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# An updated taxonomic revision of the species of *Mourasuchus* (Alligatoroidea, Caimaninae)

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**ABSTRACT**

*Mourasuchus* is one of the most well-known components of the notable South American crocodylomorph fauna of the Cenozoic. There has been a recent renewed interest in the taxonomy of *Mourasuchus*, but some issues remained. This study addressed the taxonomic problems of the genus, concluding that there are four valid species: *M. amazonensis* (Price 1964), *M. atopus* , *M. arendsi* (Bocquentin-Villanueva 1984) and *M. pattersoni* (Cidade et al. 2017). *M. arendsi* may be a junior synonym of *M. atopus*, but this can only be evaluated through an eventual reanalysis of the ventral aspect of the skull of the holotype of *M. arendsi*. The specimens LACM-160157, UFAC-1424 and UFAC-5883 may either belong to *M. amazonensis* or represent a new species, which can be evaluated only through an eventual reanalysis of the dorsal aspect of the skull of the holotype of *M. amazonensis*. *Mourasuchus nativus* is considered a *nomen dubium* as its holotype is indistinguishable from at least two other *Mourasuchus* species: *M. arendsi* and either *M. amazonensis* or the possible new species represented by LACM-160157, UFAC-1424 and UFAC-5883. This study stresses the importance of taxonomic accuracy to comprehend fossil faunas, including remarkably diverse ones like South American cenozoic crocodylomorphs.

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*Mourasuchus*; Caimaninae; Crocodylia; taxonomy; Miocene; South America

## Introduction

*Mourasuchus* is one of the most notable components of the highly phylogenetically diverse and ecologically disparate crocodylomorph fauna of the Cenozoic of South America. Its occurrences are exclusively from the Miocene of South America and are scattered through many units of several countries, from the current Amazon region to the central and southern parts of the continent (Argentina, Bolivia, Brazil, Colombia, Peru and Venezuela) (Price 1964; Langston 1965, 1966, 2008; Bocquentin-Villanueva 1984; Gasparini 1985; Bocquentin and Souza-Filho 1990; Salas-Gismondi et al. 2007; Bona et al. 2012, 2013; Scheyer et al. 2013; Tineo et al. 2014; Scheyer and Delfino 2016; Cidade et al. 2017, 2019, 2019, 2019, 2020, 2021). *Mourasuchus* features an unusual morphology comprised of a long, broad, dorsoventrally flattened rostrum with long, slender mandibles and a dentition comprised of numerous teeth (around 40 in each hemimandible and in each maxilla) of small size (Price 1964; Langston 1965, 1966, 2008; Bocquentin-Villanueva 1984; Gasparini 1985; Bocquentin and Souza-Filho 1990; Bona et al. 2012, 2013; Tineo et al. 2014; Scheyer and Delfino 2016; Cidade et al. 2017, 2019, 2019, 2019, 2020, 2021). These morphological features have led previous authors to propose that *Mourasuchus* had distinct feeding habits from most crocodylomorphs, extinct or extant, with an analogous being proposed only for the neosuchian groups Aegyptosuchidae and Stomatosuchidae, from the Cretaceous of northern Africa (Stromer 1925, 1933; Nopcsa 1926; Sereno and Larsson 2009; Holliday et al. 2012). The feeding behaviour ascribed to *Mourasuchus* has been generally named as 'filter-feeding' (Riff et al. 2010) or, most recently, 'gulp-feeding' (Cidade et al. 2017, 2019), but several specific hypotheses about foraging strategies and prey have been proposed (Langston 1965, 2008; Cidade et al. 2019).

Currently, four species of *Mourasuchus* are valid: *M. amazonensis* (Price 1964), *M. atopus* (Langston 1965), *M. arendsi* (Bocquentin-Villanueva 1984) and *M. pattersoni* (Cidade et al. 2017). The genus has been subject to a renewed interest in the last decade, with several papers addressing the taxonomy of the group: Scheyer and Delfino (2016) considered *M. nativus* Gasparini (1985) (a species described from the Ituzaingó Formation of Argentina) as a junior synonym of *M. arendsi*, whereas the holotypes of *M. amazonensis* and *M. arendsi* have been subject to recent redescriptions (Cidade et al. 2019, 2020).

Despite these recent assessments, some lingering questions remain regarding the taxonomy of *Mourasuchus*. These are related mainly to the fact that both the dorsal aspect of the skull of the holotype of *M. amazonensis* and the ventral aspect of the skull of the holotype of *M. arendsi* are firmly attached to plaster jackets cannot be currently re-examined (Cidade et al. 2019, 2020). Furthermore, their original descriptions lack photographs of these skull areas, featuring only drawings (Price 1964; Bocquentin-Villanueva 1984). Additionally, the possible assignment of incomplete specimens at a specific level also needs to be clarified, considering the number of taxonomic revisions and holotype redescriptions published about *Mourasuchus* in the last few years (Scheyer and Delfino 2016, Cidade et al. 2019; Cidade et al. 2020).

In this context, this paper has the objective of providing an updated summary of the taxonomy of the species of *Mourasuchus*, including revised diagnoses of the four species, updated

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identifications of isolated specimens at the lowest taxonomic level, especially those previously assigned to *M. arendsi* after *M. nativus* was considered a junior synonym of that species (Cidade et al. 2019, 2021), and an update on the taxonomy status of *M. nativus* considering the recent description of specimens assigned as *Mourasuchus* cf. *M. amazonensis* (see Cidade et al. 2019).

## Institutional abbreviations

AMNH, American Museum of Natural History, New York, United States; AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Urumaco, Venezuela; CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Coro, Venezuela; DGM, Divisão de Geologia e Mineralogia, Museu de Ciências da Terra, Rio de Janeiro, Brasil; IVIC-P, Colección de Paleontología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; LACM, Los Angeles County Museum, Los Angeles, United States; MCNC-PAL, Museo de Ciéncias Naturales de Caracas, Caracas, Venezuela; MLP, Museo de La Plata, La Plata, Argentina; UCMP, University of California Museum of Paleontology, Berkeley, United States; UFAC, Universidade Federal do Acre, Rio Branco, Brasil.

