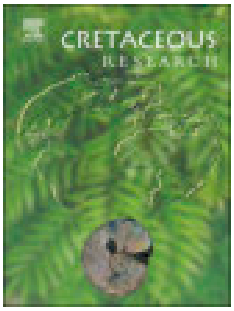

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A new Baurusuchidae (Notosuchia, Crocodyliformes) from the Adamantina Formation (Bauru Group, Upper Cretaceous), with a revised phylogenetic analysis of Baurusuchia

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ABSTRACT

Baurusuchidae is a group of notosuchian crocodyliforms ubiquitous to South American Upper Cretaceous deposits. They are distinguished by having dog-faced skulls, reduced tooth rows, and hypertrophied caniniforms. Here, we describe a new baurusuchid from the Adamantina Formation (Bauru Group), in Southeast Brazil. The new taxon consists of a right portion of the skull, cranial roof elements, fragments of the secondary palate and the lower jaw, as well as six isolated teeth. The specimen is assigned to the genus *Aphaurosuchus* due to the presence of a posterior depression on the nasal and upturned infraorbital jugal ridge. A new species, *Aphaurosuchus kaiju*, was erected based on characters that distinguish it from *Aph. escharafacies*, such as a large and deep depression occupying most of the dorsal surface of the frontal, a midline longitudinal depression on the anteriormost portion of the frontal, a well-developed crest concealed in the frontal depression, and a smooth parietal near the supratemporal fenestrae. We investigated the affinities of *Aphaurosuchus kaiju* and recently described/revised putative baurusuchians by performing an updated phylogenetic analysis that combined information from the three most up to date datasets available. We recovered the two main lineages of Baurusuchidae, Pissarrachampsinae and Baurusuchinae, with its traditional subset of taxa, but also recovered *Ogresuchus furatus* (Maastrichtian of Europe) and *Razanandrongobe sakalavae* (Batesian of Madagascar) as non-baurusuchid baurusuchians. In the light of our results, the inclusion of these two taxa in an otherwise well stablished Baurusuchia suggests that this clade had much broader spatial and temporal distributions than initially thought.

Keywords: *Aphaurosuchus. Baurusuchidae. Baurusuchia. Adamantina Formation. Bauru Basin.*

1. INTRODUCTION

Cretaceous deposits in Gondwana are distinguished by the great diversity of a peculiar group of fossil Crocodyliformes, the Notosuchia (e.g., *sensu* Ruiz et al., 2021; Turner & Sertich, 2010; Pol et al., 2014; Pol & Leardi, 2015). Notosuchians have a wide range of anatomical modifications, as specialized mandibles, heterodonty and degrees of tooth occlusion, and presumably dietary habits that can be compared to that of modern terrestrial mammals (e.g., O'Connor et al., 2010; Ösi, 2013; Melstrom & Irmis, 2019). Apart for a few putative notosuchians with a Laurasian distribution (Bunzel, 1871; Wu & Sues, 1996; Company et al. 2005; Sellés et al. 2020), members of this clade are found in most continental landmasses that once formed Gondwana, including continental Africa (Buffetaut, 1994; Gomani, 1997; Larsson & Sidor, 1999; Sereno et al., 2003; Sereno & Larsson, 2009; O'Connor et al., 2010; Pochat-Cottiloux et al., 2023), Madagascar (Buckley & Brochu, 1999; Buckely et al., 2000), and the Indian subcontinent (Wilson et al., 2001).

The greatest diversity of the group is, however, known from South American Cretaceous deposits (Bonaparte, 1991; Bronzati et al., 2015, Pol & Leardi, 2015; Langer et al., 2022), particularly the Bauru Basin, in southeastern Brazil. This yielded more than twenty species of various notosuchian lineages, such as Peirosauridae (Carvalho et al., 2007; Campos et al., 2011; Iori & Garcia, 2012) and Sphagesauria (Price, 1950; Pol, 2003; Nobre & Carvalho, 2006; Andrade & Bertini, 2008; Marinho & Carvalho, 2009; Iori & Carvalho, 2011; Martinelli et al., 2018; Pinheiro et al., 2021, Ruiz et al., 2021). Yet, Baurusuchidae (Price, 1945; Campos et al., 2001; Carvalho et al., 2005, 2011; Nascimento & Zaher, 2010; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021) is perhaps the most representative notosuchians of the Bauru Basin, particularly in the Adamantina Formation (Upper Cretaceous), which yielded eight out of the ten baurusuchid species found and described to date

(Price, 1945; Campos et al., 2001; Carvalho et al., 2005, 2011; Martinelli & Pais, 2008; Nascimento & Zaher, 2010; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021).

Baurusuchids are characterized by having short and deep rostra, reduced dental series with ziphodont teeth, hypertrophied caniniforms, and considerably large size (Price, 1945; Montefeltro et al., 2011, 2020). These characters suggest that this group represented one of the apex predators in its ecosystem (Montefeltro et al., 2011, 2020; Riff & Kellner, 2011; Godoy et al., 2016, 2018), which is supported by the direct evidence of predation on others Crocodyliformes (Godoy et al., 2014). Baurusuchids are known as early as the late XIX century (Woodward, 1896), but it was in the last 20 years that available data about the group has greatly increased, with the description of additional taxa and the investigation of its phylogeny, evolution, and paleobiology (Campos et al., 2001; Carvalho et al., 2005, 2011; Martinelli & Pais, 2008; Nascimento & Zaher, 2010; Montefeltro et al., 2011, 2020; Marinho et al., 2013; Godoy et al., 2014, 2016, 2018; Fonseca et al. 2020; Darlim et al., 2021).

Although the past decade witnesses an important increase in the knowledge about baurusuchids, just one phylogenetic matrix was published focusing on the group (Montefeltro et al., 2011, expanded in Godoy et al., 2014 and Darlim et al., 2021). However, even with a reduced number of phylogenetic analyses including a large number of baurusuchids, their results are not convergent, particularly regarding the monophyly and internal relations of its two putative main lineages: Pissarrachampsinae and Baurusuchinae (Montefeltro et al., 2011, *sensu* Darlim et al., 2021). The discrepancy among phylogenetic results is more evident if large-scale matrices are taken into account (Leardi et al., 2018; Pinheiro et al., 2018, 2021; Gerotto & Bertini, 2018; Martinelli et al., 2018; Ruiz et al., 2021).

The core problem with baurusuchid phylogeny is that the matrices focusing on its internal relations do not include other relevant notosuchians (Montefeltro et al. 2011; Godoy et al. 2014; Darlim et al. 2020). On the other hand, the analyses with a broader sample of Crocodyliformes includes comparatively few baurusuchids (Leardi et al., 2018; Pinheiro et al., 2018; Gerotto & Bertini, 2018; Martinelli et al., 2018) and a reduced number of characters that are important for defining its internal relations. Here, we describe the fragmentary skull (LPRP/USP 0634) of a new baurusuchid, collected in an outcrop of the Adamantina Formation, Bauru Group, in northwestern São Paulo state (Fig. 1), and review the systematics and taxonomy of all known baurusuchids, based on a broad notosuchian phylogeny.

2. MATERIAL AND METHODS

2.1. Collection and preparation

The specimen described here (LPRP/USP 0634) is housed at Laboratório de Paleontologia de Ribeirão Preto-USP (LPRP/USP), Ribeirão Preto, São Paulo State, Brazil. The field work that resulted in its collection was carried out in accordance with Agência Nacional de Mineração – ANM, as required by the Brazilian legislation (ordinance number 4.146 from March 4th, 1942). The fossil was mechanically prepared using pin vices and pneumatic tolls at LPRP/USP.

2.2. Phylogenetic analysis

The new specimen was included in the dataset of Ruiz et al. (2021), which encompasses a great diversity of mesoucrocodylians, including most notosuchian taxa, and a vast sample of cranial and postcranial characters. The matrix was expanded with the addition of nine taxa, including seven bauruschids - *Aplestosuchus sordidus* (Godoy et al., 2014), *Aphaurosuchus escharafacies* (Darlim et al., 2021), *Baurusuchus albertoi* (Nascimento & Zaher, 2010), *Campinasuchus dinizi* (Carvalho et al., 2011), *Gondwanasuchus scrabrosus* (Marinho et al., 2013), *Pabwehshi pakistanensis* (Wilson et al., 2001), and *Wargosuchus australis* (Martinelli & Pais, 2008) - as well as two taxa with putative close relations to baurusuchians - *Ogresuchus furatus* (Sellés et al., 2020) and *Razanandrongobe sakalavae* (Maganuco et al., 2006; Dal Sasso et al., 2017).

We also expanded the matrix with 14 extra characters (509-521, see the supplementary material for more information), three of which (515-517) are newly proposed, three (509, 510, 518) gathered from the dataset of Pol et al. (2014), four (511-514) from that of Geroto and Bertini (2018), and four (97, 519-521) from that of Darlim et al. (2021). The final data matrix is composed of 108 taxa and 521 characters and was analyzed using equally weighted parsimony in TNT 1.5 (Goloboff & Catalano, 2016), via a heuristic search (10,000 replicates). Tree Bisection Reconnection (TBR) was applied for branch swapping, saving 20 cladograms per round, and random seed was set as "0". The trees were collapsed after each replicate, and the Most Parsimonious Trees were summarized in strict consensus.

Institutional Abbreviations

CPPLIP: Centro de Pesquisas Paleontológicas L. I. Price, Universidade Federal do Triângulo Mineiro (UFTM), Uberaba, Brazil; **DGM**: Diretoria de Geologia e Recursos Minerais, Rio de Janeiro, Brazil; **DNPM**: Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; **LPRP-USP**: Laboratório de Paleontologia de Ribeirão Preto-USP, Ribeirão Preto, Brazil; **MOZ-PV**: Museo Profesor-Dr. Juan Augusto Olsacher, Zapala, Argentina; **MPMA**: Museu de Paleontologia de Monte Alto, Monte Alto, Brazil; **MZSP-PV**: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **UFRJ-DG**: Coleção de Paleontologia de Vertebrados da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

3. RESULTS

3.1. Systematic Palaeontology

Crocodyliformes Hay, 1930 (by subsequent designation of Clark, 1986)

Mesoeucrocodylia Whetstone & Whybrow, 1983

Notosuchia Gasparini, 1971 (by subsequent designation of Ruiz et al., 2021)

Baurusuchia Walker, 1968 (by subsequent designation of Darlim et al., 2021)

Baurusuchidae Price, 1945 (by subsequent designation of Darlim et al., 2021)

Aphaurosuchus Darlim et al., 2021

Diagnosis: Baurusuchidae that differs from other Crocodyliformes by the presence of a depression on the posterior portion of nasal which bears a distinct longitudinal ridge, of an upturned jugal infraorbital ridge (*sensu* Montefeltro et al., 2011), and the lack of foramina flanking the medial contact of the palatines (not observed in *Aphaurosuchus kaiju* sp. nov.).

Type-species: *Aphaurosuchus escharafacies*.

Aphaurosuchus kaiju sp. nov. (Fig. 2)

LSID: urn:lsid:zoobank.org:pub:9B27E004-77EC-424C-BC6D-65320E82DFB6

Derivation of the name: the specific name derives from the Japanese word *kaijū* (怪獣), which means “strange beast”, traditionally used in ancient Japanese legends to refer to monsters and now widely linked with pop-culture giant creatures, such as Godzilla, and associated Japanese media.

Holotype: LPRP/USP 0624, which includes parts of the right portion of the cranium anterior to the orbit, cranial roof elements, fragments of the snout, secondary palate, and lower jaw.

Type locality: Roadside outcrop at 9,6 km south of Jales, northwestern São Paulo State, Brazil (20º20'34"S 50º33'57"W).

Stratigraphic horizon: Adamantina Formation, Bauru Group, Bauru Basin (Fig. 1); Upper Cretaceous (ca. Coniacian-Campanian, Castro et al., 2018).

