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A new Peirosauridae (Crocodyliformes, Notosuchia) from the Adamantina Formation (Bauru Group, Late Cretaceous), with a revised phylogenetic analysis of Sebecia

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Abstract

Peirosauridae (Crocodyliformes, Notosuchia) is one of the fossil lineages of crocodyliforms ubiquitous in the Cretaceous deposits of the Bauru Basin. Here, we describe a new species of a longirostrine Peirosauridae from the Adamantina Formation (Bauru Basin, Late Cretaceous). The specimen consists of a partially preserved skull with a cranial roof, interorbital region, and fragments of the posterior portion of the rostrum, including the prefrontal and lacrimal; left hemimandible, with 14 alveoli and 12 teeth; and a single cervical rib fragment. The specimen is associated with Peirosauridae by three cranial synapomorphies, and it can be assigned to a new genus and species by presenting seven cranial and one tooth apomorphies. To clarify the position of the new taxon, an updated phylogenetic analysis was performed with increased sampling of taxa of Notosuchia, especially Peirosauridae, and phylogenetically relevant characters. Our results indicated the monophyly of Peirosauridae, formed by two main lineages, the oreinirostral and presumably terrestrial Peirosaurinae and the longirostrine and presumably semi-aquatic Pepesuchinae. The recovering of both lineages as distinct entities was also reinforced through a morphospace analysis. Pepesuchinae were notable by exploring a position of the morphospace not explored by any other Notosuchia. Their longer rostra

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and the assumption of them being gradually specialized to aquatic habits reflects the unique diversity of these crocodyliforms through the Cretaceous deposits of South America and Africa.

1 | INTRODUCTION

Notosuchia (sensu Ruiz et al., 2021) is a remarkably diverse group of extinct crocodyliforms, particularly in Cretaceous deposits of Gondwana, with more than 80 species described to date (Celis et al., 2021; Pol et al., 2012, 2014; Pol & Leardi, 2015; Turner & Sertich, 2010). Such taxonomic richness is also reflected in an unexpected ecological diversity, including completely terrestrial and semi-aquatic forms, a variety of feeding strategies, and presumably, the occupation of many different ecological niches (Bronzati et al., 2015; Godoy et al., 2014; Melstrom & Irmis, 2019; Montefeltro et al., 2020; O'Connor et al., 2010; Ösi, 2014). The notosuchian fossil record is mostly restricted to the Cretaceous of Gondwanan landmasses, including North and Central Africa, Madagascar, and the Indian subcontinent (Buckley & Brochu, 1999; Buckley et al., 2000; Buffetaut, 1994; Gomani, 1997; Larsson & Sidor, 1999; O'Connor et al., 2010; Sereno & Larsson, 2009; Sereno et al., 2003; Wilson et al., 2001), but it was in the Late Cretaceous of South America that the group achieved its peak in diversity (Bonaparte, 1991; Bronzati et al., 2015; Pol & Leardi, 2015).

The Bauru Basin is one of the South American deposits in which an abundance of notosuchians has been recovered, particularly from the Adamantina Formation (Upper Cretaceous, Bauru Basin), which yield one of the most important continental fossiliferous deposits of this period (Bandeira et al., 2018; Montefeltro et al., 2020; Pol & Leardi, 2015). This formation bears an important record of fossil vertebrates, with several species of crocodyliforms described and associated with different lineages of notosuchians (Godoy et al., 2014; Pinheiro et al., 2018; Riff et al., 2012). Notosuchians, represent the most significant components of the tetrapod paleofauna from the Bauru Group (Langer et al., 2022) and suggest the existence of an ecosystem dominated by crocodyliforms, something possibly unparalleled in the geological history of Earth (Godoy et al., 2014; Montefeltro et al., 2020; but see Bandeira et al., 2018).

One of the notosuchian lineages present in the Adamantina Formation is Peirosauridae (Campos et al., 2011; Carvalho et al., 2004, 2007; Iori & Garcia, 2012; Pinheiro et al., 2018). Originally erected by Gasparini (1982) encompassing *Peirosaurus torminni* Price, 1955 and *Gasparinisuchus peirosauroides* (Martinelli et al., 2012), new species were described and assigned to the group from the 1990s onward, including taxa from South America (Barrios et al., 2016; Campos et al., 2011; Carvalho et al., 2004, 2007; Coria et al., 2019; Filippi et al., 2018; Geroto & Bertini, 2018; Iori & Garcia, 2012; Martinelli et al., 2012; Pinheiro et al., 2018), continental Africa (Larsson & Gado, 2000; Larsson & Sues, 2007; Nicholl et al., 2021; Sertich & O'Connor, 2014), and Madagascar (Simons & Buckley, 2009).

Despite the description of several species of peirosaurids during the past 25 years and advances in the knowledge of the morphological and unique traits of the group, peirosaurids have been largely excluded from broader phylogenetic studies. This changed more recently, when Pinheiro et al. (2018) and Geroto and Bertini (2018) independently analyzed the phylogeny and diversity of Peirosauridae, each presenting different topologies. Pinheiro et al. (2018) recognized Peirosauridae as a group comprising only oreinirostral forms (e.g., *P. torminni*, *Uberabasuchus terrificus*, and *Hamadasuchus rebouli*) and the sister group of the clade comprising Mahajangasuchidae + Sebecidae; longirostrine notosuchians (e.g., *Itasuchus jesuinoi* and *Pepesuchus deiseae*) formed the clade Itasuchidae, the sister group of the clade Peirosauridae + (Mahajangasuchidae + Sebecidae). Conversely, Geroto and Bertini (2018) recovered Peirosauridae as a lineage comprising two subclades, the Peirosaurinae (equivalent to Peirosauridae in Pinheiro et al., 2018), encompassing the oreinirostrine forms, and Pepesuchinae (equivalent to Itasuchidae in Pinheiro et al., 2018), the longirostrine ones.

In 2011, a new fossil of a crocodyliform with a long, nearly tubular rostrum (MPMA 68-0001/11) was found in an outcrop of the Adamantina Formation at the municipality of Catanduva, Brazil (Figure 1). Here, we described it, identifying it as a new species of longirostrine notosuchian. Additionally, we performed a new phylogenetic analysis including the most inclusive dataset of Peirosauridae to date, aiming to better understand the morphological diversity and evolutionary history of these unique notusuchians.
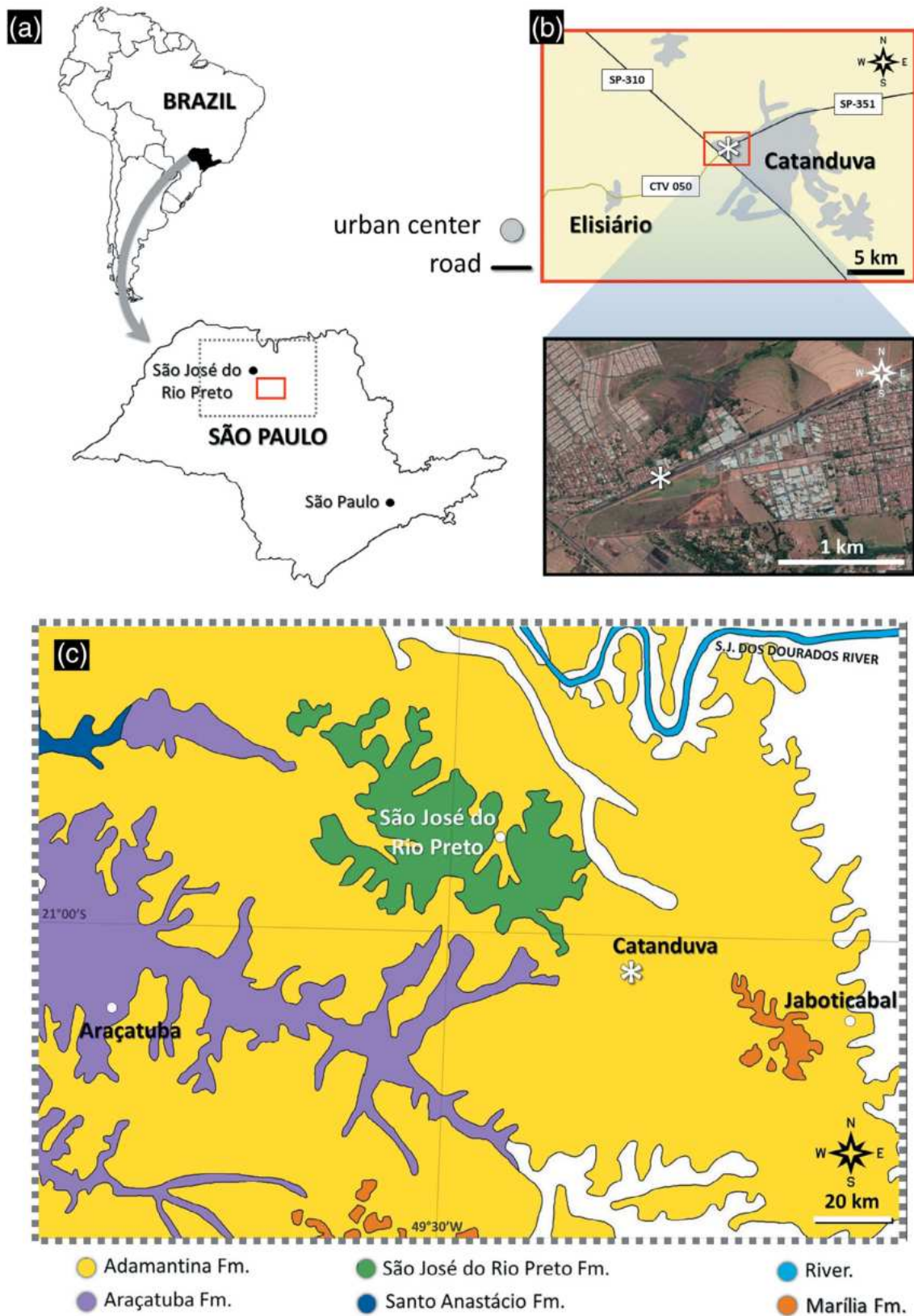
FIGURE 1 Type locality of MPMA 68-0001/11. (a) Maps of South America, Brazil, and São Paulo State, showing the provenance of the fossil; (b) the location of the outcrop where MPMA 68-0001/11 was found; and (c), surface exposure of Bauru Basin rocks around the locality. The asterisks mark the location of the outcrop. Modified from Fernandes and Ribeiro (2014).

2 | MATERIALS AND METHODS

2.1 | Collection and institutions

The specimen MPMA 68-0001/11 was collected in 2011, on a road cut (location 16 km on highway SP-351), in the municipality of Catanduva (São Paulo), Brazil. The constructions undergoing on the road at the time revealed an outcrop of the Adamantina Formation in which several fossils were revealed, collected, and sent to the Museu de Paleontologia "Professor Antonio Celso de Arruda Campos." MPMA 68-0001/11 was first assigned to Peirosauridae by Iori et al. (2011), but a more thorough morphological description and phylogenetic assessment were still lacking.

2.2 | Phylogenetic analysis

To investigate the phylogenetic relationships of MPMA 68-0001/11 within Crocodyliformes, the specimen was included in the recent version of the phylogenetic dataset of the Crocodyliformes published by Ruiz et al. (2021). This matrix encompasses a great part of the known diversity of Gondwanan Cretaceous crocodyliforms. The original matrix included nine peirosaurids: *Barreirosuchus franciscoi* Iori & Garcia, 2012; *G. peirosauroides* (Martinelli et al., 2012); *H. rebouli* Buffetaut, 1994; *I. jesuinoi* Price, 1955; *Lomasuchus palpebrosus* Gasparini et al. 1991; *Montealtosuchus arrudacamposi* Carvalho et al. 2007; *P. deiseae* Campos et al. 2011; *Stolokrosuchus lapparenti* Larsson & Gado, 2000; and *U. terrificus* Carvalho et al. 2004. We expanded the taxonomic sampling with the addition of 12 taxa previously referred as members of Peirosauridae: MPMA 68-0001/11; *Amargasuchus minor* Chiappe, 1988; *Ayllusuchus fernandezi* Gasparini, 1984; *Rukwasuchus yajabalijekunduis* Sertich & O'Connor, 2014; *Caririsuchus camposi* Kellner, 1987; *Roxochampsa paulistanus* (Roxo, 1936 comb. nov.); *Kinesuchus overoi* Filippi et al. 2018; *Colhuehuapisuchus lunai* Lamanna et al. 2019; *Bayomesasuchus hernandezi* Barrios et al. 2016; *Barrosasuchus neuquenianus* Coria et al. 2019; *Ogresuchus furatus* Sélles et al. 2020; and *Antaeusuchus taouzensis* Nicholl et al. 2021. Finally, two taxa from the data matrix of Ruiz et al. (2021), *Labidiosuchus amicum* Kellner et al. 2011 and *Lavocatchampsa sigogneaurusselae* Martin & De Broin 2016, were excluded from the phylogenetic analysis due to their fragmentary nature and tendency to destabilize the analysis (Ruiz et al., 2021).

