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# New specimens of *Mourasuchus* (Alligatorioidea, Caimaninae) from the Miocene of Brazil and Bolivia and their taxonomic and morphological implications

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*Mourasuchus* is one of the most peculiar crocodylians of all time, showing an unusual 'duck-faced' rostrum with thin, gracile mandibles. It includes four species restricted to the South American Miocene. Here, we describe ten late Miocene specimens of *Mourasuchus*, nine from the Solimões Formation of Brazil and one from Bolivia. All specimens are assigned to *M. arendsi*, but this assignment may change as the diversity and relationships within *Mourasuchus* are better understood. We also discuss several issues pertinent to the morphology of *Mourasuchus*: the presence of a braincase neomorph (the laterocaudal bridge), hypotheses about sexual dimorphism, the function of the squamosal 'horns' the presence of possible thermoregulatory functions in the genus. Additionally, the paleogeographic distribution of *Mourasuchus* in the Miocene of South America is also discussed.

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*MOURASUCHUS* Price 1964 is a caimaninae alligatorid lineage known for an unusual morphology sometimes even described as 'bizarre' (Brochu 1999, p. 29; Bona *et al.* 2013a, p. 227), 'aberrant' (Langston 2008, p. 125), having an 'almost unbelievable appearance' (Langston 1965, p. 2), resembling a 'Saturday morning cartoon' character (Brochu 2001, p. 571) and 'a surfboard with lots of small teeth' (Brochu 2011, p. S229). This is mainly due to its unusual skull, which bears a very long, broad, dorsoventrally flattened 'duck-like' rostrum with a comparatively small skull table, small supratemporal fenestrae, very thin, gracile lower jaws and with more than 40 teeth in both dentaries and both maxillae (Langston 1965, 1966, Riff *et al.* 2010, Bona *et al.* 2013b).

The first named species, *Mourasuchus amazonensis* Price 1964, is based on a nearly complete skull and mandibular remains from the Solimões Formation exposed along the Upper Juruá River, Acre state, Brazilian Amazonia. Although the type locality was initially thought to be Pliocene in age (Price 1964, Langston 1966), later work (e.g., Bocquentin-Villanueva & Souza-Filho 1990, Riff *et al.* 2010) accepted a late Miocene age, following the age attributed to the Solimões Formation as a whole (Cozzuol 2006). In fact, the geology and age of the Upper Juruá River area is unclear (Latrubesse & Rancy 1998), which takes Souza-Filho & Guilherme (2011a) to regard the Late Miocene age of the *M. amazonensis* occurrence as still uncertain. A second record of this species for the Solimões Formation, based on an isolated left jugal bone, was reported by Souza-Filho & Guilherme (2011b).

Langston (1965) described *Nettosuchus atopus* based on an incomplete, fragmented skull with postcranial remains from the Villavieja Formation, Honda Group, middle Miocene of Colombia. Based on the unusual aspect of the specimen, the author even erected a new family, Nettosuchidae, to include it. Once aware of Price's previous work, however, Langston (1966) recognized *Nettosuchus* as a junior synonym of *Mourasuchus*.

With the emergence of phylogenetic systematics, *Mourasuchus* was placed within the alligatoroid clade Caimaninae (Brochu 1999, 2010, 2011, Aguilera *et al.* 

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2006, Bona *et al.* 2013b, Cidade *et al.* 2017). Additional skull fragments attributed to *M. atopus* were later described from the of the La Victoria and Villavieja formations of the Honda Group in Colombia (Langston & Gasparini 1997), both of middle Miocene age (Hsiou *et al.* 2010).

*Mourasuchus arendsi* Bocquentin-Villanueva 1984 was described from a nearly complete skull plus cervical and dorsal vertebrae found at the late Miocene Urumaco Formation of Venezuela (see also Cidade *et al.* 2018). Later, Souza-Filho & Guilherme (2011a) referred to *M. arendsi* an almost complete skull and some other cranial fragmented remains found at the late Miocene Solimões Formation in Acre, Brazilian Amazonia.

Carandaisuchus nativus (Gasparini 1985) was based on two specimens comprising the posterior part of the skull table from the late Miocene Ituzaingó Formation of Argentina. However, Bocquentin-Villanueva & Souza-Filho (1990), based on a more complete skull table and mandibular fragments from the Solimões Formation in Brazil, concluded that Carandaisuchus is a junior synonym of Moursuchus. Later, Oliveira & Souza-Filho (2001) reported the occurrence of M. nativus in several fossiliferous localities of the Solimões Formation in the Brazilian state of Acre but did not provide detailed descriptions of the fossils. Bona et al. (2013a) provide a detailed description of the cranial anatomy of of the the Ituzaingó material originally assigned by Gasparini (1985) to M. nativus, while Schever et al. (2013) reported the presence of in the same species for the Urumaco Formation of Venezuela. However, Scheyer & Delfino (2016) argued that M. nativus is a junior synonym of M. arendsi, as some of the characters previously considered as autapomorphic of M. nativus, such as the presence of a horn-like intumescence of the squamosals and an elevated parietal sagittal crest (see Gasparini 1985 and Cidade et al. 2013, 2018), are also present in the holotype of M. arendsi. As such, occurrences of M. nativus from the Miocene of Argentina can be considered as referable to M. arendsi.

The fourth and most recently described species is Mourasuchus pattersoni, described by Cidade et al. (2017) from the late Miocene Urumaco Formation of Venezuela. This species is based on a nearly complete skull with both mandibular rami and postcranial remains (including 'a substantial part of the vertebral column, fragments of ribs, parts of the pectoral and pelvic girdles, and some osteoderms', Langston 2008, p. 125). The postcranium of *M. pattersoni* had actually been described previously by Langston (2008), who suggested the remains 'probably' represented M. arendsi.

Additionally, fragmentary fossils attributed to *Mourasuchus* were reported from the late Miocene Solimões Formation of Brazil (Souza-Filho & Kischlat

1995, Oliveira & Souza-Filho 2001; Souza et al. 2016), Urumaco Formation of Venezuela (Scheyer & Delfino 2016) and Yecua Formation of Bolivia (Tineo *et al.* 2014); from the middle Miocene Fitzcarrald Arch of Peru (Salas-Gismondi *et al.* 2007), Socorro Formation of Venezuela (Scheyer *et al.* 2013) and Pebas Formation of Peru (Salas-Gismondi *et al.* 2015); and from the late early/early middle Miocene Castilletes Formation of Colombia (Moreno-Bernal *et al.* 2016).

Furthermore, an isolated skull table housed at the American Museum of Natural History (AMNH 14441) was reported (Gasparini 1985). The specimen was purportedly from the Pleistocene of Tarija, Bolivia, which would extend the geographic and temporal distributions of the group. However, this specimen has never been fully described and its stratigraphic origin is uncertain (Gasparini 1996, Langston & Gasparini 1997, Fortier 2011). This paper provides the first description of AMNH 14441 and brings more detailed information about its stratigraphic derivation.

Between 1987 and 2001, field expeditions led by researchers of Universidade Federal do Acre (UFAC) resulted in the collection of several remains that could be attributed to *Mourasuchus arendsi*. These include nine partial skulls constituted mainly by the posterior portion of the skull table (Figs 2 and 3).

