Cretaceous Research 86 (2018) 41–52

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Cranial morphology of *Morrinhosuchus luziae* (Crocodyliformes, Notosuchia) from the Upper Cretaceous of the Bauru Basin, Brazil

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ARTICLE INFO

Article history:
Received 26 May 2017
Received in revised form
6 January 2018
Accepted in revised form 15 February 2018
Available online 17 February 2018

Keywords:
Morrinhosuchus
Notosuchia
Crocodyliformes
Bauru Basin

ABSTRACT

Although the type material of *Morrinhosuchus luziae* (Crocodyliformes, Notosuchia) permitted the diagnosis of a new genus and species, its fragmentary nature prevented a detailed analysis of its cranial anatomy. In this study, we analyzed two new specimens of *Morrinhosuchus luziae* recovered from the Adamantina Formation (Upper Cretaceous) from Cândido Rodrigues and Monte Alto cities (state of São Paulo, Brazil), in the southeastern portion of the Bauru Basin. One specimen, MPMA 12-0050/07, consists of nearly complete skull and mandible which reveals new data and characters of its cranial morphology. Another, less complete specimen, MPMA 04-0019/15, consists of a rostrum with a partially preserved dentition that include a cingulate tooth crown. The analysis of *Morrinhosuchus luziae*'s anatomy reinforces its phylogenetic position among the advanced notosuchian, allowing the inference of paleoautoecological proposals, and expanding the taxonomic knowledge of the elusive South American notosuchian.

1. Introduction

Notosuchian crocodyliforms comprise much of the Bauru Basin's (Upper Cretaceous) fossil discoveries, especially in horizons of the Adamantina Formation, source of the greatest diversity of described species (Price, 1945; Carvalho & Bertini, 1999; Pol, 2003; Nobre et al., 2007; Iori & Carvalho, 2009, 2011; Marinho & Carvalho, 2009; Marinho et al., 2013). These animals demonstrate a number of cranial and dental adaptations, usually presenting a reduced and specialized heterodont dentitions, presumably for a wide range of dietary habits, from carnivorous, herbivorous, omnivorous, and durophagous (Bertini & Carvalho, 1999; Nobre & Carvalho, 2006; Marinho & Carvalho, 2009; Iori & Carvalho, 2011; Ösi, 2013; Godoy et al., 2014; Pol et al., 2014; Fiorelli et al., 2016). As for overall body and postcranial dimensions, the Adamantina Fm. notosuchians ranged from small animals, like *Adamantinasuchus navae* Nobre & Carvalho, 2006 (about 50 cm long), to large animals, such as *Stratiotosuchus maxhechti* Campos, Suarez, Riff & Kellner, 2001 (about 4 m in length); with remarkable specializations to terrestrial environments, permitting the occupation of a wide variety of ecological niches (Carvalho & Bertini, 1999; Campos et al., 2001; Marinho & Carvalho, 2009; Nobre & Carvalho, 2013; Godoy et al., 2014; Fiorelli et al., 2016; Godoy et al., 2016; Iori et al., 2016).

Pol et al. (2014) point out that Notosuchia comprises four distinct groups: uruguaysuchids, peirosaurids, sebecosuchians and advanced notosuchians, which have diversified during two major radiation events: one during the Early Cretaceous and the other during the Late Cretaceous. The "advanced notosuchians" include

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https://doi.org/10.1016/j.cretres.2018.02.010
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the Sphagesauridae as the most derived clade (restricted, so far, both spatially and stratigraphically to the Adamantina Formation in southeastern of Brazil and the Cajones Formation in Bolivia), as well as more basal forms that occur in rocks of the Adamantina Formation (Bauru Group), Brazil, and from the Los Llanos Formation (Neuquén Group), Argentina (Carvalho & Bertini, 1999; Marinho & Carvalho, 2007, 2009; Iori & Carvalho, 2009; Novas et al., 2009; Fiorelli et al., 2016). These basal forms of advanced notosuchians are characteristically small, with oreinirostral skulls, relatively short snouts, and markedly heterodont dentitions (Carvalho & Bertini, 1999; Nobre & Carvalho, 2013; Fiorelli et al., 2016).

Morrinhosuchus luziae Iori & Carvalho, 2009 was described on the basis of fragmentary material consisting of the rostral portion of a skull and mandible, with most of the teeth missing. However, the holotype specimen permitted the diagnosis of a new genus and species, and to test its relationships through phylogenetic analysis. In the studies of Pol et al. (2014), Leardi et al. (2015) and Fiorelli et al. (2016), *Morrinhosuchus* emerges as the most basal among the advanced notosuchians, whereas, in the analysis of Iori et al. (2013) and Bronzati et al. (2015), *Morrinhosuchus* is found in a more derived position, closer to baurusuchids than to advanced notosuchians.

Specimen MPMA 12-0050/07 can be confidently referred to *Morrinhosuchus luziae,* consisting of a nearly complete skull and mandible with much of its dentition. Although fragmentary, another referred specimen (MPMA 04-0019/15) preserves the only known sixth maxillary. Here we describe these new specimens, providing new morphological data of this elusive advanced notosuchian.

Institutional abbreviation — **MPMA**, Museu de Paleontologia "Prof. Antonio Celso de Arruda Campos", Monte Alto, São Paulo State, Brazil.

2. Geological setting

The Bauru Basin (Fig. 1) is a broad cratonic depression developed during the Upper Cretaceous in the southeastern portion of the South American Plate (Fernandes & Coimbra, 1996), when its deposition occurred under semi-arid to arid climatic conditions, between the Coniacian and Maastrichtian ages (Fernandes & Coimbra, 2000). Dias-Brito et al. (2001) suggested two sedimentation intervals as part of the sequence: the deposits of the Marília Formation of Maastrichtian age, and the other units in the Turonian-Santonian interval.

The holotype of *Morrinhosuchus luziae* (MPMA 07-0009/01) and referred specimen MPMA 04-0019/15 come from the city of Monte Alto (state of São Paulo, Brazil). In this region, two lithostratigraphic units crop out: the Adamantina and Marília formations. Specimen MPMA 12-0050/07 also comes from the Adamantina Formation sandstones, but from the neighboring city of Cândido Rodrigues. The collection points of the new materials analyzed in Monte Alto (S 21° 15′ 18,7″/W 48° 33′ 09,6″) and Cândido Rodrigues (S 21° 20′ 04,8″/W 48° 34′ 54,0″) consist of fine reddish sandstones with frequent concretions and carbonate nodules.

3. Systematic palaeontology

Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1930
Mesoeucrocodylia Whetstone & Whybrow, 1983
Notosuchia Gasparini, 1971

Morrinhosuchus luziae Iori & Carvalho, 2009

Holotype. MPMA 07-0009/01, rostral region of skull and mandible.
Referred Specimens. MPMA 12-0050/07, nearly complete skull and mandible (Figs. 2 and 3), cervical vertebrae, parts of the pectoral girdle and forelimb. MPMA 04-0019/15, rostral region of skull and mandible (Fig. 4).
Comments. The original diagnosis and description of *Morrinhosuchus luziae* was based on a specimen whose preserved portions consist of the anterior regions of the snout and mandible. The characteristics observed in the holotype (MPMA 07-0009/01) are also present in the new specimens (e.g. groove on the ventral surface of the premaxilla; small lateral expansion of the dentary; medial depression on the ventral surface of the dentaries; wide incisive foramen). However, in the light of the better preservation of specimen MPMA 12-0050/07 and MPMA 04-0019/15, the