## Results

### Review of proposed characters to diagnose *Mourasuchus* species

Several characters have been proposed to diagnose *Mourasuchus* species by previous recent studies (Bona et al. 2012; Scheyer and Delfino 2016; Cidade et al. 2017, 2019, 2020). Below, a brief review is presented to illustrate which characters are deemed valid or not valid for diagnosis by this study. Some of the characters used to diagnose between *Mourasuchus* species by previous recent studies (Bona et al. 2012; Scheyer and Delfino 2016, 2017) are not regarded as valid by this study.

These include the presence of a marked knob at the anterior-medial margin of the orbits, which was considered by Bona et al. (2012) and Scheyer and Delfino (2016) to diagnose UFAC-1424 – a specimen considered by Bona et al. (2012) to belong to *M. nativus* but here considered as belonging to *Mourasuchus* cf. *M. amazonensis* following Cidade et al. (2019) – from the other *Mourasuchus* species. However, the anterior-medial margin of the orbits is incompletely preserved in UFAC-1424 (see Cidade et al. 2019, fig. 8), so the presence of the structure is unknown in this specimen.

The anterior margin of the supratemporal fenestrae being surrounded only by the postorbital bone has been proposed to diagnose *M. amazonensis* and *M. atopus* from the other species (Bona et al. 2012). However, in *M. amazonensis* this feature is only depicted in the drawing of Price (1964) and, as the dorsal portion of the skull cannot be currently observed (see below) and there are no pictures, the presence of the character in this taxon must be seen in caution. In *M. atopus*, the anterior margin of the supratemporal fenestra is not preserved enough to observe whether this feature is present (see Langston 1965).

The lateral border of the maxillae extending parallel to each other was proposed to diagnose *M. atopus* from the other species, in which the lateral borders of the maxillae would be less parallel (Bocquentin-Villanueva 1984; Scheyer and Delfino 2016). However, the maxillae are not completely preserved in *M. atopus* (see Langston 1965), so the presence of this feature is unknown in this species.

Cidade et al. (2017) considered the shape of the incisive foramen to be diagnostic among the *Mourasuchus* species, distinguishing *M. amazonensis*, *M. pattersoni* and *M. arendsi* as each species exhibits a different shape. However, intraspecific variation in the shape of the incisive foramen has been observed in extant species of *Caiman* and *Paleosuchus* (G. M. Cidade, personal observation), and the incisive foramen of *M. arendsi* has only been depicted through a drawing and cannot be currently observed. As such, the shape of the incisive foramen is not considered a valid diagnostic feature in this study.

Regarding other characters previously proposed to diagnose *Mourasuchus* species, such as a different number of premaxillary dentary teeth perforations to distinguish *M. atopus* and *M. arendsi* (Bocquentin-Villanueva 1984) and the presence of the laterocaudal bridge, a structure that is lateral to the trigeminal foramen, dividing the branches of the cranial nerve V at the level of the lateral opening of the cranial nerve V fossa, to diagnose *M. nativus* (Bona et al. 2012), we agree with the observations of Scheyer and Delfino (2016) about why these characters are not currently useful to diagnose *Mourasuchus* species. Concerning the premaxillary perforations, it is also notable that intraspecific variation regarding the number of perforations has been recorded for extant crocodylians (Kälin 1933), which argues for caution against using this feature to diagnose fossil crocodylian taxa. In relation to the diagnostical potential of the laterocaudal bridge, this structure is only completely preserved in two specimens of *Mourasuchus*, assigned as *Mourasuchus* sp. (see below): AMNH-14441 and UFAC-2515 (see Cidade et al. 2019). As such, whereas this feature may be considered diagnostic for *Mourasuchus,* as it is not present in any other taxa (Cidade et al. 2019), it is not diagnostic at a specific level within the genus.

Three characters are considered valid to diagnose *Mourasuchus* species by this study: the shape of the jugal (Figure 1); the size of the external naris (Figure 2); and the lateromedial width of the palatines (Figure 3). Bona et al. (2012) and Scheyer and Delfino (2016) used the morphology of the jugal to differentiate *Mourasuchus* species based on the presence or absence of a notch on the lateral edge of the bone: its absence in *M. atopus* would distinguish it from the other species. However, we consider the shape of the jugal as a whole as more informative, as it clearly varies significantly among *Mourasuchus* species (see also Cidade et al. 2017). Three different jugal morphologies are present in *Mourasuchus*: lateromedially slender and dorsoventrally flattened (*M. atopus* and *M. arendsi*; Figure 1, A and D, Cidade et al. 2020, fig. 13 A – B), lateromedially expanded and dorsoventrally flattened (*M. amazonensis* and *Mourasuchus* cf. *M. amazonensis*; Figure 1, B and E, Cidade et al. 2019, Figure 2), and lateromedially and dorsoventrally expanded (*M. pattersoni*; Figure 1, C and F). In this context, the presence or absence of a notch on the lateral edge of the jugal used by Bona et al. (2012) and Scheyer and Delfino (2016) is considered here as correlated with the overall shape of the jugal, which is considered more informative. Namely, the presence of the notch is correlated with the lateromedially expanded and dorsoventrally flattened seen in *M. amazonensis* and *Mourasuchus* cf. *M. amazonensis*, whereas its absence is correlated with the morphologies seen in *M. atopus*, *M. arendsi* and *M. pattersoni*.

The external naris is also informative as it varies among the species. Two morphologies are present: small and circular (*M. atopus* and *M. arendsi*; Figure 2A-B) and wider than long (*M. amazonensis* and *M. pattersoni*; Figure 2-D, Price 1964, Figure 1). The external naris of *M. amazonensis* is only depicted in the drawing of the original description (Price 1964, Figure 1); however, as the drawing clearly depicts a wider than long external naris, similar to the one in *M. pattersoni*, the presence of this feature