This paper includes the formal description of AMNH 14441 from Bolivia and the nine specimens from the Solimões Formation of Brazil, their taxonomic identity, and the implications of the new data obtained by this study for understanding the cranial anatomy of *Mourasuchus*. Additionally, this study discusses hypothesized thermoregulatory mechanisms in the taxon, as well as possible sexual dimorphism and a role in mating behavior of the squamosal eminences ('horns') of *Mourasuchus*. Moreover, this paper updates what we know about the paleogeographic distribution of *Mourasuchus* in the Miocene of South America.

# Geological background

Nine of the ten specimens described in this work are from the Niteroi locality, an outcrop of the late Miocene Solimões Formation exposed on the right bank of the Acre River (Fig. 1) between the cities of Rio Branco and Senador Guiomard (10°08'30.0" S, 67°48'46.3" W, Bona *et al.* 2013b; UTM 19L 15 629983 E/8879539 S, datum WGS84—Kerber *et al.* 2018).

Continental sediments of the Solimões Formation are composed mainly of claystones with calcareous concretions as well as calcite and gypsum veins, lying in horizontal to subhorizontal beds that can reach thicknesses of over 1000 m (Latrubesse *et al.* 2010). The depositional environment is primarily floodplain-lacustrine-swampy, with the Andes as the main sedimentary source (Latrubesse *et al.* 1997, 2010). Although



*Fig. 1.* Map of the Brazilian state of Acre modified from Hsiou (2010) and Lopes (2016), with markings indicating the approximate location of the Niteroi Site, near the city of Rio Branco, where all the 'UFAC' specimens are from, and to the area between the cities of Bolpebra (Peru) and Cobija (Bolivia) where AMNH 14441 is likely to have been collected.

originally assigned a late Miocene/Pliocene age (e.g., Latrubesse 1992, 1997), recent geological, palynological and sedimentological data indicate a late Miocene age for the unit as a whole (Cozzuol 2006, Latrubesse et al. 2010), corresponding to the Huayquerian South American Land Mammal Age (SALMA; Latrubesse et al. 2010, Fortier et al. 2014). The Niteroi locality comprises moderately consolidated claystone layers, with smaller quantities of sandstones and siltstones, deposited in a low-energy environment (Campbell et al. 2006; see also Latrubesse 1992, Negri 2004, Bissaro-Junior et al. 2019). Recent U-Pb dating of an in situ detrital zircon resulted in an age of  $8.5 \pm 0.5$  Ma for the Niteroi locality (Bissaro-Junior et al. 2019), which confirms it as being from the late Miocene (within the Tortonian age). Regarding the SALMA time-scale, the Niteroi locality is considered to be either in the Chasicoan or in the Huayquerian ages (Bissaro-Júnior et al. 2019).

The fossil record of the Solimões Formation is diverse, comprising plants to invertebrate and vertebrate animals (Latrubesse *et al.* 2010). The crocodylian record from this unit, specifically, is remarkable, with genera described so far for this Formation including the putative crocodyloid *Charactosuchus*—although this group may actually be outside crown-group Crocodylia (Vélez-Juarbe & Brochu in press)—the gavialoids *Gryposuchus* and *Hesperogavialis*, and the caimanines *Caiman*, *Mourasuchus* and *Purussaurus* (Riff *et al.* 2010).

## Materials and methods

All UFAC specimens are in the Laboratório de Pesquisas Paleontológicas in Rio Branco, Acre. These were collected at Niteroi, and details in the catalog about these specimens are transcribed and translated as follows:

- 1. UFAC-2515: collected in 1989. The catalog refers it to *Mourasuchus nativus* and mentions UFAC-2513 and UFAC-2514, vertebrae evidently found articulated with the skull. However, those were not found in the collection.
- 2. UFAC-4925: collected in 02 August 2002; no identification or further notes.
- 3. UFAC-3717: collected between 31 October and 2 November 1992 by a UFAC team. Referred to *Mourasuchus*.
- 4. UFAC-1666: collected from 7 to 9 October 1988 and referred to Nettosuchidae.
- 5. UFAC-3530: collected in July 1992. Identified as *Mourasuchus*.
- 6. UFAC-1477: collected in October 1987. Named as *Carandaisuchus* in the catalog.
- 7. UFAC-4259: collected from 20 to 22 August 1993. Identified as *Mourasuchus*.

- 8. UFAC-4885: collected from 10 to 11 August 2001; no identification or further notes.
- 9. UFAC-1431: collected in October 1987. Identified as *Mourasuchus* sp.

The other specimen, deposited in the American Museum of Natural History, New York, United States (AMNH 14441, Fig. 4), has a rather complex history. Upon describing Mourasuchus nativus, Gasparini (1985) referred AMNH 14441 to this species stating that its origin was 'probably' the Pleistocene of Tarija in southern Bolivia (see MacFadden 2000 and Tonni et al. 2009, for information about these deposits). Langston & Gasparini (1997) state that this specimen was found along the Acre River in northern Bolivia, near the Brazilian border). However, these authors still regard AMNH 14441 as from the Pleistocene of Tarija, albeit with uncertainty. Fortier (2011), based on the absence of any other occurrence of Mourasuchus outside the Miocene (Riff et al. 2010), interpreted this specimen as having come instead from an unnamed middle Miocene unit (MacFadden 1990) close to Tarija.

However, information at the American Museum of Natural History indicates that AMNH 14441 was 'within 2 days trip upstream from Cobija by motorized canoe, northwest of Bolivia, near Brazilian border, Pando Province' in the possession of an unnamed collector, who was using it as a canoe anchor. The specimen then passed through the hands of several people until finally being donated to the AMNH. The information also states that AMNH 14441 is derived from an 'unnamed Formation' situated below the Iñapari Formation 'restricted', while assigning such 'unnamed Formation' to the late Miocene Huayquerian SALMA (see Flynn & Swisher 1995).

As AMNH 14441 was not found in a stratigraphic context, it is not possible to pinpoint the locality in which it was found nor to assess the accuracy of the information available in the AMNH. Nevertheless, if it was collected along the Acre River, a Tarija origin for the specimen is unlikely. Futhermore, in the area where the specimen is assumed to have been collected (upstream from Cobija), there are two formations cropping out, one at each side of the river: the Cobija Formation on the Bolivian side (Carrasco 1986, Fortier 2011) and the Solimões Formation on the Brazilian side (Cozzuol 2006). The Cobija and Solimões Formations are considered correlative (Fortier 2011) and late Miocene in age (Cozzuol 2006). As such, AMNH 14441 is interpreted in this work as likely being from either of these two late Miocene units, which limits known occurrences of Mourasuchus to the Miocene (Riff et al. 2010, Cidade et al. 2019).

We follow Iordansky (1973) for the nomenclature of bones, musculature, vasculature and other anatomical structures. However, for other specific anatomical structures, we make use of the nomenclature of other works that are accordingly cited throughout the text.

# Systematic paleontology

The suprageneric names used in this Systematic Paleontology section are those of clades, not of Linnean categories. Both the authors whom first erected the names (regardless of whether it was in a traditional Linnean or in a phylogenetic nomenclature context) and those whom later provided the definition of these clade names are given following each taxonomic name.