Diagnosis: Baurusuchidae that differs from other Crocodyliformes by the following unique set of traits (autapormorphies marked with asterisks): a longitudinal depression on the anterior portion of the frontal; frontal with a longitudinal depression deeper at its posterior portion*; a robust jugal infraorbital ridge with the same thickness along its preserved length*; a midline crest on the nasal; a depression on the nasal with a rugose surface; a smooth posterior portion of the parietal, without the hypertrophied border overhanging the supratemporal fenestrae*.

3.2. Description

3.2.1. Cranium

The holotype cranium consists of three main fragments: the right side region, anterior to the orbit (including disarticulated fragments of the maxilla, the anteriormost portion of the jugal, complete posterior palpebral, and parts of the lacrimal and anterior palpebral, forming part of the orbit; Fig. 3A-D); the skull roof (including an almost complete frontal, fragments of the prefrontal, right lacrimal, postorbital, and the anterior and posterior portions of the parietal, forming part of the right supratemporal fenestra; Fig. 3E-F); and a fragment of the dorsal region of the snout (including most of the nasals, parts of both maxillae, and anteriormost portions of the palpebrals and prefrontals; Fig. 3G-H). In dorsal view, the preserved portions of the specimen suggest a general skull shape similar to that of other baurusuchids, with a long and straight maxilla and large, laterally expanding palpebrals (Fig. 3C-D). The external surfaces of most preserved dermal bones are ornamented with ridges and irregular pits. These ornamentations are more evident on the posterior portion of the nasal and the anterior portions of the jugal and frontal.

Only the anteroventral portion of the right **orbit** is preserved (Fig. 3A-D). It is delimited by the anterior and posterior palpebrals dorsally, and by the lacrimal and jugal both anteriorly and ventrally. The preserved portion of the orbit is anterolaterally oriented, with the ventral border laterally displaced in relation to the dorsal. Due to the fragmentation of the specimen, it is not possible to assess the exact shape for the orbit, but its preserved portion suggests that it is like that of other baurusuchids, with an oval to circular shape.

The right **supratemporal fenestra** (Fig. 3E-F, 4-C) is not complete, lacking its lateral margin, but includes the contact between the frontal and both the postorbital and parietal. Both the external and the internal supratemporal fenestrae (*sensu* Montefeltro et al., 2011) are visible, with a well-developed supratemporal fossa (*sensu* Montefeltro et al., 2011) between them, as also seen in other baurusuchids (Campos et al., 2001; Carvalho et al., 2005; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021).

The **prefrontals** (Fig. 3E-F) are mostly preserved, with a distinct medial contact between the pair, near the posterior portion of the nasal, excluding the contact between nasal and frontal, as in some baurusuchids (Fig. 7; Martinelli & Pais, 2008). Nevertheless, it is not possible to infer the exact length of the medial contact between the prefrontals.

The **frontals** (Fig. 3G-H) are fused into a single element and almost completely preserved; isolated, each bone presents a triangular shape, as in other baurusuchids (Campos et al., 2001; Carvalho et al., 2005; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021). It tapers anteriorly and wedges between the posterior margins of the prefrontals, widening posteriorly. Its lateral edges are medially curved near the point of contact with the palpebrals. On its posterior portion, the frontal contacts the parietal in a nearly transverse suture and the postorbital posterolaterally. Together with the postorbitals, it forms the anterior margin of the internal and external supratemporal fenestrae and fossae.

The dorsal surface of the frontal is mostly smooth and only scattered ornamentation is present next to the medial margins on the orbital rim. On the midline portion, the frontal bears a sagittal crest, as also present in *Aplestosuchus sordidus* (Godoy et al., 2014), *Pissarrachampsa sera* (Montefeltro et al., 2011), *Baurusuchus salgadoensis* (Carvalho et al., 2005) and *Stratiotosuchus maxhechti* (Campos et al., 2001). The sagittal crest in LPRP/USP 0634 extends from the level of the posterior end of the prefrontals to that of the middle portion of the frontal, being approximately 40 mm long. Along its extension, the crest presents variable lateromedial widths, being more developed at the middle (maximum width about 6 mm; total width of the frontal at the same level about 60 mm) and gradually tapering at both ends.

LPRP/USP 0634 shows a transversally bowed depression on the dorsal surface of the frontal, similar to that of *B. salgadoensis* (Carvalho et al., 2005), *S. maxhecthi* (Campos et al., 2001), and *A. escharafacies* (Darlim et al., 2021). However, this depression is uniquely wide and deep posteriorly in LPRP/USP 0634, i.e., three times deeper than the sagittal crest, whereas it has roughly the same depth thorough as the frontal crests in the others bauruschids (Campos et al., 2001; Carvalho et al., 2005; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021).

The **nasal** is represented by one large fragment (Fig. 3G-H) corresponding to the dorsal surface of its posterior portion, close to the contact with the prefrontals. The preserved bone is laminar and anteroposteriorly elongated, forming the median section of the dorsal portion of the rostrum. The left lateral edge indicates that the nasal tapers anteriorly, i.e., the posterior portion is wider than the anterior, as in other baurusuchids (Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021). The nasal contacts the maxillae laterally, whereas its posterior portion contacts the anterior projection of the anterior palpebrals, a condition similar to that of *Stratiotosuchus maxhechti* (Campos et al., 2001). The nasal is limited posteriorly by the prefrontal, which prevents contact to the frontal.

On the posteromedial portion of the dorsal surface of the nasal, next to the prefrontal pair, a slightly rugose depression is seen, as in pissarrachampsines (Montefeltro et al., 2011) and *Aph. escharafacies* (Darlim et al., 2021). A faint crest extends along the midline of that depression, from the middle of the nasal to the level of the anterior edges of the prefrontals. A similar crest is seen in *Aplestosuchus sordidus* (Godoy et al., 2014) and *Aph. escharafacies* (Darlim et al., 2021).

The **maxillae** are highly fragmented. The better preserved right maxilla (Fig. 3A-D) includes the posterior portion of the bone and has a nearly vertical orientation on the lateral surface of the rostrum. It contacts the jugal posteriorly and the lacrimal at the level of the anterior palpebral, but the poor preservation precludes tracing the exact suture between them. In other baurusuchids, the maxillae do not participate on the orbital margin (Price, 1945; Campos et al., 2001; Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Godoy et al., 2014; Darlim et al., 2021); but this condition is unknown in LPRP/USP 0634. The other maxillary fragments include the posterodorsal portions of the left and right bones, which are preserved in articulation with the lateral portions of the nasal, comprising the sidewalls of the snout (Fig. 3G-H). The maxillae do not appear to have had a great participation on the dorsal surface of the snout, at least on the posterior portion of the rostrum.

Only a small fragment of the **lacrimal** is preserved on the right side of the cranium, restricted to the anterodorsal edge of the orbit (Fig. 3A-B). The lacrimal contacts the anterior palpebral via a nearly horizontal suture, forming a lateral, dorsally facing platform for the support of that bone. Despite its fragmentary nature, it is possible to define that the lacrimal articulated with the anterior process of the jugal, at the anterior border of the orbit, and to the posterior edge of the maxilla, anterior to the orbit, what is consistent with the anatomy of other baurusuchids (Campos et al., 2001; Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Godoy et al., 2014; Darlim et al., 2021).

Three **jugal** fragments are preserved, the largest corresponding to the anterior portion of the right jugal (Fig. 3A-D). The bone is transversally narrow and expands dorsoventrally, with its anterior ramus forming the ventral margin of the orbit. Due to the fragmentation and disarticulation of the skull, it is not possible to precisely assess the contacts of the jugal with both the maxilla and lacrimal, but its shape and arrangement indicate that it contacted the posterior margin of the maxilla at the anterior margin of the orbit, with the contact with the lacrimal placed on the level of the anterior margin of the orbit.

On its lateral surface, a hypertrophied longitudinal infraorbital ridge (*sensu* Montefeltro et al., 2011) is present, extending posteroventrally from the lacrimal suture to the suborbital portion of the bone (Fig. 3A-B), as also seen in others baurusuchids (Carvalho et al., 2005; Nascimento & Zaher, 2010; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021). The infraorbital ridge of LPRP/USP 0634 is robust with the same development thorough its entire extension, from near the lacrimal to the suborbital region, whereas the crest is more restricted anteriorly in other baurusuchids (Carvalho et al., 2005; Nascimento & Zaher, 2010; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021). The infraorbital ridge separates the jugal in dorsal and ventral surfaces. The former forms the ventral margin of the orbit, and it is lateromedially narrower than the ventral portion. The ventral surface bears a shallow fan-shaped depression (*sensu* Monfeltro et al., 2011), with three neurovascular foramina at its ventral portion. Additionally, two other isolated fragments of the jugal are preserved and correspond to the infraorbital portion of the left bone (Fig. 4A-B), including the ventral margin of the orbit and the infraorbital ridge. Yet, due to its fragmentation, it is not possible to assess further details on these fragments.

Both right **palpebrals** are preserved (Fig. 3A-D). The bones are thick and have strongly sculptured dorsal surfaces. The anterior palpebral is hook-shaped, with a process extending posteriorly from its lateral margin, dorsoventrally flattened, larger than the posterior palpebral, and covers the anteromedial portion of the orbit, as seen in other baurusuchids (Campos et al., 2001; Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021). The anterior palpebral extends onto the anterolateral projection of the lacrimal and continues posteriorly to contact the posterior palpebral via the hook-shaped lateral process. It also presents an anterolateral projection that contacts the posterior margin of the nasal.

The posterior palpebral is smaller and covers the posterior portion of the orbit. It is dorsally convex, with an almost rounded dorsal outline. As in other baurusuchids (Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021), LPRP/USP 0634 has a supraorbital fenestra set between the anterior and posterior palpebrals. However, due to fragmentation, it is not possible to define its exact shape. The left anterior palpebral is also preserved, but it is displaced from its original position, covering part of the left prefrontal.

There are two preserved **parietal** fragments. A larger fragment corresponds to the anteriormost portion of the bone and forms the interfenestral bar between the supratemporal fenestrae (Fig. 3E-F). The parietal articulates anteriorly to the posterior portion of the frontal, along a nearly transverse suture at the cranial roof. The other fragment corresponds to the posterior limit of the parietal, which is firmly attached to the **supraoccipital** via a transverse suture (Fig. 4C). The posterior portion of the parietal is smooth at the level of the supratemporal fenestrae, without a hypertrophied border overhanging the supratemporal fossae and fenestrae, a unique condition compared to other baurusuchids, in which the parietal expands over the supratemporal fenestrae (Campos et al., 2001; Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Godoy et al., 2014; Darlim et al., 2021).

Only a small fragment of the left **pterygoid** wing is preserved (Fig. 4G-I), corresponding to its distal tip. The ventral surface of that fragment is slightly convex, whereas the facet for the articulation with the ectopterygoid is flat. On the lateral surface, the pterygoid wing presents a small piece of bone identified as a fragment of the right **ectopterygoid** (Fig. 4G), corresponding to the dorsolateral ramus of the bone (Fig. 4D-F). The fragment has a flat articular dorsal surface, which is identified as the facet for the reception of the jugal, following the anatomy of more complete baurusuchid specimens (Price, 1945; Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021). On the inner side, the ectopterygoid is concave, contacting a small unidentified bone fragment (Fig. 4F).

3.2.2. Mandible

Only two fragments of the right hemimandible are preserved (Fig. 4J-M). One is composed of the portion where the triple contact between dentary, splenial, and angular is seen (Fig. 4J-K), inferred to be near the lateroventral anterior edge of the mandibular fenestra, as in other baurusuchids. The dentary portion of this fragment is heavily ornamented with tiny shallow pits, forming the outer surface of mandible. Its inner surface is smoother, without ornamentation, and corresponds to the posterior portion of the splenial. In dorsal view, the angular contacts the dentary and splenial, with a short projection wedged between those bones. The other fragment of the lower jaw corresponds to a surangular portion set at the dorsal portion of the mandibular fenestra (Fig. 4L-M). Its outer surface is sculpted with irregular grooves. The meckelian canal is seen in ventral view, indicating the presence of the mandibular fenestra near the level of the surangular.