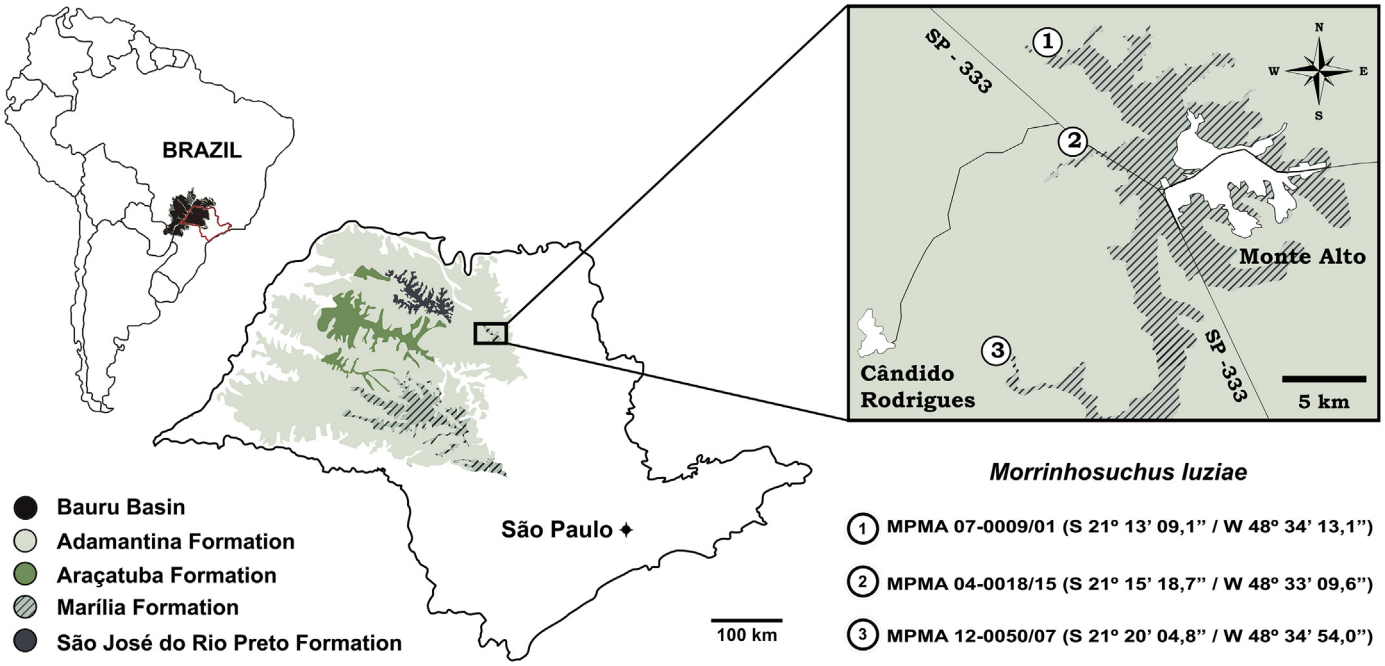

Fig. 1. Bauru Group in the state of São Paulo (modified from Iori et al., 2016). Numbered localities of *Morrinhosuchus luziae* fossils.

morphology of the posterior teeth has been reinterpreted as being conical and cingulate teeth, unlike interpretation of Iori & Carvalho (2009) of "posterior teeth of globular crowns". The lateral notch at the junction of the premaxilla with the maxilla discussed by Iori & Carvalho (2009) was indeed the result of slight disarticulation of these bones, as indicated by the new specimens.

Amended diagnosis. Advanced notosuchian crocodyliform characterized by the following combinations of features (autapomorphies marked with an asterisk): anteroposteriorly long mandibular symphysis, with participation of splenial (about 15% and 40% in ventral and dorsal views, respectively); dentary with small lateral expansion forming ridge that marks the boundary between lateral and lateroventral plains; long and narrow maxilla with six circular alveoli; flat and narrow anterior process of palatine contacting the maxilla anterolaterally (Iori & Carvalho, 2009); crown bases and roots of second and fourth teeth of premaxilla contact the third hypertrophied tooth; several fenestrae in area of quadrate bordering the otic recess; *premaxilla with anteroposteriorly directed groove on ventral surface between ridge bordering the hypertrophied tooth and ridge bordering incisive foramen; medial depression on ventral surface of dentary and splenial along mandibular symphysis; presence of cingula on maxillary/dentary teeth.

4. Comparative description (MPMA 12-0050/07)

The skull and mandible of MPMA 12-0050/07 are almost complete. There was some breakage and minimal displacement of some elements during deposition e diagenesis, but the observation and interpretation of morphological characters is not compromised.

Overall, the skull of *Morrinhosuchus* is triangular in dorsal view and the lateral edge of the snout and maxilla are almost straight, similar to those of *Notosuchus* and *Caipirasuchus*, but unlike *Mariliasuchus* whose snout is bulbous (Bertini & Carvalho, 1999; Fiorelli & Calvo, 2008; Iori & Carvalho, 2011). The snout is short, its length about one third of the skull's total length. In lateral view, the ventral edges of the premaxilla and maxilla are in the same level and consequently with the same height, as in Sphagesauridae, and unlike *Araripesuchus*, *Montealtosuchus* and *Baurusuchus*, where the edges are curved and there is a height difference between premaxilla and maxilla (Pol, 2003; Carvalho et al., 2005, 2007; Sereno & Larsson, 2009; Iori et al., 2013). The basicranium is complete and most of it is exposed posteroventrally. The mandible is arched anteroposteriorly in two plains; in lateral view, it is anteriorly concave and posteriorly convex, showing a subtle sigmoid contour; in dorsal or ventral view it presents a "V" shape; the mandibular symphysis is about one quarter of the total length of the mandible; it is relatively longer than in *Mariliasuchus*, but shorter than in Sphagesauridae (Zaher et al., 2006; Iori et al., 2013).

External nares — The external naris is rimmed laterally and ventrally by the premaxilla, and dorsally by the nasal. The anterior portion is lost to erosion, the internarial bar not preserved.

Antorbital fenestra — The antorbital fenestra is relatively small and in this specimen is not as obvious as it is in the holotype (MPMA 07-0009/01). It is rimmed almost exclusively by the maxilla, though the posterior edge of the fossa is ventral to a small portion of the lacrimal which juts anteriorly into the fenestra. This morphology is shared with *Caipirasuchus* and *Notosuchus* while *Mariliasuchus* and other sphagesaurids show no evidence of fenestra (Nobre & Carvalho, 2006; Zaher et al., 2006; Fiorelli & Calvo, 2008; Marinho & Carvalho, 2009; Novas et al., 2009; Iori et al., 2013).

Orbit — although part of the frontal have collapsed, it can be assumed that the orbit was nearly circular; it is bordered anteriorly by the jugal and lacrimal, ventrally by the jugal, posteriorly by the jugal, postorbital, and frontal, and dorsally by the frontal and prefrontal. The postorbital possesses a relatively large articular facet, suggesting the occurrence of a large posterior palpebral.

Supratemporal fenestra — The supratemporal fenestra is nearly circular, rimmed by the frontal and postorbital anteriorly, by the parietal medially and by the postorbital and squamosal laterally; the fossa, located posteriorly, is elongated anteroposteriorly; the parietal-squamosal contact occurs inside of the fenestra and its posterior edge is almost at the posterior margin of the skull. In *Mariliasuchus,* it is much broader than in *Morrinhosuchus*, the morphology of the fenestra and of the supratemporal fossa of *Morrinhosuchus* is very similar to that of *Notosuchus*; however, in the latter, the frontal does not participate in the fenestra (Zaher et al., 2006; Fiorelli & Calvo, 2008). The infratemporal fenestra is triangular in appearance, not very wide, with a maximum length similar to that of the orbit.

Suborbital fenestra — The palatines are not preserved, thus making it difficult to determine the size of the suborbital fenestra. However, it is possible to assume that they were not very wide; their maximum length was approximately 12% of skull length. The ectopterygoids constitute the posterior and part of the lateral edge of the suborbital fenestra. Most of the medial and part of the anterior edge was composed of the palatines; the maxilla bordered the fenestra anterolaterally.

Internal choana — The main structures of the choanae are not present. In ventral view, there is a circular corner on the ectopterygoid and pterygoid which precedes the dorsal depression that made up part of choana.

Caudal intermandibular foramen — The intermandibular foramen is small and circular, bordered exclusively by the splenial and located at the level as the tenth tooth.

Mandibular fenestra — The external mandibular fenestra has an elongated oval aspect oriented anteroposteriorly, its length corresponds to 30% of the total length of the mandible, similar to *Notosuchus*, while in *Mariliasuchus* this ratio is 20%. The internal mandibular fenestra is about 35% of the length of the mandible.

Cranial and mandibular ornamentation — The skull and mandible ornamentation is comprised of grooves and shallow slots, more conspicuous in certain regions. Laterally, the rostrum shows two surfaces, a ventral smooth surface marked by countless and aligned neurovascular foramina, and an adjacent, ornamented dorsal surface. The boundary between these two surfaces begins posteriorly in the jugal, almost at the postorbital bar and proceeds anteriorly to the external nares. The jugal foramen is ventral to this line. The jugal is laterally ornamented around the orbita with a cracked appearance arising from various anastomosing slots. A groove delimits the smooth and ornamented surfaces on the posterior half of the maxilla. Above this groove is a slight intumescence marked by shallow grooves which precedes the region of the antorbital fenestra. In dorsal view, subtle ornamentation is present on the dorsal surface of the rostrum, frontal, and medial portion of the parietal, in addition to the dorsal surface of the postorbital and squamosal. The frontal shows well-marked slots in the anterior portion as well as a shallow sagittal crest. The mandible is marked by a lateral crest that delimits the boundary between smooth and ornamented surfaces; the smooth region is ventral to the alveolar margin, and is characterized by the presence of neurovascular foramina. The ornamented surface is marked by grooves oriented anteroposteriorly. Ventrally, the grooved region is present from the anterior margin of the mandible posterior to the beginning of the mandibular fenestra.