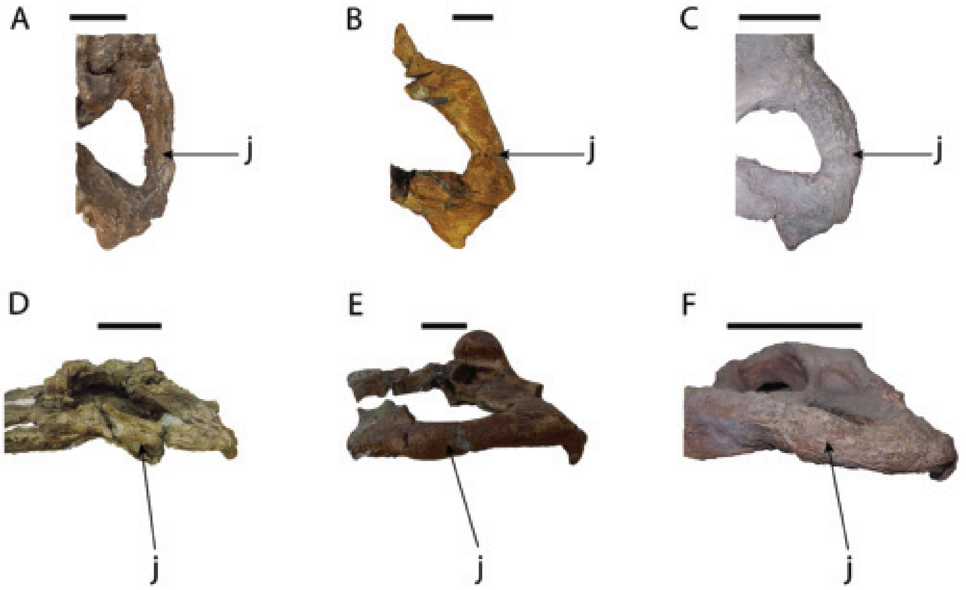

**Figure 1.** Morphological diversity of the jugals in *Mourasuchus*. *M. arendsi* (CIAAP-1297, holotype) in dorsal (right jugal, A) and lateral (left jugal, D) views; *Mourasuchus* cf. *M. amazonensis* (UFAC-1424) in dorsal (right jugal, B) and lateral (left jugal, E) views; *M. pattersoni* (MCNC-PAL-110-72 V, holotype) in dorsal (right jugal, C) and lateral (left jugal, F) views. Abbreviations: **j**, jugal. Scale bar = 10 cm. Modified from Cidade et al. (2017, fig. 8).

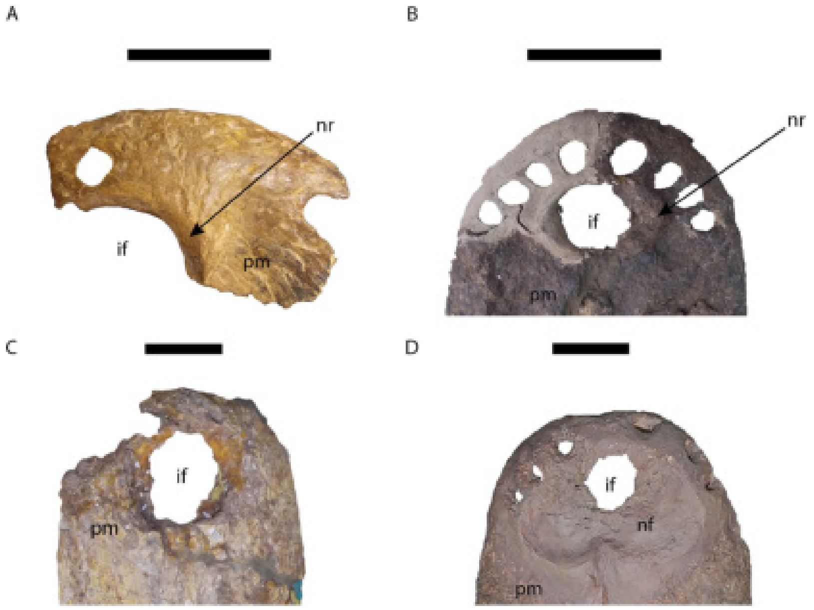

**Figure 2.** Morphological diversity of the premaxillae in *Mourasuchus*: *M. atopus* (UCMP-38012, holotype, right premaxilla; A); *M. arendsi* (CIAAP-1297, holotype; B); *Mourasuchus* sp. (UFAC-5776; C); *M. pattersoni* (MCNC-PAL-110-72 V, holotype; D). Abbreviations: if, incisive foramen; pm, premaxilla; nf, nasal fossa; nr, nasal rim. Scale bars = 5 cm (A and C) and 10 cm (B and D). Modified from Cidade et al. (2017, fig. 5).

in *M. amazonensis* is considered valid until an eventual re-examination of the holotype. An additional state may be present in *Mourasuchus*: UFAC-5776, an isolated rostrum assigned to *M. arendsi* by Souza-Filho and Guilherme (2011, Figure 2; in which is referred to as 'UFAC-5716' due to a typo), has a circular external naris that is larger than the ones in *M. atopus* and in the holotype of *M. arendsi*, but smaller than the ones in *M. amazonensis* in *M. pattersoni*, not covering all the dorsal surface of the premaxillae (Figure 2-C). Whether the size of the external naris in *Mourasuchus* is subject to individual or ontogenetic variation is unknown. A sexual dimorphism in the size of external naris regarding the presence of the 'ghara' in male individuals is well known in the extant gavialoid *Gavialis gangeticus* (Martin and Bellairs 1977); the presence of the 'ghara' is also related to the presence of a shelf and a rim around the external naris in males of that species (P. Bona, personal communication, 2023). The difference among *Mourasuchus* species has been hypothesised to be related to the presence of a similar structure (Langston 1966; Scheyer and Delfino 2016). Whether this is the case has to be investigated in further studies. Regarding ontogenetic variation, pictures of an ontogenetic series of *Caiman crocodilus* do not show a significant variation of the size of the external naris in this species (Augusta 2013). However, further studies with other species or newly found specimens of *Mourasuchus* may show otherwise. In the meantime, this