3.2.3. Dentition

In addition to the skull materials, six isolated teeth (Fig. 5) were found, without obvious association with specific cranial or mandibular elements. Apart from having the shape and size matching that expected for a similar sized baurusuchid, it is hard to identify the position of each tooth along the dental series. Three of the preserved teeth are hypertrophied (Fig. 5A-C), and probably correspond to the caniniforms of the maxillae and dentaries, based on comparison with other baurusuchids (Montefeltro et al., 2011, 2020; Godoy et al., 2014; Darlim et al., 2021). These are labiolingually compressed and posteriorly curved, with distinct denticles on the mesial and distal cutting edges (Fig. 5E); i.e., true ziphodont teeth *sensu* Prasad & De Broin (2002). The denticles are placed along most of the distal and mesial edges of the crowns, but do not occur near their bases. The other three preserved teeth are smaller, with a triangular-shaped crown, but lacking a well-marked distal curvature. These teeth also have denticles on the mesial and distal cutting edges.

4. DISCUSSION

4.1. Morphological variation within Baurusuchidae

Three remarkable traits of the baurusuchid frontal are variable among taxa and have been treated as taxonomically relevant: the depth of the dorsal depression, the position of the sagittal crest, and the presence of the midline anterior depression. A shallow frontal depression is observed in *Aplestosuchus sordidus* (Godoy et al., 2014), *Pissarrachampsa sera* (Montefeltro et al., 2011), *Campinasuchus dinizi* (Carvalho et al., 2011), and *Wargosuchus australis* (Martinelli & Pais, 2008), whereas a strongly transversally bowed depression is seen in *Baurusuchus salgadoensis* (Carvalho et al., 2005), *Stratiotosuchus maxhechti* (Campos et al., 2001), and *Aphaurosuchus escharafacies* (Darlim et al., 2021). Although the depth of the depression varies, its anterior and posterior portions are equally deep in both groups. On the contrary, LPRP/USP 0634 has a unique and easily distinguishable condition, in which the depression is much deeper as a whole, but even deeper at its posteriormost portion, near the contact with the parietal. Given that the maximal rostro-caudal length of the LPRP/USP 0634 frontal (ca. 6,4 cm) is similar to that of other Baurusuchidae, as *B. salgadoensis* (ca. 6,6 cm), *P. sera* (ca. 6,7 cm), *Aph. escharafacies* (ca. 7,2 cm) and *Apl. sordidus* (ca. 6,9 cm), we suggest this condition is not ontogeny related, but a diagnostic feature of the taxon.

A sagittal crest along the dorsal surface of the frontal is present in most baurusuchids (Campos et al., 2001; Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Godoy et al., 2014; Fig. 6), except for *Wargosuchus australis* (Martinelli & Pais, 2008) and *Aphaurosuchus escharafacies* (Darlim et al., 2021). In *Pissarrachampsa sera* (Montefeltro et al., 2011), *Campinasuchus dinizi* (Carvalho et al., 2011), and *Aplestosuchus sordidus* (Godoy et al., 2014), it extends as a sharp crest displaced anteriorly to the frontal mid-length, whereas it is smoother and restricted to the posterior portion of the frontal in *Baurusuchus salgadoensis* (Carvalho et al., 2005) and *Stratiotosuchus maxhechti* (Campos et al., 2001). The condition in LPRP/USP 0634 is similar to that of *P. sera* (Montefeltro et al., 2011), *C. dinizi* (Carvalho et al., 2011), and *Apl. sordidus* (Godoy et al., 2014), but given the greater depth of its frontal depression, the crest is fully contained within it. In this configuration, the dorsal edge of the crest is set below the level of the lateral edges of the frontal.

Some baurusuchids have a modified condition in which the dorsal surface of the anterior portion of the frontal is excavated by a conspicuous midline longitudinal depression (*sensu* Montefeltro et al., 2011). This has been previously reported for *Wargosuchus australis*

(Martinelli & Pais, 2008) and *Pissarrachampsa sera* (Montefeltro et al., 2011; Godoy et al., 2014; Darlim, et al., 2021), but is also seen in LPRP/USP 0634 (Fig. 6).

The jugal of baurusuchids bears an infraorbital ramus with a hypertrophied infraorbital ridge (*sensu* Montefeltro et al., 2011), which spans anteriorly from the level of the lacrimal to the midlength of the ramus (Fig. 7). In *Pissarrachampsa sera* (Montefeltro et al., 2011), *Campinasuchus dinizi* (Carvalho et al., 2011), *Baurusuchus pachecoi* (Price, 1945), *Baurusuchus salgadoensis* (Carvalho et al., 2005) and *Gondwanasuchus* scabrosus (Marinho et al., 2013), the infraorbital ridge merges gradually with the jugal surface near the lacrimal-maxilla contact. In addition, the anterior end of the ridge is almost straight, nearly parallel to the ventral edge of the jugal. On the other side, LPRP/USP 0634 resembles *Aphaurosuchus escharafacies* (Darlim et al., 2021) in that the anterior end of the infraorbital ridge curves dorsally onto the dorsal surface of the skull, near the contact with the lacrimal. Also, although not fully preserved, its anterior end does not merge gradually with the jugal but remains as developed as more posterior portions, ending abruptly (Fig. 7I). Due to the dorsoventral compression of the *Aplestosuchus sordidus* skull (Godoy et al., 2014), it is not possible to properly assess the morphology around the lacrimal. In *Stratiotosuchus maxhechti* (Campos et al., 2001), the infraorbital ridge overcomes the anterior border of the orbit, as in other baurusuchids, even though the ridge is smaller and less prominent than in other taxa.

The parietal of baurusuchids is restricted to the medial margin of the supratemporal fenestrae, with that of most forms bearing a short shelf that overhangs the posterior border of the aperture (Fig. 8, Campos et al., 2001; Carvalho et al., 2005, 2011; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014, Darlim et al., 2021). The parietal of LPRP/USP 0634 lacks that shelf, presenting a smoother posterior edge near the supratemporal fenestrae (Fig. 8G).

The nasal of baurusuchids does not vary greatly among most species. Two exceptions are the broader bone of *Stratiotosuchus maxhechti* (Campos et al., 2001) and the unfused condition of the pair in *Gondwanasuchus scabrosus* (Marinho et al., 2013). Few other minor differences are restricted to the posterior region of the bone. Montefeltro et al. (2011) observed that the nasal of pissarrachampsines has a longitudinal depression (Fig. 9) on the posterior portion of its dorsal surface, so that the lateral borders of the bone are placed above its central portion, as also seen in *G. scabrosus*, *Aph. escharafacies*, and LPRP/USP 0634 (Fig. 9). In baurusuchines, the central surface of the posterior portion of the nasal is at the same level of the lateral borders (e.g., *S. maxhechti*; *Aplestosuchus sordidus*, Godoy et al., 2014), or is even above them (e.g., *Baurusuchus salgadoensis* Carvalho et al., 2005). Additionally, in the posterior surface of the nasal, a slender crest is observed in *Apl. sordidus*, *Aph. escharafacies*, and LPRP/USP 0634 (Fig. 9), a character unknown to other known notosuchians.

4.2. Phylogenetic relationships

Our phylogenetic analysis resulted in eight most parsimonious trees of 2300 steps. A simplified version of their strict consensus, focusing on Notosuchia, is shown in Fig. 10, and its complete topology is presented in the supplementary material. Here, we highlight four main results: **1.** The placement of *Aphaurosuchus kaiju* as the sister taxon of *Aphaurosuchus escharafacies*; **2.** The sister-group relation between Baurusuchia and Sphagesauria, forming Xenodontosuchia (*sensu* Ruiz et al., 2021); **3.** The taxonomic content of the two Baurusuchidae lineages (Pissarrachampsinae and Baurusuchinae) matching that of previous works; **4.** The placement of *Ogresuchus furatus* and *Razanandrongobe sakalavae* within Baurusuchia.

4.2.1. The clade *Aphaurosuchus*

LPRP/USP 0624 is included in the clade *Aphaurosuchus* for which we erected the species *Aphaurosuchus kaiju*. The sister relation between *Aphaurosuchus kaiju* and *Aphaurosuchus escharafacies* is supported by the postero-dorsal depression on the nasal (char. 57 st. 1) and the upturned infraorbital ridge on the jugal (char. 517 st.1). Additionally, *Aphaurosuchus kaiju* could be assigned to a new species due to three autapomorphies in relation to *Aph. escharafacies*: 1. a well-developed depression on the dorsal surface of the frontal, a condition unknown in any other notosuchian; 2. a smooth parietal near the supratemporal fenestrae, without the overhanging processes, a condition unique among baurusuchids; 3. a sagittal crest within the frontal depression, a unique trait among notosuchians.

4.2.2. *Pakasuchus kapilimai* (O'Connor et al., 2010), Baurusuchia (*sensu* Darlim et al., 2021), and Sphagesauria (*sensu* Ruiz et al., 2021)

Our phylogenetic analysis places *Pakasuchus kapilimai* as the sister taxon of Xenodontosuchia (Sphagesauria + Baurusuchia), as also recovered in some previous works (Sertich & O'Connor, 2014; Meunier & Larsson, 2018). This contrasts with both its position as sister of *Malawisuchus mwakasyungutiensis* (Pol et al., 2014; Martin & De Broin, 2016; Pinheiro et al., 2018, 2021) and its nesting within Baurusuchia, as sister of all other members of the clade, as recovered using a previous version of the matrix employed here (Ruiz et al., 2021). The clade composed of *Pakasuchus kapilimai* + Xenodontosuchia is supported by four unambiguous synapomorphies. Firstly, *Pakasuchus kapilimai* and most of Sphagesauria and Barusuchia lacks the antorbital fenestra (char.12 st. 1), which is present in *Gondwanasuchus scabrosus*, *Campinasuchus dinizi*, *Morrinhosuchus luziae*, *Notosuchus terrestris*, and *Caipirasuchus* spp.. Also, members of this clade have the lateral margins of the squamosal and postorbital diverging posteriorly in dorsal view (char. 104 st. 1), with the condition reversed in the sphagesaurids *Yacarerani boliviensis* and *Caipirasuchus* spp., and in the baurusuchid

Baurusuchus pachecoi, in which those margins are parallel. A hook-shaped anterior palpebral (char. 107 st. 1) is also synapomorphic for the *Pakasuchus kapilimai* + Xenodontosuchia clade, as seen in all preserved taxa except for the baurusuchid *Stratiotosuchus maxhechti*, the anterior palpebral of which has a rounded shape. Finally, an unambiguous synapomorphy is the presence of longitudinal keels restricted to the posterior edge of the osteoderms dorsal surface (char. 464 st. 1; Montefeltro, 2019).

Xenodontosuchia, i.e., Sphagesauria plus Baurusuchia, is here supported by five unambiguous synapomorphies. The dorsal exposure of the supraoccipital is restricted to a thin surface attached to the posteriormost portion of the parietal and squamosal (char. 122 st. 1), a condition that seems to be exclusive within Notosuchia. A second synapomorphy is the laterally diverging palatines, which become rod-like, forming the palatine bars posteriorly (char. 229. St. 1); in other notosuchians, such as *Mallawisuchus mwakasyungutiensis*, *Simosuchus clarki*, *Libycosuchus brevirostris*, *Araripesuchus* spp., *Uruguaysuchus aznarezi*, sebecids, peirosaurids, and mahajangasuchids, the palatines extend parasagittally along the midline, a condition also found as a possible reversal in *Ogresuchus furatus*. The thirty synapomorphy is the exclusion of the pterygoid from the suborbital fenestrae by the ectopterygoid-palatine contact (char. 238 st. 1); in other notosuchians, the pterygoid enters the margin of the fenestrae. The fourth unambiguous synapomorphy is the splenial-dentary V-shaped suture (char. 334 st. 0). Finally, the absence of accessory cusps in the teeth (char. 359 st. 0) also supports Xenodontosuchia.