We also expanded the character sampling for anatomical phylogenetic relevant traits in peirosaurids with the addition of 13 characters (see Appendix S1) proposed or modified by newly published papers of Geroto and Bertini (2018) and Pinheiro et al. (2018). In addition, two characters already in the character list were rewritten (333 and 354), and four were created to add new character states (521–524, see Appendix S1).

The final matrix has 110 taxa and 524 characters. For phylogenetic analysis, the search for the most parsimonious trees was conducted in the software TNT v. 1.5 (Goloboff & Catalano, 2016) with a heuristic search with random seed set as "0," 10,000 replicates of Wagner Tree, TBR (Tree bisection and reconnection) as the rearrangement algorithm, and saving 20 cladograms per round. After each repetition, the MPTs were collapsed, and the most parsimonious trees were summarized in a strict consensus tree.

2.3 | Morphological disparity analysis

To provide a quantitative examination of the morphological disparity displayed by peirosaurids and other crocodyliforms, we used the ordination method non-metric multidimensional scaling (nMDS; Kruskal, 1964) to create a morphospace based on the morphological data matrix used for the phylogenetic analysis. Despite other options available (such as principal component analysis [PCA] or principal coordinate analysis [PCoA]), the nMDS multivariate ordination method was selected both because of the robustness of this method (Minchin, 1987) and also for visualization purposes, given that the individual axes of the PCA or PCoA analyses might explain only a small amount of the total morphological variation, which makes the visual assessment of the morphospace potentially misleading (Gómez & Pérez-Ben, 2019). As the taxon-character matrix used for this analysis, we used the same 524 characters, but a reduced number of taxa (i.e., 80 taxa), to maximize the comparison between the morphospace occupation of the groups of interest (i.e., notosuchians and neosuchians). We used the R (version 4.2.2; R Core Team, 2022) package *Claddis* (version 0.6.3; Lloyd, 2016) to create a distance matrix from the taxon-character matrix using the "Maximum Observable Rescaled Distance" (or "MORD"; Lloyd, 2016). Subsequently, we used function *metaMDS ()* from the R package *vegan* (version 2.6.4; Oksanen et al., 2022) to perform the nMDS, with "wascores" and "autotransform" arguments set to "FALSE," but keeping the remaining default parameters. Finally, we used Analysis of Similarities (Warton et al., 2012), from the *vegan* function *anosim()*, to statistically test if the morphospace occupation of distinct taxonomic groups are significantly different. For that, the euclidean distance of the nMDS scores of each species was used for pairwise comparisons between taxonomic groups, using 1000 permutations.

2.4 | Institutional abbreviations

CPPLIP, Centro de Pesquisas Paleontológicas L. I. Price, Uberaba, Brazil; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MN, Museu Nacional, Rio de Janeiro, Brazil; MNN, Musée National du Niger, Niamey, Niger; MPMA, Museu de Paleontologia "Professor Antonio Celso de Arruda Campos," Monte Alto, Brazil; RM, Redpath Museum; ROM, Royal Ontario Museum, Toronto, Canada.

3 | RESULTS

3.1 | Systematic paleontology

CROCODYLIFORMES Hay, 1930 sensu Clark, 1986
MESOEUCROCODYLIA Whetstone & Whybrow, 1983
NOTOSUCHIA Gasparini, 1971 sensu Ruiz et al. 2021
SEBECIA Larsson & Sues 2007
PEIROSAURIDAE Gasparini, 1982
PEPESUCHINAE Geroto & Bertini, 2018
EPOIDESUCHUS TAVARESAE gen. et sp. nov.

3.1.1 | Etymology

Epoidesuchus, in which "epōidé" (ancient Greek), meaning enchantment, in reference to the city of Catanduva where it was collected, which is known as "Magic Spell City", and "souchus" (ancient Greek), in reference to crocodile-headed god of ancient Egypt. The specific name, *tavaresae*, honor Sandra Simionato Tavares, paleontologist and director of the Museu de Paleontologia "Professor Antonio Celso de Arruda Campos."

3.1.2 | Holotype

MPMA 68-0001/11 includes a fragmentary skull and one postcranial element. Cranial elements include cranial roof, interorbital region, and fragments of the posterior portion of the rostrum, including prefrontal and lacrimal (Figure 2); mandibular elements include left hemimandible with 14 alveoli and 12 teeth (Figure 3); postcranial elements restricted to one isolated cervical rib fragment (Figure S1).

3.1.3 | Stratigraphic horizon

Adamantina Formation, Bauru Group, Bauru Basin. Late Cretaceous (Campanian to Maastrichtian, Castro et al., 2018).

3.1.4 | Type locality

Outcrop on the side of the SP highway 351, between km 16 and 17, municipality of Catanduva, Northwestern São Paulo state, Brazil (21°07′54.8″ S 49°00′58.8″ W; Figure 1).

3.1.5 | Diagnosis

The new taxon is a Peirosauridae with a long rostrum that differs from the other members of the clade due to a set of unique characters (autapomorphies in bold and marked with an asterisk): distance at the anterior margin of the orbit to posterior margin of the antorbital fossa longer than the height of the antorbital fossa at the posterior margin; lateral insertion of the postorbital over the jugal in the post-orbital bar*; supratemporal rims at the level of the cranial roof; squamosal post-lateral process without ornamentation* and projected upwards*; posteroventral edge of the quadratojugal does not reach the quadrate condyles*; distal edges of the quadrate with only one plane facing posteriorly*; quadratojugal dorsal extent in medial surface ending at the same level the dorsal tip of laterotemporal fenestrae*; horizontal orientation of the paraoccipital process in occipital view*; elongated mandibular symphysis; dentary not compressed, presenting a convex lateroventral surface anterior to the mandibular fenestra; dentary with lateral concavity for reception of enlarged maxillary tooth; 14 teeth per hemimandible; 7th and 8th teeth of the dentary apart from each other and closer to 6th and 9th, respectively; teeth with smooth carinae*.

3.2 | Description

3.2.1 | General comments

The holotype MPMA 68-0001/11 is composed of a partial cranium sectioned in three fragments (one being the cranial roof and the two others encompassing the posterior part of the rostrum; Figure 2), the left hemimandible in a single fragment (Figure 3), and one isolated cervical rib. The outer surface of the preserved fragments is well-preserved, allowing visualization of most sutures and deep ornamentations, particularly distinct on the rostral bones and in the dorsal surface of the cranial roof. However, MPMA 68-0001/11 shows taphonomic deformations, slightly distorting the longitudinal axis, especially in the hemimandible.

The posterior portion of the rostrum is preserved in two fragments, one of which includes most of the bones on the left lateral posteriorly to limits of the nasal and
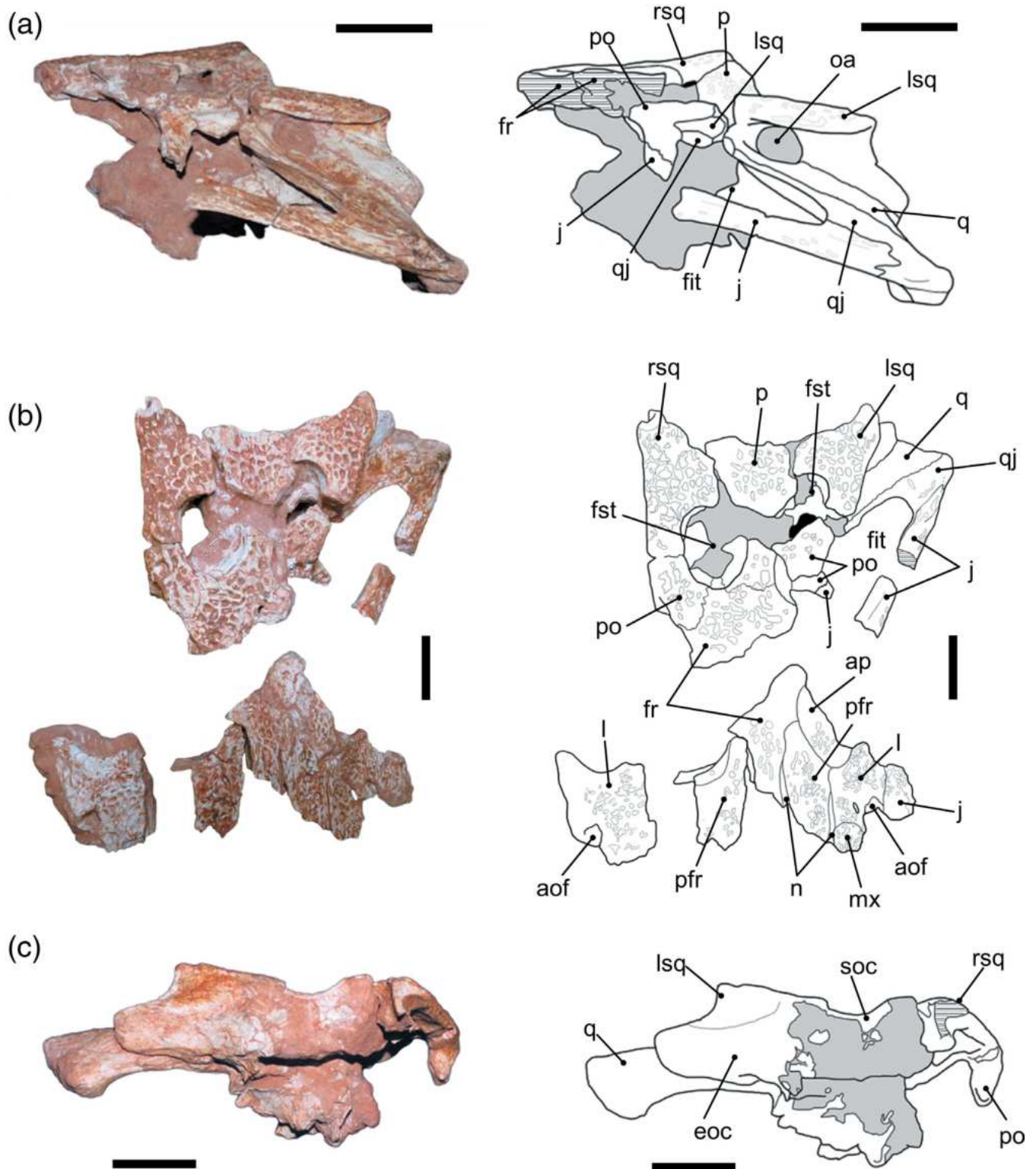
FIGURE 2 Cranial fragments of *Epoidesuchus tavaresae* gen. et sp. nov. MPMA 68-0001/11, holotype; interpretative drawings at right. (a) Left lateral view of the main cranial fragment; (b) dorsal view of the three cranial fragments; and (c) occipital view of the main cranial fragment. The gray and hatched areas indicate the presence of rock matrix and broken surfaces, respectively. aof, antorbital fenestra; ap, anterior palpebral; eoc, exoccipital; fit, infratemporal fenestra; fr, frontal; fst, supratemporal fenestra; j, jugal; l, lacrimal; lsq, left squamosal; mx, maxilla; n, nasal; oa, otic aperture; p, parietal; pfr, prefrontal; po, postorbital; q, quadrate; qj, quadratojugal; rsq, right squamosal; soc, supraoccipital. Scale bars equal to 5 cm.
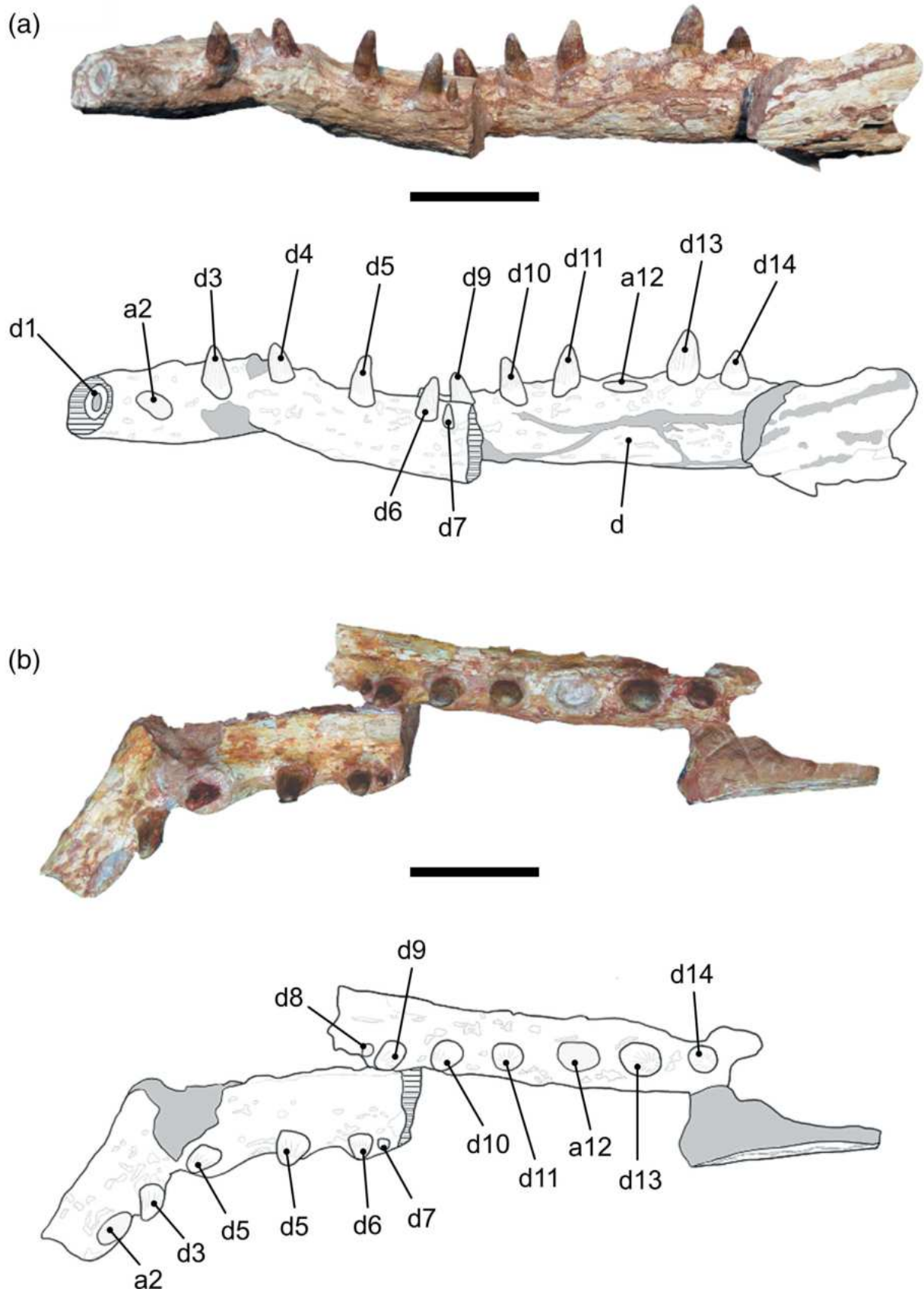
FIGURE 3 Left hemimandible of *Epoidesuchus tavaresae* gen. et sp. nov. MPMA 68-0001/11, holotype; interpretative drawings at right. (a) Left lateral view and (b) oclusal view of hemimandible. a2–12, alveoli; d, dentary; d1–14; dentary teeth. Scale bars equal to 5 cm.