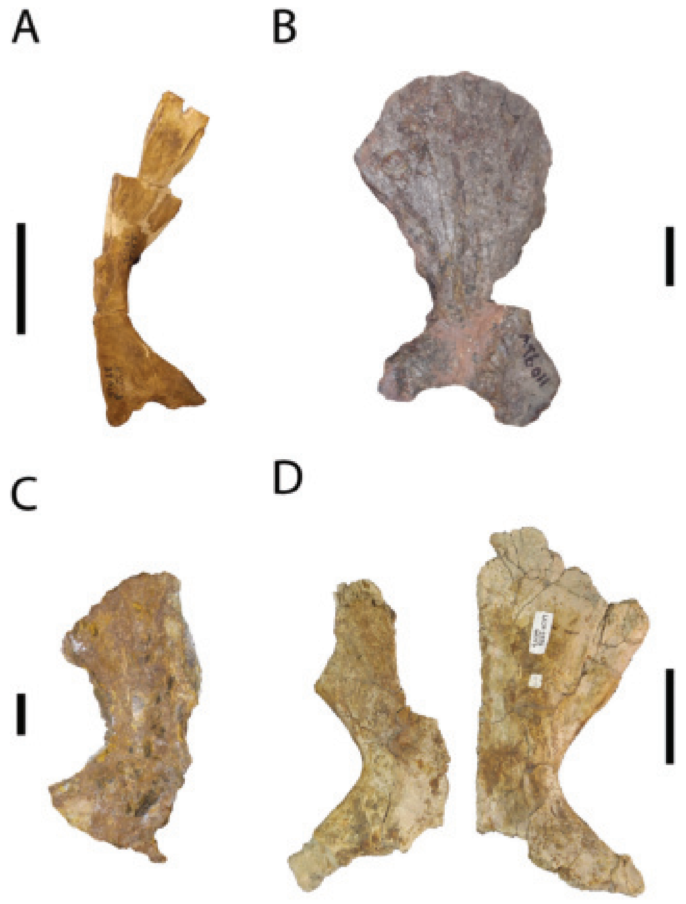

**Figure 3.** Morphological diversity of the palatines in *Mourasuchus*: *M. atopus* (UCMP-38012, holotype, left palatine; A); *M. pattersoni* (MCNC-PAL-110-72 V, holotype, both palatines; B); *Mourasuchus* cf. *M. amazonensis* (UFAC-5883, right palatine and part of the left; C); *Mourasuchus* cf. *M. amazonensis* (LACM-160157, both palatines; D). Scale bars = 5 cm. D is modified from Cidade et al. (2019, fig. 19).

study considers the morphology of UFAC-5776 to be closer to the one seen in *M. atopus* and *M. arendsi* and assigns it to *Mourasuchus* sp. (see below).

The morphology of the palatines is also considered informative. Lateromedially constricted palatines are present in *M. atopus* and *M. pattersoni* (Figure 3, A – B). Lateromedially expanded palatines are depicted in the drawing of the holotype of *M. arendsi* by Bocquentin-Villanueva (1984) (Figure 1). A re-examination of the ventral portion of the skull of the holotype is necessary to definitely settle whether this morphology is present. An eventual absence would lead *M. arendsi* to be considered a junior synonym of *M. atopus*, and this study considers that such a taxonomic change should be done only following the re-examination of the holotype. Lateromedially expanded palatines are present in other specimens (LACM-160157, UFAC-1424 and UFAC-5883, *Mourasuchus* cf. *M. amazonensis*; Figure 3, C – D, Cidade et al. 2019, figs. 10 and 19). In the holotype of *M. amazonensis*, the palatines are not complete; although they resemble the lateromedially expanded morphology seen in *M. arendsi*, this cannot be affirmed with certainty (see Cidade et al. 2019, Figure 2). Scheyer and Delfino (2016) proposed that the variation in the lateromedial width of the palatines could be due to intraspecific variation or ontogeny – the latter would be reinforced by the small size of *M. atopus*, which could be a juvenile (Langston 1965). However, the presence of lateromedially constricted palatines in the holotype of *M. pattersoni*, a large adult individual (Cidade et al. 2017), and ontogenetic studies in *Caiman crocodilus* that found only a slight lateromedial ontogenetic enlargement of the palatines (Augusta 2013) – not as severe as the variation observed in *Mourasuchus* species – suggest that the feature is not only a product of ontogenetic variation. Intraspecific variation in the lateromedial width of the palatines is also observed in the extant *Caiman latirostris* (Freiberg and Carvalho 1965), but these are not as accentuated as in *Mourasuchus*. As such, current evidence does not indicate that the different morphologies of the palatines in *Mourasuchus* are more likely to be ontogenetic or the result of intraspecific variations, but more studies are required to settle this issue. In the meantime, the variation in the lateromedially width of the parietal is considered a valid diagnostic character in this study.

Two additional characters are considered as potentially diagnostic among the *Mourasuchus* species: large eminences in the dorsal surfaces of the squamosals ('horns') and an elevated dorsal crest in the parietal. The reasons why these two characters are only potentially diagnostic among the *Mourasuchus* species are related to the fact that it is currently unknown whether they are present or not in the holotype of *M. amazonensis* (see below): if they are absent, this absence differentiates *M. amazonensis* from the other *Mourasuchus* species; if they are present, the two features would be exhibited by the two *Mourasuchus* species (*M. arendsi* being the other) in which the squamosals and the parietal are preserved and can be fully observed, and would then be a synapomorphy of the genus.

## Updated diagnoses of the *Mourasuchus* species

### *Systematic paleontology*

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)

### *Type species*

*Mourasuchus amazonensis* (Price 1964).

### *Included species*

*M. amazonensis* (Price 1964); *M. atopus* (Langston 1965); *M. arendsi* (Bocquentin-Villanueva 1984); *M. pattersoni* Cidade et al. (2017).

### *Diagnosis*

*Mourasuchus* is diagnosed by the following characteristics: dentary symphysis very short, extending only to the level of the first alveolous; orbits smaller than infratemporal fenestrae; prefrontal and frontal thickened, forming a marked knob at the anteromedial margin of the orbits; dentary linear between fourth and tenth alveoli; posterior teeth and alveoli of maxilla and/or dentary laterally compressed; nasals excluded, at least externally, from the naris, with premaxillae and nasals still in contact; dorsal premaxillary processes long, extending beyond the level of the third maxillary alveolus; frontoparietal suture linear between supratemporal fenestrae; an extremely wide, compressed and long rostrum related with a very small skull table; lateral border of rostrum without festooning; prefrontals contacting at the midline, so that nasals do not contact the frontal in dorsal view; slender U-shaped mandibles that curve from first to fifth alveoli and then are straight posteriorly to sixth alveolus; upper and lower tooth rows with more than 40 teeth; osteoderms with conspicuous spines on the dorsal surface; presence of the laterocaudal bridge, lateral to the trigeminal foramen. Emended from Price (1964), Langston (1965, 1966), Bocquentin and Souza-Filho (1990), Bona et al. (2012) and Cidade et al. (2017).