4.2.3. Baurusuchia (*sensu* Darlim et al., 2021)

Our phylogenetic analysis places *Comahuesuchus brachybuccalis* within Baurusuchia as the sister taxon of all other baurusuchians, as also recovered in previous phylogenetic analysis (Montefeltro et al., 2013; Pol et al., 2014; Martin & De Broin, 2016; Martinelli et al., 2018;

Ruiz et al., 2021). *Razanandrongobe sakalavae* was for the first time recovered within Baurusuchia, as sister to *Ogresuchus furatus* + Baurusuchidae. Previous analyses that included *O. furatus* (Sellés et la., 2020; Nicholl et al. 2021); and *R. sakalavae* (Dal Sasso et al., 2017; Nicholl et al. 2021) recovered both taxa as sebecosuchians (*sensu* Martinelli et al., 2018), with *O. furatus* within Sebecidae (Sellés et al., 2020; Nicholl et al. 2021). Our analysis, however, does not recover the Sebecosuchia (Sebecidae + Baurusuchidae) clade.

The clade Baurusuchia is supported by seven unambiguous synapomorphies, including species with a short rostrum and hypertrophied caniniforms. This condition leads to the presence of a maxillary tooth wave in lateral/medial views (char. 372 st. 1), as homoplastically seen in other notosuchians, such as Uruguaysuchidae, Sebecidae, *Mahajangasuchus insignis*, *Uberabasuchus terrificus*, *Anatosuchus minor*, *Yacarerani boliviensis*, and *Adamantinasuchus navae*. Another cranial synapomorphy of baurusuchians is the short and broad prefrontal, displaced anteriorly to the orbits (char. 69 st. 1), whereas sphagesaurians exhibit elongated prefrontals disposed in parallel to the anteroposterior axis of the skull (except for *Notosuchus terrestris* and *Mariliasuchus amarali*).

Two synapomorphies of Baurusuchia are related to the dentary. This bone presents a single dorsal expansion on its dorsal edge, which is concave posteriorly (char. 318 st. 2). In ventral view, the symphysis of baurusuchians has a U-shape (char. 333 st. 1), as also found in Mahajangasuchidae and *Libycosuchus brevirostris* among Notosuchia. Sebecids show a similar morphology, but the U-shape of the symphysis is not so evident. Another mandibular synapomorphy of baurusuchians is the presence of a large and slot-like *foramen intramandibularis oralis* (char. 311 st. 1), whereas most sphagesaurians have a small foramen.

The last two baurusuchian synapomorphies are unambiguous and regard their dentition, with all the maxillary teeth isolated in their respective alveoli (char. 376 st. 0) and also lacking molariform teeth (char. 379 st. 0); within Notosuchia, molariform teeth are only present in Spaghesauria, *Malawisuchus mwakasyungutiensis*, and *Pakasuchus kapilimai*.

4.2.4. Baurusuchidae

The Baurusuchidae (*sensu* Darlim et al., 2021) clade includes thirteen species, with *Cynodonthosuchus rothi* and *Gondwanasuchus scabrosus* as successive sister-taxa of the clade formed by Pissarrachampsinae + Baurusuchinae. It is supported by four unambiguous cranial synapomorphies. A septum dividing the external nares of baurusuchids (char. 10 st 1), a condition also homoplastically found in Uruguaysuchidae, Sebecidae, Peirosauridae and Mahajangasuchidae. Baurusuchids also exhibit an open premaxilla-maxilla contact on the ventral edge of the rostrum, resulting in a large notch that at least partially encompasses the opposite dentary tooth (char. 45 st. 1); this is also observed in some peirosaurids, such as *Gasparinisuchus peirosauroides*, *Hamadasuchus rebouli*, *Lomasuchus palpebrosus*, *Montealtosuchus arrudacaposi*, and *Uberabasuchus terrificus*, as well as in the sebecid *Bretesuchus bonapartei*. The third cranial synapomorphy of baurusuchids is the suture between the maxilla and the palatine positioned transverse to the midline skull axis (char. 218 st. 3), but the palatine is evaginated instead in *Bau. salgadoensis* and *Bau. pachecoi*. The palatine also presents an anterior extension which does not reach the level of the anterior margin of the suborbital fenestrae (char. 221 st. 1).

4.2.5. Phylogenetic relationships within Baurusuchidae

Within Baurusuchidae, our phylogenetic analysis recovered *Gondwanasuchus scabrosus* as the sister taxon of Pissarrachampsinae + Baurusuchinae, a configuration supported by two synapomorphies: first, the teeth are highly laterally compressed (char. 356, st. 2, Fig. 10); secondly, a row of foramina flanks the medial contact of the palatines (char. 224 st. 1). The latter feature is unique among crocodyliforms, with *Cynodontosuchus rothi* and *Aph. escharafacies* being the only baurusuchids to lack these foramina, interpreted as a reversal in the latter.

Our analysis also recovered the two main Baurusuchidae lineages, Pissarrachampsinae and Baurusuchinae, as proposed by Montefeltro et al. (2011; see also Godoy et al., 2014; Geroto & Bertini, 2018; Darlim et al., 2021). The Pissarrachampsinae clade is supported by two synapomorphies. The incisive foramen is absent (char. 198 st. 1), a condition also found in some baurusuchines such as *Bau. salgadoensis* and *Bau. Pachecoi*. Pissarrachampsines also have a mediolaterally wide and anteroposteriorly thin cross section of the distal end of the quadrate (char. 280 st. 0), whereas baurusuchines present a subquadrangular cross section (char. 280 st. 1).

We recovered a polytomy within Pissarrachampsinae, composed of the Brazilian species *Pissarrachampsa sera* and *Campirasuchus dinizi*, the Argentinean *Wargosuchus australis*, and the Pakistani *Pabwehshi pakistanensis*. Previous works have recovered *Pi. sera* as sister to *W. australis* (e.g. Montefeltro et al., 2011; Godoy et al., 2014; Darlim et al., 2021) and *Pa. pakistanensis* within Baurusuchidae (Turner, 2006; Turner & Calvo, 2005; Nascimento & Zaher, 2010; Pol & Powell, 2011; Dal Sasso et al., 2017; Pinheiro et al., 2018). The clade composed of *Pi. sera*, *Pa. pakistanensis*, and *Wa. australis* is supported by the presence of three premaxillary teeth (char. 365 st. 3), a condition present in the former two taxa, but unknow for *Wa. australis*. This condition is also seen in some non-Pissarrachampsinae baurusuchids, such as *Cynodontosuchus rothi* and *Stratiotosuchus maxhechti*. The latter also shares a hypertrophied last premaxillary tooth with pissarrachampsines (char. 521 st. 1).

Baurusuchinae is supported by six unambiguous synapomorphies, all restricted to the cranium. The prefrontals have a medial contact along most of their medial edge (char. 73 st. 1), as seen in *Bau. salgadoensis*, *St. maxhechti*, and *Aph. kaiju*. *Aphaurosuchus. escharafacies* has a restricted contact between the prefrontals (char. 73 st. 2), as in pissarrachampsines, whereas *Aplestosuchus sordidus* exhibits a transitional condition. Another baurusuchine synapomorphy is a short anterior extension of the frontal, which does not overcome the level of the anterior edge of the orbits (char. 79 st. 1).

The cranial table in baurusuchines is as wide as the ventral portion of the skull, so that the quadrates are covered by the squamosals (char. 102 st. 0), whereas pissarrachampsines show a narrower cranial table. Two other synapomorphies are the presence of multiple subtympanic foramina internalized in a bony otic aperture (char. 194 st. 1) and a large nutrient foramen on the palatal surface of premaxilla-maxilla contact (char. 207 st. 1). A ridged ventral surface of the choanal septum (char. 251 st. 2) is also synapomorphic for baurusuchines, as previously recovered by Darlim et al. (2021), even though the choanal septum of *Aph. escharafacies* is reversed to a slightly depressed condition.

The clade including *Aplestosuchus sordidus*, *Aphaurosuchus escharafacies*, and *Aphaurosuchus kaiju* is supported by two unambiguous synapomorphies. First, the sculpturing in the outer surface of the mandible is restricted to the dentary (char. 302 st. 0), as also seen in *Gondwanasuchus scabrosus*, whereas *Pissarrachampsa sera*, *Campinasuchus dinizi*, *Stratiotosuchus maxhechti*, and *Bau. salgadoensis* has the outer surface of the splenial also sculptured. The second synapomorphy of the clade is the presence of a ridge on the posterior portion of the nasal (char. 515 st. 1), a unique condition among notosuchians.

The clade encompassing the three *Baurusuchus* species is supported by one synapomorphy: an ectopterygoid not extending until the posterior tip of the pterygoid flange at maturity (char. 256 st.1). The plesiomorphic condition is present in other baurusuchids. The clade uniting *Bau. salgadoensis* and *Bau. pachecoi* is supported by two synapomorphies: a post-temporal fenestra (char. 28 st. 0) and a ridge at the ectopterygoid-jugal suture continuous to the ventral ridge of the infratemporal portion of the jugal (char. 154 st. 0). This condition is also present in *G. scabrosus* and *Aph. escharafacies*.

4.3. Distribution of Baurusuchia

Baurusuchians have been recognized as a typical South American clade (Price, 1945; Campos et al., 2001; Carvalho et al., 2005, 2011; Martinelli, 2003; Martinelli & Pais, 2008; Nascimento & Zaher, 2010; Montefeltro et al., 2011; Marinho et al., 2013; Godoy et al., 2014; Darlim et al., 2021). However, our phylogenetic results indicate that fragmentary taxa from other landmasses are nested to this clade, extending the temporal and spatial range of the group as well as it less inclusive groups such as Baurusuchidae. As in several previous works (Nascimento & Zaher, 2010; Dal Sasso et al., 2017; Geroto & Bertini, 2018; Pinheiro et al., 2018), our study found *Pabwehshi pakistanensis* (Wilson et al., 2001), from the Maastrichtian Pab Formation of Pakistan, as a Baurusuchidae. If confirmed, *Pabwehshi pakistanensis* would be the only known baurusuchid outside South America (Pol & Leardi, 2015; Wilson et al., 2001). The Indian Subcontinent was already isolated from other Gondwanan landmasses since the Aptian-Cenomanian (Krause et al., 2019), suggesting that baurusuchids originated previous to that event or expanded across oceanic barriers by the end of the Cretaceous.

Additionally, the recovery of *Ogresuchus furatus* (Sellés et al., 2020) and *Razanandrongobe sakalavae* (Maganuco et al., 2006) as baurusuchians further expands the spatial and temporal distribution of the group. *Ogresuchus furatus*, from the Tremp Formation (Lower Maastrichtian) of Catalonia, represents the only European and non-Gondwanan baurusuchian. As discussed by Sellés et al. (2020), the similarity between the Cretaceous faunas of Europe and North Africa indicates that these landmasses could be connected by intermittent landbridges, which can explain the presence of a few notosuchians in European deposits.

The oldest-known putative notosuchian, the enigmatic *Razanandrongobe sakalavae*, from the Bathonian Sakahara Formation of Madagascar (Maganuco et al., 2006; Dal Sasso et al., 2017), expands the geographical range of Baurusuchia to that landmass. More remarkably, it expands the temporal range of this clade to the Middle Jurassic in an unprecedented way. The occurrence of a Baurusuchia in that timeframe reinforces the hypothesis that the radiation of the group took place before the final fragmentation of Gondwana (Turner & Sertich, 2010; Pol & Leardi, 2015). The position of theses three taxa in our novel phylogenetic analysis are in line and, if confirmed, imply the occurrence of baurusuchians in Africa. However, at this point there is no robust evidence corroborating this hypothesis.