CROCODYLIA Gmelin, 1789, sensu Benton & Clark, 1988

ALLIGATOROIDEA Gray, 1844, *sensu* Brochu, 2003 ALLIGATORIDAE Cuvier, 1807, *sensu* Norell *et al.*, 1994 CAIMANINAE Brochu, 2003 (following Norell 1988) *Mourasuchus* Price, 1964

Mourasuchus arendsi Bocquentin-Villanueva, 1984

#### Holotype

CIAAP-1297, an almost complete skull with a complete right mandibular ramus and fragments of the left mandibular ramus, first six cervical vertebrae in articulation, two isolated putative cervical vertebrae, three isolated putative dorsal vertebrae and an articulated left scapulocoracoid (Bocquentin-Villanueva 1984 and Cidade *et al.* 2018).

#### Emended diagnosis

Differs from *M. amazonensis*, *M. atopus* and *M. pattersoni* by having the incisive foramen enlarged anteriorly and narrorw posteriorly and the dorsal surface of the squamosal highly hypertrophied, forming a protuberance ('horn'); differs from *M. amazonensis* and *M. pattersoni* by having a lateromedially slender and dorsoventrally low jugal and a small, circular external naris; differs from *M. atopus* and *M. pattersoni* by having lateromedially expanded palatines. Emended from Bocquentin-Villanueva 1984 and Cidade *et al.* 2018.

#### Referred material

AMNH 14441, UFAC-4925, UFAC-2515, UFAC-3530, UFAC-1666, UFAC-3717, UFAC-1477, UFAC-4885, UFAC-4259 and UFAC-1431, all posterior parts of the skull table (Figs 2, 3 and 4) with variable degrees of preservation (see General Preservation Status below).

#### Occurrence

The UFAC specimens come from the Solimões Formation, late Miocene of Brazil. AMNH 1441 comes from an unknown locality from the Cobija or Solimões Formation on the Bolivian side of the Acre River. *Mourasuchus arendsi* also occurs in the late Miocene Urumaco Formation of Venezuela (Bocquentin-



*Fig.* 2. Four of the ten specimens of *Mourasuchus arendsi* described in this paper: UFAC-3717 in dorsal (A) and posterior (B) views; UFAC-3530 in dorsal (C) and posterior (D) views; UFAC-1666 in dorsal (E) and posterior (F) views; UFAC-4925 in dorsal (G) and posterior (H) views. Scale = 5 cm.

Villanueva 1984, Scheyer & Delfino 2016) and Ituzaingó Formation of Argentina (Scheyer & Delfino 2016).

## Results

### Description

*General preservation status.* The ten specimens comprise posterior portions of the skull table (Figs 2, 3 and 4). That this part of the skull seems to be preferentially preserved may reflect the unusual morphology of the skull in *Mourasuchus*, in which the long, broad rostrum is a very wide but very thin fragile structure (Price 1964, Souza-Filho & Guilherme 2011a). This makes the rostral area of *Mourasuchus* more liable to postmortem fragmentation and destruction than the smaller, more compact and relatively more robust skull table, despite the fact that the skull table is pneumatized.

Despite the variable preservation status of the specimens (Figs 2–4), some patterns can be distinguished. All preserve the posteriormost part of the skull table, including the parietal, supraoccipital and both



*Fig. 3.* Four of the ten specimens of *Mourasuchus arendsi* described in this paper: UFAC-4885 in dorsal (A) and posterior (B) views; UFAC-1477 in dorsal (C) and posterior (D) views; UFAC-4259 in dorsal (E) and posterior (F) views; UFAC-1431 in dorsal (G) and posterior (H) views. Scale = 5 cm.

squamosals (except UFAC-1477 and UFAC-4885, which preserve only the right or left squamosal respectively). Four of these specimens (UFAC-2515, UFAC-1431, UFAC-3717, UFAC-1666) preserve at least one quadrate. Beyond this, preservation varies.

AMNH 14441, UFAC-2515, UFAC-4925 and UFAC-1431 preserve the basioccipital posteriorly, the posteriormost portion of the frontal in dorsal view, and from this point to the basisphenoid and the dorsal portion of the pterygoid anteriorly. Of these, UFAC-2515 is the most complete and best preserved (Figs 5 and 6), with a larger number of sutures clearly preserved, and it contributed most to the following description. UFAC-4925 has a rougher surface texture and is marked by brown and white surficial mottling, whereas the other specimens have a predominant brown/beige coloration.

UFAC-3717 and UFAC-1666 preserve the dorsal and part of the lateral borders of the foramen magnum and, in dorsal view, the postorbitals. UFAC-1666 preserves a small portion of the frontal. In anterior view, the specimens are complete until the area of the dorsal margin of the trigeminal foramen.

UFAC-3530 is the least complete. In posterior view, the preserved area extends from the posterior



*Fig. 4.* AMNH 14441 in anterior (A), posterior (B) and dorsal (C) views. Scale = 5 cm.

margin of the skull table until the dorsal border of the foramen magnum, but this can be seen only through the preservation of the right exoccipital, as the left one has its medial portion damaged. In dorsal view, the preservation extends until just beyond the parietal, with only portions of the right quadrate, the squamosals and the parietal bone itself visible in the area in which the supratemporal fossae would be situated.

Preservation of UFAC-1477, UFAC-4259 and UFAC-4885 is somewhat similar to that of UFAC-3530: the preserved area extends, in posterior view, from the posterior margin of the skull table to the dorsal and lateral borders of the foramen magnum, though in these three specimens, only one exoccipital reaches this point (the right exoccipital in UFAC-1477 and UFAC-4259, the left in UFAC-4885). In dorsal view, preservation extends only to the level of the parietal, comprising all the area of the parietal sagittal crest. Only UFAC-4259 exhibits an eroded portion of the

frontal. In anterior view, these specimens are restricted to incomplete, eroded laterosphenoids and the medialmost portions of the quadrates which do not extend much beyond their contacts with the squamosals.

Ornamentation. Bone ornamentation varies among specimens, none of which is strongly sculptured (which is typical for Mourasuchus; Steel 1973, Bona et al. 2013a). Bones in the anterior portion of the skull table and occipital region are predominately smooth, with only scarce rugosities, bosses or pits, although none of them is prominent. The reduced ornamentation in the occipital region distinguishes Mourasuchus from most extant caimans (Bona et al. 2013a). The external dorsal surface of the skull table, however, has a markedly rugous, irregular (and, in the case of UFAC-4925, also rough and abrasive) surface. The hypertrophied squamosals are visually the most rugous part of the skull in all specimens, with marked rugosities distributed all along the surface that are interpreted as vascular grooves (Bona et al. 2013a). The squamosals also preserve, at their anterior bases in dorsal view, several small bosses and elevations. In the specimen with the best-preserved external aspect, UFAC-2515, the parietal and frontal surfaces exhibit several slight rugosities. On the frontal, these rugositites, which also may be vascular grooves, are horizontally orientated and distributed along the elevated lateral borders of the bone, delimiting the orbits. The parietal also bears small bosses near the medial borders of the supratemporal fenestrae. UFAC-1666 also bears small pits on the squamosals, while UFAC-1431 preserves few pits on the occipital area along the squamosal-supraoccipital suture.

#### Individual description of the bones

*Frontal.* The frontal is not completely preserved on any specimen. Among those in which it is at least partially preserved, the best is observed on UFAC-2515 and UFAC-4925 where the frontal extends from the posterior portions of both orbit medial rims to the contact surfaces for the parietal and postorbitals. The frontal does not contact the supratemporal fenestrae, with the frontoparietal suture on the skull table entire, as in most members of Brevirostres (see Brochu 2011).