## *Mourasuchus amazonensis* (Price 1964)

### *Holotype*

DGM 526-R

### *Geographic and stratigraphic origin*

From the left bank of the Juruá River, approximately 4 km upstream from the mouth of the São João stream, tributary of the Juruá River, municipality of Marechal Thaumaturgo, state of Acre, Brazil (Price 1964); Solimões Formation, late Miocene.

### *Diagnosis*

Jugal lateromedially expanded and dorsoventrally flattened (autapomorphy; Cidade et al. 2019, fig. 2); differs from *M. atopus* and *M. arendsi* in having an external naris wider than long (Price 1964, fig. 1).

## *Mourasuchus* cf. *M. amazonensis*

### *Referred specimens*

LACM-160157, UFAC-1424, UFAC-5883.

### *Geographic and stratigraphic origin*

LACM-160157 and UFAC-1424 are from the 'Niteroi' locality, right bank of the Acre River, between the cities of Rio Branco and Senador Guiomard (S 10ºo08'30.0'', W 67ºo48'46.3''– Bona et al. 2012; UTM 19 L 629,983 E/8879539 S, datum WGS84 –; Kerber et al. 2018), state of Acre, Brazil (Cidade et al. 2019); UFAC-5883 is from the 'Morro do Careca' locality, in the margin of the BR-364 highway (S 08° 10'; W 69°31'), state of Acre, Brazil (Souza-Filho and Guilherme 2011); both localities are from Solimões Formation, late Miocene.

### *Remarks*

All *Mourasuchus* specimens in which the dorsal portion of the skull table is preserved and can be observed exhibit squamosal eminences and the elevated crest on the parietal. However, it is currently not known whether these structures are present in the holotype of *M. amazonensis*: the drawing of Price (1964, fig. 1) does not clearly depict the presence of both structures, and the dorsal portion of the skull, housed at Museu de Ciências da Terra in Rio de Janeiro, Brazil, is currently firmly attached to a plaster jacket. Any attempt to observe the dorsal portion of the skull would result in a serious risk of damaging the fossil. According to the institution where the specimen is housed, procedures for the restoration of the specimen are planned, but not in the short term (R.C. Silva, personal communication, 2022).

This uncertainty on the presence of the squamosal eminences and the parietal crest creates a lingering taxonomic issue in *Mourasuchus*, which regards the assignment of other specimens to *Mourasuchus amazonensis*. Other specimens with a lateromedially expanded, dorsoventrally flattened jugal (an autapomorphy of the species, present in the holotype) have been described – LACM-160157 and UFAC-1424 (Fig. 1, B and E) (Cidade et al. 2019) and UFAC-5883 (Souza-Filho and Guilherme 2011, fig. 3 – even though the presence of a resin precludes a complete visualisation of the jugal in this specimen). The three specimens also exhibit large squamosal eminences (Souza-Filho and Guilherme 2011, fig. 3; Cidade et al. 2019, figs. 8 and 14), whereas the elevated parietal crest is partially preserved in LACM-160157 (Cidade et al. 2019, fig. 14) and, in UFAC-1424, an eroded area denotes the presence of the crest though the structure itself is not preserved (Cidade et al. 2019, fig. 8); in UFAC-5883, the area is completely eroded and the crest may have been destroyed (see Souza-Filho and Guilherme 2011, fig. 3). Though the shape of the jugal shows a proximity of the specimens to *M. amazonensis*, the fact that the presence of the squamosal eminences and the parietal crest cannot be confirmed in the holotype creates two possibilities: while an eventual presence would ensure the assignment of LACM-160157, UFAC-1424 and UFAC-5883 to *M. amazonensis*, an eventual absence raises the possibility that these three specimens could represent a new species. Only the re-evaluation of the dorsal portion of the holotype of *M. amazonensis* can clarify this situation. In the meantime, it is advised that LACM-160157, UFAC-1424, UFAC-5883 and specimens similar to them are assigned as *Mourasuchus* cf. *M. amazonensis*.

This scenario also has consequences for the synonymy of *Mourasuchus nativus* with *M. arendsi*. The fact that the holotype of *M. amazonensis* may have squamosal eminences and the parietal crest – and, if it does not, then a new species of *Mourasuchus* could be erected based on the specimens LACM-160157, UFAC-1424 and UFAC-5883, which exhibit both features – means that, in either scenario, the holotype of *M. nativus* is indistinguishable from two *Mourasuchus* species. This means that *M. nativus* is a *nomen dubium* and not only a junior synonym of *M. arendsi*.

## *Mourasuchus atopus* (Langston 1965)

### *Holotype*

UCMP-38012

### *Geographic and stratigraphic origin*

Unnamed locality 6.5 km northeast of Villavieja, department of Huila, Colombia (Langston 1965); Honda Group, middle Miocene.

### *Diagnosis*

Differs from *M. amazonensis* and *M. pattersoni* in having the jugal lateromedially slender and dorsoventrally flattened and a small, circular external naris (Cidade et al. 2020, fig. 13); differs from *M. arendsi* in having lateromedially constricted palatines (Fig. 3–A).

## *Mourasuchus arendsi* (Bocquentin-Villanueva 1984)

### *Holotype*

CIAAP-1297

### *Geographic and stratigraphic origin*

Locality approximately 1 km to the southeast of the hamlet Corralito, Urumaco municipality, Democracía Department, Falcón State, Venezuela (S 11º 18′, W 70º 18′; Bocquentin-Villanueva 1984); the same locality known as 'Corralito' in Scheyer et al. (2013) and Scheyer and Delfino (2016); Urumaco Formation (upper member), late Miocene.

### *Diagnosis*

Differs from *M. amazonensis* and *M. pattersoni* in having the jugal lateromedially slender and dorsoventrally flattened (Fig. 1, A and D) and a small, circular external naris (Fig. 2–B); differs from

*M. atopus* in having lateromedially expanded palatines (as per the drawing of Bocquentin-Villanueva 1984, fig. 1).