Nasals — The anterior extent of the nasals is not well defined, but it is assumed that they dorsally rimmed the external nares. Though the largest surface exposure occurs dorsally; the nasal is ventrally projected at the point of the premaxilla-maxilla contact where the largest area of lateral exposure occurs. The nasals contact the

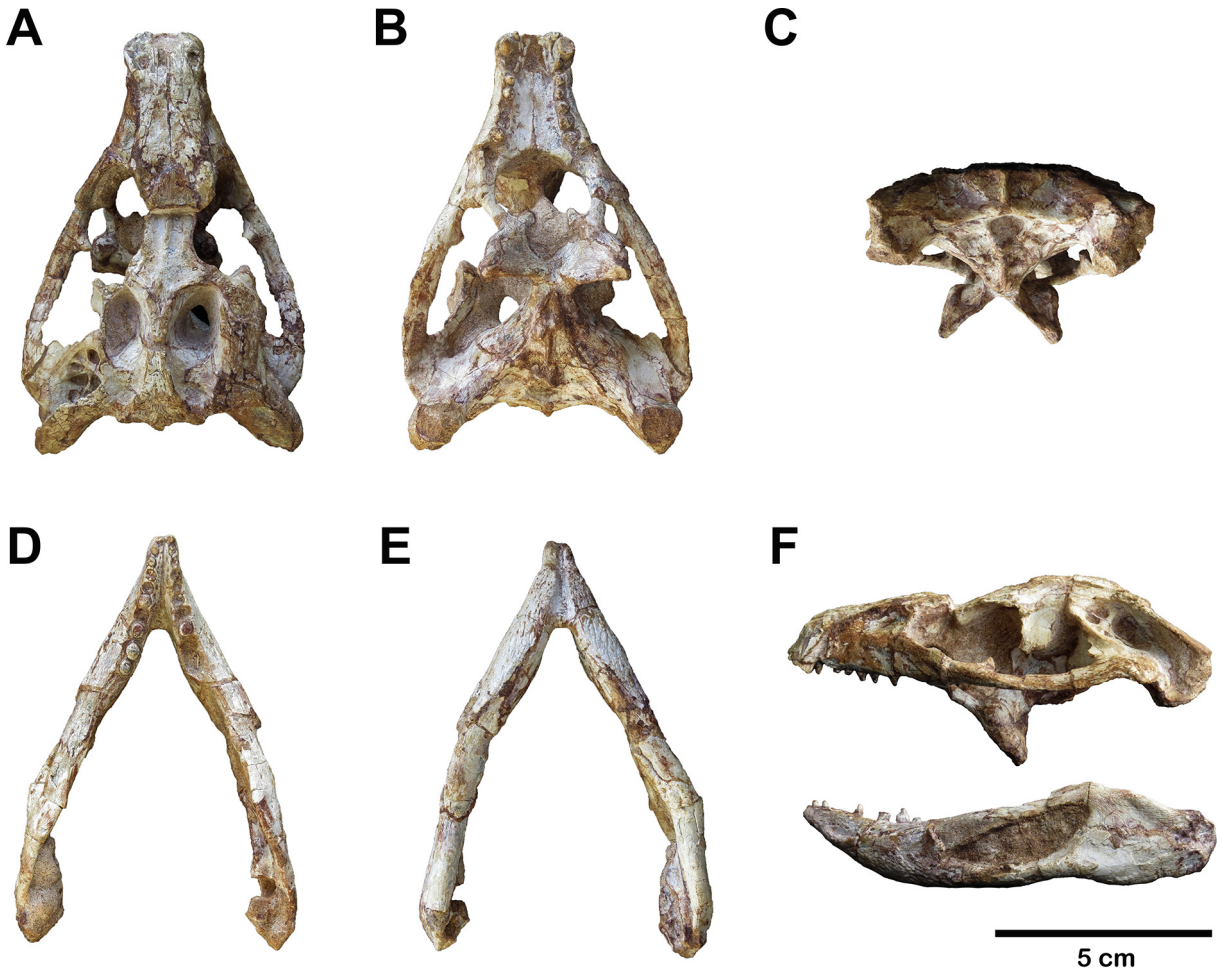

Fig. 2. Skull and mandible of *Morrinhosuchus luziae* (MPMA 12-0050/07) in dorsal (A and D), ventral (B and E), posterior (C), and left lateral (F) views.

premaxilla anteroventrally, the maxilla posteroventrally, the frontals posteromedially, and the prefrontal posterolaterally. It is not possible to determine whether or not the nasal contacts the lacrimal. The posterior process that contacts the frontal and prefrontal is cuneiform, similar to that observed in *Notosuchus.* On the other hand, in *Yacarerani* and *Mariliasuchus* the suture between the nasals and the frontals is almost perpendicular to the sagittal axis (Zaher et al., 2006; Novas et al., 2009).

Premaxilla – The premaxillae are eroded at their anteriormost extent, exposing the inner edge of the right first alveolus and part of its root. The dorsal surface is also eroded and shows the dorsal extremities of the roots of the two hypertrophied teeth. In lateral view, there is a small prominent posterior process that contacts the nasal dorsally and the maxilla posteriorly. The ventral surface is quite narrow and marked by a longitudinal groove where it contacts the maxilla posteriorly and make up the lateral and anterior edges of a large incisive foramen. The presence of this foramen is pointed forward in *Caipirasuchus*, *Sphagesaurus*, *Mariliasuchus*, among others (Pol, 2003; Zaher et al., 2006; Iori et al., 2013). However, it does not occur in *Notosuchus* (Fiorelli & Calvo, 2008).

Maxilla – The lateral contact between the maxilla and the premaxilla is marked by the presence of a wide foramen situated along the neurovascular foraminal line. From this position to the contact with the nasal, it follows the premaxillary-maxillary suture. The lateral surface of the maxilla is subtriangular and almost vertical to its contacts with the nasal anterodorsally, the jugal posterodorsally, and the lacrimal posteriorly. An antorbital fossa rims the antorbital fenestra on the maxilla and includes a large contact area with the lacrimal. In ventral view, the anterior edge of the maxilla shows a recess at the point of contact with the premaxilla followed by a medial protrusion that borders the incisive foramen. The posterior process of the maxilla contacts the jugal posterodorsally and posteromedially, and the ectopterygoid posteriorly. Neurovascular foramina are present near the inner edge of the alveoli on the palatal process. The palatines are not preserved in specimen MPMA 12-0050/07, but the holotype (MPMA 07-0009/01) shows the small anterior portion of the palatine that contacts the maxilla and there is no occurrence of a maxillo-palatine fenestrae as is present in *Notosuchus* and *Mariliasuchus* (Zaher et al., 2006; Fiorelli & Calvo, 2008).

Lacrimal – The lacrimal contacts the maxilla anteriorly and borders a small part of the antorbital fenestra; contacts the prefrontal dorsally and the jugal ventrally; and participates in the anterior edge of the orbit. It does not surpass the anterior rim of the antorbital fenestra, unlike in *Caipirasuchus montealtensis*, in which the lacrimal is more anterodorsally projected.

Prefrontal – The prefrontal contacts the nasal anteromedially and the frontal posteromedially. It dorsolaterally overlaps the lacrimal and participates in the orbital margin. Generally speaking, the prefrontal has a semicircular shape as in *Caipirasuchus* and *Mariliasuchus*.

Frontal –The frontal is fragmented and its posterior portion has shifted ventrally. However, almost the entire dorsal surface can be observed. It contacts the nasal and prefrontal