maxilla, also including part of the lacrimal, jugal, anterior palpebral, and frontal; the anterior margin of the orbits is marked by incomplete pieces of the lacrimal and prefrontal, but their lateroventral limits have been lost. The second rostrum fragment is restricted to the right lacrimal. The cranial roof is the most complete known fragment of *E. tavaresae* and is mostly preserved in its dorsal, left lateral, posterior part of the right lateral, and posterior view; the bones preserved include the frontal, postorbital, parietal, squamosal, quadrate, quadratojugal, posterior portion of the jugal, supraoccipital, and exoccipital. The ventral part of the skull including the neurocranium is heavily fragmented and covered by a rocky matrix. In the occipital view, the supraoccipital and exoccipital are present with poorly preserved limits.

The left hemimandible of *E. tavaresae* comprises most of the dentary, which extends from the distal end to almost the margins of the external mandibular fenestra and the contact with the surangular. The size and shape of the dentary indicate a long rostrum. Among the 14 preserved alveoli, only teeth D2 and D12 are absent. The splenial is covered by a rocky matrix.

3.2.2 | Nasal

Only the posterior part of the left nasal is preserved in MPMA 68-0001/11, limited to two wedge-shaped and very thin processes. Both processes present smooth sculptures, ornamented with pits and grooves. The dorsal process is located between the ventral limit of the frontal and the dorsal limit of the prefrontal; the ventral process is located between the ventral limit of the prefrontal and the dorsal limit of the maxilla and lacrimal (Figure 2). A similar nasal shape (i.e., with two posteriorly extending wedge-shaped processes separating anteriorly frontal-prefrontal and prefrontal-lacrimal) is observed in other peirosaurids, such as *Pepesuchus*, *Caririsuchus*, and *Barreirosuchus* but also in *Cricosaurus araucanensis*, *Cr. suevicus*, *Cr. vignaudi*, and *Metriorhynchus casamiquela*, longirostrine thalattosuchians of aquatic habits.

3.2.3 | Lacrimal

The lacrimal extends from a notched suture with the nasal and maxilla, anteriorly, to the anterior margin of the orbit and the contact with the prefrontal, posteriorly. It also has a short and straight lateral extension, forming the posterior border of the elliptical fossa of the preserved antorbital fenestra, and contacting the anterior ramus of the jugal. The lacrimal presents a slight lateral concavity

next to the suture with the jugal, and its surface bears heaving ornamentation. Both left and right lacrimals are incomplete and it is not possible to trace their most anterior limits and, therefore, its total length. As in other longirostrine peirosaurids, the antorbital fenestra of *E. tavaresae* is low and elongated, and the distance between its posterior margin and the anterior portion of the orbit is longer than in most peirosaurids, similar to *Stolokrosuchus* and *Hamadasuchus* (Figure 4).

3.2.4 | Prefrontal

The prefrontal is preserved in both lateral surfaces of the rostrum. It is an anteroposteriorly elongated bone placed between the frontal and lacrimal, being separated by the posterior processes of the nasal on its anterior preserved half (see above, Figure 4). The relation between the anterior region of the prefrontals and the frontals cannot be accessed due to the incompleteness of the frontal; however, taxa that have this region preserved, as *Pepesuchus*, *Rukwasuchus*, *Caririsuchus*, and *Barreirosuchus*, present the anterior limit of the prefrontals at the same level to the boundary of the frontal; presumably, *Epoidesuchus* also possessed a similar condition. Posteriorly, the prefrontal has a process that contacts the frontal dorsally, anterior to the orbit. This process has a dorsal concavity for the reception of the anterior palpebral.

3.2.5 | Palpebral

Only the left anterior palpebral is preserved in MPMA 68-0001/11. It is composed of a robust element with a slightly convex and heavily ornamented dorsal surface. The elliptical anterior palpebral is anterolaterally inclined in relation to the dorsal surface of the skull and has an articulation with the posterior projections of the prefrontal and lacrimal, fitting on a notch present on the posterior edge of these structures. Its posteromedial portion also fits into a small lateral facet of the frontal. This anchoring surface for the palpebral is convex in both the frontal and prefrontal.

3.2.6 | Frontal

The frontal is fully fused at midline and presents a heavily marked ornamentation (Figure 2). In the dorsal view, the frontal is laterally limited by the prefrontals and nasals anterior to the orbits. Although not preserved in MPMA 68-0001/11, its most anterior edge would likely
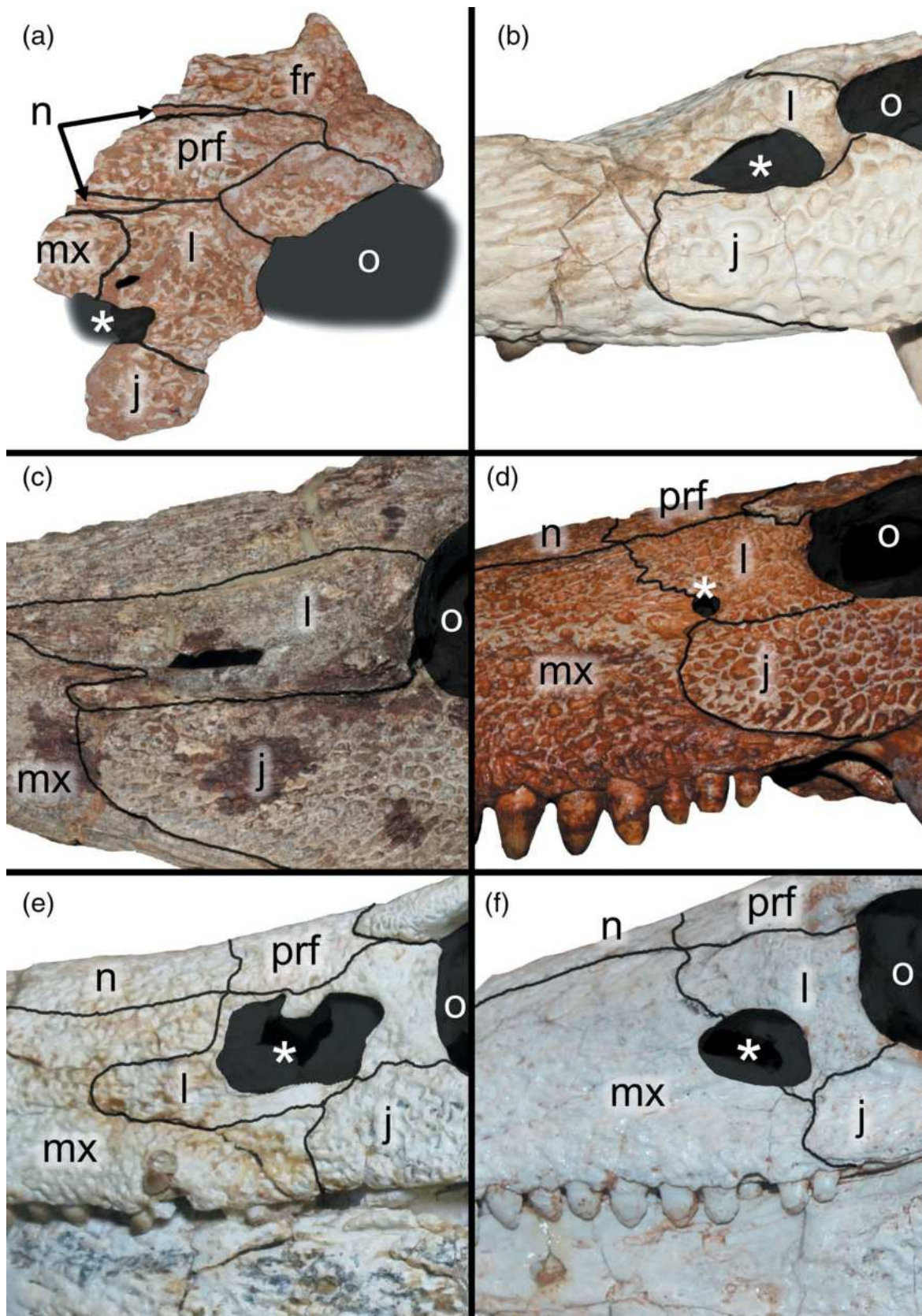
FIGURE 4 Antorbital region of peirosaurids. (a) *Epoidesuchus tavaresae* MPMA 68-0001/11; (b) *Pepesuchus deiseae* MN 7005-V (mirrored); (c) *Stolokrosuchus lapparenti* MNN GDF600; (d) *Hamadasuchus rebouli* ROM 52620; (e) *Uberabasuchus terrificus* CPPLIP-630; and (f) *Montealtosuchus arrudacamposi* MPMA-16-0007/04. fr, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; o, orbit; prf, prefrontal. The asterisk marks the position of the antorbital fenestra. Not to scale.

form the wedge-shaped process between the nasals due to the similarity of the configuration of the frontals, nasals, and prefrontals seem in the better preserved *Pepesuchus* and *Barreirosuchus*. On its posterior portion, the frontal extends to the contact with the postorbitals laterally and the anterior parietal medially, contributing only to a minor part of the anterior margin of the upper temporal fenestra. Between the orbits, the frontal presents a lateral convex notch for insertion of the anterior palpebral (see above). As in other peirosaurids, the orbital margins of the frontal are moderately elevated, and the dorsal surface of the bone is gently concave.