### *Remarks*

The holotype of *Mourasuchus atopus* and *M. arendsi* exhibit only one taxonomically relevant difference: the palatines of *M. atopus* are lateromedially constricted, whereas those of *M. arendsi* are depicted as lateromedially expanded by the original description of the holotype of *M. arendsi*, which does not include pictures (Bocquentin-Villanueva 1984). The holotype is currently firmly attached to a plaster jacked that precludes the observation of its ventral portion, where the palatines are situated. As the drawing in the original description of *M. arendsi* clearly depicts lateromedially expanded palatines (Bocquentin-Villanueva 1984, fig. 1), this study still considers *M. atopus* and *M. arendsi* as distinct species until an eventual re-examination of the holotype of *M. arendsi*, as it is here considered that an eventual synonymy between the two species should only be performed followed by the re-examination of the holotype, which can also reveal other differences between the two species and further justifies caution regarding assigning such a synonymy. The hypothesis of synonymy between *M. arendsi* and *M. atopus* has already been discussed by Scheyer and Delfino (2016) and Cidade et al. (2020), and the reasons why the differences in the palatine morphology are considered a valid diagnostic character are discussed by Cidade et al. (2020) and above.

## *Mourasuchus pattersoni* (Cidade et al. 2017)

### *Holotype*

MCNC-PAL-110-72 V

### *Geographic and stratigraphic origin*

Locality recorded as '3 1/2 km N 30° W of El Picacho, on the up side of the Chiguaje fault", about 6.5 km N 24° E of the town Urumaco, state of Falcón, Venezuela (Langston 2008; Cidade et al. 2017), although whether this is the exact locality is controversial (see Langston 2008); Urumaco Formation (upper member), late Miocene.

### *Diagnosis*

Jugal both lateromedially and dorsoventrally expanded (Fig. 1, C and F) (autapomorphy); differs from *M. atopus* and *M. arendsi* in having an external naris wider than long (Fig. 2–D); differs from *M. arendsi* and in having lateromedially constricted palatines (Fig. 3–B).

## *Mourasuchus* sp.

### *Referred specimens*

AMNH-14441, AMU-CURS-212, AMU-CURS-218, IVIC-P-2907, MLP 73-iv-15–8 (holotype of *Mourasuchus nativus*), MLP 73-iv-15–9, UFAC-1431, UFAC-1477, UFAC-1666, UFAC-2515, UFAC-3530, UFAC-3717, UFAC-4259, UFAC-4885, UFAC-4925, UFAC-5776.

### *Geographic and stratigraphic origin*

AMNH-14441: possibly in a locality 'within 2 days trip upstream from Cobija by motorized canoe, northwest of Bolivia, near Brazilian border, Pando Province', though the specimen has been found in a non-stratigraphic context and other stratigraphic origins have been put forward (see Cidade et al. 2019); possibly Cobija Formation (Bolivia) or Solimões Formation (Brazil), since it is reported to have been found in Bolivia near the Brazilian border; both units are considered correlated and are from the late Miocene (see Cidade et al. 2019). AMU-CURS-212: west of El Mamon, Venezuela (Scheyer and Delfino 2016); Urumaco Formation, late Miocene. AMU-CURS-218: Puente Rio Urumaco/Playa Larga, Venezuela (Scheyer and Delfino 2016); Urumaco Formation, late Miocene. IVIC-P-2907: locality at N 11°11′3.29'; W 70°20′49.54', Venezuela; Urumaco Formation, late Miocene. MLP 73-iv-15–8 and MLP 73-iv-15–9: banks of the Paraná River, in the area of Paraná, province of Entre Ríos, Argentina (Bona et al. 2012); Ituzaingó Formation, late Miocene. UFAC-1431, UFAC-1477, UFAC-1666, UFAC-2515, UFAC-3530, UFAC-3717, UFAC-4259, UFAC-4885, UFAC-4925: 'Niteroi' locality, right bank of the Acre River, between the cities of Rio Branco and Senador Guiomard (S 10º08'30.0", W 67º48'46.3"– Bona et al. 2012; UTM 19 L 629,983 E/ 8879539 S, datum WGS84 –; Kerber et al. 2018), state of Acre, Brazil (Cidade et al. 2019); Solimões Formation, late Miocene. UFAC-5776: locality in the margin of the BR-364 highway, in the city of Manuel Urbano (S 8°47'33", W 69°24'11"), state of Acre, Brazil; Solimões Formation, late Miocene.

### *Remarks*

There are two sets of specimens that are assigned as *Mourasuchus* sp. in this study. The synonymy between *M. nativus* and *M. arendsi* was proposed by Scheyer and Delfino (2016) based on their sharing of features such as large squamosal eminences and the elevated parietal crest. Following this synonymy, several isolated specimens of *Mourasuchus* comprised only or mostly by the skull table have been assigned or proposed to have affinities to *M. arendsi*, mostly due to the sharing of the squamosal eminences and the parietal crest. Scheyer and Delfino (2016) assigned to *M. arendsi* the holotype and a referred specimen of *M. nativus* described by Gasparini (1985), and specimens initially assigned to *M. nativus* by Scheyer et al. (2013), whereas Cidade et al. (2019) and Cidade et al. (2021) assigned several specimens either containing or comprised only by the skull table to *M. arendsi*.

However, the assignment of the specimens LACM-160157, UFAC-1424 and UFAC-5883 to *Mourasuchus* cf. *M. amazonensis*, which also exhibit squamosal eminences and parietal crests (see Souza-Filho and Guilherme 2011; Cidade et al. 2019; and above), forces a change in the taxonomic assignment of these specimens. The presence of these structures in the *Mourasuchus* cf. *M. amazonensis* means that all specimens that exhibit these features but not exhibit any other diagnostic feature of one *Mourasuchus* species must be assigned to *Mourasuchus* sp., as the presence of squamosal eminences and parietal crests is either, based on whether they are present or absence in the holotype of *M. amazonensis* (see above), a shared feature between *M. amazonensis* and *M. arendsi* or between *M. arendsi* and the possible new species represented by LACM-160157, UFAC-1424 and UFAC-5883. As such, in any possibility, the presence of the two features is not exclusive to *M. arendsi* and should not be used to assign specimens to this species. Because of this perspective, many specimens previously assigned to *M. arendsi* by previous studies (Scheyer and Delfino 2016; Cidade et al. 2019, 2021) must be assigned to *Mourasuchus* sp.: these include most of the specimens included in the 'referred specimens' above, except AMU-CURS-218 and UFAC-5776 (see below). In this context, we also recommend that any *Mourasuchus* specimen that contains squamosal eminences and the parietal crest but not any other of the valid diagnostic characters for the *Mourasuchus* species presented above (as it is the case for many isolated skull tables) must be assigned to *Mourasuchus* sp.