5. CONCLUSION

Aphaurosuchus kaiju sp. nov. is the 12th baurusuchid species described for South America, and the 10th for the Bauru Group, expanding the morphological and taxonomic diversity of the clade. The recovery of *Pabwehshi pakistanensis* (Maastrichtian of Pakistan) in Baurusuchidae, and of *Ogresuchus furatus* (Maastrichtian of Catalonia) and *Razanandrongobe sakalavae* (Bathonian of Madagascar) in Baurusuchia, suggests that both groups were not limited to South America, but expanded its range to other Gondwnan and Laurasian landmasses, and that Baurusuchia originated much earlier than previously anticipated.

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Fig. 1. Type locality of *Aphaurosuchus kaiju* sp. nov. (LPRP/USP 0634). A. maps of South America, Brazil, and São Paulo showing the areas detailed in B and C; B. location map of the outcrop where LPRP/USP 0634 was found; C. surface exposure of Bauru Basin rocks around the locality. LPRP/USP 0634 site marked with an asterisk. Modified from Fernandes & Ribeiro (2015).

Fig. 2. Reconstructed skull of *Aphaurosuchus kaiju* sp. nov. (LPRP/USP 0634). A. Portion with maxilla, jugal, lacrimal, anterior and posterior palpebral (seen in detail in Fig. 3); B. Portion with frontal and parietal (the dorsally projected structures above the orbit result from fragmentation and are not real features of the taxon; seen in detail in Fig. 3); C. Fragment with nasal, the contact between the prefrontals, and the anterior projection of the anterior palpebral (seen in detail in Fig. 3); D. Fragmentary angular (seen in detail in Fig. 4); E. Fragment with the triple contact between dentary, angular, and splenial (seen in detail in Fig. 4); F. Hypertrophied associated caniniform teeth (seen in detail in Fig. 5).

Fig. 3. Holotype of *Aphaurosuchus kaiju* sp. nov. (LPRP/USP 0634) and interpretative drawings. **A-B.** right lateral view of the main fragment; **C-D.** dorsal view of the main fragment; **E-F.** Dorsal view of the cranial roof; **G-H.** Dorsal view of the snout fragment. Grey and hatched areas indicate matrix and broken surfaces, respectively. Abbreviations: **ap**, anterior palpebral; **fr**, frontal; **j**, jugal; **jir**, jugal infraorbital ridge; **l**, lacrimal; **lap,** left anterior palpebral; **mx**, maxillae; **n**, nasal; **o**, orbit; **p**, parietal; **po**, postorbital; **prf**, prefrontal; **pp**, posterior palpebral; **rap**, right anterior palpebral; **stf**, supratemporal fenestrae. Scale bars: 3 cm.

Fig. 4. Skull fragments of *Aphaurosuchus kaiju*. **A.** fragment of the left jugal in lateral view; **B.** fragment of the left jugal near the border of the orbit in lateral view; **C.** parietal and supraoccipital in dorsal view; **D-F.** ectopterygoid in posterior (D), right lateral (E), and left lateral (F) views; **G-I.** left pterygoid wing in dorsal (G), ventral (H), and lateral (I) views; **J-K.** fragment of the right surangular in lateral (J) and ventral (K) views; **L-M.** fragment of the right hemimandible in lateral (L), showing the dentary, and ventral (M) views, showing the triple contact of dentary, angular, and splenial. Abbreviations: **ang**, angular; **de**, dentary; **ecpt**, ectopterygoid; **mkc**, meckelian canal; **p**, parietal; **ptw**, pterygoid; **soc**, supraoccipital; **sp**, splenial; **un,** unidentified bone fragment. Scale bars: 1 cm.

Fig. 5. The isolated teeth of *Aphaurosuchus kaiju* **A.** hypertrophied caniniform (on the left) and smaller teeth (on the middle and the right); **B-C.** hypertrophied caniniforms; **D.** a smaller tooth; **E.** Detail of the tooth shown in C in lateral view, with denticules seen along its distal edge. Scale bars: 1 cm.

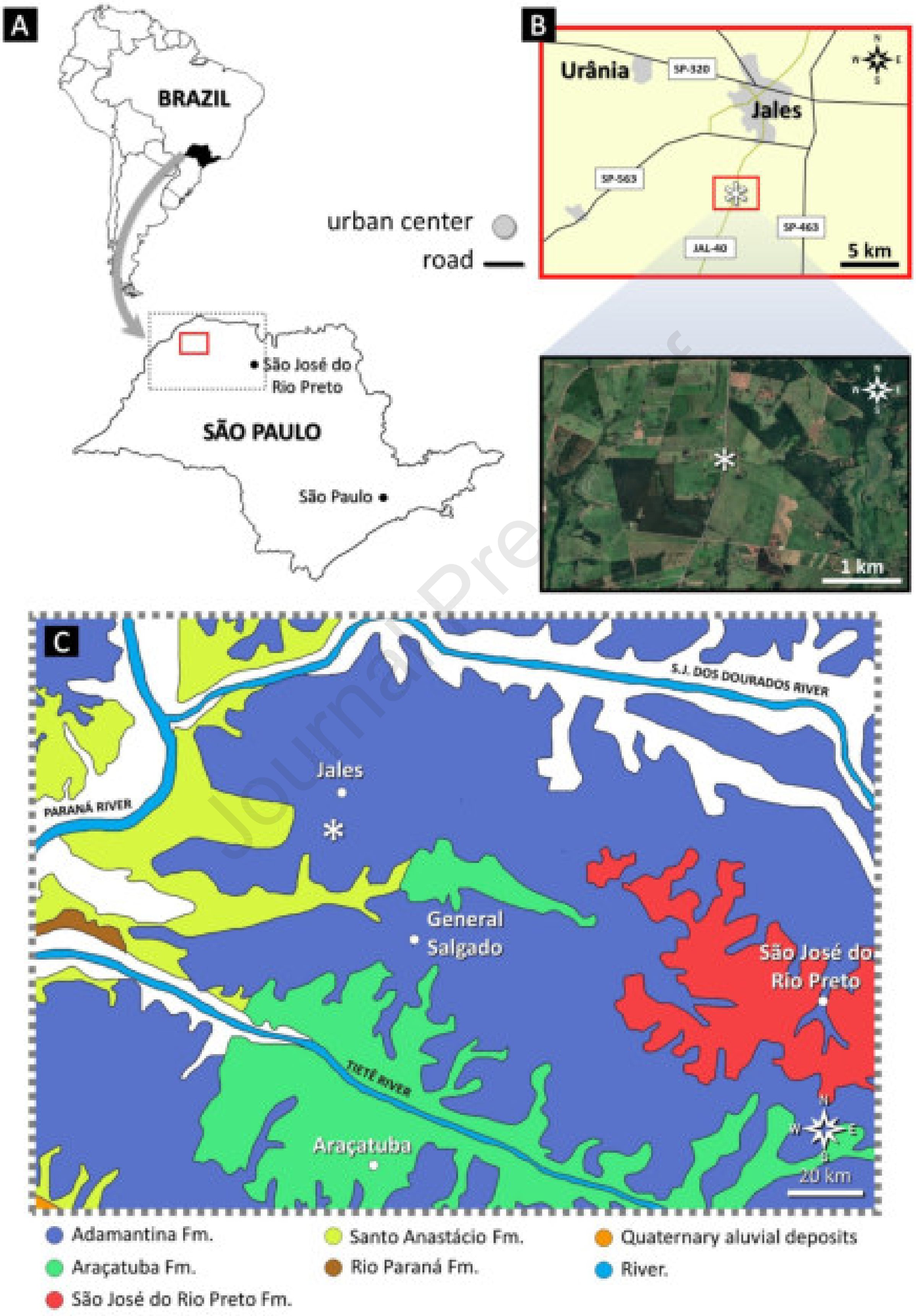
Fig. 6. Dorsal surface of baurusuchid frontals. 1, *Campinasuchus dinizi* (CPPLIP 1235); 2, *Wargosuchus australis* (MOZ-PV 6134); 3, *Pissarrachampsa sera* (LPRP/USP 0019); 4, *Stratiotosuchus maxhechti* (DNPM DGM 1477-R); 5, *Aplestosuchus sordidus* (LPRP/USP 0229a); 6, *Baurusuchus salgadoensis* (MPMA 62-0001-02); 7, *Aphaurosuchus escharafacies* (LPRP/USP 0697); 8, LPRP/USP 0634. Abbreviations: **ap**, anterior palpebral; **fr**, frontal; **l**, lacrimal; **n**, nasal; **p**, parietal; **po**, postorbital; **pp**, posterior palpebral; **prf**, prefrontal. Dotted lines indicate the sagittal crests, the brackets indicate the midline longitudinal depressions.

Fig. 7. Lateral surface of baurusuchid jugals. 1, *Gondwanasuchus scrabrosus* (UFRJ DG 408-R); 2, *Campinasuchus dinizi* (CPPLIP 1235); 3, *Pissarrachampsa sera* (LPRP/USP 0019); 4, *Stratiotosuchus maxhechti* (DNPM DGM 1477-R); 5, *Baurusuchus pachecoi* (DGM 299-R, mirrored); 6, *Baurusuchus salgadoensis* (MPMA 62-0001-02); 7, *Aplestosuchus sordidus* (LPRP/USP 0229a, mirrored); 8, *Aphaurosuchus escharafacies* (LPRP/USP 0697, mirrored); 9, LPRP/USP 0634. Abbreviations: **de**, dentary; **j**, jugal; **l**, lacrimal; **mx**, maxillae. Dotted lines indicates the infraorbital ridge.

Fig. 8. Dorsal surface of baurusuchid parietals. 1, *Campinasuchus dinizi* (CPPLIP 1235); 2, *Pissarrachampsa sera* (LPRP/USP 0019); 3, *Stratiotosuchus maxhechti* (DNPM DGM 1477-R); 4, *Baurusuchus salgadoensis* (MPMA 62-0001-02); 5, *Aphaurosuchus escharafacies* (LPRP/USP 0697); 6, *Aplestosuchus sordidus* (LPRP/USP 0229a); 7, LPRP/USP 0634. Abbreviations: **fr**, frontal; **p**, parietal; **po**, postorbital; **soc**, supraoccipital; **sq**, squamosal. Dotted lines indicate the parietal shelf overhanging the supratemporal fenestrae.

Fig. 9. Dorsal surface of baurusuchid rostrum showing the posterior portion of the nasals. 1, *Gondwanasuchus scabrosus* (UFRJ DG 408-R); 2, *Wargosuchus australis* (MOZ-PV 6134); 3, *Pissarrachampsa sera* (LPRP/USP 0019); 4, *Stratiotosuchus maxhechti* (DNPM DGM 1477-R); 5, *Aplestosuchus sordidus* (LPRP/USP 0229a); 6, *Baurusuchus salgadoensis* (MPMA 62-0001-02); 7, *Aphaurosuchus escharafacies* (LPRP/USP 0697); 8, LPRP/USP 0634. Abbreviations: **ap**, anterior palpebral; **fr**, frontal; **l**, lacrimal; **mx**, maxillae; **n**, nasal; **prf**, prefrontal. Dotted lines indicate the nasal crests, whereas the brackets indicate the postero-dorsal depressions.