3.2.7 | Postorbital

The postorbitals are preserved on both sides of the cranium in MPMA 68-0001/11 and are formed by three processes that radiate from its central body, a dorsal process, a posterodorsal process, and a ventral process. The dorsal process contacts the frontal and separates the orbit from the supratemporal fenestra, contributing to the posteromedial and anterior margins of these openings, respectively (Figure 5). The posterodorsal process meets the squamosal posteriorly on the dorsal surface of the cranial roof, making up the lateral margin of the supratemporal fenestra. In dorsal view, these two processes form a surface ornamented with pits and grooves located at the anterolateral corner of the cranial roof (Figure 2).

The descending process of the postorbital is directed lateroventrally, being concave in its most dorsal limit. It contacts the ascending process of the jugal, forming the dorsal portion of the postorbital bar. In this contact, the postorbital is positioned laterally to the jugal, unlike all other peirosaurids. In contrast to the other postorbital processes, the ventral process is unsculpted, with a vascular opening on the dorsal surface of the postorbital bar positioned posterolaterally (in lateral view). Although this vascular opening can also be found in other crocodyliforms, as some Neosuchia, *Araripesuchus*, and other peirosaurids (*Pepesuchus*, *Rukwasuchus*, *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus*), the posterolateral position of this foramen is shared only by the platyrostral *Pepesuchus* and *Rukwasuchus*.

3.2.8 | Parietal

The parietal forms a single midline bone with a horizontally oriented dorsal surface ornamented with an irregular pattern of rounded, deep pits (Figure 2). Although preserved in most of its extension, including its anterior and posterior portions, the middle section of the parietal,

between the supratemporal fenestrae, where it originally formed the medial margin of these apertures, is missing and/or covered by the rock matrix in MPMA 68-0001/11. Even so, it is possible to identify the descending portion of the parietal forming a considerable part of the margins of the fossa of the supratemporal fenestrae.

At its most anterior limit, the parietal is wider and contact the frontal in a transversely oriented suture. In its posterior portion, the dorsal surface extends laterally, reaching the medial processes of the squamosal and forming the posteromedial margins of the supratemporal fenestrae. Posteriorly to the supratemporal fenestrae, the dorsal surface of the parietal is broad, markedly depressed at its center, and completely covers the supraoccipital (in dorsal view), a condition also shared with other pepesuchines of the Adamantina Formation, *Pepesuchus* and *Barreirosuchus*.

3.2.9 | Squamosal

In MPMA 68-0001/11, the squamosals are well-preserved. The dorsal surface is heavily ornamented and covers much of the posterolateral corner of the cranial roof, forming part of the posterior and lateral margins of the supratemporal fenestrae (Figure 2). The squamosal has three ventrally directed processes that form a triradiate structure: the anterior, medial, and posterior processes.

The anterior process of squamosal (hereafter APS) extends laterally in the dorsal view, margining the posterolateral half of the supratemporal fenestra. Anteriorly, the squamosal contacts the posterior process of the postorbital in a clear transverse suture. This squamosal-postorbital suture extends to the lateral edge of the cranial roof and have an anteroventrally inclination. The lateroventral surface of the APS extends ventrally toward the orbital margin, overlapping the postorbital laterally and reaching the level of the dorsal tip of the lateral temporal fenestrae. This extension forms a wedge-like suture overlapping the base of the postorbital bar. This feature is shared with other pepesuchines such as *Pepesuchus*, *Stolokrosuchus*, and *Rukwasuchus*. The APS has a large descending surface. Laterally, this surface covers most of the dorsal margins of the bony otic aperture and contacts the anterodorsal process of the quadrate.

The medial process of the squamosal is short and robust. This postorbital process extends medially, bordering the supratemporal fenestra posteriorly until it reaches the parietal in a posterolaterally inclined suture.

The posterior squamosal process in MPMA 68-0001/11 projects posteriorly and upwards and is unornamented in most of its posterior surface,
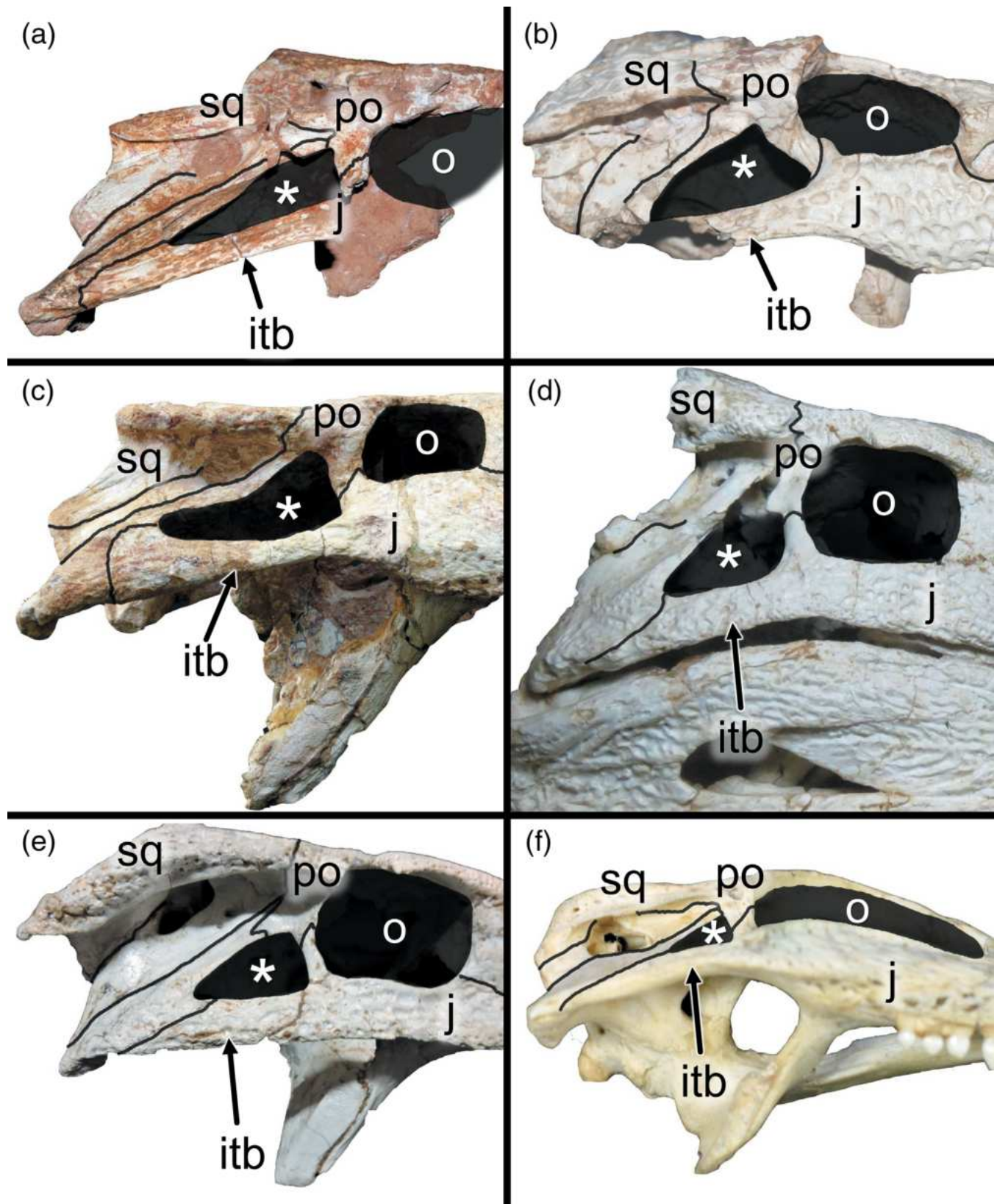
FIGURE 5　Lateral view of the cranial region of peirosaurids and alligatorid. (a) *Epoidesuchus tavaresae* MPMA 68-0001/11 (mirrored); (b) *Pepesuchus deiseae* MN 7005-V; (c) *Barreirosuchus franciscoi* MPMA 04-0012/00; (d) *Uberabasuchus terrificus* CPPLIP-630; (e) *Montealtosuchus arrudacamposi* MPMA-16-0007/04; and (f) *Alligator mississippiensis* RM 2790. itb, infratemporal bar; j, jugal; o, orbit; po, postorbital; sq, squamosal. The asterisk marks the position of the infratemporal fenestra. Not to scale.

presenting a notch on its posterior edge. The external surface of the occipital portion of the squamosal has a posterior inclination in pepesuchines (*Barreirosuchus*, *Caririsuchus*, and *Pepesuchus*), a different condition from peirosaurines (*Barrosasuchus*, *Bayomesasuchus*, *Hamadasuchus*, *Barrosasuchus*, *Lomasuchus*, *Montealtosuchus*, and *Uberabasuchus*) and Xenodontosuchia.

3.2.10 | Jugal

Only the left jugal is present, but it is incomplete (Figure 2). Although its complete limits are not preserved, it is possible to identify that its anterior process extends anteriorly to the orbits (Figure 4). The dorsal process of the jugal projects at the midpoint of the bone, contacting the postorbital dorsally and forming the ventral portion of the postorbital bar. Posteriorly, the jugal borders a large infratemporal fenestra lateroventrally, forming the infratemporal bar, and contacts the quadratojugal in an interdigitated suture. Unlike peirosaurines (*Barrosasuchus*, *Hamadasuchus*, *Lomasuchus*, *Montealtosuchus*, and *Uberabasuchus*), which presents a laterally flattened infratemporal bar, in MPMA 68-0001/11 this structure is rod-shaped, as in the other pepesuchines (*Barreirosuchus*, *Caririsuchus*, *Pepesuchus*, and *Stolokrosuchus*, Figure 5). The infratemporal bar surface has ornamentations composed of pits and grooves.

3.2.11 | Quadrate

As in all crocodyliforms, the quadrate is a complex bone that contacts other structures of the cranial roof and the neurocranium, presenting a main body, a dorsal, and pterygoid processes, and also an anterodorsal region subdivided in a dorsal head and anterodorsal process (Iordansky, 1973; Sertich & O'Connor, 2014). In MPMA 68-0001/11, it is not fully preserved and only the left quadrate is visible on its lateral and occipital surfaces. Due to the cranial taphonomic deformation of MPMA 68-0001/11, the quadrate is flattened in its longitudinal axis and extends more laterally than it would have originally been (Figure 6).

The anterior region of the quadrate extends dorsally, overlapping the quadratojugal at the level of the otic aperture (Figure 5). This structure is closed posteriorly by the quadrate and exoccipital and possesses a triangle-shaped outline, with the apex directed dorsally. In ventral view, the anterodorsal branch of the quadrate is well developed and forms more than half of the lateral border of the internal supratemporal fenestra. The medial-lateral surface of the quadrate is wide, ornamented with several longitudinally oriented straight striae of

muscular attachment, aligned to the broad suture with the quadratojugal placed above the lateral temporal fenestra.