Two specimens must also be assigned to *Mourasuchus* sp., but for different reasons. AMU-CURS-218, a specimen described and illustrated by Scheyer and Delfino (2016, f. 19), is a posterior portion of the skull containing the skull table, quadrates, and parts of the quadratojugals and jugals. The specimen has squamosal eminences, a scar indicating the presence of the parietal crest, and a fragmented jugal lateromedially slender; this last feature is shared with *M. atopus* and *M. arendsi*. UFAC-5776, an isolated rostrum, exhibits a circular external naris that, although larger than in *M. atopus* and *M. arendsi*, is also smaller than in *M. amazonensis* and *M. pattersoni* (Fig. 2–C); such morphology is here considered as closer to the one exhibited by *M. atopus* and *M. arendsi*, although further studies on the external naris may change this scenario (see above). As both specimens do not preserve the palatines, an assignment to either of the species is not possible. In this way, both specimens are referred to *Mourasuchus* sp.

## Discussion

This study concludes that there are four valid species of *Mourasuchus*: *M. amazonensis* (Price 1964), *M. atopus* (Langston 1965), *M. arendsi* (Bocquentin-Villanueva 1984) and *M. pattersoni* (Cidade et al. 2017). Three taxonomic perspectives are lingering in *Mourasuchus*. One is that *M. arendsi* may be a junior synonym of *M. atopus*, but this can only be evaluated through a reanalysis of the ventral aspect of the skull of the holotype of *M. arendsi*. Another is that the specimens LACM-160157, UFAC-1424 and UFAC-5883 may either belong to *M. amazonensis* or represent a new species – this can be evaluated only through a reanalysis of the dorsal aspect of the skull of the holotype of *M. amazonensis*; in the time being, these specimens are referred to as *Mourasuchus* cf. *M. amazonensis*. The specimen UFAC-5776 is assigned as *Mourasuchus* sp. as the size of its external naris, although larger, is closer to those of *M. atopus* and *M. arendsi*; however, it may represent a new species if new fossil specimens or future studies on the ontogeny of living crocodylians show that this difference in the size of external naris is a taxonomically relevant character.

*Mourasuchus nativus* (Gasparini 1985) is considered a *nomen dubium*, and not only a junior synonym of *M. arendsi*, due to the fact that, regardless of whether the holotype of *M. amazonensis* has squamosal eminences and a parietal crest or not, the holotype of *M. nativus* is indistinguishable from at least two other *Mourasuchus* species: *M. arendsi* and either *M. amazonensis* or the possible new species represented by specimens LACM-160157, UFAC-1424 and UFAC-5883. Within this perspective, any *Mourasuchus* specimen containing squamosal eminences and the parietal crest but not any other of the valid diagnostic characters for the *Mourasuchus* species presented in this study should be assigned to *Mourasuchus* sp. Additionally, the specimens AMU-CURS-218 and UFAC-5776 are referred to *Mourasuchus* sp. as they are not distinguishable from *M. atopus* and *M. arendsi*.

This study highlights the importance of taxonomic works on fossil crocodylomorph taxa, especially on the Cenozoic of South America, which have been historically overlooked (see Cidade et al. 2019). More efforts on the taxonomy and nomenclature of these taxa are needed so a better, more accurate understanding of the outstandingly rich, diverse South American crocodylomorph fauna of the Cenozoic is reached.

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## References

Augusta BG 2013. Revisão sistemática e ontogenética dos materiais cranianos atribuídos ao gênero *Mariliasuchus* (Crocodyliformes, Notosuchia) e suas implicações taxonômicas e paleobiológicas [master's thesis]. São Paulo (Brazil): University of São Paulo.

Benton MJ, Clark JM. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: MJ B, editor. The phylogeny and classification of the tetrapods. Vol. 1, Oxford: Clarendon Press; pp. 295–338.

Bocquentin J, Souza-Filho JP. 1990. O crogodiliano sul-americano *Carandaisuchus* como sinonímia de *Mourasuchus* (Nettosuchidae). Rev Brasi Geoc. 20(1):230–233. doi: 10.25249/0375-7536.1990230233.

Bocquentin-Villanueva J. 1984. Un nuevo Nettosuchidae (Crocodylia, Eusuchia) proveniente de la Formación Urumaco (Mioceno Superior), Venezuela. Ameghiniana. 21:3–8.

Bona P, Degrange FJ, Fernández MS. 2013. Skull anatomy of the bizarre crocodylian *Mourasuchus nativus* (alligatoridae, caimaninae). Anat Rec. 296 (2):227–239. doi: 10.1002/ar.22625.

Bona P, Riff D, Gasparini Z. 2012. Late Miocene crocodylians from Northeast Argentina: new approaches about the austral components of the Neogene South American crocodilian fauna. Ear Environ Sci Tran Roy Soc Edin. 103 (3–4):551–570. doi: 10.1017/S175569101300042X.

Cidade GM, Fortier D, Rincón AD, Hsiou AS. 2019. Taxonomic review of two fossil crocodylians from the Cenozoic of South America and its implications for the crocodylian fauna of the continent. Zootaxa. 4656(3):475–486. doi: 10.11646/zootaxa.4656.3.5.

Cidade GM, Riff D, Hsiou AS. 2019. The feeding habits of the strange crocodylian *Mourasuchus* (Alligatoroidea, caimaninae): a review, new hypotheses and perspectives. Rev Bras Paleo. 22(2):106–119. doi: 10.4072/rbp.2019.2.03.

Cidade GM, Riff D, Souza-Filho JP, Hsiou AS. 2019. A reassessment of the osteology of *Mourasuchus amazonensis* Price, 1964 with comments on the taxonomy of the species. Palaeo Electr. 22(2.44A):1–23. doi: 10.26879/893.

Cidade GM, Rincón AD, Solórzano A. 2021. New cranial and postcranial elements of *Mourasuchus* (Alligatoroidea: Caimaninae) from the late Miocene of Venezuela and their palaeobiological implications. Hist Biol. 33 (10):2387–2399. doi: 10.1080/08912963.2020.1795844.

Cidade GM, Solórzano A, Rincón AD, Riff D, Hsiou AS. 2017. A new *Mourasuchus* (Alligatoroidea, Caimaninae) from the late Miocene of Venezuela, the phylogeny of Caimaninae and considerations on the feeding habits of *Mourasuchus*. PeerJ. 5:e3056. doi: 10.7717/peerj.3056.