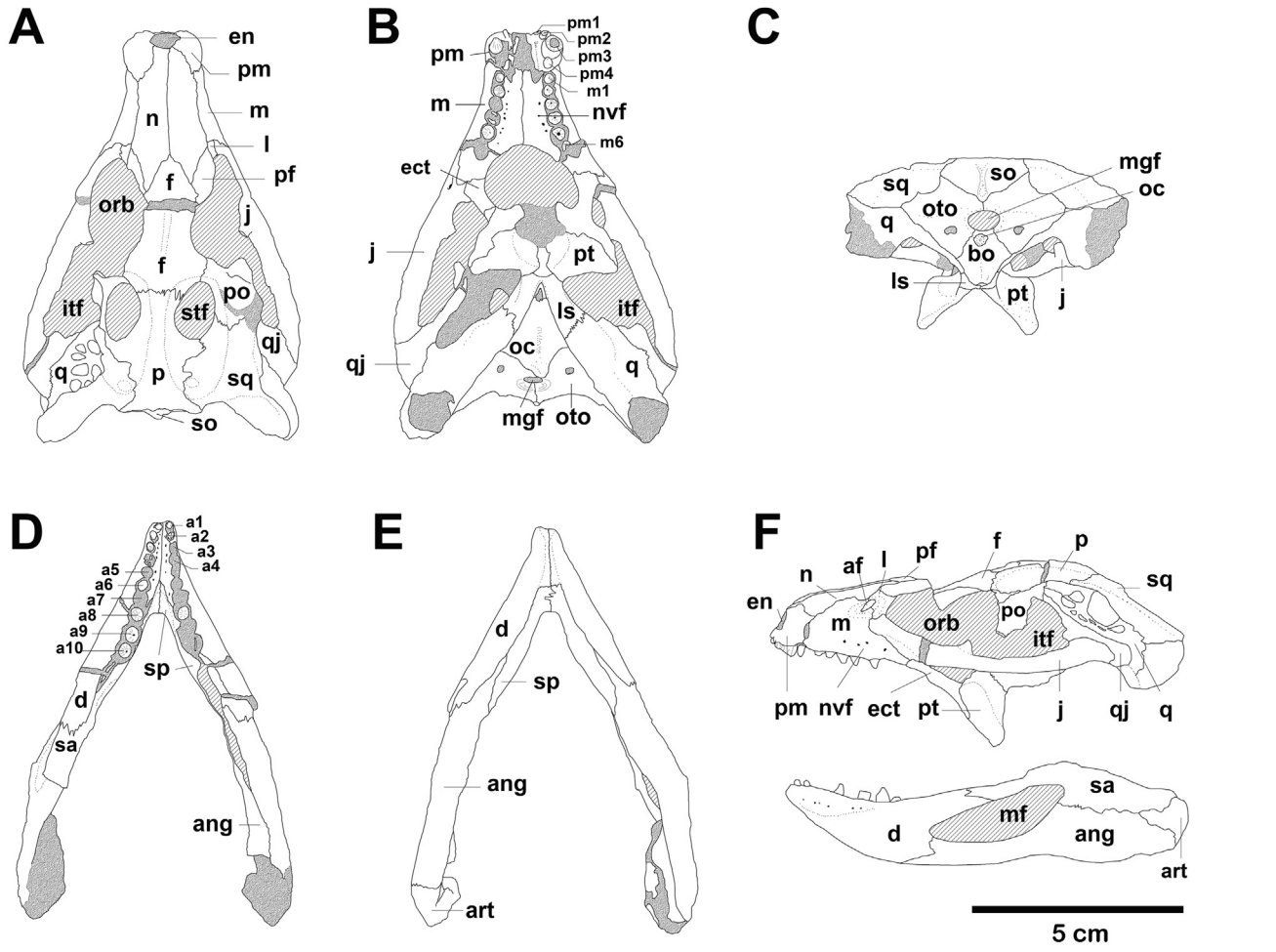

Fig. 3. Schematic drawing of the skull and mandible of the *Morrinhosuchus luziae* (MPMA 12-0050/07) in dorsal (A and D), ventral (B and E), posterior (C), and left lateral (F) views. **a1**–**a10**, alveolus of the dentary; **af**, antorbital fenestra; **ang**, angular; **art**, articular; **bo**, basioccipital; **d**, dentary; **dlr**, dentary lateral ridge; **ect**, ectopterygoid; **en**, external nostril; **f**, frontal; **itf**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **ls**, laterosphenoid; **ltf**, laterotemporal fenestra; **m**, maxilla; **m1**–**m6**, maxillary teeth; **mf**, mandibular fenestra; **mgf**, *foramen magnun*; **n**, nasal; **nvf**, neurovascular foramina; **oc**, occipital condyle; **orb**, orbit; **oto**, otoccipital; **p**, parietal; **pm**, premaxilla; **pm1**–**pm4**, premaxillary teeth; **pf**, prefrontal; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sp**, splenial; **sq**, squamosal; **so**, supraoccipital; **sof**, suborbital fenestra; **stf**, supratemporal fenestra.

anterolaterally in unornamented region. From here, the sagittal crest appears posteriorly and extends almost to the suture with the parietal. The frontal rims the orbit dorsally and supratemporal fenestra anteriorly contacts the postorbital laterally and meets the parietal posteriorly. The anterior contact with the nasals is marked by a V-shaped groove in the region of the sutures. It is an elongated and relatively narrowed bone, unlike *Mariliasuchus* whose frontal is short, and that of the *Yacarerani,* which has a rectangular aspect and smooth dorsal surface (Zaher et al., 2006; Novas et al., 2009).

Parietal – The parietal contacts the frontal anteriorly on the dorsal surface and across the medial wall of the supratemporal fenestra. The lateral contact with the squamosal occurs both within supratemporal fossa and on the dorsal surface of the cranial roof. The contact with the supraoccipital occurs on the dorsal surface, almost at the posterior edge of the cranial roof. Here, it presents obvious ridges bordering the fossa which border the supratemporal fenestrae, as noted in *Caipirasuchus paulistanus* (Iori & Carvalho, 2011).

Postorbital – In dorsal view two distinct surfaces of the postorbital can be observed, one lower and smooth near the orbit, and the other ornamented in the same plane as the dorsal squamosal surface. Contact with a posterior palpebral would probably occur on this smooth region, though none is preserved. The contact with the right squamosal is partially covered dorsally and laterally by matrix. The entire dorsal surface of the left postorbitalis eroded, but it is possible to observe its lateral surfaces. It shows a dorsoventrally oriented corner which divides the lateral surface from the anteromedial one that composes part of the orbit; its contact with the quadrato-jugal is not preserved.

Squamosal – In dorsal view, the squamosal is triradiate, with a main axis directed anteriorly to its contacts with the postorbital, a medial ramus that contacts the parietal, and a posterolateral branch directed beyond the posterior edge of the cranial roof as a distinct posterior process. The squamosal is ornamented on the dorsal surface between the supratemporal fossa and the lateral edge of the skull. The portion that contributes to the floor of the fossa is smooth along with the most posterior region and lateral otic portion. In lateral view, the squamosal is strongly arched posteroventrally. Laterally, it forms a thin lamina protruding over the otic region. The squamosal contacts the parietal medially and anteriorly, the supraoccipital posteriorly, and the otoccipital and quadrate ventrally. The wide posterodorsal exposure of the squamosal is similar to the expanded posterolateral process observed in *Araripesuchus patagonicus* unlike *Mariliasuchus* and *Caipirasuchus* (Ortega et al., 2000; Zaher et al., 2006; Iori et al., 2013).

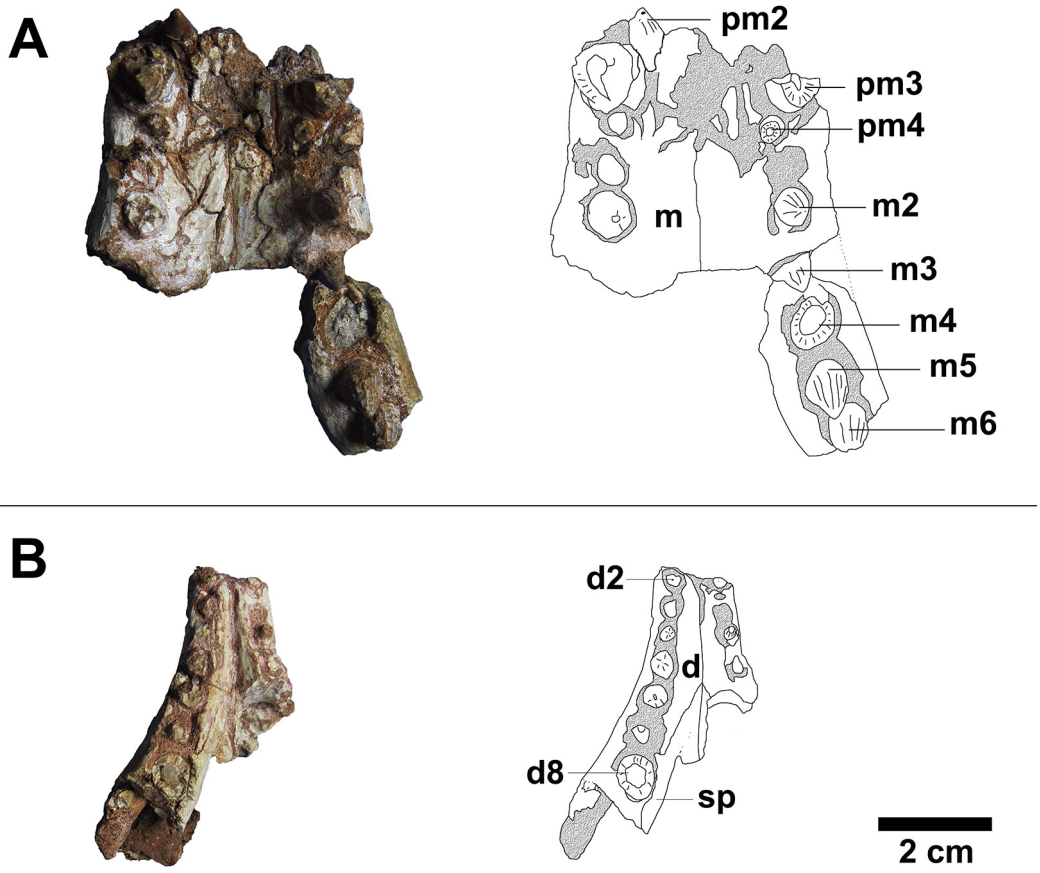

Fig. 4. Skull in ventral view (A) and mandible in dorsal view (B) of *Morrinhosuchus luziae* (MPMA 04-0019/15). **d**, dentary; **d2**–**d8**, teeth of the dentary; **m**, maxilla; **m2**–**m6**, teeth of the maxilla; **pm**, premaxilla; **pm2**–**pm4,** teeth of the premaxilla; **sp**, splenial.

