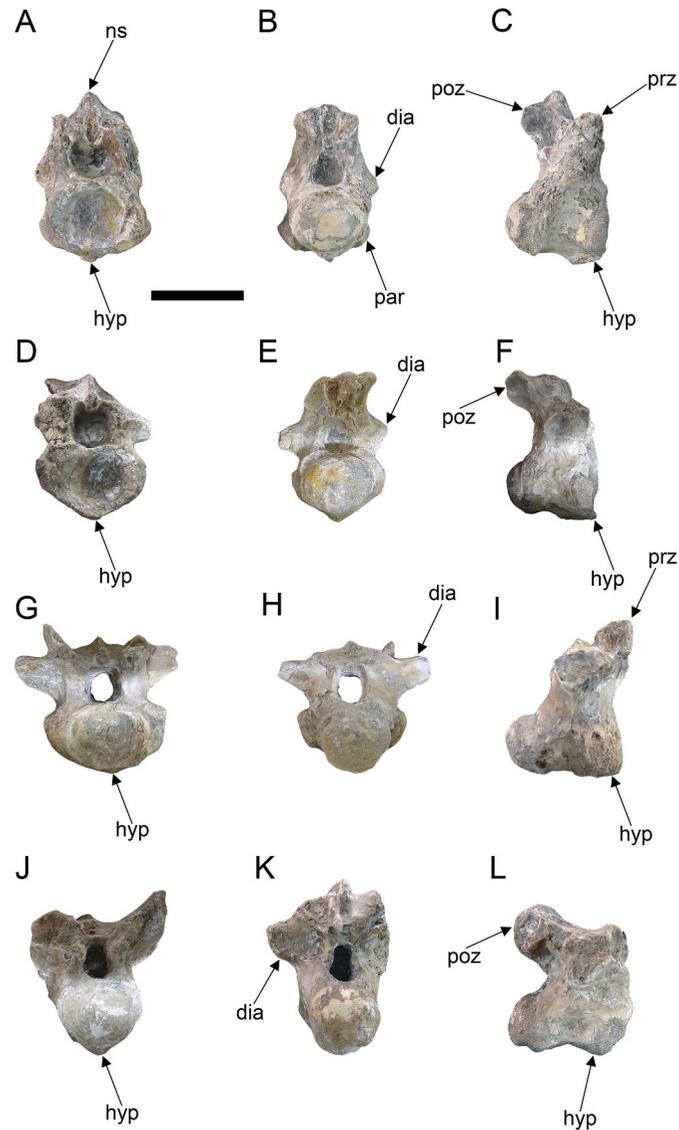


Figure 8. *Mourasuchus arendsi* (IVIC-P-2907): thoracic vertebrae in anterior (left row), posterior (middle row) and right lateral (right row) views. Possible first thoracic vertebra (a, b and c); possible second thoracic vertebra (d, e and f); possible third thoracic vertebra (g, h and i); posterior thoracic vertebra (tentatively, the ninth or the tenth) (j, k and l). Abbreviations: dia = diapophysis; hyp = hypapophysis; ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis. Scale bar = 5 cm.

Table 1. Measurement (in mm) of vertebral centra of *Mourasuchus arendsi* (IVIC-P-2907) from the lower member of the Urumaco Formation (late Miocene, Venezuela). *estimated measurements.

Catalogue number	Description	Length	Height	Width
IVIC-P-2907	Third cervical	368	360*	390
IVIC-P-2907	Fifth cervical	375	374	394
IVIC-P-2907	Six cervical	405	380	434
IVIC-P-2907	First thoracic	401	366	443
IVIC-P-2907	Second thoracic	368	366	468*
IVIC-P-2907	Third thoracic	365	379	477
IVIC-P-2907	Posterior thoracic	425	363	426
IVIC-P-2907	Lumbar	428	>350*	407
IVIC-P-2907	Sacral vertebra	265	357	588

Discussion

The specimen herein described exhibits a small skull table, a slender dentary, cervical vertebrae with relatively short centra and

a humerus with a dorsoventrally flattened posterior lobe of the humeral head. The combination of these features is distinctive for the endemic South American caimanine *Mourasuchus* (Price 1964; Langston 1965, 1966, 2008; Bocquentin-Villanueva 1984; Gasparini 1985; Bocquentin and Souza-Filho 1990; Brochu 1999; Riff et al. 2010; Bona et al. 2012, 2013; Tineo et al. 2014). Previous palaeontological studies in the Urumaco area recognised two *Mourasuchus* species: *M. arendsi* (Bocquentin-Villanueva 1984) and *M. pattersoni* (Cidade et al. 2017).