The frontal is narrow, in accordance with the medial position of the orbits characteristic of *Mourasuchus*. The lateral margins of the frontal are elevated abruptly adjacent to the orbital margins, as in most caimanines (Brochu 2011, Hastings *et al.* 2013, Scheyer *et al.* 2013, Salas-Gismondi *et al.* 2015). Such elevation is present along the lateral surface of the frontals; the postorbitals exhibit a similar morphology as discussed below. Despite this elevation, it is not possible to confirm whether these specimens bore the marked knob around the orbit that is reported in *M. amazonensis*, *M. atopus* and *M. arendsi* (Bona *et al.* 2013b, Cidade *et al.* 2018). The only known specimen attributed to *M. nativus* to preserve the prefrontals is UFAC-1424



Fig. 5. UFAC-2515 in dorsal view (A) and schematic drawing (B). f: frontal; p: parietal; po: postorbital; q: quadrate; sq: squamosal; so: supraoccipital; stf: supratemporal fenestra. Scale: 5 cm.



*Fig. 6.* UFAC-2515 in posterior view (A) and schematic drawing (B). bo: basioccipital; ex: exoccipital; fm: foramen magnum; oc: occipital condyle; ptf: postemporal fenestra; so: supraoccipital; sq: squamosal. Scale = 5 cm.

(Bocquentin-Villanueva & Souza-Filho 1990), but the area is only poorly preserved and does not allow further assessment of this feature.

Ventrally, still in UFAC-2515 and UFAC-4925, the *cristae cantii frontales* are distinguishable. Posteriorly, the frontal comprises the dorsal floor of the braincase. In five other specimens (AMNH 14441, UFAC-1666, UFAC-1477, UFAC-4259, UFAC-1431) only the posteriormost part of the frontal is preserved, with no meaningful anatomical details observable.

*Parietal.* The parietal is preserved in all specimens. It contacts the frontal anteriorly, the postorbital anterolaterally, the squamosals posterolaterally, and the supraoccipital posteriorly, but as with most caimanines (see Brochu 2011; Fig. 5), it does not reach the posterior edge of the skull table. The bone is rectangular, in accordance with the small size of the supratemporal fenestrae. This correlation was observed among crocodylians by Iordansky (1973). The parietal has a wide, plain aspect anteriorly, but it abruptly expands posteriorly as it approaches the supraoccipital, in accordance with the overall elevation of the posterior portion of the skull table (Gasparini 1985, Bona *et al.* 2013a and 2013b).

The parietal constitutes the lateral and a portion of the anterior borders of the supratemporal fenestrae, with the other part of the anterior border being comprised by the postorbital. The rims of the supratemporal fenestrae are overhung by the dermal bones, as in most caimanines (Brochu 2011). The supratemporal fenestrae in most of these specimens is trilobate (e.g., UFAC-2515, Fig. 5) regardless of size. The right fenestra of AMNH 14441 appears to be roughly oval in shape, but this can not be confirmed due to distortion of the area. The supratemporal fenestrae display a more variable outline in the two specimens of *Mourasuchus* from Argentina—subcircular in MLP 73-IV-15-8, but trilobate in MLP 73-IV-15-9 (Bona *et al.* 2013a).

Bona *et al.* (2013a) also report three marked vascular grooves surrounding each trilobate supratemporal fenestra, each corresponding to a lobe. These grooves are also present in the specimens described here. Additionally, these grooves can have a physiological function, such as thermoregulation (Bona *et al.* 2013a), as will be discussed below. One of those grooves (the one that emerges from the caudolateral lobe) is deeper in the larger specimens, as noted by Bona *et al.* (2013a). The *cristae cranii parietalis*, which constitute



Fig. 7. UFAC-2515 (A) and UFAC-4259 (B) showing respectively the elevated and the inconspicuous aspects of the parietal crest (pc). Scale = 5 cm.

the medial walls of the supratemporal fenestrae and the opening for the orbitotemporal artery and vein, can be seen on the posterior wall of the supratemporal fossa, where these vessels, in crocodylians, connect with the temporal artery and vein (SedImayr 2002, Bona *et al.* 2013a) between the parietal and the squamosal.

The parietal sagittal crest (Fig. 7) varies among the specimens. In UFAC-2515, UFAC-1477, UFAC-4885 and UFAC-1431, the crest is conspicuous and elevated, with a longitudinally thin dorsal extremity. In other specimens, the crest is represented only by a slight convexity. In UFAC-4925, UFAC-3717, UFAC-3530, and UFAC-4259, the crest is a small inconspicuous elevation (Fig. 7). This feature may vary intraspecifically or taphonomically. On either side of the parietal crest, fossae argued by Bona *et al.* (2013a) that would bear vascular vessels emerging from the nearby supratemporal fenestrae are present. The parietal sagittal crest separates these fossae.

*Supraoccipital.* The supraoccipital contacts both squamosals laterally and the exoccipitals ventrolaterally. The exposure of the supraoccipital is large in dorsal view, and in posterior view, the bone is tall and narrow as indicated by Bona *et al.* (2013a). In occipital view, the bone is triangular and comprises the medial border and half of the ventral borders of the postemporal fenestrae.

The supraoccipital bears a prominent sagittal crest (Fig. 6) that may be the attachment area for cervical muscles (Bona *et al.* 2013a). The morphology of this structure varies, but in most specimens (AMNH 14441, UFAC-2515, UFAC-1477, UFAC-3717, UFAC-3530, UFAC-4259, UFAC-1431) the crest is singular, dorso-ventrally expanded, and medially compressed along the midline. In the others (UFAC-4925, UFAC-1666, UFAC-4885), the crest is a group of isolated elevations. Such differences may reflect individual variation, possibly resulting from the activity of the muscle on the crest during the life of the individual, although this must be tested in future studies.

In all specimens, the dorsal surface of the supraoccipital is dorsoventrally elevated, following the elevation of the squamosals, but the degree of elevation varies among specimens. In AMNH 1441 and UFAC- 1666, this elevation reaches such a degree that the supraoccipital is as highly elevated as the squamosals. In the other UFAC specimens, the surface of the supraoccipital lies below those of the squamosals. These differences may be due to individual or ontogenetic variation as proposed by Bona *et al.* (2013a).

On the supraoccipitals of the specimens here described, unlike those of other crocodylians, the *processus postoccipitales*, a pair of posteriorly orientated processes, are practically absent, as reported by Bona *et al.* (2013a) for the Argentine specimens of *Mourasuchus*.

Postorbitals. The following specimens preserve both dorsal plates of the postorbital entirely: UFAC-2515, UFAC-4925, UFAC-1666. AMNH 1441 preserves both almost completely. UFAC-1431 preserves the right dorsal plate entirely but the left one just partially. UFAC-3717 preserves only the right postorbital dorsal plate, but in its entire form, and UFAC-4259 preserves the same structure partially. The postorbital descending process can be seen in UFAC-3717, UFAC-4925, UFAC-1477, and UFAC-1666, but only a small part of the posterior portion is preserved. This portion hints that the descending process was slender, as in most alligatoroids and crocodyloids (see Brochu 1997, 2011), but this can not be assured completely. The process was also inset from the anterolateral edge of the skull table. The postorbital contacts the frontal and the parietal medially, the squamosal posteriorly, and the quadrate laterally.