Posteriorly, the articular facet of the quadrate extends posteriorly and lateroventrally, well beyond the lateral limit of the cranial roof, giving a more wide than tall aspect to the cranium in occipital view, a condition similar but even more accentuated to the pepesuchinae *Stolokrosuchus* (Figure 6). The distal articular surface is also displaced ventroposteriorly to the occipital condyle. The posterior surface of the mandibular condyle is faced posteriorly, perpendicularly to the cranium axis (Figure 7).

3.2.12 | Quadratojugal

As with the quadrate, only the left quadratojugal is preserved. It is mostly unsculpted, except for its lateroposterior portion (Figures 2 and 7). The anterodorsal branch of the quadratojugal is narrow, forming the entire posterior margin of the infratemporal fenestrae and contacts the quadrate in a long suture (Figure 5). In the anterodorsal portion of the infratemporal fenestrae, the quadratojugal is overlapped by the postorbital, excluding the quadrate and squamosal from the dorsal margin of the fenestra. The medial surface of this anterodorsal branch ends at the same level as the dorsal tip of the infratemporal fenestrae, a similar anatomy observed in some eunotosuchians (e.g., Sphagesauria). A short anteroventral process of the quadratojugal contacts medially the jugal, forming an interdigitated suture on the infratemporal bar and comprising the posterior margin of this aperture. The posteroventral portion of the quadratojugal follows the axis of the quadrate and gradually tapers posteriorly, not taking part in the mandibular articulation, as also seen in Mahajangasuchidae (Figure 7) and Xenodontosuchia.

3.2.13 | Supraoccipital and exoccipital

The occipital bones of MPMA 68-0001/11 are mostly visible on the left side, being covered by the rock matrix on its central portion and lost on its right side (Figures 2 and 6). The supraoccipital is preserved only on its dorsal limits and exposed on the occipital surface of the cranium, presenting a U-shape. It is obscured from the dorsal view by the parietal (see above). The exoccipital forms most of the occipital surface of the cranium, bearing a smooth surface with a slight concavity on the lateromedial axis. Dorsally, it presents a poorly marked suture contacting the supraoccipital, forming the descending surface of the posterior squamosal process. Its lateral process is posterolaterally projected, presenting a horizontal
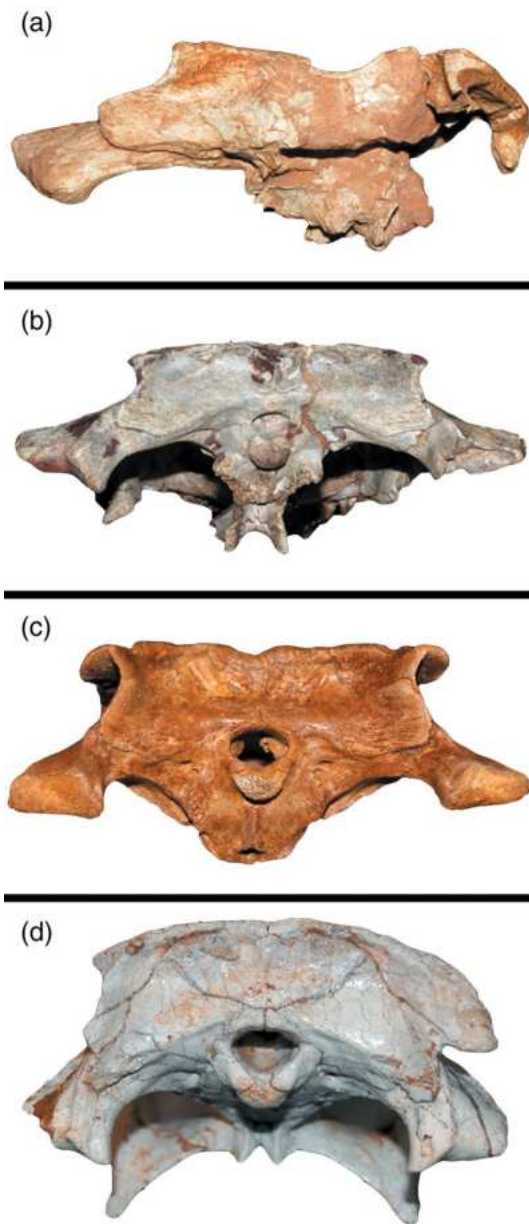
FIGURE 6 Occipital view of the cranium of peirosaurids. (a) *Epoidesuchus tavaresae* MPMA 68-0001/11; (b) *Stolokrosuchus lapparenti* MNN GDF600; (c) *Hamadasuchus rebouli* ROM 52059; and (d) *Montealtosuchus arrudacamposi* MPMA-16-0007/04. Not to scale.

orientation. The lateral limit of the paraoccipital process extends further laterally than the squamosal (Figures 2 and 6), a trait unique among peirosaurids.

3.2.14 | Dentary

Although sectioned in four parts, with abrupt breakages at the limits of d3-4, d7-8, and just posteriorly to d14
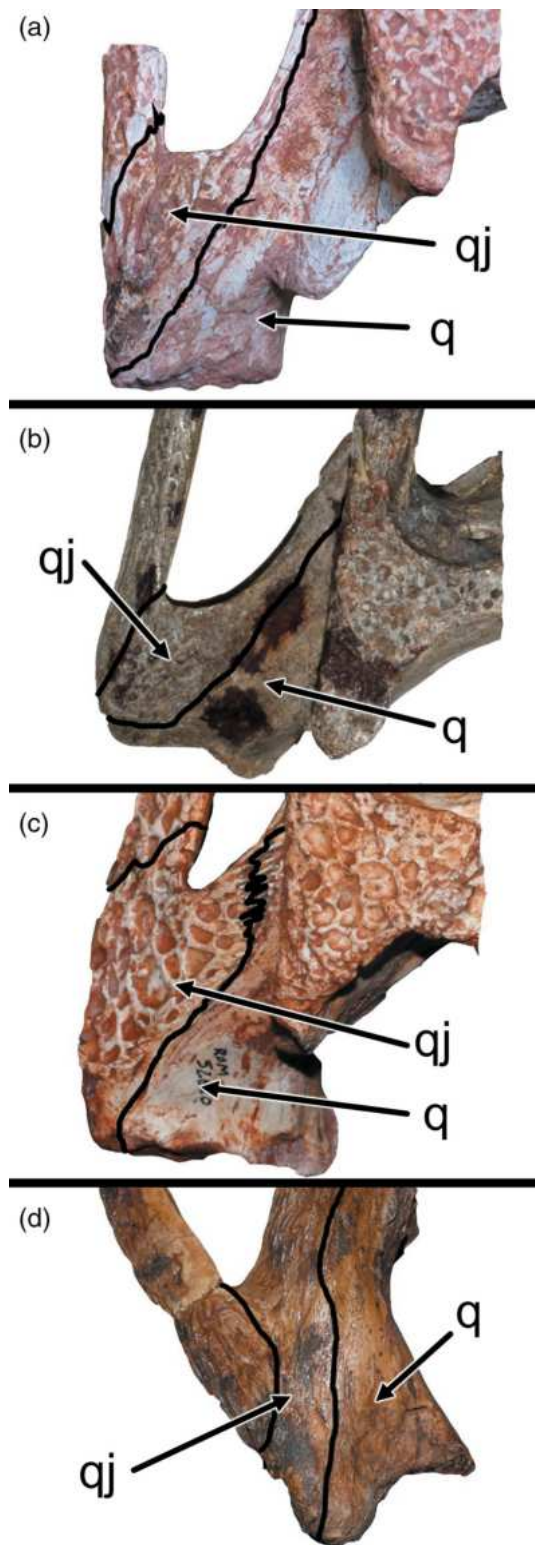

FIGURE 7 The mandibular articulation of quadrate in peirosaurids and mahajangasuchid. (a) *Epoidesuchus tavaresae* MPMA 68-0001/11; (b) *Stolokrosuchus lapparenti* MNN GDF600; (c) *Hamadasuchus rebouli* ROM 52620; and (d) *Kaprosuchus saharicus* MNN IGU12. q, quadrate; qj, quadratojugal. Not to scale.

(Figures 3 and 8), the left dentary is well preserved, missing only its posteriormost end near the putative contact with the surangular and angular. The position and extent of the symphysis are unclear as its medial surface and, presumably, the splenial are covered by a rocky matrix. Considering the proportions, the symphysis can be considered long, perhaps displaced along most of the preserved tooth row (Figure 8).

The dentary is elongated (35 cm preserved length), with almost the same height along its entire length, with a slightly gradual increase posteriorly in comparison to its anterior portion. The dentary is not lateromedially compressed, and the lateroventral surface anterior to mandibular fenestra is slightly convex.

Along the alveolar margin, the edge of the dentary is straight and subparallel to the longitudinal axis of the skull, without presenting an alveolar shelf, although there is a small concavity on the side of the dentary, close to d4, possibly for the insertion of a hypertrophied maxillary tooth (Figure 8). The dentary lateral and ventral surfaces are ornamented with striations and small pits, while the dorsal/alveolar surfaces are smooth. There are 14 alveoli preserved, 12 of it possessing teeth (see below). While the first alveolus is procumbent, the others are all positioned on the same sagittal axis as the dentary. This big and well-preserved bone indicates that MPMA 68-0001/11 is at least 50% larger than other peirosaurids from the Adamantina
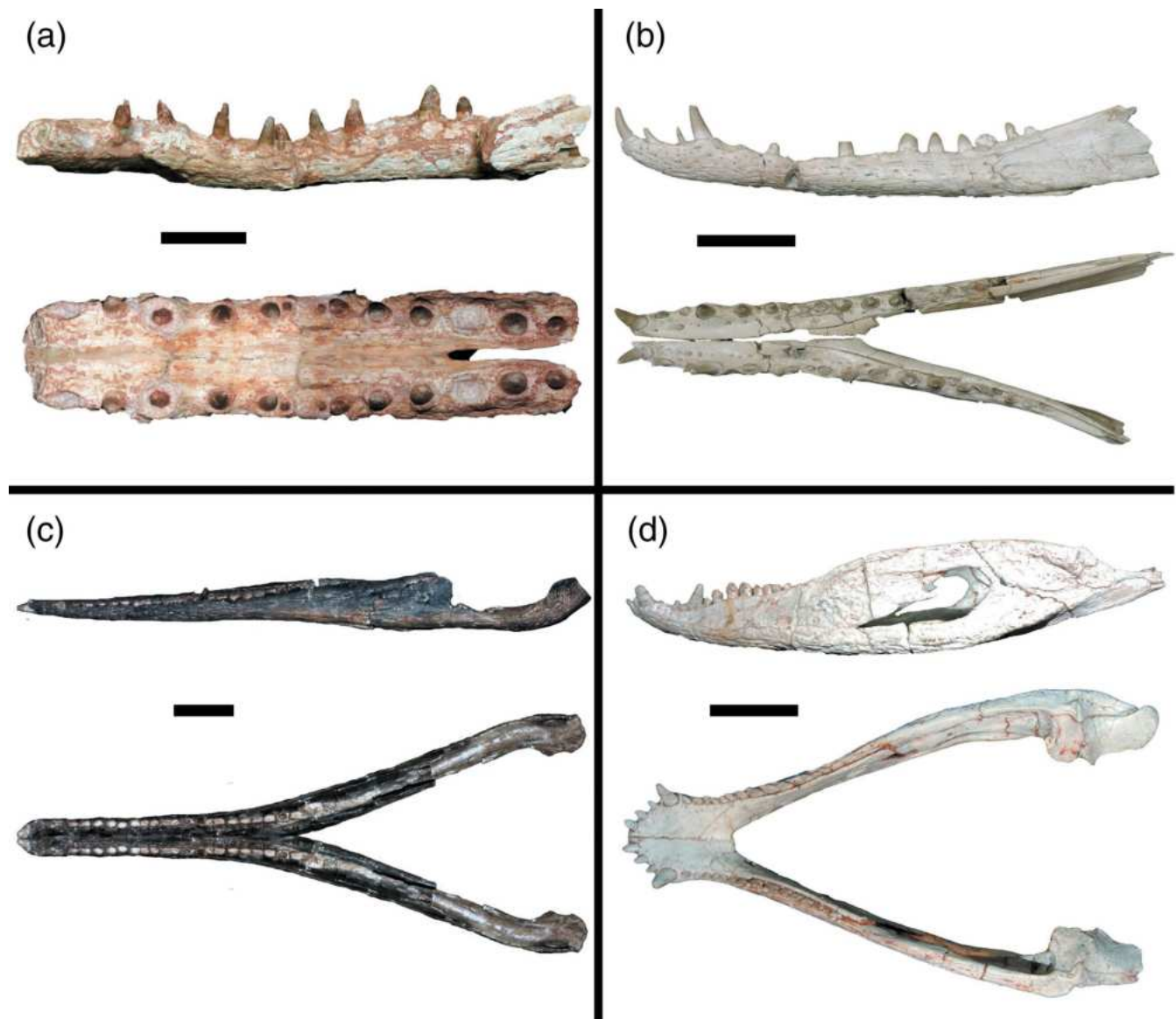

FIGURE 8 Lateral and dorsal views of the mandible of peirosaurids. (a) *Epoidesuchus tavaresae* MPMA 68-0001/11 (dorsal view reconstructed); (b) *Pepesuchus deiseae* MCT 1788-R; (c) *Stolokrosuchus lapparenti* MNN GDF600 (dorsal view reconstructed); and (d) *Montealtosuchus arrudacamposi* MPMA-16-0007/04. Scale bars equal to 5 cm.

Formation (*Itasuchus*, *Montealtosuchus*, *Pepesuchus*, and *Roxochampsa*).

3.2.15 | Dentition

Judging by the preserved dentary (see above), MPMA 68-0001/11 had 14 preserved teeth in each hemimandible, varying in size and diameter (see Table S1 for approximate width and length of the tooth alveoli and crown height). *Itasuchus* and *Pepesuchus* present 18 teeth per hemimandible, while *Roxochampsa* has at least 19 teeth and *Caririsuchus* has a minimum of 22 teeth (Pinheiro et al., 2018). The dentary alveoli are very separated from each other, probably to accommodate the opposing maxillary teeth during jaw occlusion. Although most alveoli are uniformly displaced through the mandible, the alveoli of d6-7 and d8-9 are very close to each other and separated by a diastema from d5 and d10, respectively (Figures 3 and 8). This unique condition is in paired with other pepesuchines from Adamantina Formation, *Pepesuchus*, *Itasuchus*, and *Roxochampsa*, and possibly with *Caririsuchus*.

The smallest tooth is d8, bearing a total crown height of approximately 0.8 cm, while the largest are d11 and d13, each with a crown height of 2 cm. The teeth have laterally compressed crowns arranged obliquely to the longitudinal axis of the skull. From the middle to posterior toothrow, the crowns have smooth grooved ornamentation on the enamel surface extending from its base to the apex. Differently from other peirosaurids, whose teeth are ziphodont or false-ziphodont, the teeth of MPMA 68-0001/11 have smooth carinae, similar to *Stolokrosuchus*.

3.3 | Phylogenetic relationships

The six most parsimonious trees (MPTs) of 2577 steps each were recovered. The new results (Figure 9) shed light on the phylogenetic relationships among the Gondwanan notosuchians, especially about the internal relationship within Peirosauridae. Here, we address the main clades recovered within Notosuchia, their internal relationships, and significant variance from previous works. We discuss four main aspects of our results: (A) the recovering of the clade Sebecia; (B) Peirosauridae comprising two lineages, Peirosaurinae and Pepesuchinae; (C); the nesting of *E. tavaresae* sp. et gen. nov. within Pepesuchinae; and (D) the recovering of *A. fernandezi* as a Sebecidae, *C. lunai* as a Mahajangasuchidae, and *O. furatus* as a Baurusuchia.

3.3.1 | Sebecia

Our phylogenetic results show Notosuchia under the "Sebecia hypothesis" (Larsson & Sues, 2007), with Sebecia comprising Mahajangasuchidae as the sister group of Peirosauridae + Sebecidae (Figure 9). It differs from the competing "Sebecosuchia hypothesis," in which Sebecidae and Baurusuchidae are nested together (Martinelli et al., 2018; Pol et al., 2014; Pol & Leardi, 2015). Additionally, our results show Baurusuchidae and Sphagesauria forming the clade Eunotosuchia together with forms such as *Araripesuchus*, similar to the topology recovered by Ruiz et al. (2021).

In the topology presented here, Sebecia contains *Doratodon* + (Mahajangasuchidae + (Peirosauridae + Sebecidae)). It is supported by three synapomorphies: the supratemporal rims are raised and hypertrophied (char. 96, st. 1); a complex dentary/surangular suture, with well-developed interlocking prongs from both surangular and dentary, three posterior prongs from dentary, and two from surangular (char. 318; st. 2); and an arched dorsal edge of the surangular (char. 338 st. 1).

The relationship of Mahajangasuchidae to other notosuchians is another major topic in mesoeucrocodylian phylogeny. This lineage was usually recovered as either closer to Sebecidae (Geroto & Bertini, 2018; Pinheiro et al., 2018) or to Peirosauridae (Bravo et al., 2021; Sertich & O'Connor, 2014) but here it appears as the sister clade of a clade formed by these two lineages. This is similar to results from previous studies that conducted phylogenetic analyses using a data matrix representing previous iterations of the one used here (Martins et al., 2024; Montefeltro et al., 2013; Ruiz et al., 2021). This relationship is supported by six unambiguous synapomorphies: the posterior extent of maxilla in the lateral surface of the rostrum is anterior to anterior margin of orbit (char. 141, st. 1); the absence of unsculpted region in the dentary below the tooth row (char. 316, st. 0); dentary with dorsal edge sinusoidal, with two concave waves (char. 317, st. 3); a dorsally robust splenial posterior to symphysis (char. 334, st. 1); dentary teeth opposite to premaxilla-maxilla contact with more than twice the length (char. 381, st. 1); and tooth row immediately posterior to caniniform (d4) characterized by d5-9 converging to the main axis of the symphysis and d10-12 diverging (char. 522, st. 1).

The composition of the clade Sebecidae + Peirosauridae refers to the initial proposition of the clade Sebecia by Larsson and Sues (2007); however, contrary to the first proposition of the clade, in our analysis, Sebecia is placed within Notosuchia and not as the sister group of Neosuchia. The clade Sebecidae + Peirosauridae is supported by six unambiguous synapomorphies: the presence of perinarial fossa
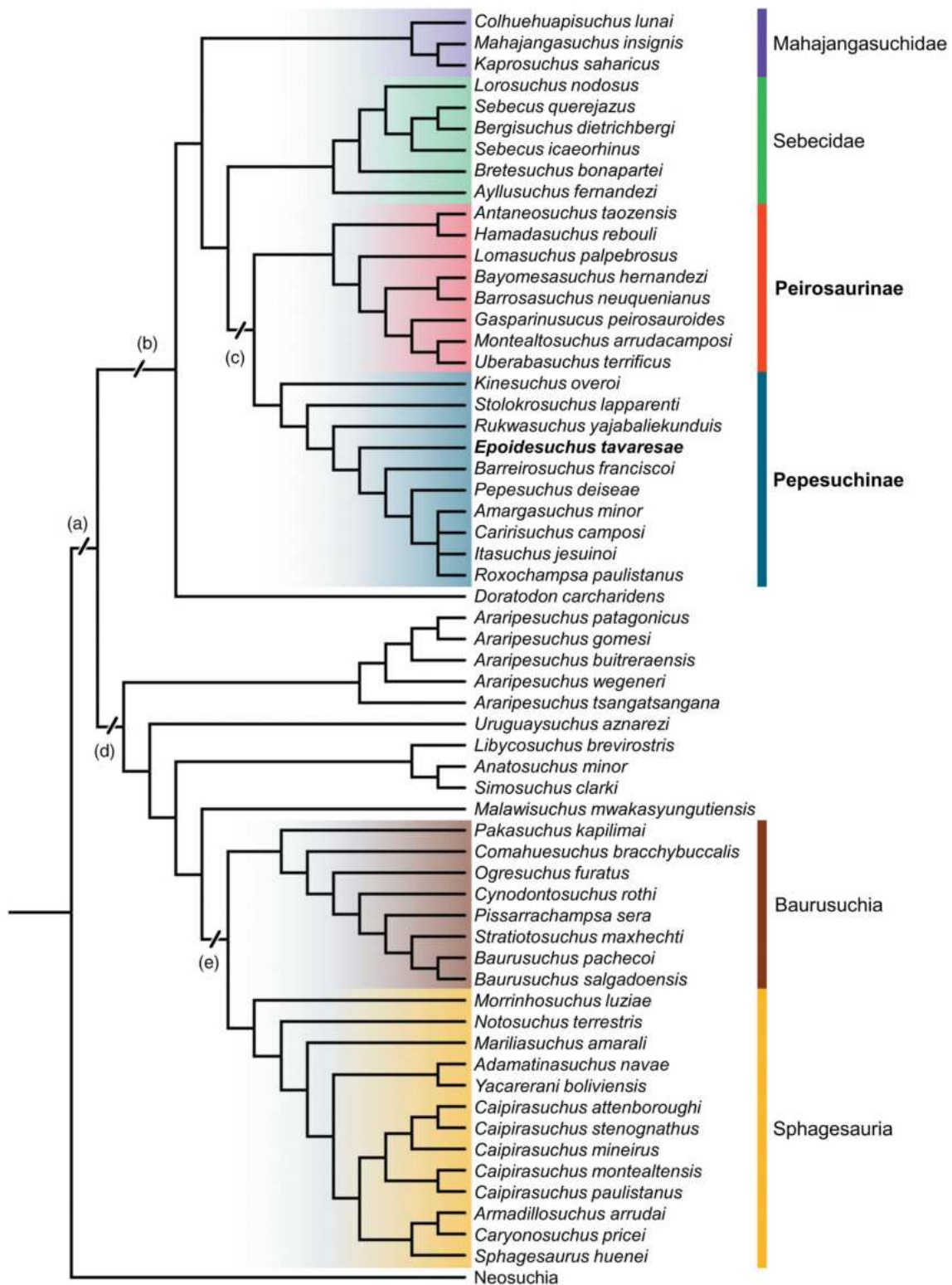
FIGURE 9 Reduced strict consensus tree depicting the phylogenetic relationship among Notosuchia. (a) Notosuchia; (b) Sebecia; (c) Peirosauridae; (d) Eunotosuchia; and (e) Xenotontosuchia.

(char. 127, st. 1); the jugal portion of the postorbital bar is anteriorly continuous, but posteriorly inset (char. 159, st. 0); posterior pterygoid processes well developed, projecting posteriorly (char. 248, st. 1); external mandibular fenestra slit-like, proportionally very long and with both ends acute (char. 306, st. 2); cheek teeth base constricted (char. 377, st. 1); many more neurovascullary foramen in the maxilla than teeth (char. 510, st. 1).

3.3.2 | The inner relationships of Peirosauridae

In our topology, Peirosauridae encompasses 18 species of Gondwana notosuchians forming the sister group of Sebecidae (Figure 9). Peirosauridae is supported by nine unambiguous synapomorphies: otic aperture closed posteriorly and triangle-shaped, with the apex directed dorsally (char. 30, st. 1); supratemporal rims not raised and hypertrophied (char. 96, st. 0); the concave lateral surface of postorbital descending flange (char. 175, st. 1); ectopterygoid abutted by the maxilla (char. 213, st. 0); anterior half of interfenestral bar between suborbital fenestrae flared anteriorly (char. 224, st. 1); dentary with lateral concavity for the reception of enlarged maxillary tooth (char. 312, st. 1); premaxillary teeth 1 and 2 nearly confluent (char. 368, st. 1); maxillary teeth occur in two waves (char. 371, st. 2); and the presence of robust otic butters (char. 487, st. 1).

Our phylogenetic analysis recovered the division of Peirosauridae in Peirosaurinae and Pepesuchinae. Peirosaurines are distinguished by an oreinirostral morphology associated with terrestrial and semi-aquatic habits (Geroto & Bertini, 2018; Pinheiro et al., 2018; Sertich & O'Connor, 2014). This clade received a phylogenetic definition first by Larsson and Sues (2007) and later by Geroto and Bertini (2018). Here, we recovered Peirosaurinae with eight taxa: *G. peirosauroides*, *H. rebouli*, *L. palpebrosus*, *M. arrudacamposi*, *U. terrificus*, *B. hernandezi*, *B. neuquenianus*, and *A. taouzensis* (Figure 9).