Cidade GM, Solórzano A, Rincón AD, Riff D, Hsiou AS. 2020. Redescription of the holotype of the Miocene crocodylian *Mourasuchus arendsi* (Alligatoroidea, caimaninae) and perspectives on the taxonomy of the species. Hist Biol. 32(6):733–749. doi: 10.1080/08912963.2018.1528246.

Cidade GM, Souza-Filho JP, Hsiou AS, Brochu CA, Riff D. 2019. New specimens of *Mourasuchus* (Alligatoroidea, Caimaninae) from the Miocene of Brazil and Bolivia and their taxonomic and morphological implications. Alcheringa. 43(2):261–278. doi: 10.1080/03115518.2019.1566495.

Freiberg MA, Carvalho AL. 1965. El yacare sudamericano *Caiman latirostris (Daudin)*. Physis XXV. 70:351–360.

Gasparini Z. 1985. Un nuevo cocodrilo (Eusuchia) Cenozoico de América del Sur. Col Trab Paleont MME–DNPM. Sér Geol. 27:51–53.

Gmelin J. 1789. Linnei Systema Naturae. Leipzig: G.E. Beer.

Gray JE. 1844. Catalogue of tortoises, crocodilians, and amphisbaenians in the collection of the British Museum. London: British Museum (Natural History).

Holliday CM, Gardner NM, Farke AA. 2012. A new Eusuchian Crocodyliform with novel cranial integument and its significance for the origin and evolution of Crocodylia. PloS One. 7(1):e30471. doi: 10.1371/journal.pone.0030471.

Kälin JA. 1933. Beiträge zur vergleichenden Osteologie des Crocodilidenschädels. Zool Jahrb Abteil Anat Ont Tie. 57:535–714.

Kerber L, Bissaro-Junior MC, Negri FR, Souza-Filho JP, Guilherme E, Hsiou AS. 2018. A new rodent (Caviomorpha: Dinomyidae) from the upper Miocene of southwestern Brazilian Amazonia. Hist Biol. 30(7):985–993. doi: 10.1080/08912963.2017.1327529.

Langston W. 1965. Fossil crocodylians from Colombia and the Cenozoic history of the Crocodilia in South America. Berkeley and Los Angeles: University of California 157. p. Publications in Geological Sciences.

Langston W. 1966. *Mourasuchus* Price, *Nettosuchus* Langston, and the family Nettosuchidae (Reptilia: Crocodilia). Copeia. 4(4):882–885. doi: 10.2307/1441424.

Langston W. 2008. Notes on a partial skeleton of *Mourasuchus* (Crocodylia, Nettosuchidae) from the upper Miocene of Venezuela. Arq Mus Nac. 66:125–143.

Martin BG, Bellairs ADA. 1977. The narial excrescence and pterygoid bulla of the gharial, *Gavialis gangeticus* (Crocodilia). J Zool. 182(4):541–558. doi: 10.1111/j.1469-7998.1977.tb04169.x.

Nopcsa F. 1926. Neue Beobachtungen an *Stomatosuchus*. Centr Miner Geol Paläont B 1926:212–215.

Norell MA 1988. Cladistic approaches to paleobiology as applied to the phylogeny of alligatorids [Phd thesis]. New Haven (CT): Yale University.

Norell MA, Clark JM, Hutchison JH. 1994. The late Cretaceous alligatoroid *Brachychampsa montana* (Crocodylia): new material and putative relationships. Am Mus Nov. 3116:1–26.

Price L. 1964. Sobre o crânio de um grande crocodilídeo extinto do Alto de Rio Juruá, Estado do Acre. An Acad Brasil Ciên. 56:59–66.

Riff D, Romano PSR, Oliveira GR, Aguilera OA. 2010. Neogene crocodile and turtle fauna in northern South America. In: Hoorn C Wesselingh F, editors. Amazonia landscape and species evolution: a look into the past. London: Wiley-Blackwell; pp. 259–280. doi:10.1002/9781444306408.ch16.

Salas-Gismondi R, Antoine PO, Baby P, Brusset S, Benammi M, Espurt N, De Franceschi D, Pujos F, Tejada J, Urbina M. 2007. Middle Miocene crocodiles from the Fitzcarrald Arch, Amazonian Peru. Cuader Mus Geomin. 8:355–360.

Scheyer TM, Aguilera OA, Delfino M, Fortier DC, Carlini AA, Sánchez R, Carrillo-Briceño JD, Quiroz L, Sánchez-Villagra MR. 2013. Crocodylian diversity peak and extinction in the late Cenozoic of the northern neotropics. Nat Commun. 4:1907. doi: 10.1038/ncomms2940.

Scheyer TM, Delfino M. 2016. The late Miocene caimanine fauna (Crocodylia: Alligatoroidea) of the Urumaco Formation, Venezuela. Palaeontol Electron. 19(3.48A):1–57. doi: 10.26879/657.

Sereno PC, Larsson HCE. 2009. Cretaceous crocodyliforms from the Sahara. ZooKeys. 28:1–143. doi: 10.3897/zookeys.28.325.

Souza-Filho JP, Guilherme E. 2011. Ampliação da diagnose e primeiro registro de *Mourasuchus arendsi* (Crocodylia-Nettosuchidae) no Neógeno da Formação Solimões, Amazônia Sul-Ocidental. In: Carvalho I, editor. Paleontologia: cenários de Vida. 1st ed. Vol. 4. Rio de Janeiro (Brazil): Interciencia; pp. 399–408.

Stromer E. 1925. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 7 *Stomatosuchus inermis* Stromer, ein schwach bezahnter Krokodilier und 8. Ein Skelettrest des Pristiden *Onchopristis numidus* Huag sp. Abhan Bay Akad Wis, Math-natur Abteil. 30:1–22.

Stromer E. 1933. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Würsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman), 12; die procoelen Crocodilia. Abhan Bay Akad Wis, Math-natur Abteil. 15:1–55.

Tineo DE, Bona P, Pérez LM, Vergani GD, González G, Poiré DG, Gasparini ZN, Legarreta P. 2014. Palaeoenvironmental implications of the giant crocodylian *Mourasuchus* (Alligatoridae, Caimaninae) in the Yecua Formation (late Miocene) of Bolivia. Alcheringa. 39(2):224–235. doi: 10.1080/03115518.2015.967162.