Fig. 10. Simplified strict consensus tree depicting the phylogenetic relations among Notosuchia.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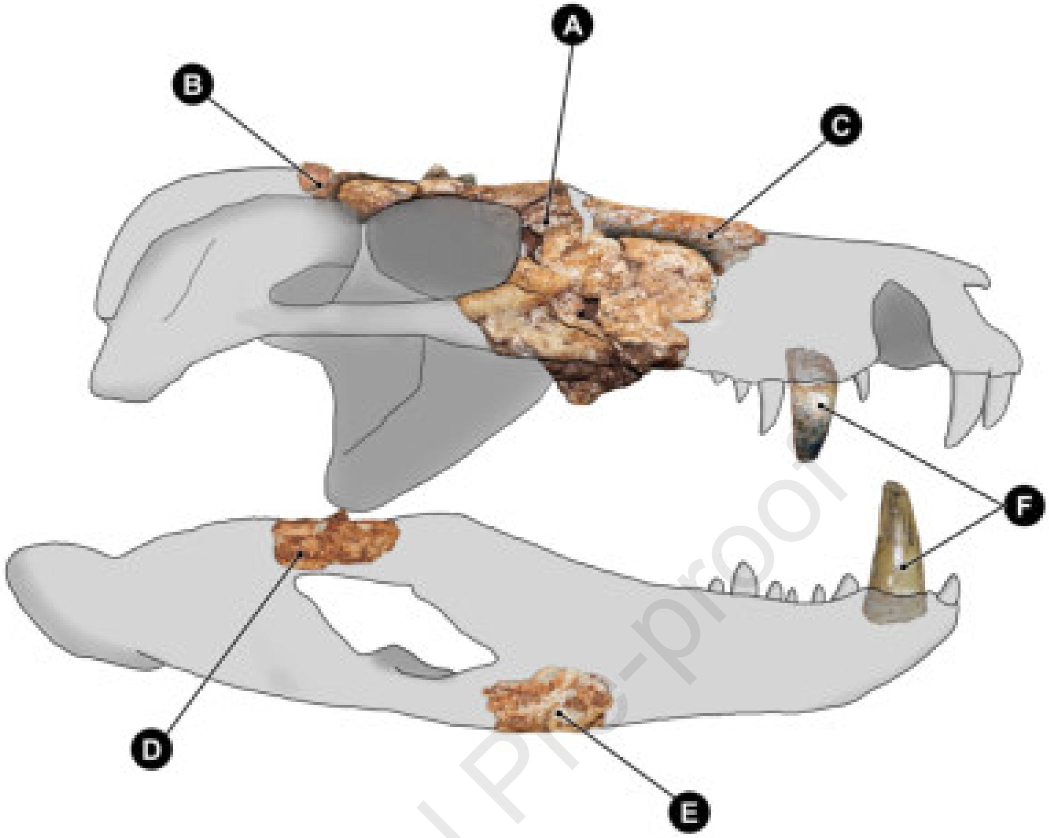
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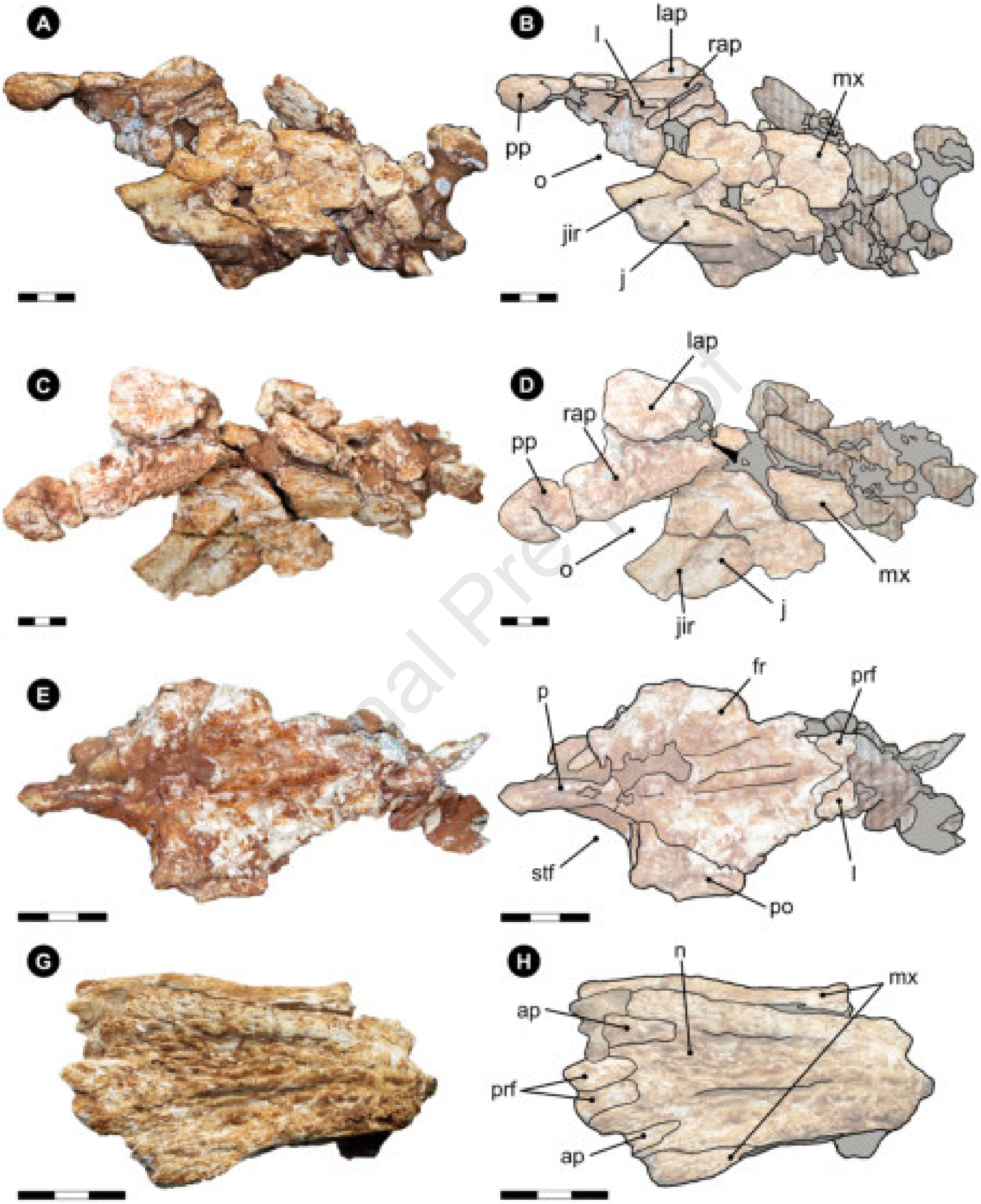
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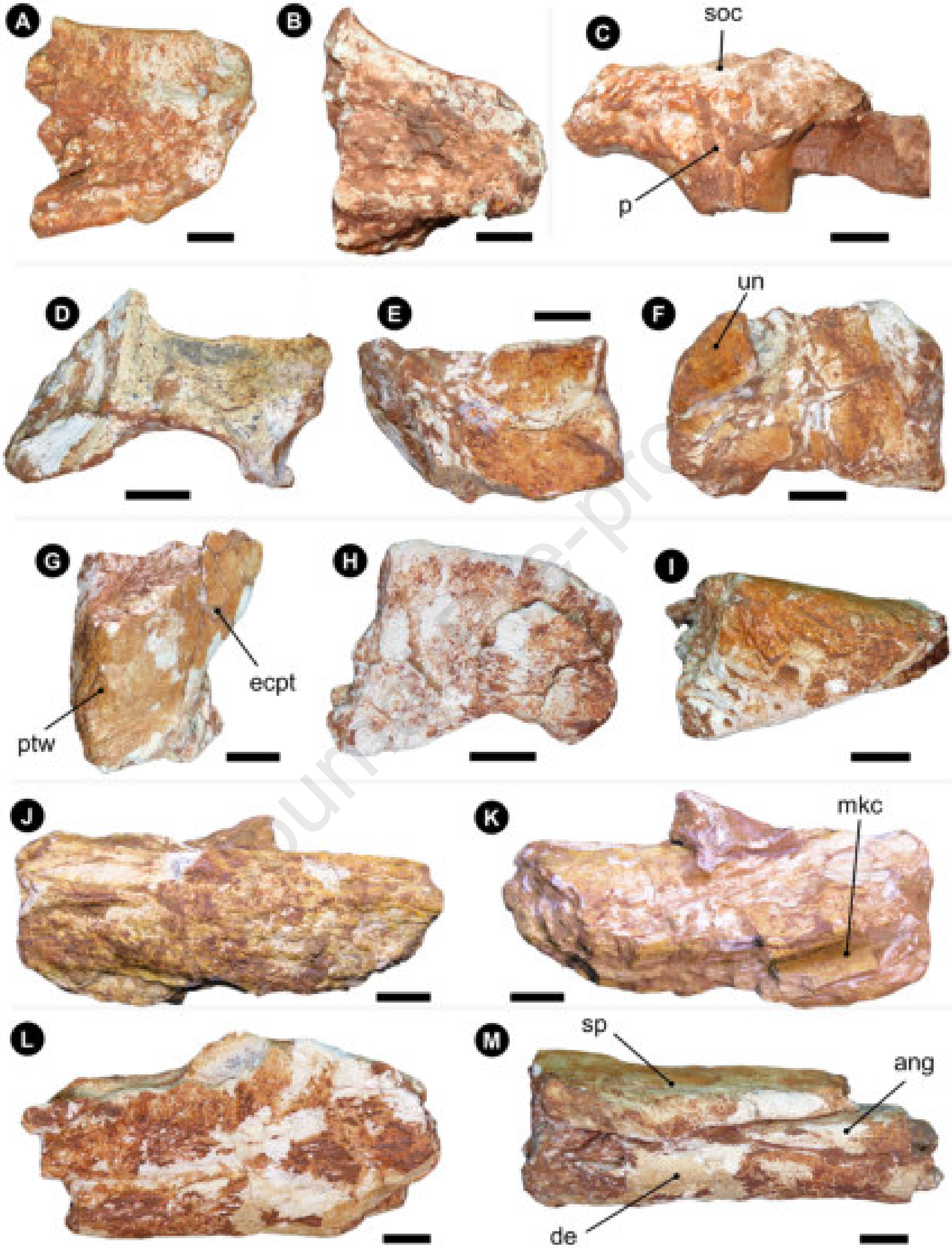
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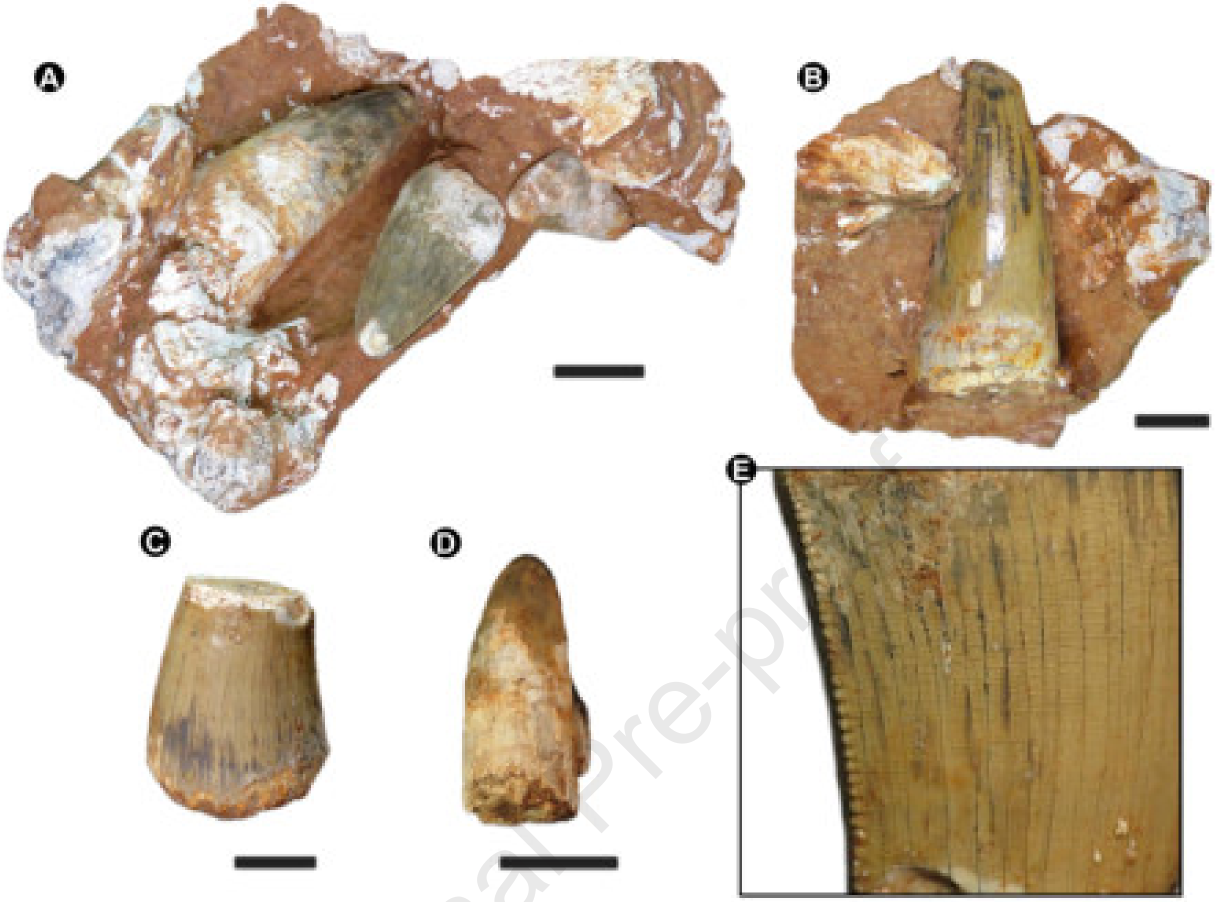
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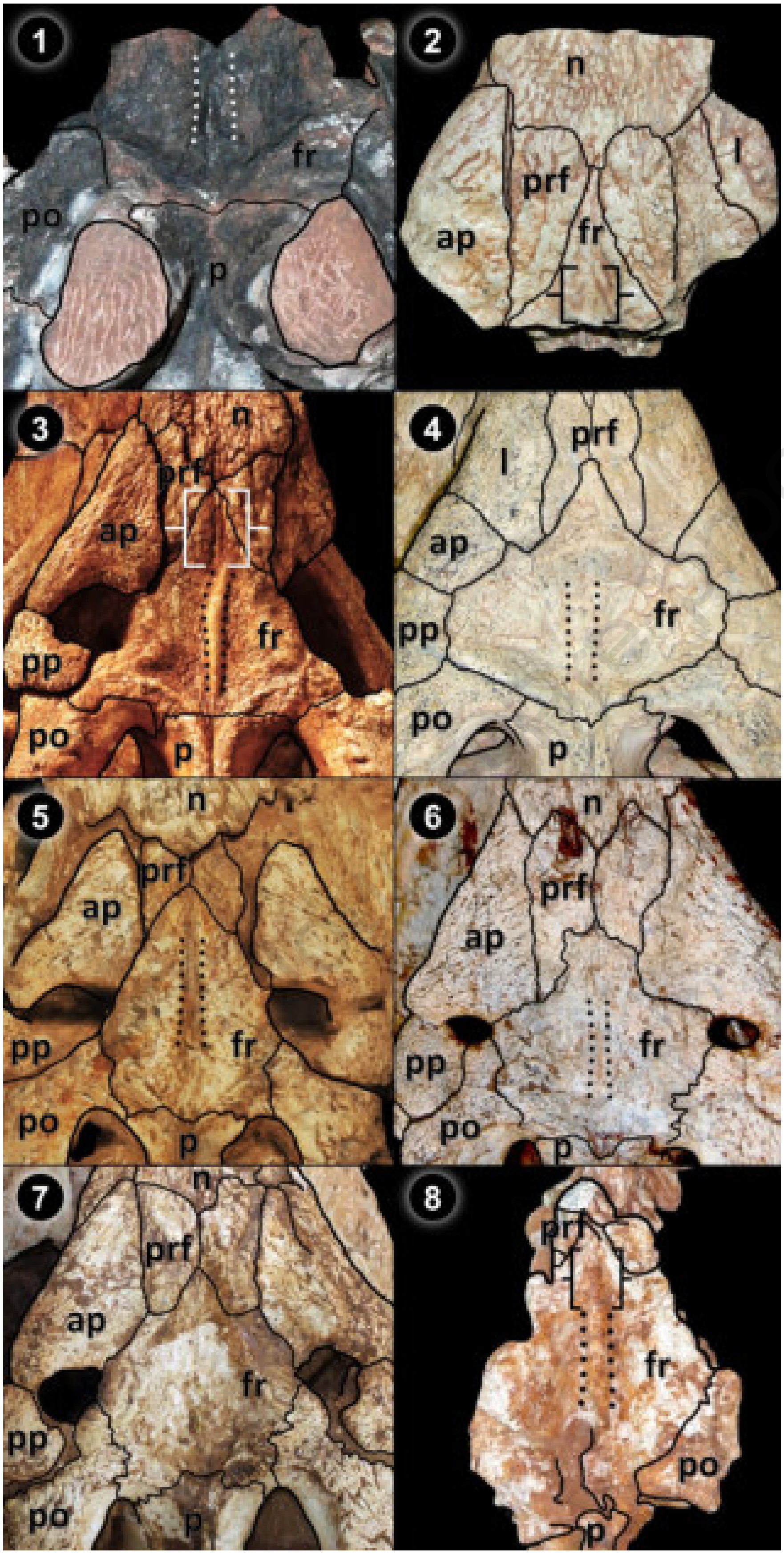
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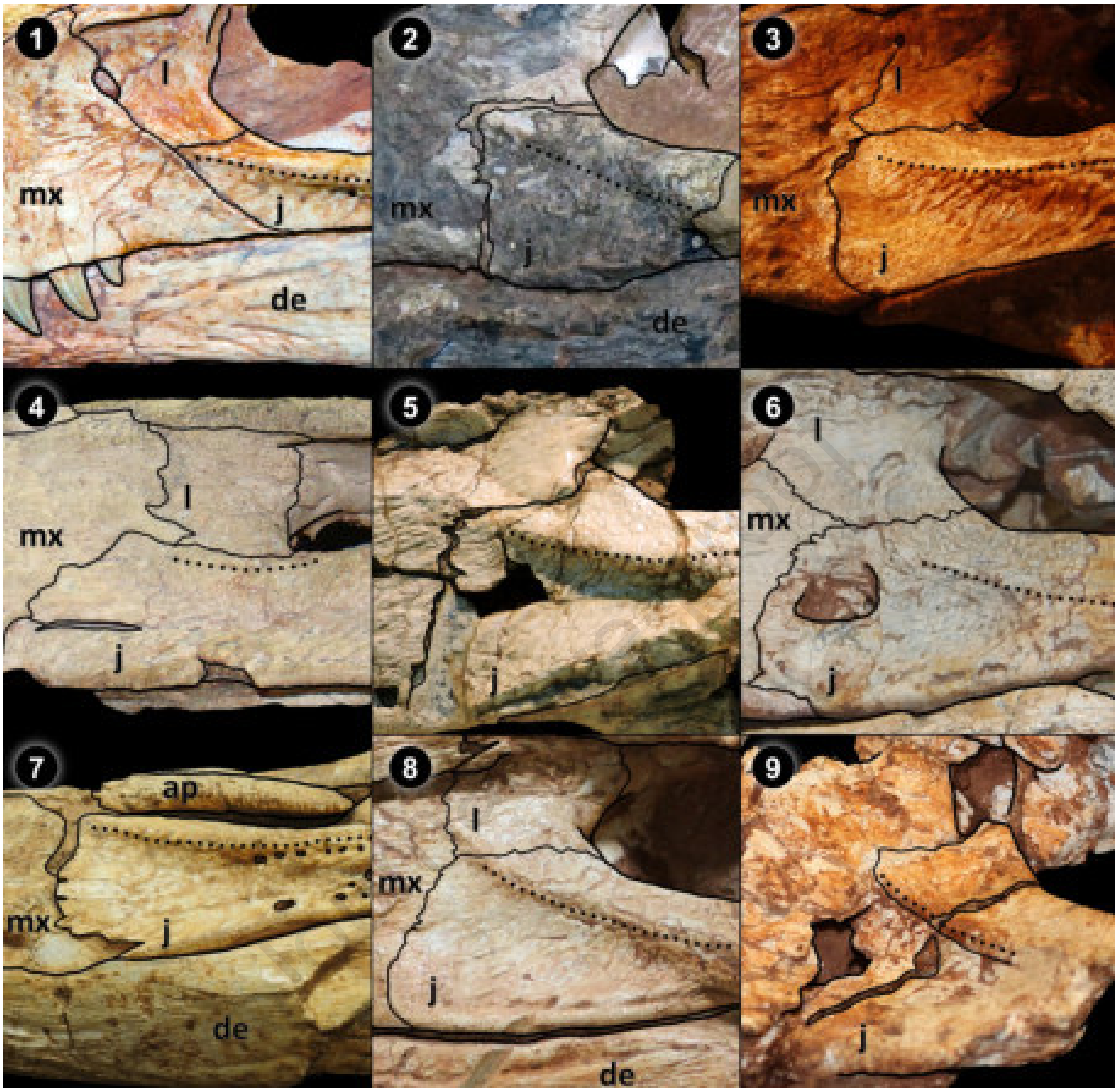
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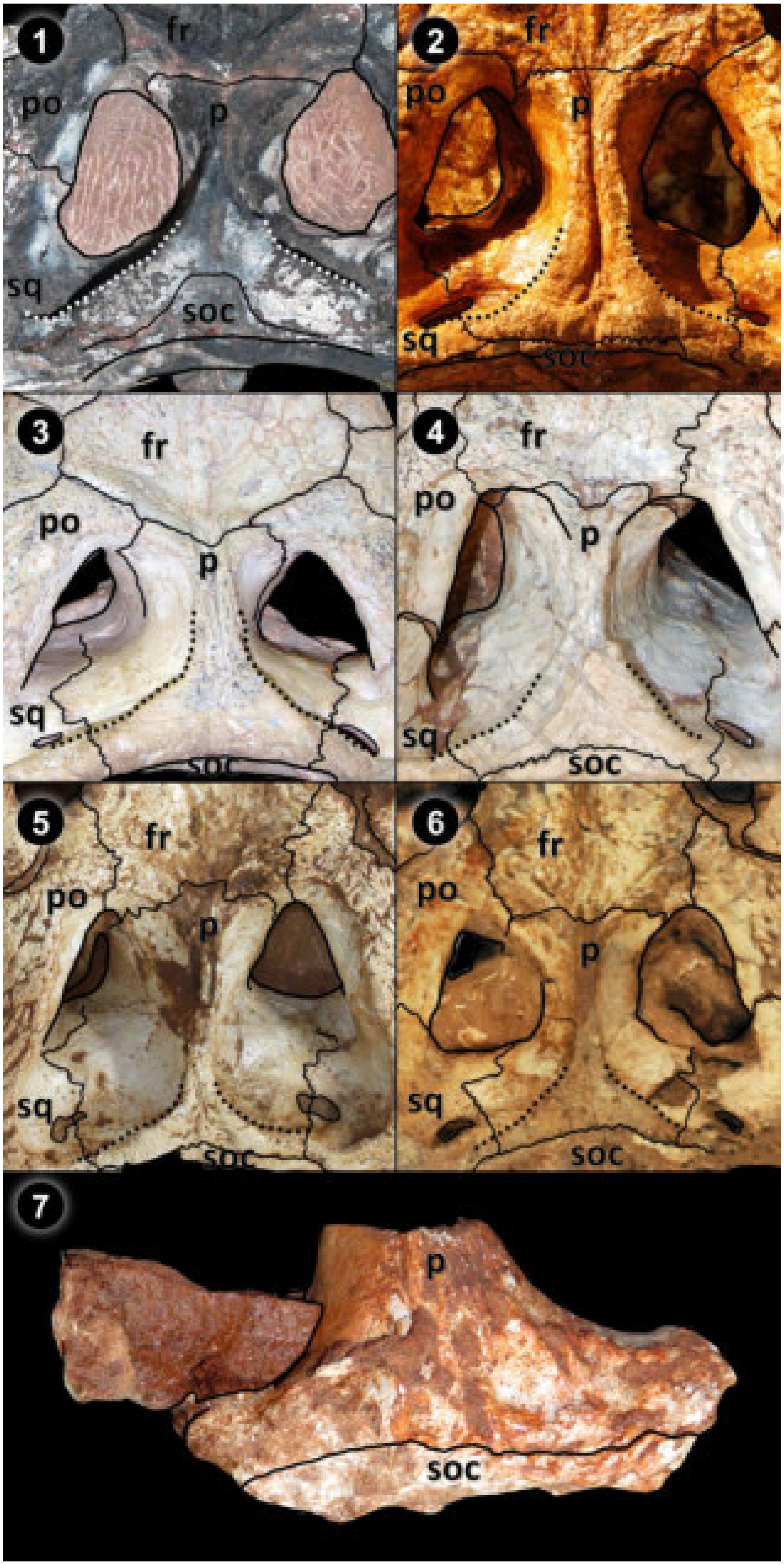
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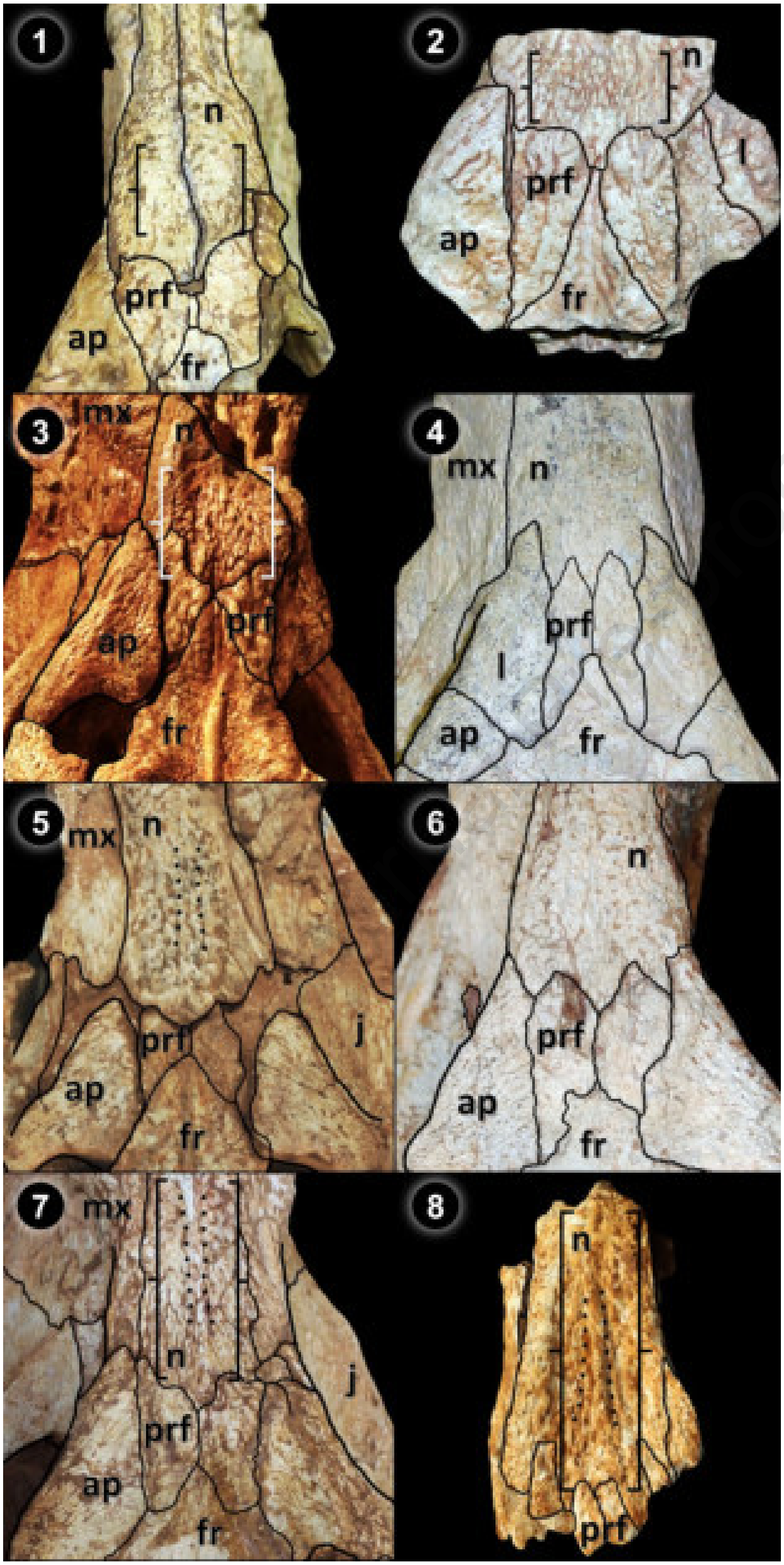
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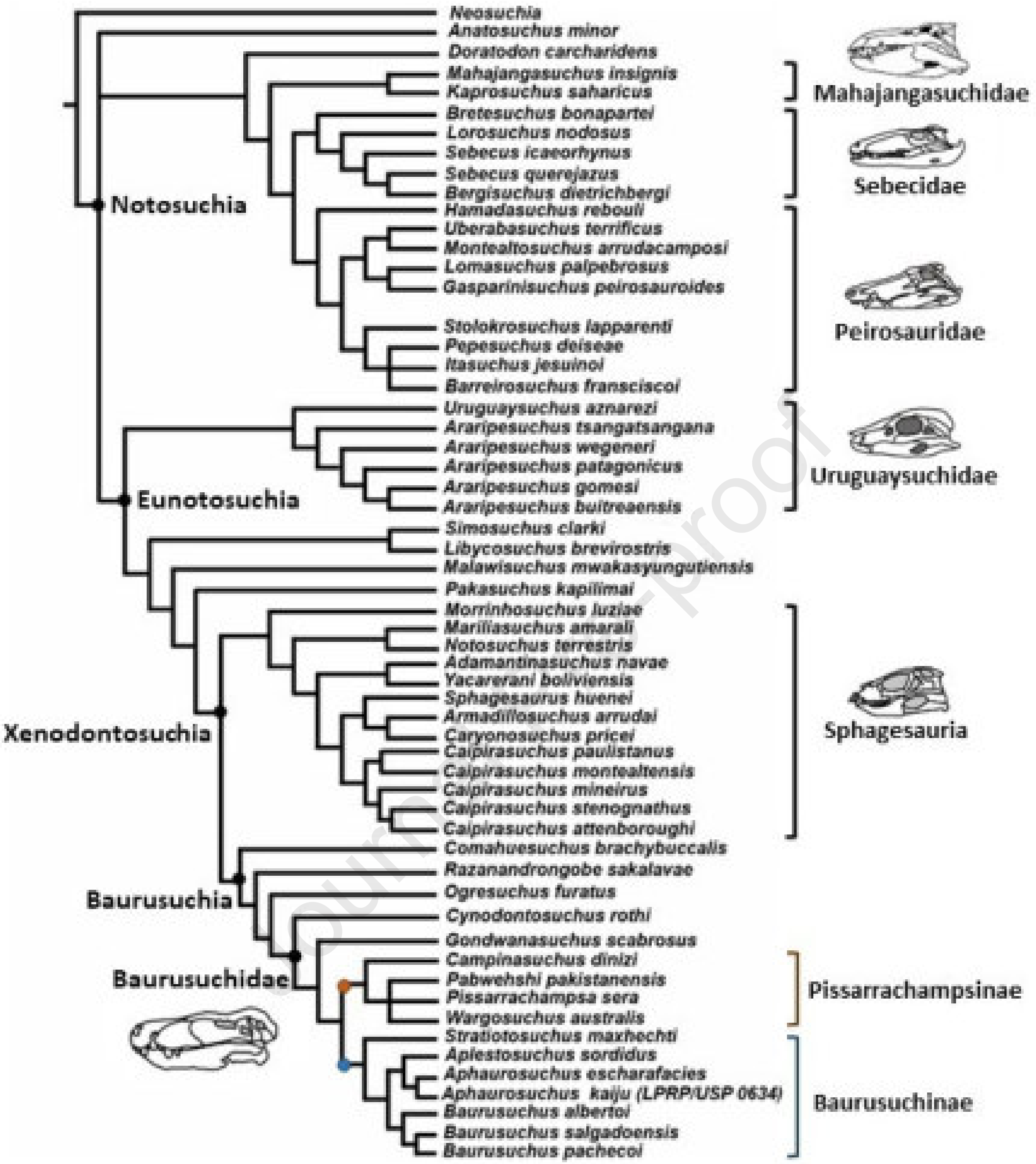
Neosuchia