Peirosaurinae is supported by 11 synapomorphies: the presence of foramen in perinarial depression (char. 41 st. 1); opened contact on ventral edge of premaxilla–maxilla contact as a large notch encompassing at least partially the opposite dentary tooth (char. 45 st. 1); maxilla with wedge-like process in lateral surface of premaxilla–maxilla contact (char. 135 st. 1); the presence of vascular opening in dorsal surface of postorbital bar (char. 172 st. 1); the presence of prominent depression on the palate near alveolar margin at the level of the 6th or 7th alveolus (char. 203 st. 1); the presence of posteroventral symphyseal depressions (char. 323, st. 1); splenial participating in the distalmost mandibular alveoli, supporting teeth (char. 327, st. 1); intermediary-shaped of splenial-dentary suture at symphysis on ventral surface (char. 333 st. 2); premaxilla with anteroposterior length long in relation to the rostrum (char. 509 st. 1); postorbital bar with a narrow structure (char. 516 st. 0); and external surface of the occipital portion of the squamosal with inclination posterodorsally (char. 517 st. 1).

The second clade of Peirosauridae, Pepesuchinae, includes taxa characterized by a long rostrum with nearly tubular or platyrostral shape, (hereafter longirostrine), presumably related to more aquatic habits in relation to the oreinirostrine forms (Geroto & Bertini, 2018; Pinheiro et al., 2018; Sertich & O'Connor, 2014). The clade comprises 10 species in our topology: *B. franciscoi*, *I. jesuinoi*, *P. deiseae*, *S. lapparenti*, *A. minor*, *R. yajabalijekunduis*, *C. camposi*, *R. paulistanus*, *K. overoi*, and *E. tavaresae* gen. et sp. nov. (Figure 9). It is supported by one unambiguous mandibular synapomorphy: the dentary is not compressed and its lateroventral surface anterior to mandibular fenestra is convex (char. 315, st. 1). This condition is also found in some Neosuchia with semi-aquatic habits, such as *Sarcosuchus imperator*, *Goniopholis simus*, *Susisuchus anatoceps*, and most living neosuchians.

3.3.3 | *E. tavaresae* gen. et sp. nov. within Pepesuchinae

All most parsimonious trees placed the specimen MPMA 68-0001/11 as the sister group of all other members of Pepesuchinae. The nesting of *Ep. tavaresae* with other longirostrine peirosaurids is supported by the presence of vascular opening in dorsal surface of postorbital bar (char. 172 st. 1); dorsal surface of parietal markedly depressed from skull roof (char. 100 st. 2); and caudal tip of nasals separated by anterior sagittal projection of frontals (char. 61 st. 1).

The specimen MPMA 68-0001/11 was assigned to a new genus and species *E. tavaresae* gen. et sp. nov. due to the presence of eight autapomorphies that distinguishes it from other peirosaurids; lateral insertion of the postorbital over the jugal in the post-orbital bar (char. 89, st. 2); squamosal post-lateral process without ornamentation (char. 118, st. 0) and projected upwards (char. 115, st. 2); posteroventral edge of the quadratojugal does not reach the quadrate condyles (char. 167, st. 0); distal edges of the quadrate with only one plane facing posteriorly (char. 196, st. 0); quadratojugal dorsal extent in medial surface ending at the same level the dorsal tip of laterotemporal fenestrae (char. 214, st. 1); horizontal orientation of the paraoccipital process in occipital view (char. 290, st. 0); and teeth with smooth carinae (char. 354, st. 4).

3.3.4 | *A. fernandezi* as a Sebecidae, *C. lunai* as a Mahajangasuchidae, and *O. furatus* as a Baurusuchia

In our topology, *A. fernandezi* is recovered within Sebecidae, contrary to Pinheiro et al. (2018), who recovered this taxon as the sister clade of *B. franciscoi*, a position closer to other longirostrine taxa. Our results are supported by six synapomorphies: rostrum with narrow oreinirostral

proportion (char. 8, st. 0); the absence of external antorbital fenestrae (char. 12, st. 1); rostrum narrower than width of premaxilla at the level of alveoli 4 or 5 (char. 35, st. 1); nasal elevated above dorsal surface of maxilla forming a sagittal bar (char. 53, st. 1); posterolateral region of nasal deflected ventrally, forming part of the lateral surface of the snout (char. 56, st. 1); and the presence of paired foramen located ant anterior region of palatal ventral surface, not homologous to maxillo-palatine fenestrae and palate canals (char. 479, st. 1).

Another novel arrangement regards *C. lunai*, originally identified as a Peirosauridae (Lamanna et al., 2019), recovered as a Mahajangasuchidae in our analysis. This newly proposed phylogenetic position is supported by three characters related to the mandibular symphysis and one related to the position of the first teeth of the dentary: dentary with anterior alveoli procumbent (char. 319 st. 1); dentary symphysis in ventral view U-shaped and smoothly curving anteriorly (char. 332 st. 1); splenial-dentary suture at symphysis on the ventral surface (char. 333 st. 1); and with a transversal orientation on occlusal view, with the angle between hemimandible and the main axis of the symphysis >70° (char. 521 st. 1).

The inclusion of *O. furatus* in our analysis retrieved divergent results from what was proposed in its original description. In Sellés et al. (2020), *Ogresuchus* is recovered as Sebecidae, while our phylogeny finds *Ogresuchus* nested with Baurusuchia, as seen in Martins et al. (2024), an analysis also based on a modified version of the dataset of Ruiz et al. (2021). The synapomorphies includes an opened contact between the premaxilla and maxilla on the ventral edge of the rostrum (char. 44, st. 1); nasals participating medially and laterally on the dorsal/posterior margin of the nares (char. 46, st. 2); and the absence of an unsculptured surface along alveolar margin on the lateral surface of maxilla (char. 139, st. 0).

3.4 | Morphospace occupation

The results of our morphological disparity analysis show a clear separation between the morphospace occupied by the notosuchian and neosuchians included in the dataset (Figure 10), highlighting the differences in morphology exhibited by both clades. The results also show a separation between the two Peirosauridae subgroups (Pepesuchinae and Peirosaurinae), providing further support to the phylogenetic analysis results, which recovered these two subgroups as separate clades. This visual assessment of the morphospace occupation is reinforced by the Analysis of Similarities, which indicates that the values exhibited by both
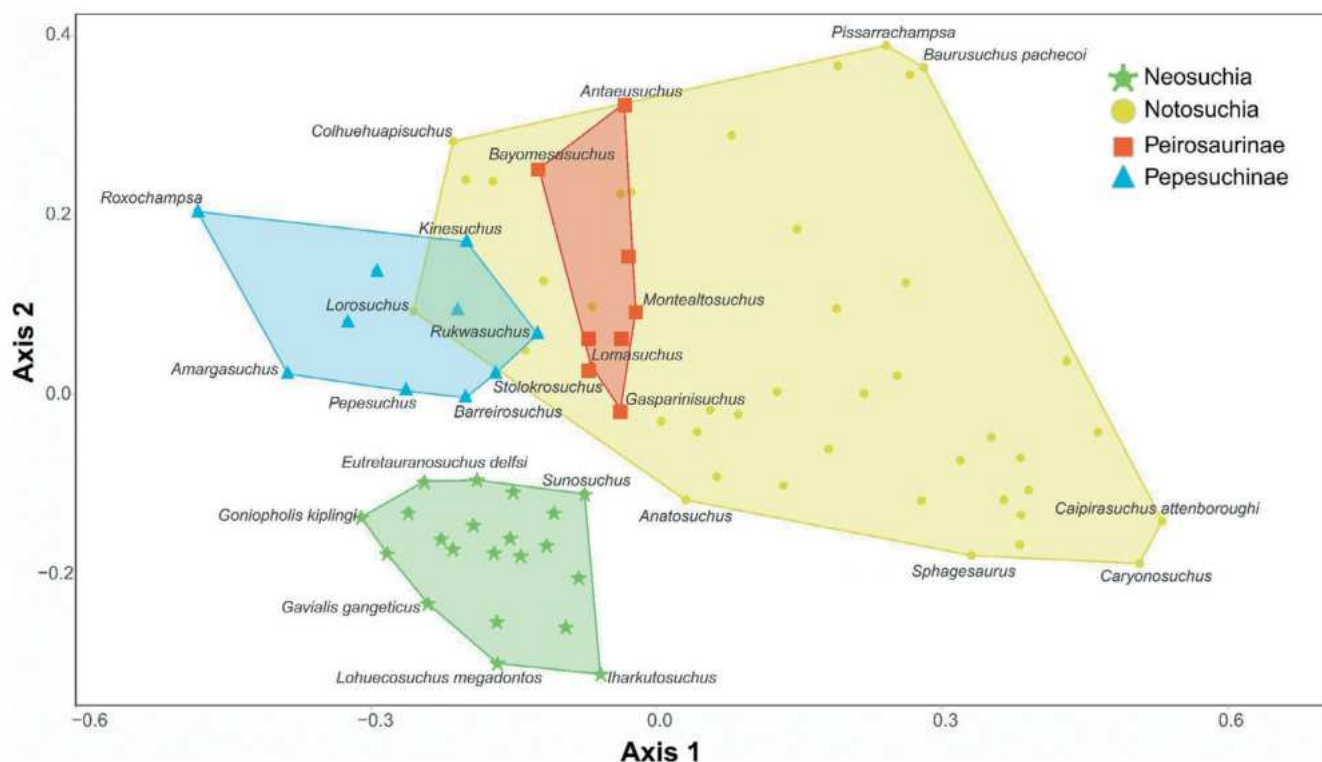

FIGURE 10 nMDS plot showing the morphospace occupied by different mesoeucrocodylian groups. The analysis was produced with the same discrete characters used for the phylogenetic analysis, but focusing on a subset of taxa (i.e., only notosuchians and neosuchians). The group "Notosuchia" (in yellow) includes all notosuchians except for peirosaurids (i.e., Pepesuchinae + Peirossaurinae).
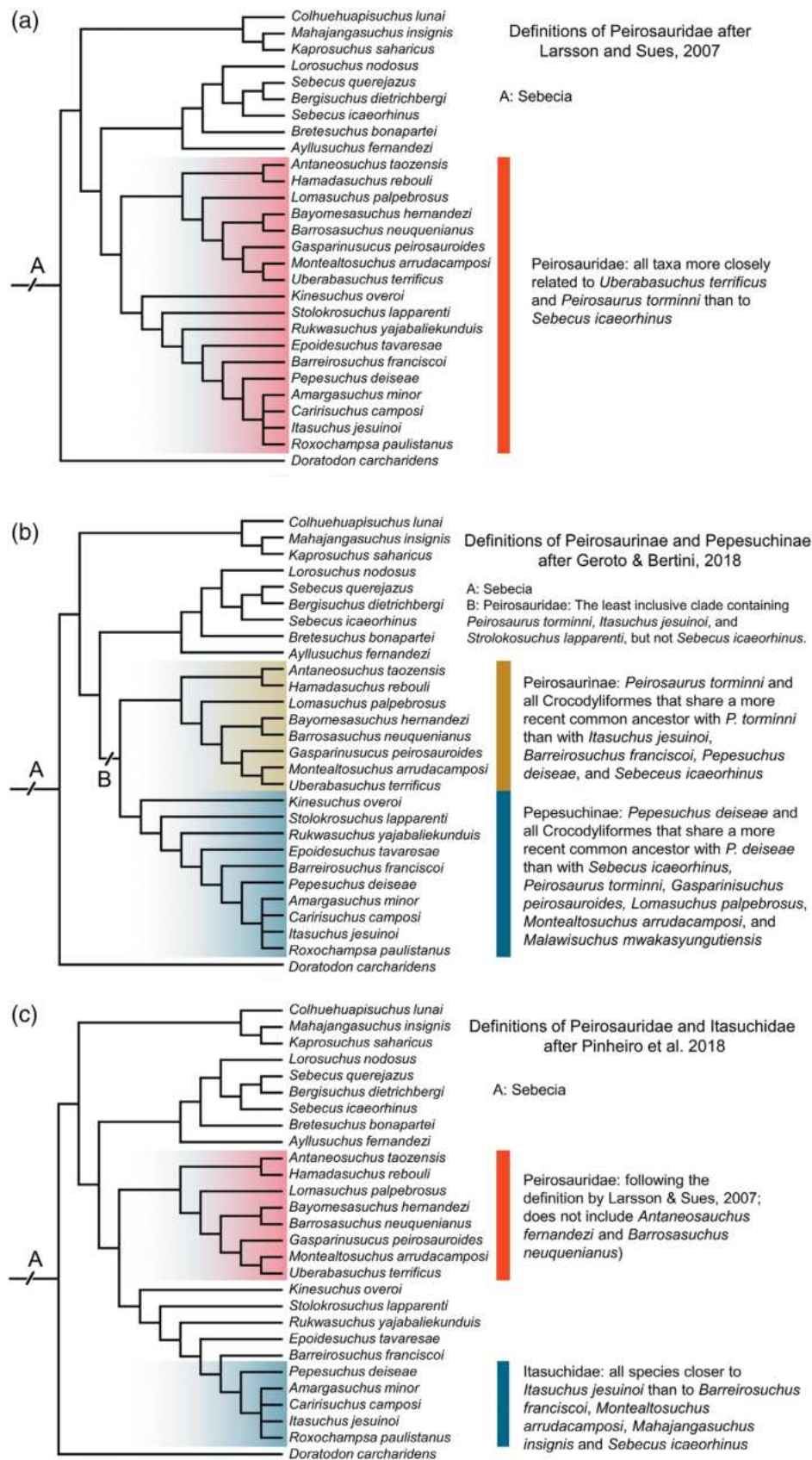
FIGURE 11 Clade definitions discussed in the text applied to the new phylogenetic hypothesis presented in this study. Each definition is related to the mentioned study. (a) Peirosauridae by Larsson and Sues (2007); (b) Peirosauridae, Peirosaurinae, and Pepesuchinae by Geroto and Bertini (2018); and (c) Peirosauridae and Itasuchidae by Pinheiro et al. (2018). Definitions included only Sebecia taxa and/or notosuchians species discussed in the text.