In specimens preserving at least one postorbital (e.g., UFAC-2515, UFAC-3717, UFAC-1666, UFAC-4925 and UFAC-1431), the portion of the bone comprising the posterior rim of the orbit is markedly elevated relative to the rest of the skull table. This is continuous with what has been previously described for the lateral margins of the frontal, which comprises the posterior portions of the medial borders of the orbits.

*Squamosals.* UFAC-1477 preserves the right squamosal, UFAC-4885 preserves the left squamosal, and the other specimens preserve both. In all, the squamosals are elevated relative to the anterior part of the skull table. This elevation includes the supraoccipital (most notably in AMNH 14441, as described above),

which the squamosals contact medially in dorsal view, and the parietal behind the sagittal crest.

The most distinctive aspect of the squamosals is their remarkably hypertrophied form, bearing very accentuated, voluminous horn-like bosses. These are present in all *Mourasuchus* specimens preserving the dorsal surface of the squamosal, including the holotypes of both *Mourasuchus arendsi* and *Mourasuchus nativus* (see Gasparini 1985, Scheyer & Delfino 2016, Cidade *et al.* 2018), and CT scan images performed by Bona *et al.* (2013a) showed that these structures are solid and not invaded by the paratympanic sinus system. These hypertrophied bosses are surrounded by vascular grooves that generally become more pronounced in larger structures (Bona *et al.* 2013a).

The squamosal contacts the postorbital anteriorly, and the sutural area is very thickened in most specimens, most notably in UFAC-4925. The squamosal surface is markedly rugose along its extent, and there are smaller bosses along the base of the main bosses.

In occipital view (Fig. 6), the squamosal expands ventrolaterally, contacting the supraoccipital medially, the paraoccipital process of the exoccipital ventrally, and the quadrate laterally. The squamosal comprises the dorsal and lateral border of the postemporal fenestra. These fenestrae are the openings for the orbitotemporal canals. In Mourasuchus, the fenestrae are dorsoventrally large, and the openings for the orbitotemporal canals are anteroposteriorly deep, such that the exoccipitals form a platform on the ventral margin of each postemporal fenestra. The fenestrae have a subcircular aspect, as observed by Gasparini (1985), and allowed passage for ramifications of the temporal artery and vein (Sedlmayr 2002, Bona & Desojo 2011, Bona et al. 2013a). The squamosal surface dorsal and dorsolateral to the postemporal fenestra is large, and it may have been a surface attachment for the musculus spinalis capitis in the absence of the posteriorly orientated process of the supraoccipital, as well as the longitudinal axial musculature (Bona et al. 2013a).

*Exoccipitals.* Only four specimens (AMNH 14441, UFAC-3717, UFAC-2515 and UFAC-1431) preserve substantial amounts of the exoccipitals. They contact the squamosals dorsally and laterally, the quadrates ventrolaterally through the paroccipital processes, the supraoccipital medially, and the basioccipital ventrally (Fig. 6). The exoccipitals contact each other dorsal to the foramen magnum (Fig. 6). They comprise the medial parts of the ventral borders of the postemporal fenestrae. Ventrally, in UFAC-2515 and UFAC-1431, the exoccipitals contact the basioccipital, bearing slender descending processes on each side, as in most caimanines (see Brochu 1997, 2011).

In UFAC-3717 and UFAC-2515, the tympanic bullae can be seen through the opening of the foramen magnum. In crocodylians, these are formed by the



*Fig. 8.* UFAC-1477 in posterior view (A; scale = 5 cm), with the area marked in the square detailed in (B; scale = 1 cm), showing the foramen vagus (fv) and the XII cranial nerve (XII) in the exoccipital.

exoccipital, supraoccipital and prootic bones (Iordansky 1973).

There are several foramina on the ventralmost portion of the exoccipital close to the suture with the basioccipital (Fig. 8). The largest and lateralmost opening is the vagus foramen, which is preserved and distinguishable in UFAC-2515 (both exoccipitals), UFAC-1477 and UFAC-1431 (right exoccipital) and UFAC-3717 (left exoccipital). It provides passage for cranial nerves IX, X and XI, and for the jugular vein (Bona et al. 2013a). Medial to the vagus foramen are the foramina for the XII cranial nerve (foramina hypoglossi; Bona et al. 2013a) on UFAC-2515 (both exoccipitals), UFAC-3717 (left) and UFAC-1477 (right). In the latter specimen, there are three such openings; in the others there are two, as observed in Caiman latirostris (see Bona & Desojo 2011), although the number of the foramina hypoglossi is subject to individual variation in all crocodylian species (CAB personal observation). On UFAC-2515, UFAC-3717, UFAC-1477 and UFAC-1431, the posterior carotid foramen is preserved on the ventral margin of the exoccipital.



*Fig. 9.* UFAC-2515 (A) in left lateral view and AMNH 14441 (B) in right lateral view of the anterior region of the braincase, exhibiting the laterocaudal bridge (lcb). bsr: basisphenoid rostrum; fV2: foramen for the maxillary branch of the trigeminal nerve (V2); fV3: foramen for the mandibular branch of the trigeminal nerve; ls: laterosphenoid; pt: pterygoid; q: quadrate.

The ventral opening of the cranioquadrate passage may be seen on UFAC-1431 (both exoccipitals), UFAC-3717 and UFAC-2515 (on the left). The hyomandibular branch of the facial nerve (VII), orbitotemporal artery, lateral cephalic vein, ceratohyal nerve, stapedial artery and vein, and tympanical branch of the glossopharyngeal nerve have been proposed to pass through this passage in different crocodylians, including *Mourasuchus* (Iordansky 1973, Bona & Desojo 2011, Bona *et al.* 2013a).

*Basioccipital.* The basioccipital, preserved only in four specimens (AMNH 14441, UFAC-2515, UFAC-4925 and UFAC-1431), includes the occipital condyle, the hexagonal basioccipital plate bearing a median crest and a pair of laterally positioned tubera. It contacts the exoccipitals dorsally and the basisphenoid anteriorly. The basioccipital forms the medialmost part of the ventral margin of the foramen magnum and the posterior floor of the cerebral cavity.

The occipital condyle, which is completely preserved only in AMNH 14441, UFAC-2515 and UFAC-1431, is spherical. The basioccipital crest, which serves as attachment for the tendons of the *basioccipitovertebralis* and *occipitotransversalis profundus* muscles (Iordansky 1973), is preserved on all four specimens cited above and is longitudinally thin along its posterior extremity (see UFAC-2515 in Fig. 6).

*Basisphenoid.* The basisphenoid is partially preserved on AMNH 14441, UFAC-2515, UFAC-4925, and UFAC-1431. It contacts the laterosphenoids anterodorsally and the basioccipital posteriorly. The baisphenoid also forms the anterior surface of the cranial cavity. An anteroposteriorly expanded and mediolaterally compressed basisphenoid rostrum is preserved on UFAC-2515. A sulcus separates the basisphenoid rostrum from the lateral braincase wall, and the basisphenoid is not exposed extensively anterior to the trigeminal foramen (see Brochu 2011). Posteriorly, the basisphenoid is an anteroposteriorly thin sheet, as in most crocodylians (see Brochu 2011).

*Laterosphenoids*. Although all specimens preserve at least small portions of the laterosphenoids, the best preserved are those of AMNH 14441, UFAC-2515, UFAC-4925 and UFAC-1431, in which they are almost complete. Details are best seen in AMNH 14441 and UFAC-2515.