IVIC-P-2907 has tall, rounded squamosal eminences. Among the holotypes of currently recognised species of *Mourasuchus*, only the holotype of *Mourasuchus arendsi* exhibits them (Scheyer and Delfino 2016; Cidade et al. 2018). The holotype of *M. nativus* (Gasparini 1985) also exhibits this feature (Gasparini 1985; Bona et al. 2013), but this species is now considered a junior synonym of *M. arendsi* (Scheyer and Delfino 2016). Regarding the other three valid species, the holotype of *M. atopus* does not preserve the squamosals (Langston 1965), whereas in that of *M. pattersoni* the squamosals were covered by plaster in a restoration (Cidade et al. 2017), and for the holotype of

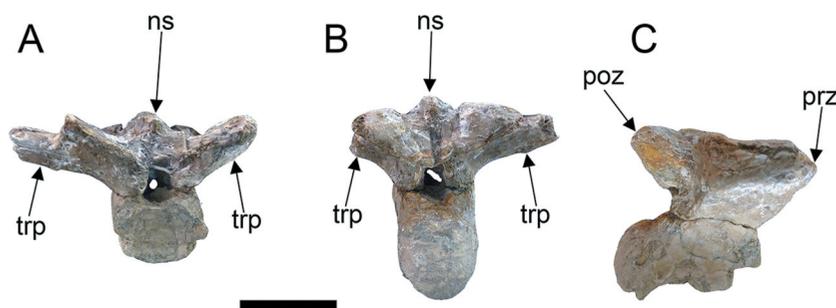


Figure 9. *Mourasuchus arendsi* (IVIC-P-2907): possible third lumbar vertebra in anterior (a), posterior (b) and right lateral (c) views. Abbreviations: ns = neural spine; poz = postzygapophysis; prz = prezygapophysis; trp = transverse process. Scale bar = 5 cm.

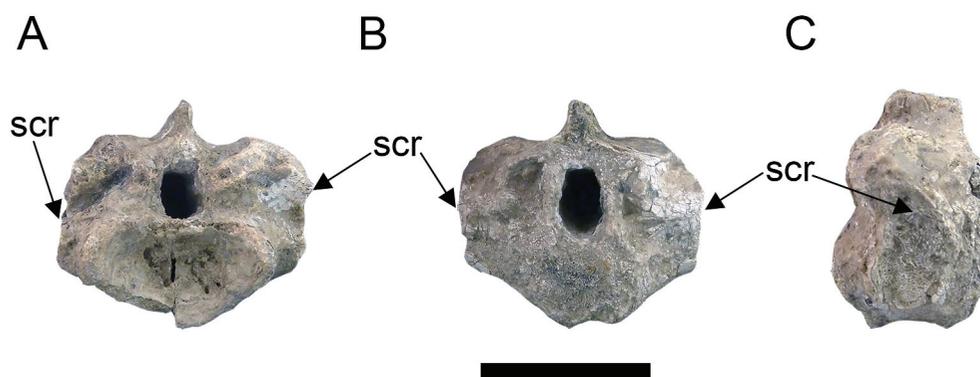


Figure 10. *Mourasuchus arendsi* (IVIC-P-2907): possible first sacral vertebra in anterior (a), posterior (b), and right lateral (c) views, with arrows pointing to the remnants of the sacral ribs (scr) in the lateral portions of the vertebra. Scale bar = 5 cm.

Table 2. Total body length (TL in cm) and body mass (BM in Kg) estimations for *Mourasuchus* spp. based on the dorsal cranial length (DCL in mm). The DCL of IVIC-P-2907 (denoted with an asterisk) was estimated using the equation of Solórzano et al. (2019). TL₁ = total length based on the equation of Hurlburt et al. (2003); TL₂ = total length based on the equation of Aureliano et al. (2015); BM₁ = body mass based on the equation of Aureliano et al. (2015); BM₂ = body mass based on the equation of Grigg (2015). The calculations used the equations shown in Table S1 (Supplemental Online Material).

Taxa	DCL	DCL data	TL ₁	TL ₂	Mean _{TL}	BM ₁	BM ₂	Mean _{BM}
<i>M. amazonensis</i>	1114	Price 1964	904	990	947	3742	5032	4387
<i>M. arendsi</i>	910	Cidade et al. 2018	743	806	774	2079	2525	2302
<i>M. arendsi</i>	640*	IVIC-P-2907; present work	528	563	546	748	761	754
<i>M. atopus</i>	739	Langston and Gasparini 1997	607	652	630	1136	1242	1189
<i>M. pattersoni</i>	1050	Cidade et al. 2017	853	933	893	3151	4113	3632

Table 3. Results from DRCI calculations for *Mourasuchus arendsi* holotype (CIAAP-1297). Abbreviations: **HI**, skull length in cm; **a**, skull half-diameter in metres; **b**, skull half-height at the upper caniniform tooth level in metres; **DRCI**, 'death roll' capability indicator values. Note that DRCI values close to or greater than 1 were observed in extant species that perform or that have the potential to perform the 'death roll' (mainly as a feeding behaviour), while DRCI values well below 1.0 were observed in extant species that do not perform it (see Blanco et al. 2014 for details).

HI (cm)	a	b	DRCI
95	0.14	0.0171	0.14

M. amazonensis the only available depiction of the dorsal side of the skull is a drawing by Price (1964) that does not clearly depict the squamosal eminences (Cidade et al. 2019c). The dorsal side of the skull of the holotype of *M. amazonensis* cannot be currently assessed (see Cidade et al. 2019c) and, as such, there is the possibility that the squamosal eminences are present in it as well. The fact that the eminences are present in all *Mourasuchus* specimens that preserve the squamosals hints that this feature is a synapomorphy of the genus and not an autapomorphy of *M. arendsi* (Cidade et al. 2019b). However, until the holotype of *M. amazonensis* can be reassessed and specimens that preserve this feature can be assigned to the other species

of the genus, this remains only a perspective. As such, the presence of the squamosal eminences allows IVIC-P-2907 to be assigned to *Mourasuchus arendsi*, although the eventual discovery of this feature in other *Mourasuchus* species may require revising this assignment to *Mourasuchus* sp.

The supratemporal fenestrae of IVIC-P-2907 are elliptical to sub-triangular in shape, similar to morphology observed in the holotype of *M. arendsi* (Bocquentin-Villanueva 1984). However, in other specimens of *M. arendsi*, these fenestrae are also variable in size and shape, varying from trilobed with medial, rostralateral, and caudolateral lobes to subcircular (Bona et al. 2013; Cidade et al.

2019b). As such, the shape of the supratemporal fenestrae is not considered as having taxonomic value.

Unequivocal remains of *Mourasuchus arendsi* are known only in the late Miocene, from Solimões Formation, Brazil (Souza-Filho and Guilherme 2011; Cidade et al. 2019b), Urumaco Formation, Venezuela (Bocquentin-Villanueva 1984; Cidade et al. 2018), Ituzaingó Formation, Argentina (Gasparini 1985; Bona et al. 2012, 2013; Scheyer and Delfino 2016; Cidade et al. 2019b), whereas one specimen may be either from the Cobija Formation, Bolivia, or from the Solimões Formation, Brazil (Cidade et al. 2019b). *Mourasuchus arendsi* was previously recovered just from the middle and upper members of the Urumaco Formation (Scheyer et al. 2013) and, consequently, IVIC-P-2907 represents the first record of this species from the lower member of the Urumaco Formation.

During most of the Cenozoic, until the Great American Biotic Interchange (GABI, late Neogene), South America was isolated from other continents (Woodburne 2010). The dominant predators in South America were crocodyliforms, large snakes, large birds (Phorusrhacidae), and metatherian mammals (Sparassodonta) (Prevosti et al. 2013). Besides the record of snakes (see Head et al. 2006 for details), among the aforementioned groups of predators only the crocodylian crocodyliforms have been so far recovered from the Urumaco Formation, including alligatoroids (seven species), gavialoids (six species) and one putative tomistomine crocodyloid, *Brasilosuchus mendesi* Souza-Filho and Bocquentin-Villanueva (1989) (Bocquentin-Villanueva 1984; Sánchez-Villagra et al. 2010; Riff et al. 2010; Scheyer and Moreno-Bernal 2010; Scheyer et al. 2013; Scheyer and Delfino 2016; Cidade et al. 2019a).

The occurrence of at least seven sympatric species with distinctive body sizes and skull morphologies in the Urumaco Formation strongly indicates the existence of niche partitioning and suggests the existence of a complex food web (Aguilera et al. 2006; Riff and Aguilera 2008; Riff et al. 2010; Scheyer and Moreno-Bernal 2010; Scheyer et al. 2013). The main palaeoecological hypotheses indicate that during the Miocene the ecosystems contained numerous huge water bodies in which gavialoids traversed the channels preying on fish, *Purussaurus* loitered in the margins for aquatic mammals, turtles, and riparian mammals, *Caiman* and *Melanosuchus* lived on the riparian lands catching small vertebrates and invertebrates and *Globidentosuchus*, with its blunt and robust teeth, possibly caught crustaceans, molluscs, insects and small turtles (Langston 1965, 2008; Riff et al. 2010; Scheyer et al. 2013; Cidade et al. 2019a, 2019d). Regarding *Mourasuchus*, several hypotheses for the palaeoecology and feeding habits have been proposed. These indicate that *Mourasuchus* likely was unable to capture and consume large prey, and instead was specialised for small animals, such as molluscs, crustaceans, and small fish. It likely inhabited quiet, shallow bodies of water that would have provided a broad range of suitable habitats for their prey (see Cidade et al. 2019d). However, empirical assessments of the palaeoecology and feeding habits of *Mourasuchus* are still lacking.

Recent work suggested the prevalence of death rolling behaviour across extant Crocodylia (Drumheller et al. 2019). Indeed, this behaviour is not solely, or maybe even primarily, a feeding behaviour but it also might be utilised during inter- and intra-specific conflict as a means to escape from or harm an opponent (Drumheller et al. 2019). Besides, the death roll behaviour appears not to be restricted to any specific snout morphotype (Drumheller et al. 2019). Therefore, inferring its presence in extinct taxa must be done with caution especially in the case of taxa like *Mourasuchus*, which does not have a modern analogue

(Langston and Gasparini 1997). This notwithstanding, our results (based only on skull proportions) indicate that *Mourasuchus* was unlikely to have performed the 'death roll' as a feeding behaviour. Other uses cannot be ruled out, however, especially for escaping an opponent during inter- or intra-specific conflict. Regarding feeding behaviours, it is also significant that most of the upper and lower teeth of *Mourasuchus* are much reduced relative to the size of the skull (Langston 1965, 2008; Riff et al. 2010; Bona et al. 2012, 2013; Cidade et al. 2018, 2019d), which makes them difficult to be used in catching large prey. This last perspective, together with DRCI results, strongly suggests that *Mourasuchus* was incapable of executing the 'death roll' (a typical tactic used by living crocodylian species that feed on medium to large animals) and, in consequence, was unable to predate large mammals like giant caviomorph rodents or giant sloths, which are common in the Urumaco Formation (e.g. Rincón et al. 2015).

Previous descriptions of postcranial elements of *Mourasuchus* include Langston (1965), who described the scapula, coracoid, proximal end of the humerus, femur, ilium, and ischium of *M. atopus*. Bocquentin-Villanueva (1984), in the description of the holotype of *M. arendsi*, reported the presence of six articulated cervical vertebrae and other isolated vertebrae; upon redescribing the holotype, Cidade et al. (2018) described the six articulated cervical vertebrae, two probable isolated cervical vertebrae, three probable isolated dorsal vertebrae, and articulated left scapula and coracoid. Langston (2008) described postcranial materials of the specimen MCNC-PAL-110-72 V, initially referred to *M. arendsi* but later the holotype of *M. pattersoni* (Cidade et al. 2017), which includes vertebrae, ilium, scapula, coracoid, and osteoderms. Tineo et al. (2014) described three vertebrae and six rib fragments assigned to *Mourasuchus* sp. from the late Miocene Yecua Formation of Bolivia, and Souza et al. (2016) described six isolated osteoderms of *Mourasuchus* sp. from the late Miocene Solimões Formation of Brazil.

The long, slender, almost complete humerus of IVIC-P-2907 represents the most complete described for *Mourasuchus*. The only comparable material already described corresponds to the proximal portion of a left humerus of *M. atopus* (Langston 1965). The humerus of IVIC-P-2907 also differs from *M. atopus* in having the angle formed by the lateral humeral process and the glenohumeral condyle (humeral head) more closed with respect to the position of the medial humeral process and the glenohumeral condyle (around 150°, Figure 6; see Langston 1965, p. 64, Figure 25). A comparison between the width of the proximal end of the holotype of *M. atopus* and IVIC-P-2907 suggests that the first has a significantly smaller size (60 mm in *M. atopus* in comparison with 83 mm in the specimen herein described of *M. arendsi*). In general, the cervical, thoracic, lumbar and sacral vertebrae here described resemble those of *M. pattersoni* as described by Langston (2008).

Given these perspectives on the palaeoecology of *Mourasuchus*, the slender humerus of IVIC-P-2907 (as per the comparisons above) may indicate the presence of weak forelimbs in *M. arendsi*. However, a relatively large body mass has been estimated for the same individual (~750 kg). This would suggest that *M. arendsi* would spend much time in the water (at least when they were juvenile), in agreement with previous assessments of *Mourasuchus* that describe it as an aquatic crocodylian (Langston 1965; Cidade et al. 2017, 2019d). Whether *Mourasuchus* inhabited preferably shallow waters, as suggested by previous authors (Langston 1965; Cidade et al. 2017, 2019d), or venturing into deeper water bodies is to be assessed by future studies.

Conclusions

This paper describes IVIC-P-2907, a specimen comprised of cranial and postcranial remains from the late Miocene Urumaco Formation of Venezuela. The presence of rounded, tall squamosal eminences allows its assignment to *Mourasuchus arendsi*, a species already present in the Urumaco Formation, but further studies of the other species of the genus may change the assignment to *Mourasuchus* sp. Estimations of total body length and total body mass for several specimens of *Mourasuchus* yielded results of above 9 m and weighed more than 4 tons. But even juvenile specimens of *Mourasuchus*, like the one described here, reached more than 5 metres. This study also included the first empirical assessment of the palaeoecology and feeding habits of *Mourasuchus*. Our analysis of the ‘death roll’ capability indicator (DRCI), based on the holotype of *M. arendsi*, indicates that the genus was unlikely to have been able to perform the ‘death roll’ manoeuvre as a feeding behaviour. Additionally, the slender humerus described here may indicate that *Mourasuchus arendsi* had weak forelimbs, and would spend much time in the water.

The crocodylian assemblage of the Urumaco Formation is critical to improving our understanding of the morphological variation within South American caimanine and gavialoid faunas and for testing the phylogenetic relationships of both groups. In this context, this study provides a step towards much needed detailed morphological descriptions of the Urumaco crocodylian fauna, as well as the first empirical assessments on the feeding habits of *Mourasuchus*. Future studies are also needed to evaluate and test general assumptions about the palaeoecology of the crocodylian assemblage of the Urumaco sequence, including *Mourasuchus*, in conjunction with biological, histological and morpho-functional analyses of postcranial elements and isotopic analyses of teeth and associated coprolites, whenever possible. Due to the complex tectonic evolution of northern South America, and its ancient hydrographic basins, during the Cenozoic (e.g. Hoorn et al. 2010), additional geological evidence will also be necessary for a better understand these issues.

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Disclosure statement

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