subgroups are significantly different ($p = 0.0002$). Perhaps even more interestingly, the results show that peirosaurines are not significantly separated ($p = 0.454$) from "other notosuchians" (excluding pepesuchines, shown in yellow in Figure 3), whereas the morphospace occupied by pepesuchines is significantly different from that of "notosuchians" ($p = 0.0001$).

4 | DISCUSSION

The clade Peirosauridae was originally erected as a family (in the context of Linnaean taxonomy) by Gasparini (1982) to encompass *P. torminni* specimens from Brazil and Argentina (the Argentinean specimen was later recognized as a distinct genus, *G. peirosauroides*, by Martinelli et al., 2012). A clade including *Peirosaurus* from Gasparini (1982) and other forms such as *L. palpebrosus* was also recovered in posterior studies (e.g., Gasparini et al., 1991), and it was firstly phylogenetically defined by Larsson and Sues (2007) as all the taxa more closely related to *P. torminni* and *U. terrificus* than to *Sebecus icaeorhinus*. Nevertheless, the affinities of Peirosauridae to other crocodyliforms remained uncertain. For instance, the topology of Larsson and Sues (2007) shows Peirosauridae more closely related to neosuchians than to notosuchians, similar to some previous hypotheses (e.g., Pol & Norell, 2004). Furthermore, in Larsson and Sues (2007), peirosaurids were found as the sister group of some traditional notosuchians such as *Sebecus* and *Bretesuchus* (e.g., Pol & Norell, 2004).

Differently from these works, Carvalho et al. (2004) advocated for Peirosauridae as a member of Notosuchia, and recovered it as the sister group of Itasuchidae, a clade defined by those authors, as the most inclusive clade containing *I. jesuinoi* and *Malawisuchus mwakasyungutiensis*. The notosuchian affinity of peirosaurids has also been recovered in most recent analyses (e.g., Pol et al., 2014; Ruiz et al., 2021). However, Itasuchidae, as originally proposed by Carvalho et al. (2004) found no support in subsequent analyses (e.g., Pol et al., 2014) and a redefinition of Itasuchidae was presented by Pinheiro et al. (2018).

Pinheiro et al. (2018) is one of two recent studies that revisited the systematics of Peirosauridae and Itasuchidae by conducting phylogenetic analyses including broad sampling of taxa with putative association to both groups in the past. Following the definition of Larsson and Sues (2007) for Peirosauridae, Pinheiro et al. (2018) recovered Peirosauridae as comprising only oreinirostrine taxa, and as the sister group of the clade Mahajangasuchidae + Sebecidae (clades' definitions on Figure 11). In their analysis, longirostrine taxa, putatively associated with Peirosauridae, were grouped within Itasuchidae, which was

recovered as the sister group of the clade Peirosauridae + (Mahajangasuchidae + Sebecidae) (clades' definitions on Figure 11). Additionally, *S. lapparenti*, *B. franciscoi*, and *A. fernandezi* were recovered as consecutive sister taxa of Itasuchidae.

Differently from Pinheiro et al. (2018), Geroto and Bertini (2018) recovered Peirosauridae comprising two main lineages, the oreinirostrine Peirosaurinae and the longirostrine Pepesuchinae (clades' definitions on Figure 11). Apart from these main lineages, they also recovered *A. minor*, *Miadanasuchus oblita*, and *S. lapparenti* as Peirosauridae and successive taxa to Peirosaurinae + Pepesuchinae.

Our results mostly agree with those presented by Geroto and Bertini (2018), with Peirosauridae comprising a taxonomically diverse clade composed of two main lineages, one comprising the oreinirostrine taxa (taxonomically equivalent to Peirosaurinae in Geroto & Bertini, 2018 and to Peirosauridae in Pinheiro et al., 2018) and another one encompassing the longirostrine taxa (equivalent to Pepesuchinae in Geroto & Bertini, 2018; Figure 11). Hence, our preference for here is to adopt the terminology of Geroto and Bertini (2018) in this study (Figure 9).

Historically, longirostrine peirosaurids were not considered in most phylogenetic analyses, perhaps reflecting the fragmentary nature of most specimens, the relative difficulty to access the materials, and its geographical distribution mostly confined to South America, especially Brazil. This low sampling of longirostrine taxa is likely one of the factors behind the discrepant results regarding the inclusivity of Peirosauridae and their affinity to other notosuchians. In analyses where Peirosauridae is not recovered within Sebecia (e.g., Larsson & Sues, 2007; Geroto & Bertini, 2018; Pinheiro et al., 2018; this study), but rather as more closely related to other taxa such as uruguaysuchids, as it is the case in Pol et al. (2014) and subsequent studies based on their dataset (e.g., Barrios et al., 2016; Coria et al., 2019; Martinelli et al., 2018; Nicholl et al., 2021), there is a low representativity of longirostrine taxa apart from *Stolokrosuchus*. This low sampling of longirostrine taxa might be one of the factors causing this result. For instance, the analysis by Pinheiro et al. (2018), which is also based on a modified version of the dataset of Pol et al. (2014) but considered a richer sampling of longirostrine taxa, found Peirosauridae within Sebecia. Thus, future works based on larger samplings of longirostrine notosuchians would potentially bring new perspectives to the phylogeny of this morphologically diverse group of crocodyliforms.

The recognition of longirostrine and oreinirostrine peirosaurids as different lineages is also expressed in our morphospace analysis (Figure 10). According to that, pepesuchines (in blue, Figure 10) and peirosaurines (in red,

Figure 10) are well decoupled in the morphospace, with peirosaurines displaced near or among other Sebecia (represented with other notosuchians in yellow, Figure 10). Although some forms (*Kinesuchus*, *Caririsuchus*, and *Rukwasuchus*) are within the variation of other notosuchians, most pepesuchines are far positioned on the negative side of the NDMS1, a position similar to that of the sampled Neosuchia (in green, Figure 10). This configuration indicates a peculiar morphological specialization of pepesuchines compared to other notosuchians.

One of the most striking characteristics of pepesuchines is the elongation of the rostrum. This is a unique feature among notosuchians and its relative similarity to the condition of most neosuchians permits assuming a similar ecology for both pepesuchines and neosuchians such as goniopholidids and crocodylians (Campos et al., 2011; Chiappe, 1988; Pinheiro et al., 2021). The elongation of the rostrum is widespread in crocodyliforms and associated to an aquatic lifestyle (Drumheller & Wilberg, 2020; McCurry et al., 2017; Morris et al., 2021). Some skull elements, such as the platyrostral to tubular rostrum, related to a longirostrine condition, and the dorsal position of nostrils and orbits, are directly tied to the habit of lurking in the water (Iordansky, 1973; Wilberg et al., 2019). However, pepesuchines in general present eyes more lateralized when compared to semi-aquatic crocodilians as *Alligator* (Figure 5), allowing the suggestion that, although semiaquatic, they were not so dependent on water bodies when compared to living crocodilians.

Semi-aquatic habits were assumed for other notosuchian lineages in addition to pepesuchines. That includes mahajangasuchids (Wilberg et al., 2019), from the Upper Cretaceous of Madagascar and Africa, and the sebecid *Lorosuchus* (Pol & Powell, 2011), from the Eocene of South America. Our morphospace analysis shows mahajangasuchids near terrestrial Sebecia; interestingly, *Lorosuchus*, known only for a complete skull, is the only notosuchian that overlaps with the morphospace of pepesuchines (Figure 10). This could suggest that the skull morphology underwent evolutionary pressures associated with semiaquatic habits in these two lineages, indicating a convergence between *Lorosuchus* and Cretaceous pepesuchines.

5 | CONCLUSIONS

We describe a new Peirosauridae from the Adamantina Formation, *E. tavaresae* gen. et. sp. nov. The new species reinforces the Bauru Group of Southeastern Brazil not only as the most important rock unit for notosuchian diversity anywhere in the world but also for members of the longirostrine peirosaurids. The description of this new specimen became even more relevant after the fire in the Museu Nacional, in Rio de Janeiro, Brazil in 2018. During this tragedy, the holotype and referred materials of one of the best preserved Brazilian pepesuchines, *P. deiseae*, were lost. In addition to this incident, there is also the disappearance of two specimens, including the almost complete holotype, of *C. camposi*, another Brazilian pepesuchine, which could help in the task of elucidating the internal relationships of this diverse group.

Our dataset, with the most inclusive sampling of Peirosauridae to date, represents a solid framework to test the different phylogenetic hypotheses for Peirosauridae presented in recent years. Our results provide additional evidence for the presence of Peirosauridae comprising two lineages, the oreinirostrine Peirosaurinae and the longirostrine Pepesuchinae. Additionally, the results of our morphospace analysis indicate that peirosaurids were ecomorphologically diverse, with taxa exhibiting either a more putative terrestrial ecology or more semi-aquatic habits, and with a great range of morphospace occupation, including spaces not explored by other notosuchians or neosuchians.

According to our results, Pepesuchinae was widespread in Africa and South America during the Cretaceous. This lineage is notable among notosuchians by possessing longer rostra, similar to generalist living crocodilians such *Crocodylus* and some caimans. Pepesuchines are recorded from formations where semiaquatic neosuchians are absent or rare. In Africa, *Stolokrosuchus* co-occurred with *Sarcosuchus* (Sereno & Larsson, 2009), while in the great pole of diversity of pepesuchines, the Bauru Group in Brazil, only one putative neosuchian was described to date (Fachini et al., 2022) and there is no other record of large, predatory tetrapods with semi-aquatic habits (Langer et al., 2022). In this scenario, we suggest that pepesuchines were occupying vacant freshwater systems of Western Gondwana during the Late Cretaceous.

AUTHOR CONTRIBUTIONS

Juan V. Ruiz: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; formal analysis; data curation; software; validation. **Marcos V. L. Queiroz:** Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; formal analysis; data curation; software; validation. **Kawan C. Martins:** Conceptualization; investigation; writing – review and editing; methodology; software; visualization. **Pedro L. Godoy:** Methodology; software; data curation; investigation; writing – review and editing; visualization. **Fabiano V. Iori:** Investigation; writing – review and editing;

CONFLICT OF INTEREST STATEMENT
The authors declare no competing interests.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.