The laterosphenoids comprise the anterior lateral walls of the braincase. They articulate dorsally with the frontal and, with a nonsutural contact through the capitate process, with the postorbital. As such, the laterosphenoids form the anteromedial areas of the supratemporal fossae (dorsotemporal fossae *sensu* Holliday & Witmer 2009, Bona & Desojo 2011). The anterior opening of these fossae are limited dorsally by the postorbital and are slightly ventrolaterally inclined in anterior view.

The dorsalmost portion of the lateral surface of the laterosphenoid (postorbital process) is the primary attachment site for the *pseudotemporalis superficialis* muscle in crocodylians (Holliday & Witmer 2009, Bona *et al.* 2013a). It is possible to see on UFAC-2515 the cotylar crest of the laterosphenoid (*sensu* Holliday & Witmer 2009), a distinct longitudinal structure that serves for the attachment of the *pseudotemporalis* muscle (Iordansky 1964, Holliday & Witmer 2007; Bona *et al.* 2013a). This crest in *Mourasuchus* is more vertically orientated than in other caimanines (Bona *et al.* 2013a).

The laterosphenoids contact the quadrates laterally, and along this suture, there is a large foramen for the trigeminal ganglion (Fig. 9). A smaller foramen and groove dorsal to the primary trigeminal foramen, which is also along the contact between the laterosphenoid and the quartate, traces the pathway of the supraorbital branch of the trigeminal nerve (Fig. 9). The trigeminal foramen is delimitated medially and dorsally by the lateral and caudal bridges respectively. Besides these two bridges, the right laterosphenoid of AMNH 14441 and both elements of UFAC-2515 preserve an additional anatomical feature—an extra 'bridge', situated across the trigeminal foramen, that may be a neomorph.

This laterocaudal bridge (*sensu* Bona *et al.* 2011; = caudolateral bridge of Bona *et al.* 2013a) is formed by an anteroventral extension of the quadrate together with a smaller posterodorsal expansion of the laterosphenoid. This structure may separate the maxillary and mandibular branches ( $V_2$  and  $V_3$ , respectively) of the trigeminal nerve. Although the laterocaudal bridge is

preserved entirely only on UFAC-2515 and the right laterosphenoid of AMNH 14441, the left laterosphenoid of the last specimen and both laterosphenoids of UFAC-1477 and UFAC-1431 preserve the proximalost parts of the expansions that form the bridge. As such, we infer that the bridge was also present in these two specimens.

Medial to the trigeminal foramen is the foramen for the tympanic trigeminal branch (Holliday & Witmer 2009), which in these specimens is almost the same size as the trigeminal foramen. This foramen is exposed in lateral view, as described by Bona *et al.* (2013a). Bona *et al.* (2013b) includes this feature in their diagnosis of *Mourasuchus nativus*, but the status of this structure in other *Mourasuchus* species is not known.

*Pterygoids*. The posterodorsal portions of the pterygoids, contacting the laterosphenoids and basisphenoid, are preserved only on AMNH 14441, UFAC-2515, UFAC-4925 and UFAC-1431 (Fig. 9). These are also the specimens also exhibit better-preserved laterosphenoids.

*Quadrates.* No specimen preserves both quadrates completely. UFAC-2515, UFAC-3717 and UFAC-1431 preserve complete left quadrates, and UFAC-1666 preserves a complete right quadrate.

The quadrate is broadly expanded laterally and dorsally (Figs 2 and 3), as described for other *Mourasuchus* specimens (e.g., Price 1964; Bocquentin-Villanueva & Souza-Filho 1990; Bona *et al.* 2013b) and consistent with the large, broad rostrum of the genus. It contacts the postorbital and squamosal dorsally; the laterosphenoid, basisphenoid and pterygoid anteroventrally; and the exoccipital and squamosal medially. The quadrate bears a process on the lateral braincase wall rendering the quadrate-pretygoid suture nonlinear, as in most crocodylians (Brochu 2011).

The quadrate mandibular condyles are completely preserved on all complete specimens listed above, except for the medial hemicondyle of UFAC-1431, which is eroded. The medial and lateral hemicondyles are nearly the same size in all specimens. The *foramen aëreum* is visible only on the preserved quadrate of UFAC-1666 and lies on the dorsal surface of the quadrate, a common feature among alligatoroids (Brochu 1997, 2011).

In ventral view, there are crests interpreted as quadrate crests A, B and D *sensu* Iordansky (1973). Crest A, or its anterior continuation (A'), is visible in all specimens that preserve at least the proximalmost portion of a quadrate. The anterior terminus of A' is close to the laterocaudal bridge. Crest B can be seen on UFAC-1431, UFAC-2515, UFAC-1477, UFAC-3717 and UFAC-4925. Blunt convexities on the ventral surface of the quadrate anterior to the mandibular joint in UFAC-1431, UFAC-2515, UFAC-1666 and UFAC-3717 may correspond to crest D. All crests serve as origin sites for tendons and aponeuroses of the adductor muscles (Iordansky 1964, 1973), including *m. adductor mandibulae externus* and *m. adductor mandibulae posterior* (Bona *et al.* 2013a). The ventral portion of the quadrate is more laterally orientated than in other caimanines (Bona *et al.* 2013a), implying a derived orientation for the jaw musculature originating at this part of the quadrate (Bona *et al.* 2013a).

The quadrate and squamosal circumscribe a trilobate otic opening of the tympanic cavity, which has a bowed posterior margin as in most members of the Brevirostres clade (Brochu 2011). The otic opening of the tympanic cavity is preserved in both sides only on UFAC-1431. Other specimens preserve it on the left (UFAC-2515 and UFAC-3717) or the right (UFAC-1666, UFAC-4925, UFAC-3530, UFAC-1477). An external otic recess foramen is visible anterior to the otic opening of the tympanic cavity on UFAC-2515, UFAC-4925, UFAC-1477 and UFAC-2515, UFAC-4925, UFAC-1477 and UFAC-1431.

### Discussion

### Synonymy of Mourasuchus nativus (Gasparini 1985) and M. arendsi Bocquentin-Villanueva, 1984

We follow Scheyer & Delfino (2016) in regarding Mourasuchus nativus (Gasparini 1985) as a junior subjective synonym of M. arendsi Bocquentin-Villanueva 1984. Of the characteristics considered autapomorphic for M. nativus (Gasparini 1985, Bona et al. 2013b, Cidade et al. 2013), two are present on the holotype of M. arendsi (the horn-like squamosal bosses and parietal sagittal crest; Scheyer & Delfino 2016, Cidade et al. 2018; Figs 5 and 7). Others, such as the laterocaudal bridge, large postemporal fenestrae and large opening for the tympanic ramus of the trigeminal nerve, can not be assessed in other Mourasuchus species either to nonpreservation (M. atopus; see Langston 1965 and Scheyer & Delfino 2016), or poor preservation allied with the impossibility of observing the structures due to the disposition of the material in a plaster jacket (M.arendsi, Cidade et al. 2018; and M. amazonensis, GMC personal observation).

Bona et al. (2013b) argued that the absence of a pronounced knob at the anteromedial margin of the orbits differentiates М. nativus from other Mourasuchus species, but in fact none of the specimens attributed to M. nativus preserve the anteromedial margin of the orbits well enough to assess this feature (Figs 2, 3, 4 and 5), including UFAC-1424 (GMC personal observation; see Bona et al. 2013b, fig. 2C). Bona et al. (2013b) also argued that M. nativus would have short ventral exoccipital process (Bona et al. 2013b), but UFAC-2515 and UFAC-1431 display long ventral exoccpital process (see UFAC-2515 in Fig. 6), and the same morphology is present on the holotype of M. nativus (MLP 73-IV-15-8, GMC personal observation) and M. arendsi (Cidade et al. 2018). As the condition can not be assessed in other holotypes of the

genus due to nonpreservation (*M. atopus*, Langston 1965; *M. amazonensis*, GMC personal observation), this character also can not be currently regarded as diagnostic for *M. nativus*.

From all specimens referred to Mourasuchus nativus, including the holotype (Gasparini 1985; Scheyer et al. 2013), all but one consists mainly of isolated skull tables that can be referred to M. arendsi. The only exception is UFAC-1424, assigned to M. nativus by Bocquentin-Villanueva & Souza-Filho (1990), which is a skull table that also preserves both quadrates, quadratojugals, most of the jugals, parts of the prerygoid, ectopterygoid and palatines and most of the right mandibular ramus. The jugals of UFAC-1424 are lateromedially wide and dorsoventrally low (Character 187-1 of Cidade et al. 2017), the same morphology seen on the holotype of M. amazonensis but different from that of the holotype of *M. arendsi*, in which the jugal is also dorsoventrally low but lateromedially slender (Cidade et al. 2017, Character 187-0; Cidade et al. 2018).

This indicates that UFAC-1424 may be closer to M. amazonensis than to M. arendsi. However, it is still not known whether the holotype of M. amazonensis has horn-like squamosals or the elevated parietal sagittal crest. Price (1964) offers only a drawing of the dorsal portion of the holotype skull in which the presence of these structures is not clearly depicted, and the dorsal portion of the skull can not be currenly observed as it is tightly attached to a plaster jacket (GMC personal observation). If the holotype of M. amazonensis does preserve both characters, then UFAC-1424 could be referred to M. amazonensis. If it does not, however, the specimen could be considered as a new species of Mourasuchus based on a unique combination of characters. The presence of these two characters might also render M. nativus a nomen dubium, and not synonymous with M. arendsi, if no other differences are recognized between the holotypes of *M. amazonensis* and *M.* nativus. The dorsal view of the skull of M. amazonensis must be assessed to settle these issues.

# Laterocaudal bridge of Mourasuchus and its possible anatomical and functional implications

The laterocaudal bridge, the bony structure situated across the trigeminal foramen presumably separating the maxillary and mandibular nerves (Fig. 9), may be neomorphic among crocodylians, as a similar structure has not been described for any other species (Cidade *et al.* 2011, Bona *et al.* 2013a). A similar structure was reported in the extant crocodylid *Crocodylus palustris*, but in this case, the structure is a ventral expansion of the laterosphenoid caudal bridge that, upon contacting the ventral portion of the lateral bridge, results in a process that also divides the trigeminal foramen (Holliday & Witmer 2009). Also, this pattern is considered a matter of individual variation in *C. palustris*, as

not all the individuals of this species present it (CAB personal observation).

Bona et al. (2013a, p. 234) classified the trigeminal fossa of Mourasuchus as 'huge'. George & Holliday (2013) found a strong correlation between trigeminal fossa volume and other cranial measurements, such as skull length and endocranial volume, in modern Alligator mississippiensis. This correlation is consistent with what is known for Mourasuchus, as completely preserved skulls are indeed long when measured from the tip of the premaxillae to the posterior margin of the supraoccipital: M. amazonensis (1.11 m; Price 1964), M. pattersoni (1.06 m; GMC personal observation) and M. arendsi (0.91 m, GMC personal observation). However, George & Holliday (2013) found only a weak correlation between trigeminal fossa volume and skull length in other extant crocodylians and some fossil crocodyliforms, suggesting that differences in fossa volume relative to brain or skull size might reflect differences in sensory magnitude as well. This is also plausible for Mourasuchus, as George & Holliday (2013) also found that trigeminal fossa volume and skull length both correlate with axon count and nerve cross-section area of the maxillary and mandibular nerves of A. mississipiensis. These nerves are responsible for innervating the integumentary sensory organs (ISOs) of the crocodylian upper and lower jaws (Leitch & Catania 2012). The ISOs are mechanoreceptors responsible for detecting movements in the water from potential prey (Soares 2002), while according to Leitch & Catania (2012, p. 4228) they may also play a key role in 'discriminating objects that have been grasped in the jaws and guiding the manipulation of prey once it has been secured'. The sensitivity of this tactile system is thought to exceed that of primate fingertips (Leitch & Catania 2012), and is capable of discerning even minute water surface disturbance.

The mandibles of *M. amazonensis* and *M. atopus* bear several foramina that may be homologous with the neurovascular foramina housing the ISOs in extant species (GMC personal observation), which suggests the presence of these structures in Mourasuchus. This is interesting as Mourasuchus is thought not to have been an active predator of large prey (Langston 1965, 2008; Cidade et al. 2017). Mourasuchus may have relied on this powerful sensory tool to capture small fish and arthopods (Langston 1965; Cidade et al. 2017). According to Leitch & Catania (2012) crocodylians can distinguish edible from nonedible matter based on tactile information from the ISOs. Therefore, the concentration of ISOs in Mourasuchus could have been significantly larger than in other crocodylians. The number of ISOs and the magnitude of their sensory coverage may increase the size of the maxillary and mandibular nerves, which are correlated with the size of the trigeminal fossa (George & Holliday 2013); it is thus possible that the enlarged trigeminal fossa in *Mourasuchus* is related to a larger number of ISOs in the rostrum. This in turn can be related to the peculiar feeding habits of *Mourasuchus* reflected in its unusual cranial and postcranial anatomy (Cidade *et al.* 2017). Additionally, Bona *et al.* (2013a) propose that the large size of the trigeminal fossa could indicate a large trigeminal ganglion. In this context, the maxillary and the mandibular rami of the trigeminal nerve could also be larger in *Mourasuchus*, with the laterocaudal bridge thus being needed to separate them.

However, this is still speculative. The presence of ISOs in *Mourasuchus* needs to be confirmed, and more studies about the trigeminal nerve in this taxon and other caimanines are required. Also, hypetrophy of the surrounding trigeminal vasculature and the possibility that the *musculus adductor mandibulae externus* (mAME) used the extra surface provided by the bridge to maintain an attachment area (Bona *et al.* 2013a) must also be considered as related factors.

#### Possible thermoregulatory function in Mourasuchus

The cranioquadrate passage and the postemporal fenestrae of Argentine Mourasuchus specimens are described as 'huge' (Bona et al. 2013a, p. 232). This, along with the superficial vascularization of the head in the skull roof (e.g., in the vascular fossae of the parietal), led these authors to speculate that the vascular system was capable of transporting large amounts of blood, possibly for a physiological function such as thermoregulation. Moreno-Bernal (2007) linked the huge narial opening of Mourasuchus amazonensis (and also in M. pattersoni, but not in the holotypes of M. atopus and M. arendsi-see Cidade et al. 2017) to thermoregulation. This could be related to respiratory mechanisms that would have prevented overheating of the brain (Tattersal et al. 2006). Concentration of the large vascular vessels in the skul roof is consistent with the thermoregulatory function proposed by Bona et al. (2013a), as is the fact that these vascular channels communicate with the encephalic vessels (Holliday & Gardner 2012, Bona et al. 2013a). However, these hypotheses require further testing.

# Possible functions of the squamosal horns in Mourasuchus

In addition to *Mourasuchus*, several crocodylians bear horn-like structures. Among modern species, they are most prominent on the Cuban (*Crocodylus rhombifer*) and Siamese (*C. siamensis*) crocodiles, though they can occur on very large specimens of most species of *Crocodylus* (e.g., Mook 1921, Vliet 2001), and the presence of modest horns distinguishes one modern species of *Mecistops* from the other (Shirley *et al.* 2018). Squamosal bosses are also found on the Paleocene alligatorine *Ceratosuchus* (Schmidt 1938, Bartels 1984) and several extinct crocodylids from East Africa, Aldabra Atoll, and Madagascar (Brochu 2006, 2007, Brochu *et al.* 2010, Brochu & Storrs 2012). In all of these cases, the squamosal bosses lie along the posterolateral or lateral margin of the skull table and may incorporate part of the postorbital.

Extant *C. rhombifer* and *C. siamensis* perform social displays with the head in which the squamosal horns may play a visual role. These displays may be used by males to attract females (Souza-Filho *et al.* 2019). The squamosal eminences of *Mourasuchus* could likewise have been used in mating displays.

The squamosal eminences of Mourasuchus vary in size among specimens. In some, such as AMNH 14441, UFAC-1431, UFAC-4259 and UFAC-1477, the eminences are not only dorsoventrally larger but the supraoccipital is also markedly elevated. They are as high as the squamosal in AMNH 14441, thus forming a single continuous crest along the posterior border of the skull table. That the specimens with the largest squamosals are the largest specimens described in this paper suggests that the variation is ontogenetic, which is also true for extant crocodylians with eminences (Vliet 2001). However, the holotype of M. arendsi (CIAAP-1297) is a large specimen with a skull length of 91 cm (from the supraoccipital to the premaxillae), and yet the squamosal eminences are small relative to those described here. This in turn prompts us to consider sexual dimorphism; male crocodylians are larger than females (Grigg & Kirshner 2015), and the larger specimens in our sample might be males. This is consistent with the suggestion that the holotype of M. arendsi is female based on other characteristics (Cidade et al. 2018).

Such hypotheses must be considered cautiously. The only complete skull of *Mourasuchus* on which the eminences are preserved and accessible is the holotype of *M. arendsi*. This limits our understanding of these structures. Nevertheless, future morphometric work, even on incomplete *Mourasuchus* specimens, may shed light on the issue.

# Distribution of Mourasuchus in the Miocene of South America

The known distribution of *Mourasuchus* in South America (Fig. 10) includes, among other stratigraphic units, the Honda Group of Colombia (*M. atopus*), the Pebas Formation of Peru (*M. atopus*) the Urumaco Formation of Venezuela (*M. arendsi*, *M. pattersoni*), the Solimões Formation of Brazil (*M. amazonensis*, *M. arendsi*) and the Ituzaingó Formation of Argentina (*Mourasuchus arendsi*). Shared vertebrate taxa among at least two or more of these units has been noted previously (e.g., Cione *et al.* 2000, Cozzuol 2006, Sánchez-Villagra & Aguilera 2006, Riff *et al.* 2010, Cidade et al. 2019), with comprehensive compilations of vertebrate genera shared by all four areas provided by Cozzuol (2006) and Latrubesse *et al.* (2010).



Fig. 10. Map of South America showing the distribution of Mourasuchus along Miocene geological units. All occurrences are from the late Miocene, unless otherwise noted.

The presence of *Mourasuchus arendsi* in both the Urumaco and Solimões Formations adds to the strong similarity of their reptilian fauna, which is consistent with a north-flowing drainage of the Miocene Amazonian aquatic systems (Lundberg *et al.* 1998, Riff *et al.* 2010).

Moreover, the occurrence of Mourasuchus arendsi in the Solimões Formation in Acre, Brazil, and in the Ituzaingó Formation in Argentina reinforces the similarity of their faunas (Cione et al. 2000, Cozzuol 2006, Latrubesse et al. 2010). The northern and southern portions of South America are believed to have had, at least for continental vertebrates, greater faunal similarity in the late Miocene than in modern times, which led several authors to suggest one or more connections between these two areas during that period (Bocquentin-Villanueva & Souza-Filho 1990, Räsänen et al. 1995, Latrubesse et al. 2010, Riff et al. 2010). Such connections could have included drainage basins through swampy areas along their divides (Riff et al. 2010) that arose after regression of the Paranian Sea and before an uplift of the Andes by the middle-late Miocene, especially of the Bolivian Altiplano, which is currently the main geographical barrier between the Amazonian and Paraná drainage basins (Cozzuol 2006, Hoorn *et al.* 2010, Riff *et al.* 2010).

A marine transgression that could link those two areas was suggested (Räsänen *et al.* 1995) but later questioned (Cozzuol 2006, Latrubesse *et al.* 2007) based on the continental nature of the sediments and biota of southwestern Amazonian deposits, including freshwater crocodylians (Riff *et al.* 2010) such as *Mourasuchus.* 

### Conclusions

This paper adds to the knowledge about the genus *Mourasuchus* in describing ten specimens belonging to the species *M. arendsi.* Nine are from the Solimões Formation, from which *Mourasuchus* had already been reported; another specimen, AMNH 14441, is regarded

in this paper as probably deriving from late Miocene deposits of either the Cobija or the Solimões Formations, and not from the middle Miocene or the Pleistocene as previously proposed. This implies that *Mourasuchus* is known only from the Miocene (Fig. 10).

The morphology of the ten specimens described here does not contradict the proposed synonymy of *Mourasuchus nativus* (Gasparini 1985) with *M. arendsi* Bocquentin-Villanueva, 1984 (Scheyer & Delfino 2016). Most of the specimens formely attributed to *M. nativus*, including the holotype, may be assigned to *M. arendsi*, except for UFAC-1424, which can be considered either as belonging to *M. amazonensis* Price, 1964 or as a new species of *Mourasuchus* depending on future studies.

The laterocaudal bridge described by Bona et al. (2011) is fully preserved on two specimens described here. This structure, formed by an anteroventral extension of the quadrate and a small posterodorsal expansion of the laterosphenoid, is not known in any other crocodylian. Possible functions include attachment area for mAME, splitting hypertrophied vasculature, or separating hypertrophied maxillary and mandibulary rami of the trigeminal nerve. This last hypothesis is linked to a possible large number of ISOs in the upper and lower jaws, which in turn could be related to detection of small prey. These hypotheses require further testing. The same is true for possible thermoregulatory functions for enlarged blood vessels in the genus and the expanded external naris of M. amazonensis and M. pattersoni. Possible sexual dimorphism of Mourasuchus squamosal eminences, as well as a possible role of these structures in mating behavior, also have to be studied more in future assessments.

The distribution of *Mourasuchus* in the South American Miocene (Fig. 10) is consistent with biogrographical patterns observed in other taxa. In particular, the co-occurrence of *Mourasuchus* in the Urumaco and Solimões Formations is consistent with a north-flowing drainage of Miocene Amazonian fluvial systems, while the co-occurrence of *Mourasuchus* between those and the Ituzaingó Formation may be explained by the presence of drainages through swamps that connected setentrional and meridional South America before an uplift of the Andes by the middle-late Miocene that separated the two areas.

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