Jugal – The jugal forms the ventral borders of the orbit and infratemporal fenestra. Anteriorly, the jugal bar is robust and slightly compressed. The portion posterior to the postorbital bar is laminar and compressed dorsoventrally. In lateral view, the posterior region of the jugal is slightly sigmoid, curved slightly downward below the anterior portion of the infratemporal fenestra and curved slightly upward below the posterior region of the infratemporal fenestra to its contact with the quadratojugal. The posterior process of the jugal contacts the quadratojugal posterodorsally. The anterior process of the jugal contacts the lacrimal dorsally, the maxilla anteroventrally, and at the region near the contact with the ectopterygoid possesses a small protrusion that contacts the maxilla anterodorsally. The contact with the ectopterygoid is located on the ventral portion of the medial surface. The contact with the postorbital is not preserved. The dorsoventrally compression of the jugal is similar to that of *Adamantinasuchus,* although it is strongly dorsally arched posteriorly, unlike in Sphagesauridae, *Mariliasuchus* and *Notosuchus*, where the jugal is a straight bar allowing for effective propalinal movement (Pol, 2003; Nobre & Carvalho, 2006; Zaher et al., 2006; Fiorelli & Calvo, 2008; Marinho & Carvalho, 2009; Iori et al., 2013).

Quadratojugal – The anterior process of the left quadratojugal is not fully preserved, while the right quadratojugal is visible ventrally. It is relatively wide. The posterior most portion of the bone is nearly vertical, its long axis oriented posteriorly.

Quadrate – The quadrate protrudes posteriorly beyond the posterior-most extent of the occipital condyle. Although the quadrate condyles are not preserved, they likely protrude ventrally based on the orientation of the posterior ramus, similar to the quadrate morphology of *Mariliasuchus*, *Yacarerani* and *Caipirasuchus*. Its dorsolateral surface is broad, with a complex otic region. The otic aperture is bordered posterodorsally by the suture with the squamosal bone, the anterodorsal, lateral, and posteroventral margins of the otic aperature are bordered by a total of seven fenestrae, each approximately one third the diameter of the aperature (Fig. 5). Pol et al. (2014) indicate that among the Notosuchia, multiple fenestrae surrounding the otic aperture are observed in *Notosuchus*, *Mariliasuchus*, *Yacarerani*, and *Caipirasuchus*, a characteristic similar to that observed in basal crocodyliforms. The pattern of fenestration in *Morrinhosuchus* is very similar to that of *Notosuchus*. The quadrate contacts the quadratojugal anterolaterally along a fairly elongate suture starting in the region of the distal condyles and continuing anterodorsally to the ventral surface of the postorbital. In ventral view, the quadrate appears quite robust. Here it contacts the pterygoid anteroventrally, the otoccipital and basioccipital posteromedially, and the squamosal dorsally. A rugosity is present toward the posterior edge of the infratemporal fenestra.

Pterygoid – The pterygoid contacts the quadrate posterodorsally along an elongate suture. It is notably constricted in the posterior region the level of the transverse process. Here, the pterygoid possesses a ridge bordering the depression of the basisphenoid. The transverse process of the pterygoid is modest in size. The, posterior face of the pterygoid is almost vertical, is robust laterally, and contacts the ectopterygoid anterodorsally. On its anteroventral surface, it has a medial depression which comprises part of the parachoanal fossae. The transverse processes are solid, not pneumatic unlike *Caipirasuchus montealtenis*.

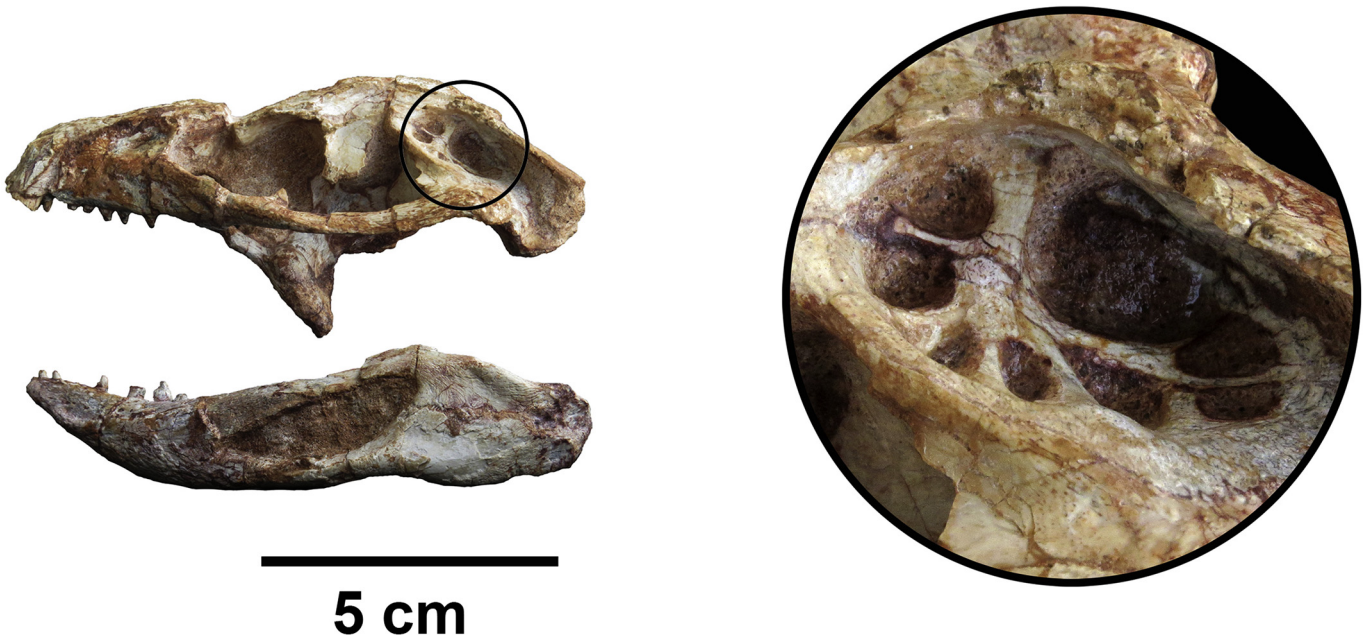

Fig. 5. Detail of the otic recess region of *Morrinhosuchus luziae* (MPMA 12-0050/07).

Ectopterygoid – The ectopterygoid is triradiate, with anterior, medial and posterior process. The posterior process contacts the pterygoid posteroventrally, a small protrusion juts medially, delimiting the suborbital fenestra posteriorly (as in *Notosuchus*), and may have contacted the palatines (which are not preserved). The anterolateral bar contacts the maxilla anteriorly and the jugal laterodorsally, bordering part of the suborbital fenestra.

Supraoccipital – The supraoccipital is exposed on the dorsal surface of the skull by a small sagittal posterior projection. At this point, the suture with the parietal is in the dorsal plane. Laterally, the contact with the parietal occurs on the edge between the dorsal and posterior planes. In posterior view, the supraoccipital is triangular and in contact with the otoccipital lateroventrally. A nuchal crest is conspicuous, as in *Simosuchus* (Kley et al., 2010).

Otoccipital – The otoccipital can be divided into posterior and posteroventral faces. The posterior face is triangular, ventrally bounded by its lateromedial edge, mediodorsally by its contact with the supraoccipital and laterodorsally by its contact with the squamosal. The posteroventral face is also triradiate, with the most lateral projection comprised by a crest aligned with the suture between the quadrate and the squamosal; the medial portion contacts the other otooccipital and borders the *foramen magnum* dorsolaterally. The ventral-most process is cuneiform, contacting the basioccipital ventromedially and the quadrate laterally. The ventral margin of the foramen for the *vagus* nerve is almost aligned with the ventral margin of the *foramen magnum*.

Basioccipital – The basioccipital is diamond-shaped and possesses a sagittal crest throughout almost the entire surface. It contacts the otoccipital posterodorsally, the quadrate lateromedially, and the depression of the parabasisphenoid ventrally. The occipital condyle is not fully preserved in any known specimen.

Dentary – In lateral view, the dorsal margin of the dentary is straight in its anterior portion; posterior to the toothrow it arches dorsally. The ventral margin is parabolic. A marked lateral keel separates a smooth dorsal surface from a ventral ornamented surface (Fig. 6). This keel begins at the fourth tooth position and proceeds posteriorly to level of the eighth tooth where it becomes an almost imperceptible intumescence. The dentary borders the mandibular fenestra posteroventrally and contacts the surangular posteriorly above the anterior half of the mandibular fenestra. This differs from *Caipirasuchus* and *Mariliasuchus* in which the surangular project anterior to the mandibular fenestra (Zaher et al., 2006; Iori et al., 2013). The dentary contacts the angular posteriorly at approximately the midpoint of the mandible. In ventral view, the suture dentary-angular begins at the level of the last tooth position and ends slightly posterior to the border of the mandibular fenestra. On the dorsal surface, the dentary symphysis extends posterior to the level of the sixth tooth position. The dentary contributes to the lateral alveolar margin of the entire dentition and to the medial border anterior to the seventh alveolus. A small projection borders the sixth and seventh alveoli, ventrally, this projection contacts the splenial. In ventral view, a medial sulcus without ornamentation is present on the mandibular symphysis and expands posteriorly. The suture with the splenial in ventral view is not visible. However, Iori & Carvalho (2009) refer to the participation of the splenial in the symphysis based on the holotype (MPMA 07-0009/01). A series of linearly arranged neurovascular foramina borders the alveoli medially and on the smooth lateral surface of the dentary. The teeth of the dentary are positioned in a straight line, as in *Notosuchus*, whereas in *Mariliasuchus* the teeth are in a parabolic line and in the Sphagesauridae, in two lines, one parallel to the sagittal axis and the other diverging laterally (Zaher et al., 2006; Fiorelli & Calvo, 2008; Novas et al., 2009; Iori et al., 2013; Pol et al., 2014).

Splenial – In medial view, the splenial is a laminar, almost flat bone posterior to the intermandibular caudal foramen. Posterior to the last tooth position, the lamina moderately inclined posterolaterally, contacting the dentary anterolaterally and the surangular posteriorly. The splenial comprises the entire anterior internal margin of the mandibular fenestra; it contacts the angular posteroventrally below the mandibular fenestra. The splenial medially borders the three last mandibular alveoli. In dorsal view, the splenial participates in almost half the anteroposterior length of the mandibular symphysis. In ventral view, the suture between the splenial and the dentary marks the ornamented outer side and the smooth inner side of the mandible. Posteriorly, this suture contacts the apex of the projection of the angular. A peg is present at the posterior surface of the mandibular symphysis.

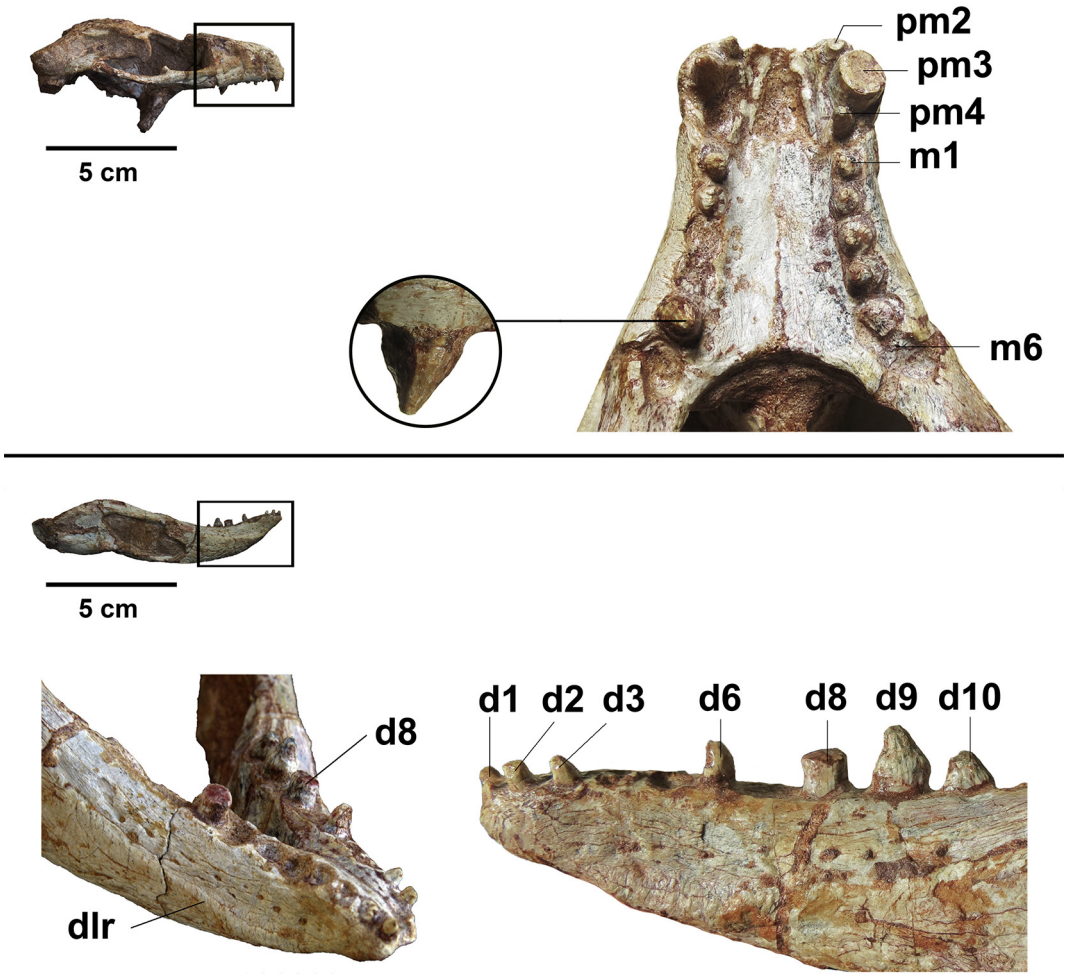

Fig. 6. Dentition of *Morrinhosuchus luziae* (MPMA 12-0050/07). **d1**–**d10, m1**–**m6, pm1**–**pm4,** teeth of the dentary, maxilla and premaxilla (respectively); **dlr**, dentary lateral ridge.

Angular – The angular possesses an anterior cuneiform projection that contacts the dentary anterolaterally and the splenial posteromedially; in lateral view, it follows the concave contour until close to the final margin of the mandibular fenestra where it presents a slightly concave contour, followed by another convex one; In lateral view, the angular is projects laterally to the posteroventral margin of the mandibular fenestra, followed posteriorly by a flat, laterally facing surface to the dorsal contact with the surangular. The posterior-most portion of the angular consists of a posterolateral facing surface that contacts the articular dorsally. In medial view, it is perceived an extensive dorsal angular-surangular contact, a formation of most of the ventral margin of the mandibular fenestra and the anterodorsal contact with the splenial.

Surangular – It contacts the dentary anteriorly over the mandibular fenestra, in lateral view, presents two exposed surfaces, one dorsolateral, more anteriorly, and another lateral where it contacts the angular in an anteroventral manner.

Articular – The articular is incompletely preserved and part is covered by matrix. The retroarticular process is quite small and has little exposure in lateral view. The articular is comprised by posterior, lateral, and ventral facing surfaces, contacting the angular anteroventrally and the surangular anterodorsally. In medial view, the articular contacts the angular ventrally and the surangular laterally.

Dentition – Few tooth crowns are preserved, and only the right third premaxillary tooth and the fifth maxillary tooth preserve considerable portions of the enamel (Fig. 6). In these teeth, the striations are evident around the entire crown from the crown base to the apex. The teeth are closely arranged, without diastemas. The sequence of the teeth in the dentary is arranged in a straight line, diverging about 15° from the sagittal plane. The sequence of the third premaxillary tooth to the sixth maxillary tooth is arranged along a parabolic line. The full dentition would be comprised by a total of 40 teeth, all circular cross-sections, 4 in each premaxilla, 6 in each maxilla, and 10 in each dentary. The crown of the first premaxillary tooth was not preserved either side; the second right premaxillary tooth is better preserved, around 3 mm in diameter, featuring a conical and pointed crown similar to the third and fourth teeth in the series. The third premaxillary tooth is large and caniniform, the diameter of the base of its crown is approximately 5 times the diameter of the other premaxillary teeth. The crown bases of the second and fourth premaxillary teeth touch the base of the third crown. The premaxillary right third tooth is a replacement tooth, and the diameter of the base of its crown is around half the measurement of its equivalent fully erupted crown. The fourth premaxillary tooth is approximately 5 mm tall, sharp, and its respective alveolus is in a groove shared with the hypertrophied third tooth. The first maxillary crown is taller than it is wide, with a cylindrical basal half. The series from the second to the fifth maxillary position is characterized by teeth of a similar morphology, though, progressively increasing in size posteriorly. These teeth are conical with sharp apices, and with crowns of the same height and width. The sixth tooth in the series is not preserved in either maxilla of MPMA 12-0050/07, or in the holotype.

However, in MPMA 04-0019/15, the crows of the fifth and sixth maxillary teeth are well preserved (Fig. 7). The fifth crown is conical and curved backward as in specimen MPMA 12-0050/07. However, the sixth tooth is peculiar among the advanced notosuchians due to the presence of a cingulum. In this tooth, the root represents about ¾ of the height, the base of the crow is constricted and the cingulum is subtle and visible on distal surface of the crown. Only one central cusp is present (Fig. 7). The anterior three teeth of the dentary are the smallest in the series. All three are conical with anterodorsally facing apexes. The fourth, fifth, and seventh teeth are not preserved; though the sixth tooth of the left dentary is partially preserved and apparently was a sharp, taller than wide. The eighth dentary tooth preserves a very peculiar morphology with a cylindrical crown, and a flat dorsal surface possible resulting from wear. The ninth crown is without enamel, however the abrupt tapering in the crown suggests the presence of a cingulum as in the sixth maxillary tooth.

Morrinhosuchus possesses a markedly different dental morphology from other advanced notosuchians. The dental formula (4 teeth in each premaxilla, 6 in each maxilla and 10 in each dentary) is the same as those of *Caipirasuchus* and *Yacarerani*, however, there are no teeth of oblique implantation in *Morrinhosuchus*, also found in *Notosuchus* and *Llanosuchus* (Pol, 2003; Fiorelli & Calvo, 2008; Lecuona & Pol, 2008; Novas et al., 2009; Iori et al., 2013; Fiorelli et al., 2016). The premaxilla of *Morrinhosuchus* has a hypertrophied third tooth and a fourth tooth in very close to contact with the maxilla, as observed in *Caipirasuchus*, *Mariliasuchus*, *Adamantinasuchus* and *Notosuchus*, among others. The peculiarity is in the placement of the second and fourth teeth, which are very close to the hypertrophied third, with roots touching each other. *Mariliasuchus* possess few teeth (4 teeth in each premaxilla, 5 in each maxillar and 9 in each dentary). Iori & Carvalho (2009) report similarities between the posterior teeth in *Morrinhosuchus* and *Mariliasuchus*, however, the analysis of the new individuals reveals that the morphology of the crowns are distinct. *Mariliasuchus* has posterior teeth with globular crowns denticulate serrations on the mesial and distal margins (Zaher et al., 2006), while in *Morrinhosuchus* most of crowns are conical, obtuse, grooved. In *Morrinhosuchus,* the eight tooth of the dentary is cylindrical with flat dorsal surface possible resulting from wear. However, there is no opposition from a tooth of the dentary with similar features. Both teeth are preserved in MPMA 12-0050/07, and in the holotype (MPMA 07-009/01), only the tooth on the left side. *Morrinhosuchus* does not possess procumbent anterior teeth as observed in *Yacarerani*, *Mariliasuchus* and *Labidiosuchus*, or hypertrophied teeth in the dentary and/or maxilla as occurs in *Araripesuchus*, *Candidodon*, and *Comahuesuchus* (Price, 1959; Nobre & Carvalho, 2002; Martinelli, 2003; Zaher et al., 2006; Novas et al., 2009). *Morrinhosuchus* possesses a cingulate tooth crown as in *Malawisuchus* and *Candidodon* (Ösi, 2013). The principal cusp is similar to *Malawisuchus*, though in *Morrinhosuchus* accessory cusps don't occur. Only Montefeltro et al. (2009) reported the occurrence of cingulate teeth in Bauru Basin with five isolated teeth from the São José do Rio Preto Formation showing similarities to dentition of *Morrinhosuchus*.

5. Phylogeny

Phylogenetic dataset and analysis – A new phylogenetic analysis was made, using TNT ver. 1.1 (Goloboff et al., 2008) and the character matrix published by Fiorelli et al. (2016) with the inclusion of the new data observed for *Morrinhosuchus* (Appendix 1) along the exclusion of *Coringasuchus*. Also, a heuristic tree search of 1000

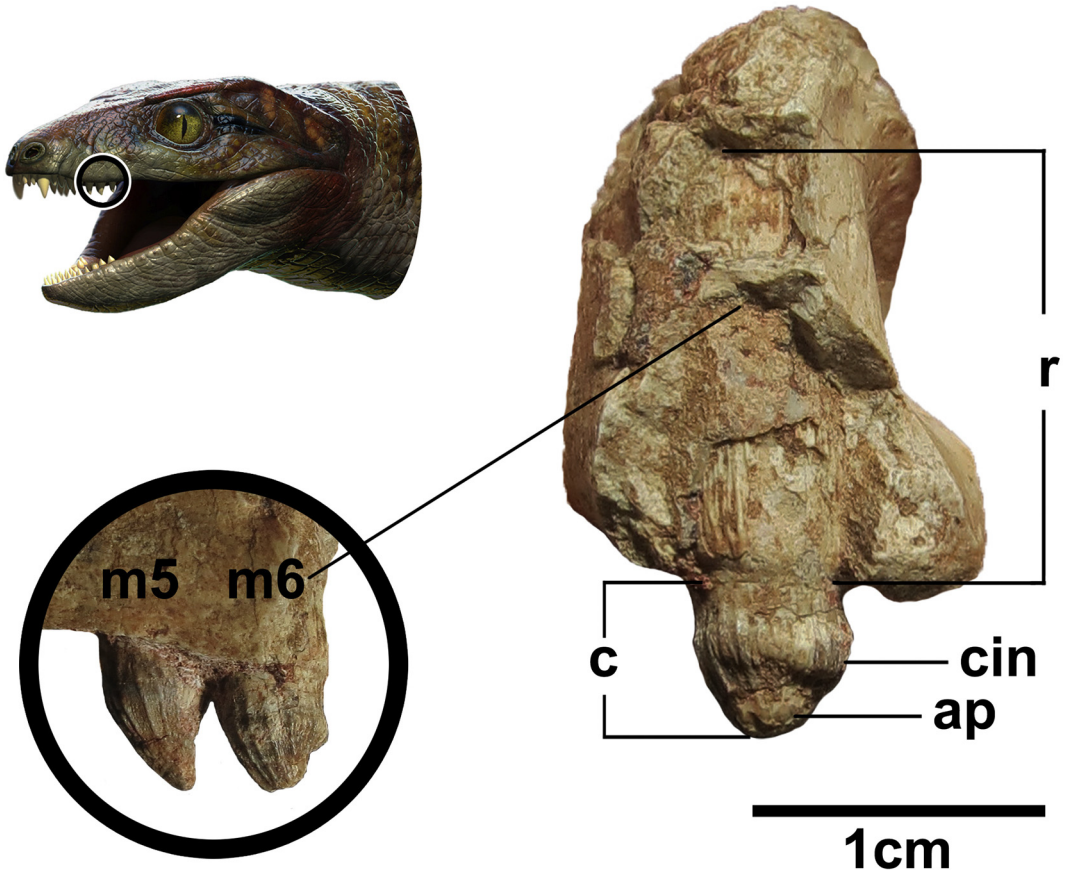

Fig. 7. Detail of last two maxillary teeth in *Morrinhosuchus luziae* (MPMA 04-0019/15). **ap**, apex; **c**, crown; **cin**, cingulum; **m5**–**m6**, teeth of maxilla; **r**, root.

replicates of Wagner trees with random addition sequences was performed, followed by TBR branch-swapping. The result was the strict consensus of the 8 most parsimonious trees with CI = 0.316, RI = 0.730 and tree length = 1673 steps.

Results – The studies confirmed the analysis by Fiorelli et al. (2016), regarding the monophyletic positioning of the advanced notosuchians, and the positioning of *Morrinhosuchus luziae* as the most basal among the Brazilian forms. However, in the new analysis, *Morrinhosuchus* occupies a more derived position inside the group, with *Notosuchus* and *Llanosuchus* arising as the most basal forms (Fig. 8).

6. Paleoautoecology

Morrinhosuchus exhibits a very small retroarticular process that infers gravity as the cause of mandible opening. On the other hand, the supratemporal fossa is relatively broad in *Morrinhosuchus,* similar to that of *Notosuchus* and much larger than in *Mariliasuchus* (Zaher et al., 2006; Barrios et al., 2017). In this fossa the *adductor mandibulae externus profundus* muscle was embedded, being one of those responsible for closing the jaw (Molnar, 2013). In the mandibular fenestra region, the insertion regions of the adductor muscles are also relatively broad, inferring the existence of robust muscles that gave a reasonably powerful bite force. Caniniform tooth along with sharp accessory teeth suggest a more effective prey grasp function, the broad incisivum foramen associated with lateral foramen at the premaxilla-maxilla junction should have relieved the stress in that region during prey hunting. The cylindrical molariforms teeth and cuspidated ones may have acted in the processing of slaughtered animals by breaking shells and bones, however, such dentition could also macerate seeds, roots and other hard foods.

In addition to the dentition of *Morrinhosuchus*, structures related to enhanced auditory function could represent advantages during predation, although these apparatuses also occur in omnivorous/herbivorous forms. Montefeltro et al. (2016) relates the chamber of the acoustic meatus to the maximization of sound wave reception in basal crocodyliforms, baurusuchids, and in certain notosuchians. These authors stated that in such groups, the meatus chamber occupies a large part of the posterior region of the head, and that this expanded region, combined with the concave aspect, could function as a resonance device. Considering Baurusuchidae, they suggest sophisticated auditory anatomy, which includes certain characteristics present in *Morrinhosuchus,* such as the posterolaterally extended region of the quadrate and of the squamosal, expanding the area of the meatus chamber, as well as a wide periotic pneumatization. The new *Morrinhosuchus* specimen has seven subtympanic foramina (or quadrate fenestrae), and as suggested by Montefeltro et al. (2016), these structures could function with multiple resonance networks of the ear. Following the proposal of Montefeltro et al. (2016), the otic complex apparatus of *Morrinhosuchus* is an indicator that this genus may have had good hearing acuity, which would imply advantages for locating prey and fast predator perception. Another possibility is that it could be related to intraspecific communication.

7. Discussion

The taxon diagnosis and previous phylogenetic analyses of *Morrinhosuchus luziae* were performed using only the holotype, consisting only rostral region. The analysis of new specimens (MPMA 12-0050/07 and MPMA 04-0019/15) permit the survey of a large number of characters, some of them, unknown in advanced notosuchians including: all crowns sub-circular in cross section; dentary with a small lateral expansion; crown bases and roots of the second and fourth teeth of the premaxilla contact the third, hypertrophied tooth; quadrate extensively fenestrated; ventral groove in premaxilla; sagittal depression on the ventral surface of the mandibular symphysis; presence of cingulated posterior teeth. The synapomorphies of the advanced notosuchians are: Anterior edge of choanae situated posterior to the suborbital fenestra; maxilla with six teeth; nasal-premaxilla suture straight; anterior region of dentary symphysis in ventral view having a distinct anterior process with parallel lateral margins; presence of a smooth elongated fossa extending along ventral margin of the external mandibular fenestra on the angular, separated from the lateral surface of the angular by a

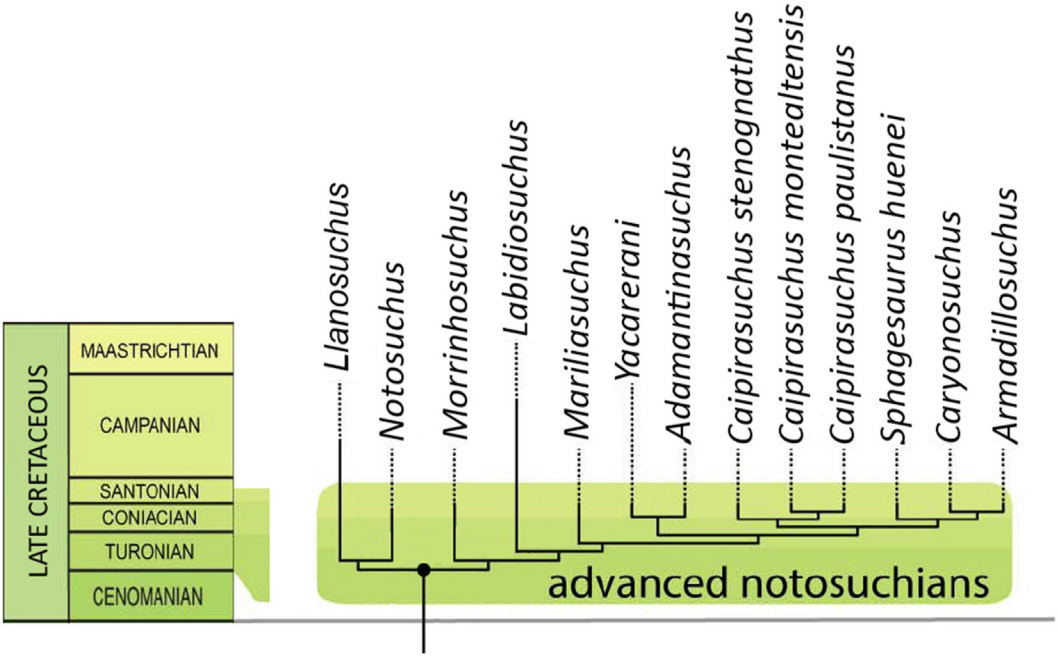

Fig. 8. Phylogenetic position of *Morrinhosuchus* (modified from Pol et al., 2014).

sharp ridge; transitional tooth located at the contact between the premaxilla and maxilla, both of which contribute to the alveolar walls; apico-basal ridges on the enamel surface of posterior teeth and; location and orientation of tooth-tooth occlusion wear facets in posterior teeth aligned along a plane that is oblique to the longitudinal and sagittal planes of the skull.

The presence of posterior teeth with keels and obliquely implanted is related to the development of molariform teeth, and the masticatory occlusion mechanism between opposing teeth of the upper and lower dental series. In the phylogenetic analysis of Fiorelli et al. (2016), this character provides the most derived positioning to *Notosuchus* and *Llanosuchus* regarding *Morrinhosuchus*, but in the analysis here presented, the Argentine species emerge as the most basal group, differing from other species by the presence of anterior palatal fenestrae.

Overall, the morphology of *Morrinhosuchus* is similar to *Notosuchus* and *Mariliasuchus*, however its dentition is distinctive. The dentition is almost exclusively composed of tapered and pointed teeth, and accessory teeth grouped adjacent to the hypertrophied third crown, suggesting the ability for prey seizure. *Morrinhosuchus* was likely not a specialized carnivore as *Pakasuchus*, but likely a generalized carnivore, and may have occupied a niche distinct from those of other advanced notosuchians, namely the Sphagesauridae (Zaher et al., 2006; Fiorelli & Calvo, 2008; Marinho & Carvalho, 2009; Novas et al., 2009; O'Connor et al., 2010; Iori et al., 2013; Pol et al., 2014).

Omnivorous and herbivorous diets have been suggested for advanced notosuchians and in the case of the peculiar teeth of Sphagesauridae suggest possible herbivory (Nobre & Carvalho, 2006; Nobre et al., 2008; Marinho & Carvalho, 2009; Iori & Carvalho, 2011; Ösi, 2013; Iori & Carvalho, 2018). However, teeth with oblique implantations are also observed in *Notosuchus*, *Labidiosuchus, Llanosuchus* and more subtly, in *Mariliasuchus* (Zaher et al., 2006; Lecuona & Pol, 2008; Iori et al., 2011; Kellner et al., 2011; Fiorelli et al., 2016). *Morrinhosuchus* is the only genus that does not possess oblique dental implantation, a feature shared with other ziphosuchian like *Malawisuchus*, *Candidodon* and *Lavocatchampsa* which also possess the peculiar character of cingulate teeth (Gomani, 1997; Nobre & Carvalho, 2002; Martin & Lapparent de Broin, 2016). Ösi (2013) associates the cingulate teeth of *Candidodon* with herbivory and those of *Malawisuchus* to insectivory. *Mariliasuchus* and *Yacarerani* possess procumbent teeth, interpreted to allowing soil foraging. However, they do not occur in *Morrinhosuchus*, where the dentition is comprised almost exclusively of sharp and conical crowns, revealing possible predatory habits.

The anterior series of teeth, composed of tapered crowns suggest an apprehension function, and the cingulated posterior teeth indicate an occlusal mechanism, as suggested for *Lavocatchampsa* (Martin & de Lapparent de Broin, 2016).

Structures possibly related to hearing acuity in *Morrinhosuchus* as well as *Baurusuchus* include a highly fenestrated periotic region that could have granted advantages in prey identification and location. However, omnivorous forms such as *Notosuchus* and *Mariliasuchus* also bear fenestrated periotic region. Refined hearing can also represent a coevolution between predators and prey, or a sign of communication between individuals of the same species (Zaher et al., 2006; Fiorelli & Calvo, 2008; Montefeltro et al., 2016).

Morrinhosuchus was relatively small, with carnivorous/omnivorous habits, and lived in an arid to semi-arid environment, as some of the current Herpestidae. Suricate and mongooses of the African savannas are less than 1 m in length, fed on insects, small vertebrates, eggs, roots, fruits and seeds, besides, they present varying social habits going from complex social systems to solitary habit species. Probably, by its size and teeth features, *Morrinhosuchus* occupied an ecological niche similar to the Herpestidae.

Fig. 9. Three-dimensional head reconstruction of *Morrinhosuchus luziae* based on tomography of fossil MPMA 12-0050/07. Art by Raul Tabajara and Deverson da Silva (Pepi).

8. Conclusions

Morrinhosuchus luziae is a peculiar crocodyliform among the advanced notosuchian. Phylogenetic analysis reinforces its position among the most basal of the group, but more derived than *Notosuchus* and *Llanosuchus*. The anterior dentition composed by sharp teeth suggests predation, whereas powerful muscles and distinguished molariforms (Fig. 9) can suggest durophagy and the possibility of processing carapace, bones, seeds, roots and other foods.

Morrinhosuchus was a small hunter with an acute hearing, that should have inhabited a niche occupied today by Herpestidae, being generalist predators who supplemented their diet with nutritional sources of plant origin.

Acknowledgement

Our thanks go to Sérgio Luiz Frare for the discovery of specimen MPMA 12-0050/07 and Antonio Celso de Arruda-Campos (*in memorian*) for providing the material for studies. We also thank the crew involved in field activities: Cledinei A. Francisco, Deverson da Silva, Flávio Machado, José A. Bugarelli, Nestor A. Costa, Paulo G. Tavares, Sandra A. S. Tavares, and Thiago S. Fachini. Thanks to the artists Deverson da Silva (Pepi) and Raul Tabajara for the life reconstruction of the animal. Special thanks are due to the Editor-in-Chief, Eduardo A. M. Koutsoukos and two anonymous reviewers' contribution, by the depth of their comments, in their respective attempts to help to improve the paper. This study was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG).

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Appendix 1. The data set used in the phylogenetic analysis was based on a set of previously published data (Fiorelli et al., 2016), with the addition of new characters (below) observed in the new specimens of *Morrinhosuchus*.

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