Anatosuchus minor
Doratodon carcharidens
Mahajangasuchus insignis
Kaprosuchus saharicus
Mahajangasuchidae
Bretesuchus bonapartei
Lorosuchus nodosus
Sebecus icaeorhynus
Sebecus querejazus
Bergisuchus dietrichbergi
Sebecidae
Notosuchia
Hamadasuchus rebouli
Uberabasuchus terrificus
Montealtosuchus arrudacamposi
Lomasuchus palpebrosus
Gasparinisuchus peirosauroides
Stolokrosuchus lapparenti
Pepesuchus deiseae
Itasuchus jesuinoi
Barreirosuchus fransciscoi
Peirosauridae
Uruguaysuchus aznarezi
Araripesuchus tsangatsangana
Araripesuchus wegeneri
Araripesuchus patagonicus
Araripesuchus gomesi
Araripesuchus buitreaensis
Uruguaysuchidae
Eunotosuchia
Simosuchus clarki
Libycosuchus brevirostris
Malawisuchus mwakasyungutiensis
Pakasuchus kapilimai
Morrinhosuchus luziae
Mariliasuchus amarali
Notosuchus terrestris
Adamantinasuchus navae
Yacarerani boliviensis
Sphagesaurus huenei
Armadillosuchus arrudai
Caryonosuchus pricei
Caipirasuchus paulistanus
Caipirasuchus montealtensis
Caipirasuchus mineirus
Caipirasuchus stenognathus
Caipirasuchus attenboroughi
Xenodontosuchia
Sphagesauria
Comahuesuchus brachybuccalis
Razanandrongobe sakalavae
Baurusuchia
Ogresuchus furatus
Cynodontosuchus rothi
Gondwanasuchus scabrosus
Baurusuchidae
Campinasuchus dinizi
Pabwehshi pakistanensis
Pissarrachampsa sera
Wargosuchus australis
Pissarrachampsinae
Stratiotosuchus maxhechti
Apiestosuchus sordidus
Aphaurosuchus escharafacies
Aphaurosuchus kaiju (LPRP/USP 0634)
Baurusuchus albertoi
Baurusuchus salgadoensis
Baurusuchus pachecoi
Baurusuchinae

KCM: conceptualization, methodology, analysis, data curation, writing (original draft, review, editing)

MVLQ: data curation, writing (review, editing)

JVR: data curation, writing (review, editing)

MCL: writing (review, editing)

FCM: supervision, writing (review, editing)

All authors have approved the final version of the manuscript.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: