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To cite this article: Thiago S. Fachini, Pedro L. Godoy, Júlio C. A. Marsola, Felipe C. Montefeltro & Max C. Langer (2022): A large-sized mesoeucrocodylian from the Late Cretaceous of Brazil with possible neosuchian affinities, Historical Biology, DOI: [10.1080/08912963.2022.2122822](https://doi.org/10.1080/08912963.2022.2122822)

To link to this article: <https://doi.org/10.1080/08912963.2022.2122822>




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Published online: 26 Sep 2022.



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A large-sized mesoeucrocodylian from the Late Cretaceous of Brazil with possible neosuchian affinities

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ABSTRACT

Most crocodyliforms of the Bauru Group were found in rocks of the Adamantina Formation, whereas the younger Marília Formation is almost devoid of such fossils. Here, we provide a detailed comparative description of MPMA 02–0005/87, a large skull roof found in Marília Formation deposits of the Monte Alto area, assigning it to a new crocodyliform. Despite its fragmentary nature and puzzling suit of characters, the new taxon possesses enough characters to reject its placement within Notosuchia, which is so far the only crocodyliform clade known from the Bauru Group. We tested its phylogenetic position with twodata matrices, both of which recovered the new taxon within Neosuchia and Eusuchia. Although the material does not preserve any eusuchian synapomorphy, a neosuchian affinity is supported by: anterior extension of the meatal chamber covered by the squamosal; constricted flange of the posterior process of the postorbital; poorly developed posterolateral process of squamosal. Finally, the large size estimated for the specimen, ranging from 2.98 to 5.88 metres, coupled with its possible neosuchian affinity, suggests a possible semiaquatic behaviour, an ecology rarely explored by the predominantly terrestrial crocodyliforms of the Bauru Group.

<http://www.zoobank.org/urn:lsid:zoobank.org:pub:3C7C9499-FFE3-4D5A-A90B-DE2E3572EF16>
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ARTICLE HISTORY

Received 10 June 2022
Accepted 2 September 2022

KEYWORDS

Notosuchia; Neosuchia;
Eusuchia; Crocodyliformes;
Bauru Group; Marília
Formation

Introduction


The Bauru Group (Figure 1) is a vertebrate-rich Late Cretaceous lithostratigraphic unit that crops-out in south-central Brazil (Menegazzo et al. 2016; Batezelli 2017), which is famous for its extensive record of crocodyliforms (Carvalho et al. 2010; Godoy et al. 2014; Martinelli and Teixeira 2015). However, this diversity is currently represented only by notosuchians (Mannion et al. 2015; Pol and Leardi 2015), a group of predominantly terrestrial, small- to medium-sized crocodyliforms, which are not directly linked to the extant crocodylians and exhibited a wide range of morphologies and ecologies (Candeiro et al. 2006; Turner 2006; Carvalho et al. 2010; Godoy et al. 2014; Godoy et al. 2020; Nascimento 2014; Pol et al. 2014; Iori and Arruda-Campos 2016; Marsola et al. 2016; Melstrom et al. 2019; Montefeltro 2019; Wilberg et al. 2019; Stubbs et al. 2021). One of the most significant fossil-bearing areas of the Bauru Group is the Monte Alto municipality, which has already yielded five formally named notosuchians: *Caipirasuchus montealtensis*, *Caipirasuchus paulistanus*, *Morrinhosuchus luziae*, *Montealtosuchus arrudacamposi*, and *Barreirosuchus franciscoi* (Carvalho et al. 2007; Iori and Carvalho 2009; 2011; Montefeltro et al. 2011; Iori and Garcia 2012; Iori et al. 2013; 2018).


All Monte Alto notosuchians have been recovered from rocks of the Adamantina Formation, the age of which has been the subject of intense debate, with high-precision U-Pb dating recently revealing a post-Turonian maximal age of around 87.8 million years ago

(Castro et al. 2018; but see Gobbo-Rodrigues et al. 1999; Dias-Brito et al. 2001; Menegazzo et al. 2016; Batezelli 2017 for alternative ages based on biostratigraphy). Yet, the Monte Alto region also contains deposits of another stratigraphic unit within the Bauru Group, the Marília Formation (Figure 1), which is slightly younger in age, loosely dated as Maastrichtian based on biostratigraphy, using both vertebrates and microfossils (Dias-Brito et al. 2001; Santucci et al. 2008; Martinelli et al. 2011; Batezelli 2017). Although outcrops of the Marília Formation are not as common around Monte Alto as those of the Adamantina Formation, it is surprising that they have so far yielded almost no unambiguous crocodyliform fossils.

The only exception is the fragmentary skull roof MPMA 02–0005/87. Given its large size and fragmentary nature, the material was initially labelled as a partial titanosaur skull in the museum exhibition, but later acknowledged as a fragmentary crocodyliform skull (Iori and De Arruda-Campos 2016). According to newly proposed stratigraphic schemes (Soares et al. 2020), this represents the only crocodyliform known from the Marília Formation. Although breakages prevent the complete removal of the rock matrix, the right side of the specimen is relatively well-preserved, which allowed Iori and Arruda-Campos (2016) to briefly describe it. Those authors compared MPMA 02–0005/87 mostly with notosuchians, but refrained from its more precise assignment to any crocodyliform subgroup.

In this study, we provide a detailed description of MPMA 02–0005/87 and a full morphological comparison to a wide range of

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 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/08912963.2022.2122822>

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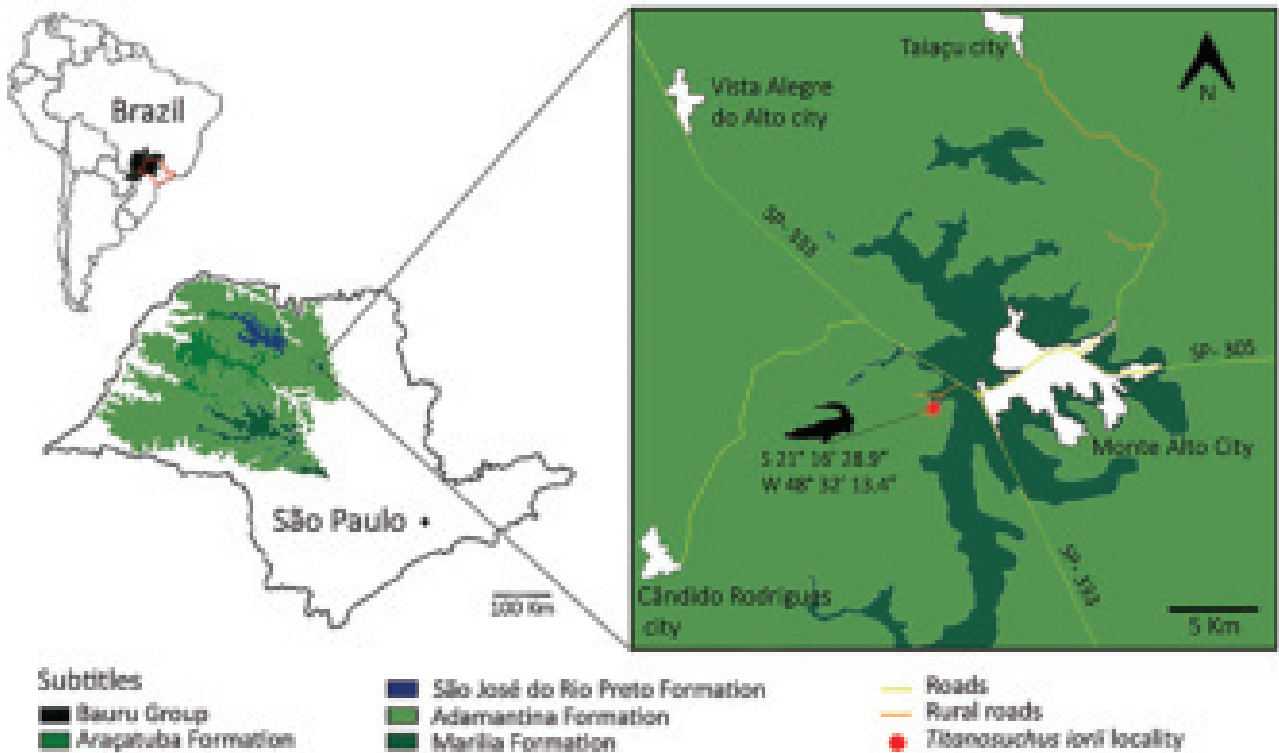


Figure 1. Geological map of the Bauru Group in São Paulo state. The type-location of MPMA 02–0005/87 is indicated by a red dot.

mesoeucrocodylians, which allowed its assignment to a new taxon. We performed a pair of phylogenetic analyses to assess its position among Crocodyliformes, by scoring the specimen into two comprehensive data matrices, with the addition of some newly proposed characters. Finally, we also estimated the total body length of the specimen, discussing its paleoenvironmental and palaeoecological implications.

Material and methods

The crocodyliform material described here includes a partially preserved skull roof, with the right side of the temporal arch, posterior portion of the orbits, right meatal chamber, and the occipital region only incompletely present. The material was collected in 1987 and is housed at the Museu de Paleontologia ‘Professor Antonio Celso de Arruda Campos’ (MPMA). We used the literature and first-hand examination of fossil specimens to conduct the morphological comparative description. The full list of specimens analysed can be found in the Supplementary Material.

Phylogenetic analysis

The phylogenetic position of MPMA 02–0005/87 was tested with its inclusion in two independent morphological datasets. First, we used the matrix of Martínez et al. (2018) with 114 taxa and 441 characters, which is one of the most recent versions of the dataset originally assembled by Pol et al. (2014). Second, we scored MPMA 02–0005/87 into the dataset of Ruiz et al. (2021) with 101 taxa and 507 characters, an updated version of the matrix first presented by Montefeltro et al. (2013). These datasets were chosen because they include a significant number of notosuchians and neosuchians, given that the affinity of the specimen within Mesoeucrocodylia is uncertain. Furthermore, to better represent the morphological information available for MPMA 02–0005/87

(i.e., cranial roof bones), we expanded both datasets by proposing seven new characters (see Supplementary Material).

Maximum parsimony equally weighted phylogenetic analyses were performed using TNT version 1.5 (Goloboff et al. 2008; Goloboff and Catalano 2016). For each data matrix, a heuristic search (‘Traditional Search’ in TNT) of 1,000 replicates was conducted using random addition sequences (RAS), with random seed value set to 0, followed by tree bisection and reconnection (TBR) branch swapping and 10 trees saved per replication. Another round of TBR was performed at the end of the replicates (i.e., trees saved in memory) and the trees were collapsed after the searches. Most parsimonious trees were summarised in strict consensus.

Body size estimation

The total body length of MPMA 02–0005/87 was estimated based on comparisons with preserved cranial elements of other mesoeucrocodylians, followed by the application of equation to estimate total body length of crocodyliforms. First, we roughly estimated the dorsal skull length (DCL) of MPMA 02–0005/87, by comparing the width of its skull roof to that of multiple crocodyliforms, given the uncertain affinity of the specimen within Mesoeucrocodylia. The skull roof width of MPMA 02–0005/87 was calculated by measuring the lateral border of the squamosal until the midpoint of the dorsal anterior surface of the parietal, which was subsequently multiplied by two to obtain the total skull roof width. The taxon sampling used for comparison prioritised specimens with skull roof width roughly similar to that of MPMA 02–0005/87, varying between 10 and 20 cm. It includes the living crocodylians *Crocodylus acutus* and *Alligator mississippiensis*, the notosuchians *Uberabasuchus terrificus* and *Stratiotosuchus maxhechti*, and the neosuchian *Eosuchus lerichei*. Subsequently, we used the range of DCL estimates to obtain the total body length (TL) by applying the equations presented by Hurlburt et al. (2003), which uses regressed data from extant crocodylian

species. All the measurements, equations and list of taxa used for the body size estimation can be found in the Supplemental Material.

Institutional abbreviations

MPMA, Museu de Paleontologia ‘Professor Antonio Celso de Arruda Campos’; LPRP/USP, Laboratório de Paleontologia da Universidade de São Paulo, Campus Ribeirão Preto.

Systematic palaeontology

CROCODYLOMORPHA Hay, 1930 (*sensu* Benton and Clark 1988)

CROCODYLIFORMES Hay, 1930 (*sensu* Clark 1986)

MESOEUCROCODYLIA Whetstone and Whybrow 1983

Titanochampsia iorii gen. et sp. nov.

Etymology

The generic name congregates the latinised Greek words ‘*titan*’ (= large/brutal) and ‘*champsia*’ (= crocodile), in reference to the large size of the animal and also its previous identification as a titanosaur dinosaur. The specific epithet ‘*iorii*’ honours the Brazilian palaeontologist Fabiano V. Iori, due to his numerous contributions to the palaeontology of the Monte Alto region.

Holotype

MPMA 02–0005/87 (Figures 2–5), a partial cranial roof including frontal, parietal, supraoccipital, right postorbital, squamosal, quadratojugal, and laterosphenoid.

Type-locality and horizon

MPMA 02–0005/87 was collected in a site located about 3.5 km west from Monte Alto, São Paulo State (21° 16′ 28.9″ S, 48° 32′ 13.4″ W; Figure 1), at an altitude of about 760 m, on the embankments of a secondary road that gives access to the rural district of Água Limpa. It exposes sediments of the Marília Formation, which is composed of whitish, fine to medium, carbonated sandstones, with frequent calcrete beds (Iori and Arruda-Campos 2016) and has

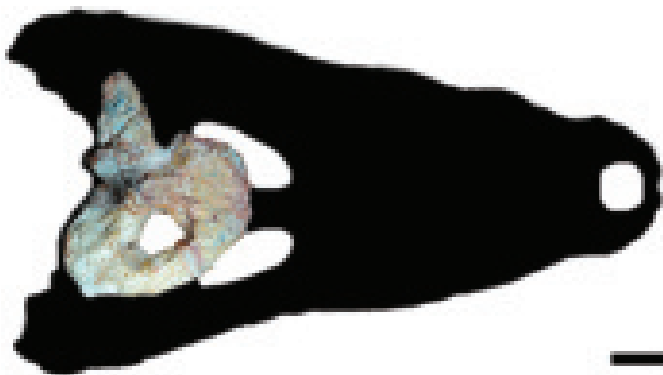


Figure 2. Position of the preserved skull roof of *Titanochampsia iorii* on a hypothetical crocodyliform skull. Scale bar – 5 cm.

a proposed Maastrichtian age (Bertini et al. 2001; Dias-Brito et al. 2001; Martinelli et al. 2011; Batezelli 2017; Soares et al. 2020).

Diagnosis

Titanochampsia iorii differs from all other Crocodyliformes by the following unique set of traits (autapomorphies marked with an asterisk): large supratemporal fenestrae, occupying over half of the area of the skull roof; flat dorsal surface of the frontal; laterally oriented capitate process of the laterosphenoid; anteroposterior projection of the parietal/squamosal set with almost the same length as the supratemporal fenestra*; dorsal end of the postorbital bar thicker than the supratemporal squamosal bar*; rudimentary crests on the dorsal surface of the anterior portion of the parietal; meatal chamber anteroposteriorly narrow; upper earlid groove placed only on the squamosal*; dorsal lamina of the frontal thicker than squamosal bar; anterodorsal process of the quadratojugal dorsally overcoming the tip of the infratemporal fenestra; dorsal, primary quadrate head articulating with prootic and laterosphenoid; small foramina piercing the dorsal surface of the postorbital bar.

Description

General morphology and ornamentation

The material is composed of a partial skull roof, including most of its right side (Figures 3–5). The squamosal, postorbital, and laterosphenoid are well-preserved, whereas the quadratojugal and supraoccipital are represented only by small fragments. Despite its incompleteness, *Titanochampsia iorii* bears several unique characters, which are discussed below. There are obvious signals of abrasion on the roof surface, but the ornamentation can still be observed, mainly on the squamosal, at the lateral corner of the skull. It is composed of small regularly spaced pits and faint grooves, mostly visible on the external surface of the frontal, parietal, postorbital, and squamosal (Figures 4–5). This ornamentation differs from that observed in baurusuchids, in which it varies between the lateral corner and the dorsal surface of the skull roof, with larger grooves in the postorbital and squamosal compared to those of the dorsal surface of the frontal (Carvalho et al. 2005, 2011; Pinheiro et al. 2008; Nascimento and Zaher 2010; Montefeltro et al. 2011). The skull roof ornamentation of *Titanochampsia iorii* contrasts with that of some peirosaurids (e.g., *Hamadasuchus rebouli*, *Pepesuchus deiseae*, *Stolokrosuchus lapparenti*, and *Rukwasuchus yajabalijekundu*), which have more developed pits and crenulations, as well as with that of most eusuchians (e.g., *Gavialis gangeticus*, *Hylaeochampsia vectiana*, *Allodaposuchus precedens*, *Crocodylus* sp., *Alligator mississippiensis*, *Susisuchus anatoceps*, *Isisfordia duncani*, *Lohuecosuchus megadontos*, *Agaresuchus fontisensis*, *Aegisuchus witmeri*, *Aegyptosuchus peyeri*, *Pietraroiasuchus ormezzanoi* and *Iharkutosuchus makadii*), which have larger and deeper pits and stronger grooves.

Skull roof

In dorsal view, the temporal bar of *Titanochampsia iorii* is posterolaterally directed, as in *Baurusuchus salgadoensis*, *Armadillosuchus arrudai*, *Lohuecosuchus megadontos*, *Iharkutosuchus makadii*, *Pietraroiasuchus ormezzanoi*, *Crocodylus porosus*, and *Montealtosuchus arrudacamposi* (Carvalho et al. 2005; Carvalho et al. 2007; Ősi et al. 2007; Marinho and Carvalho 2009; Buscalioni et al. 2011; Narváez et al. 2015). This differs from what is seen in *Barreirosuchus franciscoi*, *Hylaeochampsia vectiana*, *Gavialis gangeticus*, *Alligator mississippiensis*, *Crocodylus niloticus*, *Agaresuchus fontisensis*, *Susisuchus anatoceps*, and *Uberabasuchus*

terrificus, in which the temporal bar is roughly parallel to the lateral surface of the skull roof Holbrook 1842; Owen 1874; Salisbury et al. 2003; Carvalho et al. 2004; Iori and Garcia 2012; Narváez et al. 2016). In lateral view, the skull table of *Titanochampsia iorii* resembles the condition seen in *Aegisuchus witmeri* and *Aegyptosuchus peyeri*, being it dorsoventrally thick and buttressed by a robust laterosphenoids (Holliday and Gardner 2012). The postorbital posterior process and the squamosal anterior process are roughly horizontalized, as in *Barreirosuchus franciscoi*, *Armadillosuchus arrudai*, *Hylaeochampsia vectiana*, *Agaresuchus fontisensis*, *Osteolaemus tetraspis*, and *Gavialis gangeticus* (Carvalho et al. 2007; Marinho and Carvalho 2009; Iori and Garcia 2012), differing from the slightly convex outline seen in *Uberabasuchus terrificus* and *Baurusuchus salgadoensis* (Carvalho et al. 2004; Carvalho et al. 2005) and the sinuous outline of *Allodaposuchus precedens*, *Lohuecosuchus megadontos*, and *Crocodylus* spp. (Iordansky 1973; Delfino et al. 2008; Narváez et al. 2015).

Cranial openings

The supratemporal fenestra of *Titanochampsia iorii* has a triangle-shaped outline, slightly anteroposteriorly longer than lateromedially wide, with moderate exposure of the external supratemporal fossa (*sensu* Montefeltro et al. 2011). The lateral border of the supratemporal fenestra is slightly convex in dorsal view, whereas its medial margin is strongly concave. Such triangle-shaped fenestra is observed in some notosuchians, such as baurusuchids, mahajangasuchids, and *Armadillosuchus arrudai*. The external supratemporal fossa is moderately wide at its anteromedial portion near the parietal-postorbital contact. It extends until the anterolateral margin of the descending processes of the parietal (*crista cranii parietalis*), which borders the transition between the anterior and the middle region of the dorsal lamina of the parietal, terminating near the parietal-squamosal suture. The posterolateral surface of the external supratemporal fossa is not anteroposteriorly wide, but deeply concave (Figure 4). Such exposition of the external supratemporal fossa seems to be autapomorphic for *Titanochampsia iorii*. In dorsal view, the angle formed between medial and anterior margins of the external supratemporal fossa is approximately 90°, as in most crocodyliforms, except for thalattosuchians (e.g., *Dakosaurus andiniensis*, *Cricosaurus suevicus* and *Dakosaurus maximus*), in which the angle averages 45°.

Frontal

The frontals are fused, forming a partially preserved broad dorsal horizontal lamina and two thick descending laminae. The bone contacts the postorbitals posterolaterally via concave sutures, which resembles those of *Lohuecosuchus megadontos*, *Crocodylus acutus*, and *Alligator mississippiensis* (Martínez et al. 2018). These sutures are morphologically variable in notosuchians, from strongly concave, as in *Hamadasuchus rebouli*, baurusuchids, and *Barreirosuchus franciscoi* (Carvalho et al. 2005; Carvalho et al. 2011; Larsson and Sues 2007; Pinheiro et al. 2008; Nascimento and Zaher 2010; Montefeltro et al. 2011; Iori and Garcia 2012), to less sinuous, as in *Mahajangasuchus insignis*, *Armadillosuchus arrudai*, *Rukwasuchus yajabaliyekundu*, *Pepesuchus deiseae*, *Montealtosuchus arrudacamposi*, and *Uberabasuchus terrificus* (Carvalho et al. 2004; Carvalho et al. 2007; Turner and Buckley 2008; Marinho and Carvalho 2009; Campos et al. 2011; Sertich and O'Connor 2014).

The posterior portion of the frontal contacts the parietal via a near straight suture on the skull table similar to that of *Hamadasuchus rebouli* (Larsson and Sues 2007), becoming

posterolaterally oriented as it approaches the external supratemporal fossae. Yet, the same suture in *Barreirosuchus franciscoi*, *Montealtosuchus arrudacamposi*, *Lohuecosuchus megadontos*, and *Agaresuchus fontisensis* is transversely oriented in relation to the major axis of the skull, becoming straighter towards the external supratemporal fossae (Carvalho et al. 2007; Iori and Garcia 2012). In addition, among eusuchians, *Crocodylus* spp. shows a wedge-shaped frontal-parietal suture, with *Gavialis gangeticus* having a slightly convex one. Small posterior portions of the frontal of *Titanochampsia iorii* enter the external supratemporal fossae, contacting the parietal and postorbitals. The same is seen in *Hamadasuchus rebouli* and *Rukwasuchus yajabaliyekundu* (Larsson and Sues 2007; Sertich and O'Connor 2014), whereas extinct eusuchians (e.g., *Pierraroiasuchus ormezzanoi*, *Lohuecosuchus megadontos*, *Hylaeochampsia vectiana*) have the posterior parts of the frontal occupying a greater portion of the external supratemporal fossae, preventing the parietal-postorbital contact (Clark and Norell 1992; Buscalioni et al. 2011; Narváez et al. 2015).

The frontal of *Titanochampsia iorii* is notably thicker than that of any other taxa analysed here (Figures 3 and 5). Its descending lamina extends ventromedially, contacting the postorbital posterolaterally via a sinuous suture and the laterosphenoid via a nearly straight suture. In the ventral portion of the descending lamina, the *crista cranii frontalis* extends near the frontal-laterosphenoid suture. The groove formed by the *crista cranii frontalis* encompasses the olfactory and optic tracts and is proportionally narrower than that of *Barreirosuchus franciscoi*. The *crista cranii frontalis* forms a blunt lamina, resembling those of *Agaresuchus fontisensis* and *Allodaposuchus precedens*, whereas *Barreirosuchus franciscoi*, *Hamadasuchus rebouli*, *Pissarrachampsia sera*, *Montealtosuchus arrudacamposi*, *Rukwasuchus yajabaliyekundu*, and living crocodylians have a sharply laminated *crista cranii frontalis*.

Parietal

Only the anterior portion of the parietal is preserved, at the centre of the skull roof. The recovered part includes its dorsal body and descending laminae, which form the medial walls of the supratemporal fenestrae. The dorsal surface of the parietal is marked by two longitudinal crests near its lateral borders, where the descending laminae project ventrally. Although not as thick as in *Titanochampsia iorii*, these crests are also seen in other taxa, such as the notosuchians *Barreirosuchus franciscoi*, *Montealtosuchus arrudacamposi*, and *Uberabasuchus terrificus* (Carvalho et al. 2004; Carvalho et al. 2007; Iori and Garcia 2012), and the eusuchians *Agaresuchus fontisensis*, *Hylaeochampsia vectiana*, *Allodaposuchus precedens*, *Isisfordia duncani*, *Pierraroiasuchus ormezzanoi*, *Alligator mississippiensis*, *Crocodylus niloticus*, and *Crocodylus porosus*. Such crests of *Titanochampsia iorii* are somewhat similar to those of *Rukwasuchus yajabaliyekundu*, but lacks the sagittal crest seen in the parietal dorsal lamina of the later taxon (Figures 4A and C) (Sertich and O'Connor 2014).

The descending laminae of the parietal enter the supratemporal fenestrae, forming their entire anterolateral and medial portions, as well as most of the posterior portion. The anterior most portions of the laminae form the corners where parietal, frontal, and postorbitals contact one another. Anterior to the corners, the parietal descending laminae contact the descending laminae of the anterior portion of the postorbitals via curved, anteroventrally-directed sutures. These sutures end at the contact between the parietal, postorbitals, and laterosphenoids. Posterior to each of these triple contacts, there is a long and oblique posteroventral suture that separates the descending lamina of the parietal from the posterolateral lamina of the laterosphenoid, within the supratemporal fenestra.

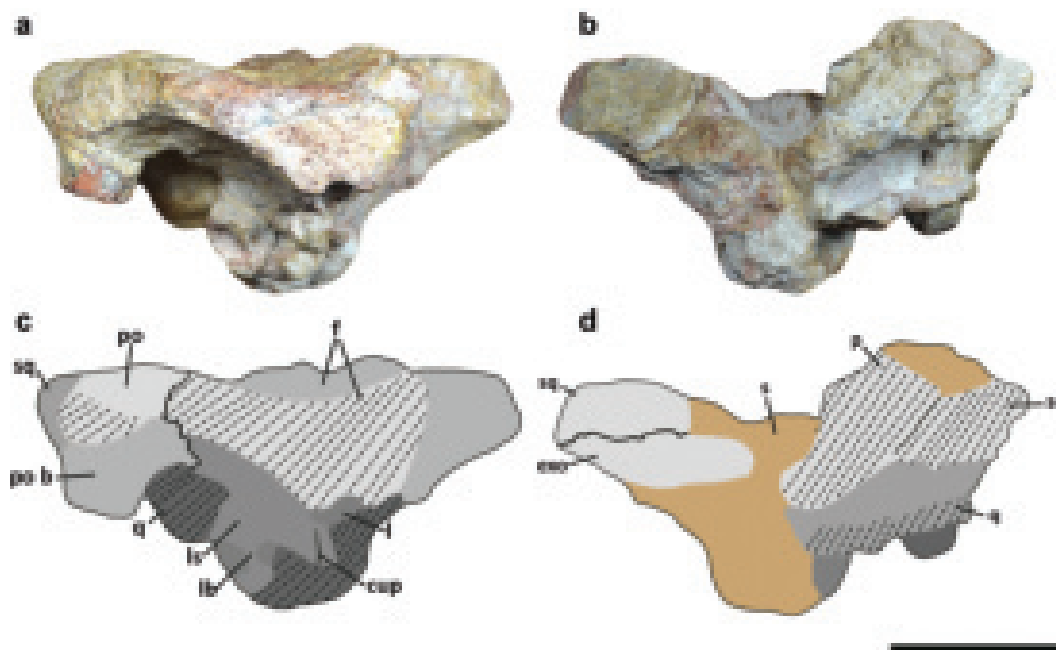


Figure 3. Partial skull roof of *Titanochampsia iorii*. in anterior (A and C) and posterior (B and D) views. Broken regions of the skull represented by hatched areas. Anatomical abbreviations: cup – cultriform process; exo – exoccipital; f – frontal; ls – laterosphenoid; lb – laterosphenoid bridge; p – parietal; po – postorbital; po b – postorbital bar; q – quadrate; sq – squamosal; l – olfactory foramen. Scale bar – 5 cm.

The posterior portion of the parietal bears an elevated and slightly sinuous suture with the squamosal, posterior to the supratemporal fenestrae. Although damaged, the posterior portion of the parietal represents more than 50% of the entire lateral extension of the cranial roof, an autapomorphy of *Titanochampsia iorii* (Figures 3B and D; Figures 4A and B). The descending laminae of the parietal briefly overlap the dorsal primary quadrate heads.

Supraoccipital

The presence of a partial suture with the parietal, suggests that the supraoccipital was a large element. Large supraoccipitals are also observed in some notosuchians, such as in baurusuchids, *Araripesuchus gomesii*, *Montealtosuchus arrudacamposi*, *Hamadasuchus rebouli*, *Lomasuchus palpebrosus*, *Pepesuchus deiseae*, and *Stolokrosuchus lapparenti*, as well as in the eusuchian *Eosuchus lerichei* (Gasparini et al. 1991; Delfino et al. 2005; Larsson and Sues 2007; Campos et al. 2011).

Postorbital

The postorbital is a triradiate bone, formed by anteromedial, posterior, and descending processes. Its anteromedial and posterior regions form the dorsal lamina of the postorbital and are relatively robust (4 cm and 3.5 cm thick, respectively) (Figure 4). This indicates a wide postorbital, even when compared to those of large taxa such as *Barreirosuchus franciscoi* and *Baurusuchus salgadoensis* (Carvalho et al. 2005; Iori and Garcia 2012). The posterior process of the postorbital forms most of the lateral border of the supratemporal fenestra, contacting the squamosal via an irregular suture. In lateral view, the suture is slightly curved and oblique. On the lateral border of the supratemporal fenestra, that suture extends anteroventrally in a zig-zag fashion along the dorsalmost portion of the descending process, until it contacts the dorsal primary head of the quadrate.

The orbital lamina of the postorbital is formed by anteromedial and descending processes. The latter is short, laterally expanded, and dorsoventrally depressed, unlike the plate descending lamina (*sensu* Pol et al. 2014) found in all notosuchians, including peirosaurids and mahajangasuchids (Pol et al. 2014). As in *Titanochampsia iorii*, most neosuchians lack the plate descending lamina, e.g., *Agaresuchus fontisensis*, *Allodaposuchus precedens*, *Gavialis gangeticus*, *Alligator mississippiensis*, *Crocodylus* spp., *Hylaeochampsia vectiana*, *Lohuecosuchus megadontos*, and *Isisfordia duncani* (Iordansky 1973; Clark and Norell 1992; Delfino et al. 2008; Narváez et al. 2015; 2016). The descending process of the postorbital meets the anterior tip of the squamosal and the anterodorsal portion of the quadratojugal, posterior to the dorsal end of the postorbital bar, but not the anterodorsal process of the quadrate, as also observed in *Allodaposuchus precedens*, *Agaresuchus fontisensis*, *Gavialis gangeticus*, *Osteolaemus tetraspis*, *Tomistoma schlegelii*, and baurusuchids.

The postorbital bar is oval-shaped in cross-section and has an anterolaterally directed small spur in its dorsal region (Figures 4–5). This spur is also observed in *Pepesuchus deiseae* and some living crocodylians, such as *Gavialis gangeticus* and Caimaninae (Iordansky 1973; Campos et al. 2011), and is quite different from the long and robust element present in dyrosaurids (de Stefano 1903; Denton et al. 1997; Jouve et al. 2006; Hastings et al. 2010). Moreover, the anterior and medial surfaces of the postorbital bar are flat, whereas the lateral and posterior surfaces possess irregular outlines. In lateral view, the dorsal part of the postorbital bar bears a moderate-sized notch, with many small foramina, which indicate some level of vascularisation. A vascularised postorbital bar is typical of some neosuchians, such as *Theriosuchus pusillus*, *Calsoyasuchus valliceps*, and *Sunosuchus junggarensis* and eusuchians, such as *Gavialis gangeticus*, *Leidyosuchus canadensis*, *Crocodylus* spp., and *Alligator* spp. The dorsal end of the postorbital bar is oriented almost vertically, as seen in *Barreirosuchus*

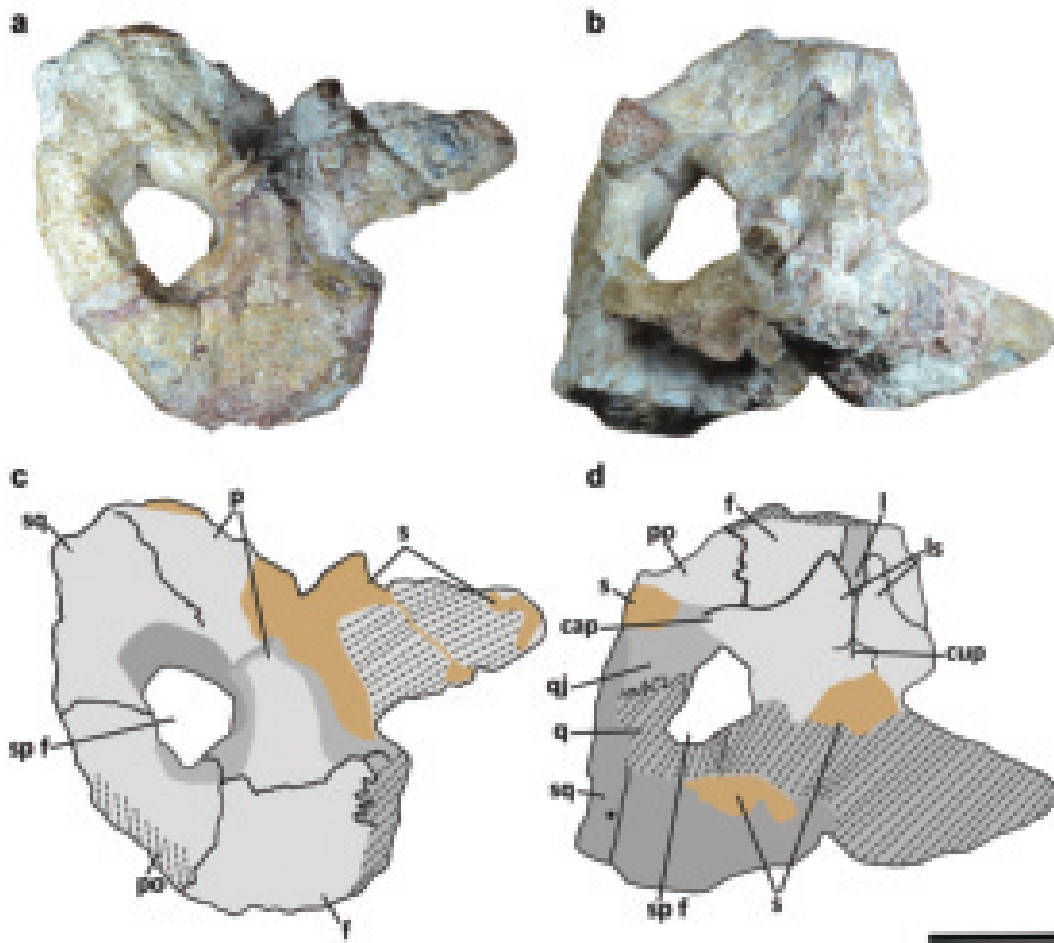


Figure 4. Partial skull roof of *Titanochampsia iorii* in dorsal (A and C) and ventral (B and D) views. Broken regions of the skull represented by hatched areas. Anatomical abbreviations: cap – capitate process; cup – cultriform process; f – frontal; ls – laterosphenoid; p – parietal; po – postorbital; q – quadrate; qj – quadratojugal; s – sediment; sp f – supratemporal fenestra; sq – squamosal; l – olfactory foramen. Scale bar – 5 cm.

franciscoi, *Hamadasuchus rebouli*, *Pepesuchus deiseae*, *Baurusuchus salgadoensis*, and *Gavialis gangeticus* (Carvalho et al. 2005; Larsson and Sues 2007; Campos et al. 2011; Iori and Garcia 2012), but diverging from *Caiman latirostris* (LPRP/USP 0008 A), in which it is more anterolaterally directed.

Squamosal

The squamosal is a triradiate bone formed by anterior, medial, and posterior processes, the confluence of which forms a thick dorsal body. The dorsal body and the descending processes border part of the posterolateral margin of the supratemporal fenestra and contact the descending lamina of the parietal via a sinuous suture. In lateral view, the anterior descending process extends ventrally dorsal to the quadratojugal, under the posterior portion of the postorbital, as a tapering process that reaches the descending process of that bone (Figure 5). This condition resembles that of *Gavialis gangeticus*, differing from the vast majority of notosuchians, in which the descending process reaches the level of the contact between the postorbital bar and the posterior palpebral (Campos et al. 2011; Iori and Garcia 2012; Pol et al. 2014; Sertich and O'Connor 2014).

There is a faint groove for the upper ear lid that extends across the lateral margin of the squamosal, as seen in most extinct and extant mesoeucrocodylians (Montefeltro et al. 2016). Intriguingly, *Titanochampsia iorii* has a small notched area just anterior to the

posterior lobe of the squamosal, which is also seen in *Shamosuchus djadochtaensis* (Pol et al. 2009; Turner 2015). The roof of the meatal chamber is formed by the anterior process and the descending lamina of the medial and posterior processes of the squamosal. The roof is not ventrally concave as in peirosaurids, baurusuchids, and extant crocodylians (Iordansky 1973; Carvalho et al. 2004; 2005, 2007; Larsson and Sues 2007; Pinheiro et al. 2008; Nascimento and Zaher 2010; Sertich and O'Connor 2014). Its ventral surface is formed entirely by the anteroventral extension of the squamosal. The anterior process of the squamosal is hypertrophied and slopes laterodorsally, gradually becoming horizontal at the level of dorsal margin of the bony otic aperture.

Despite its partial preservation, the posterior descending process of the squamosal does not seem to flare as in *Rukwasuchus yajabaliyekundu* (Sertich and O'Connor 2014). Moreover, it is distally oriented, forming a very short and shallow posterior portion of the meatal chamber. This condition resembles that of living crocodylians (e.g., *Crocodylus* spp., *Gavialis gangeticus*, *Alligator mississippiensis*, *Paleosuchus palpebrosus*, and *Tomistoma schlegelii*) and some extinct mesoeucrocodylians (e.g., *Barreirosuchus franciscoi*, *Shamosuchus djadochtaensis*, *Hylaeochampsia vectiana*, *Hamadasuchus rebouli*, *Mahajangasuchus insignis*, and *Stolokrosuchus lapparenti*) (Larsson and Gado 2000; Clark and Norell 1992; Larsson and Sues 2007; Turner and Buckley 2008; Iori and Garcia 2012; Turner 2015). The suture between the posterior descending process of the squamosal and the dorsal process of

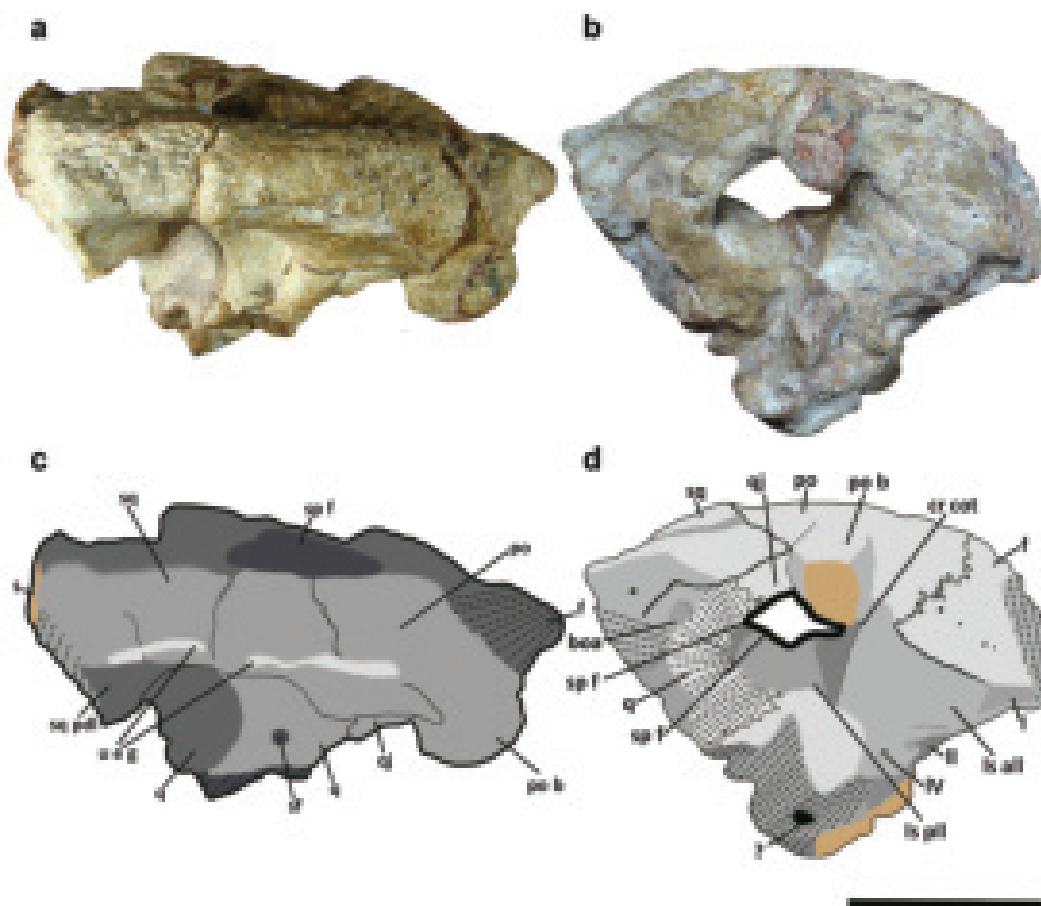


Figure 5. Partial skull roof of *Titanochampsia iorii* in lateral (A and C) and ventrolateral (B and D) views. Broken regions of the skull represented by hatched areas. Anatomical abbreviations: boa – bony otic aperture; cr cot; cotylar crest; f – frontal; ls all – laterosphenoid anterolateral lamina; ls pll – laterosphenoid posterolateral lamina; po – postorbital; po b – postorbital bar; q – quadrate; qj – quadratojugal; s – sediment; sf – foramen siphoneal; sp f – supratemporal fenestra; sq – squamosal; sq pdl – squamosal posterior descending lamina; u e g – upper earlid groove; ? – unidentified structure; I – olfactory foramen; II – optic foramen; IV – trochlear foramen. Scale bar – 5 cm.

the quadrate is posteroventrally oriented, as seen in *Barreirosuchus franciscoi* (Iori and Garcia 2012), whereas *Caiman latirostris* has a sub-horizontal suture. There is a large foramen at the ventral surface of the posterior descending process of the squamosal. The shallow meatal chamber of *Titanochampsia iorii* is clearly seen because the bony otic aperture is close to the lateral margin of the dorsal lamina of the squamosal, as in *Pepesuchus deiseae* (Campos et al. 2011).

Quadrate

The quadrate is incomplete, preserving only a partial primary head and its anterodorsal process. In lateral view, the anterodorsal process forms a dorsally oriented wall, anterior to the bony otic aperture, which is also seen in *Mahajangasuchus insignis*, *Stolokrosuchus lapparenti*, *Hamadasuchus rebouli*, *Rukwasuchus yajabaliyekundu*, *Pepesuchus deiseae*, *Montealtosuchus arrudacamposi*, and *Uberabasuchus terrificus* (Carvalho et al. 2004; Carvalho et al. 2007; Larsson and Sues 2007; Turner and Buckley 2008; Campos et al. 2011; Sertich and O'Connor 2014). Such orientation is different from that of extant crocodylians, in which the anterodorsal process forms a medially-sloped wall, probably due to the dorsoventral flattening of the skull (Iordansky 1973). In this region, the anterodorsal process of the quadrate reaches the anterior region of the periotic fossa. The posteroventral margin of the bony otic aperture is not preserved, but it is possible to infer that it was dorsally directed, with an oval-shaped outline. This orientation resembles that

of *Mahajangasuchus insignis*, *Barreirosuchus franciscoi* (Iori and Garcia 2012), *Hamadasuchus rebouli*, *Rukwasuchus yajabaliyekundu*, *Pepesuchus deiseae*, and some extant crocodylians as *Gavialis gangeticus* and *Tomistoma schlegelii* (Larsson and Sues 2007; Campos et al. 2011; Sertich and O'Connor 2014). However, it differs from that of *Montealtosuchus arrudacamposi*, *Uberabasuchus terrificus*, and baurusuchids, in which the aperture is anterodorsally directed (Carvalho et al. 2004, 2005; 2007; 2011; Montefeltro et al. 2011).

The anterodorsal process of the quadrate forms the anterior, anterodorsal, and ventral margins of the bony otic aperture. Because the meatal chamber is shallow, the dorsal otic incisure of *Titanochampsia iorii* is entirely exposed in lateral view. The incisure is located at the anteromedial, ventrally extensive broad lamina. The otic buttress is not preserved, but we infer that it met the otic incisure posteriorly. The meatal chamber is anteroposteriorly elongated and, in its posterior region, the suture between the descending lamina of the squamosal and the anterodorsal process of the quadrate is oriented dorsally. The contact between the quadrate and the squamosal occurs at the posteroventral margin of the bony otic aperture, with the quadrate occupying the whole posteroventral border of the otic aperture, as seen in *Gavialis gangeticus* and *Tomistoma schlegelii* (Iordansky 1973).

Quadratojugal

The quadratojugal is only represented by a small fragment, which reaches the edge of the external supratemporal fossa, buttressing the

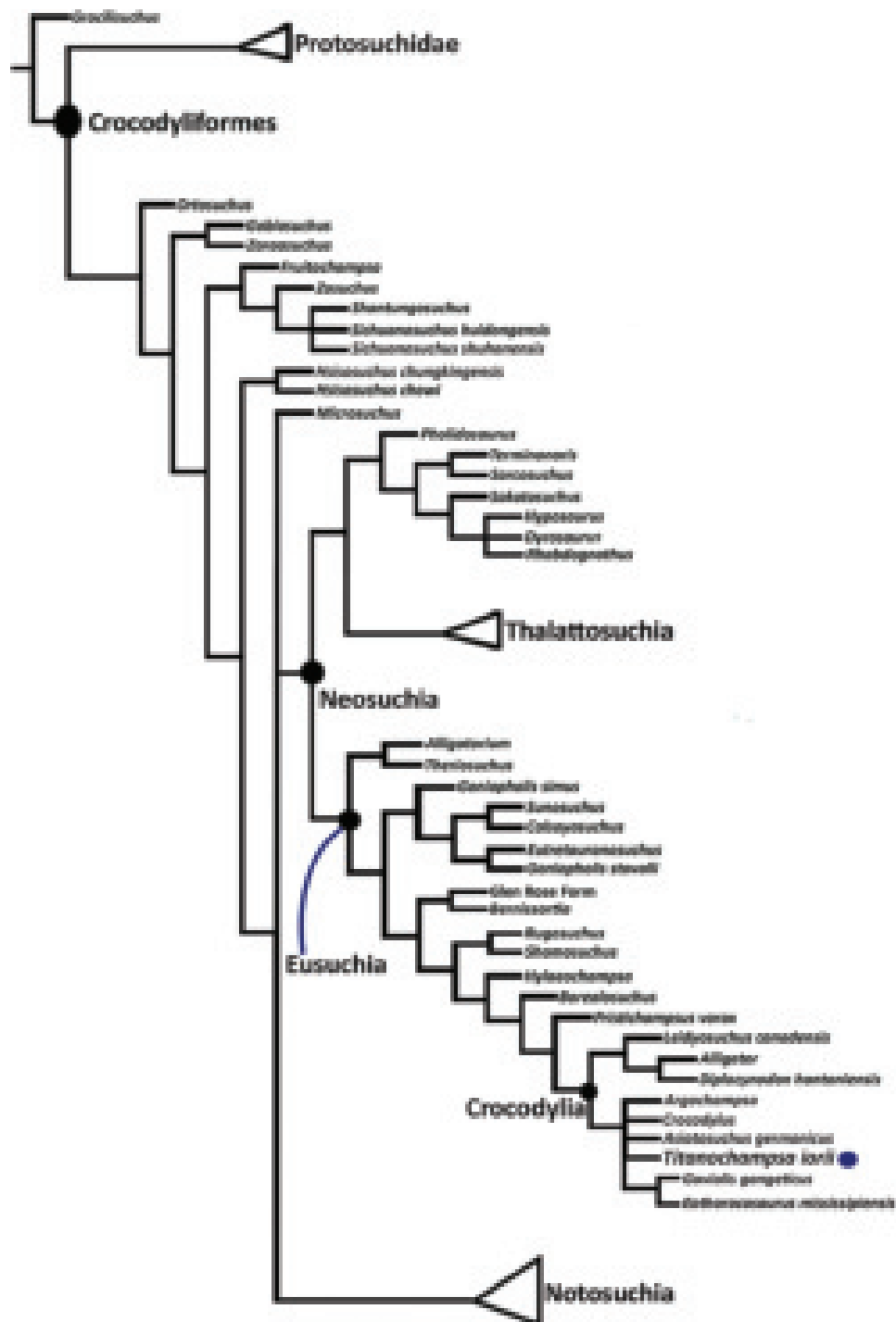


Figure 6. Resulting strict consensus cladogram illustrating the phylogenetic relations of *Titanochampsia iorii* and its position inside Crocodylia (modified matrix from Martínez et al. 2018).

anterior region of the descending lamina of the squamosal, the anterodorsal process of the quadrate, and the posterior descending lamina of the postorbital.

Laterosphenoid

The laterosphenoid forms the anterolateral walls of the braincase, and is divided in anterolateral and posterolateral laminae by a cotylar crest (Figures 4B and D; Figures 5 B and D). The

anterolateral lamina extends anteroposteriorly from the cotylar crest, buttressing the descending lamina and the posterior region of the dorsal lamina of the frontal. The surface of the anterolateral lamina of the laterosphenoid is notably concave, and the suture that separates that lamina from the descending lamina of the frontal is thick and slightly sloped ventrally. The medial tip of the anterolateral lamina meets its counterpart medially, forming a ventrally closed floor for the olfactory tract. The pair of laminae contact one another via a broad, rough, and posteriorly directed suture, forming the roof of the optic foramen. At its ventral most portion,

the laterosphenoid has a bulged area, located dorsal to the optic foramen canal. From this bulged area a crest extends dorsoventrally, meeting the roof of the optic foramen. Ventrolateral to the optic foramen, in the right anterolateral lamina, the trochlear foramen (IV) is found, distal to the ventral most portion of the anterolateral lamina and dorsal to the oculomotor foramen (III). Although present, the trigeminal region is badly preserved, precluding the proper assessment of its morphology. Posteriorly, the anterolateral lamina has a capitate process that are laterally oriented in *Titanochampsia iorii*, as well in *Aegisuchus witmeri*, *Aegyptosuchus peyeri* and gavialoids.

Results

Phylogenetic relationships

The analysis using the dataset of Martínez et al. (2018) resulted in 200,880 most parsimonious trees (MPTs) of 1,771 steps, whereas

that using the matrix of Ruiz et al. (2021) resulted in 560 MPTs of 2,318 steps. Both analyses placed *Titanochampsia iorii* nested within Neosuchia, in a close relation with eusuchians (Figures 6 and 7). The strict consensus of the first analysis, retrieved *Titanochampsia iorii* nested within Crocodylia, in a polytomy at the base of Longirostres (*sensu* Harshaman et al. 2003; i.e. Gavialoidea + Crocodyloidea), along with *Argochampsia krebsi*, *Crocodylus* spp., *Asiatosuchus germanicus*, and *Gavialis gangeticus* + *Eothoracosaurus mississippiensis*. Such arrangement is supported by only one synapomorphy, i.e., a wide posterior half of axial neural spine (character 258.1), which is not preserved in *Titanochampsia iorii*. In some MPTs, the clade is also supported by three other features (character 91.4, 100.0, and 71.0). However, none of these are preserved in *Titanochampsia iorii*. Indeed, among the fifty characters scored for *Titanochampsia iorii* in the dataset of Martínez et al. (2018), few provide some clues about its affinity to Neosuchia. These include the grooved external surface of the skull roof bones (character 1.1–2), also seen only in *Eothoracosaurus*

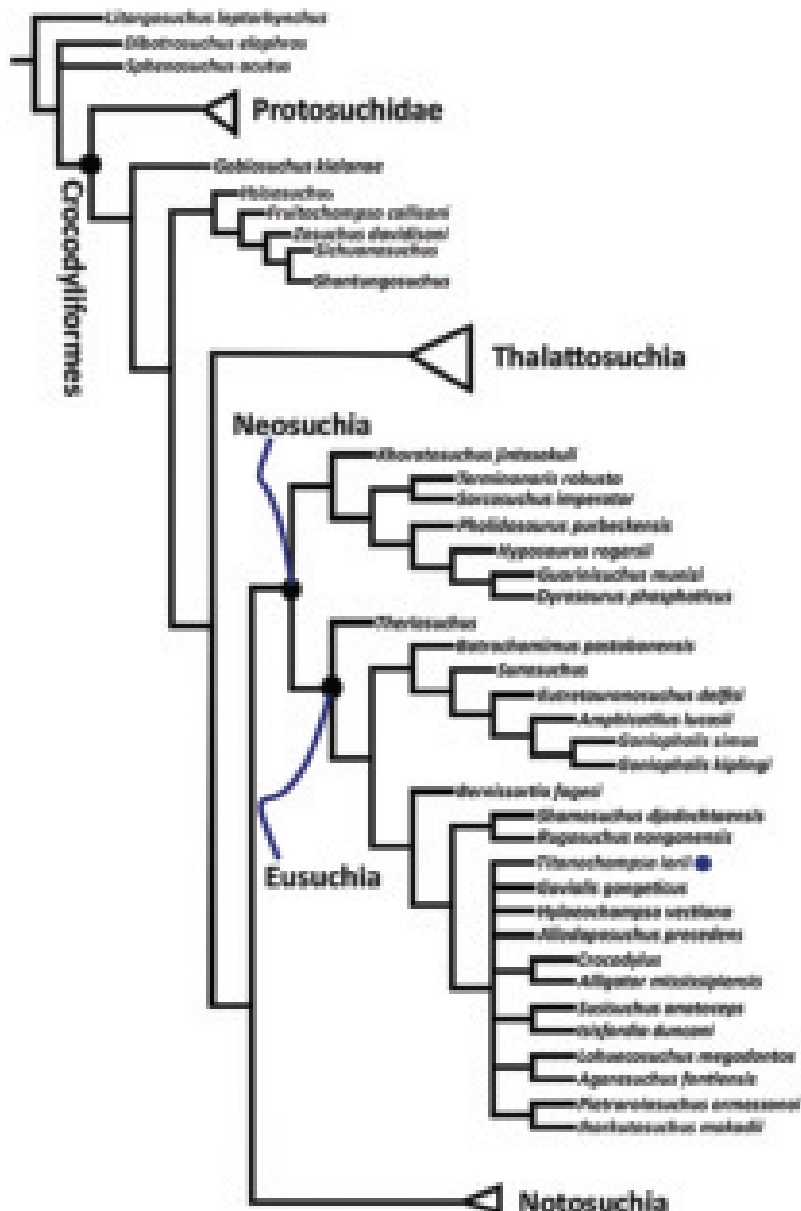


Figure 7. Resulting strict consensus cladogram illustrating the phylogenetic relationship of *Titanochampsia iorii* and its position inside Eusuchia (modified matrix from Ruiz et al. 2021).

mississippiensis; the anterolaterally facing edge of the dorsal part of the postorbital (character 29.1), observed in all neosuchians included in the dataset; and the anterior temporo-orbital opening exposed in dorsal view (character 173.0), shared only with *Sarcosuchus imperator*.

The second analysis – based on the dataset of Ruiz et al. (2021) – also recovered *Titanochampsia iorii* within Eusuchia (Figure 7), within a large polytomy that includes *Hylaeochampsia vectiana*, *Allodaposuchus precedens*, *Susisuchus anatoceps*, *Isisfordia duncani*, *Lohuecosuchus megadontos*, *Agaresuchus fontisensis*, *Pietraroiiasuchus ormezzanoii*, and *Iharkutosuchus makadii*, as well as the three extant crocodylians included in the analysis (*Gavialis gangeticus*, *Crocodylus* spp., and *Alligator mississippiensis*). Such clustering is supported by five synapomorphies (characters 1.1, 16.2, 100.2, 108.1, and 172.1), all of which are also not preserved in *Titanochampsia iorii*. Once again, very few of the sixty characters scored for *Titanochampsia iorii* in the matrix of Ruiz et al. (2021) indicate a neosuchian affinity for the taxon. The exceptions are an ornamented external surface of the sull roof bones (character 1.1), shared with Longirostres; and vascular openings in the dorsal surface of postorbital bar (character 172.1), which represents a neosuchian synapomorphy.

Discussion

Although the results of both phylogenetic analyses unambiguously place *Titanochampsia iorii* within Eusuchia, the incompleteness of the fossil material imposes caution towards a robust assignment even to Neosuchia. On the other hand, we are significantly more confident on rejecting a notosuchian affinity for this taxon. This is interesting given that the Late Cretaceous crocodyliform fauna of Gondwana is largely dominated by notosuchians, particularly in the Bauru Group (Godoy et al. 2014; Pol and Leardi 2015). The reasons for rejecting a notosuchian affinity are detailed below.

Rejecting a baurusuchid affinity for *Titanochampsia iorii*

Baurusuchids were relatively large-sized notosuchians and form the most taxonomic diverse group of crocodyliforms in the Bauru Group, with nine species described so far and several additional specimens reported (Pol and Leardi 2015; Dumont et al. 2020; Darlim et al. 2021). This justifies a tentative assignment of MPMA 02–0005/87 to the group, given that it also corresponds to a large specimen (see below). Yet, twelve characters, found in both matrices used here (Martínez et al. 2018; Ruiz et al. 2021), distinguish *Titanochampsia iorii* from baurusuchids, two of which represent synapomorphies of the clade: (1) the posterolateral process of the squamosal is elongated and ventrally directed in baurusuchids, forming an angle of approximately 90° to the skull roof, whereas it is poorly developed in *Titanochampsia iorii* and in neosuchians, projecting horizontally relative to the skull roof; (2) the dorsal surface of the frontal in baurusuchids has a broad basin-like depressed area bordered posteriorly by a transverse ridge, whereas that of *Titanochampsia iorii* and neosuchians is flat or only slightly depressed, lacking a transverse ridge.

The general architecture of the *Titanochampsia iorii* skull table is widely divergent from the morphology of all baurusuchid species. The small internal and enlarged external supratemporal fenestrae (*sensu* Montefeltro et al. 2011) create an extensive supratemporal fossa in baurusuchids, particularly at the posterior portion of the skull table, which is not seen in *Titanochampsia iorii*. In this taxon, the supratemporal fossa is reduced and equally developed around all its margins. The interfenestral bar between supratemporal fenestrae in baurusuchids is formed by a reduced surface (about half the

width of the supratemporal fenestra), whereas in *Titanochampsia iorii* the interfenestral bar is large (about the same width of the supratemporal fenestra). In addition, the lateral margins of the interfenestral bar in baurusuchids form hypertrophied rims for the fenestra, whereas in *Titanochampsia iorii* the bar has smooth edges.

Other characters that distinguish *Titanochampsia iorii* from baurusuchids include a narrow dorsal process of the quadratojugal that contacts only a small part of the postorbital, whereas the process is broad in baurusuchids, with an extensive contact with the postorbital. Additionally, the dorsal extension of the medial surface of the quadratojugal of *Titanochampsia iorii* reaches the dorsal margin of the infratemporal fenestra, whereas in baurusuchids it ends ventral to that. Likewise, baurusuchids and some other notosuchians have a midline ridge on the dorsal surface of the frontal and parietal, whereas that surface is flat in *Titanochampsia iorii*, peirosaurids, and most neosuchians. The slightly grooved ornamentation pattern seen in *Titanochampsia iorii* is similar to that of the early crocodyliforms *Zaraasuchus shepardii* and *Gobiosuchus kielanae*, as well as that of early-diverging eunotosuchians (*sensu* Ruiz et al. 2021), such as *Araripesuchus gomesii*, *Araripesuchus patagonicus*, *Pakasuchus kapilimai*, and *Malawisuchus mwakasyungutiensis*. This contrast with the heavily ornamented skulls of baurusuchids, peirosaurids, and neosuchians, with deeper pits and grooves. In addition, *Titanochampsia iorii* does not present the peculiar pebbled ornamentation at the border of external supratemporal fenestra, which has been considered a synapomorphy of Baurusuchidae (Montefeltro et al. 2011; Darlim et al. 2021). The quadrate has a ventrally directed major axis in baurusuchids, whereas that axis is posteroventrally directed in *Titanochampsia iorii* and most other mesoeucrocodylians. Finally, the quadrate with a single and anteriorly placed subtymppanic foramen (*sensu* Montefeltro et al. 2016) of *Titanochampsia iorii* is shared with Peirosauridae and well-distributed within Neosuchia, whereas multiple subtymppanic foramina are seen in Baurusuchidae.

In *Titanochampsia iorii*, as well as in Peirosauridae and Neosuchia, the meatal chamber is covered by a straight or slightly sinusoidal lateral margin of the squamosal. This differs from the condition seen in most eunotosuchians, including baurusuchids, which have a strongly convex ventral outgrowth of the squamosal, located anterior to a small, but marked concavity at the level of the bony otic aperture. Overall, the bony otic aperture of *Titanochampsia iorii* is posteriorly closed and triangle-shaped, with its apex directed dorsally. Such morphology is very similar to that of neosuchians and peirosaurids, whereas the bony otic aperture in Eunotosuchia, including baurusuchids, is subpolygonal to elliptical and posteriorly open. Finally, the anterodorsal ramus of the quadrate of *Titanochampsia iorii* corresponds to more than 50% of the lateral edge of the internal supratemporal fenestra, as in the majority of the mesoeucrocodylians, but not in Baurusuchidae.

Rejecting a peirosaurid affinity for *Titanochampsia iorii*

Peirosaurids are also common components of the Bauru Group fauna and, although most hypotheses place them within Notosuchia, their possible affinity to Neosuchia (e.g., Iori et al. 2018) warrants further comparisons. A short anterior extension of the meatal chamber is seen in *Titanochampsia iorii* and neosuchians, in which such anterior ending is represented by the squamosal. This condition diverges from that of Peirosauridae, in which the meatal chamber extends into the dorsal part of the postorbital bar (Pol et al. 2014). In addition, the anterior limit of the meatal chamber in peirosaurids corresponds to a concave surface formed by the posteroventral process of the postorbital

and the anterodorsal process of quadrate and quadratojugal. This concave surface is more restricted in longirostrine peirosaurids such as *Stolokrosuchus lapparenti* and *Pepesuchus deiseae* (Larsson and Gado, 2000, Campos et al. 2011), but much more developed in other peirosaurids such as *Montealtosuchus arrudacamposi*, *Hamadasuchus rebouli*, and *Rukwasuchus yajabalijekundu* (Carvalho et al. 2007; Larsson and Sues 2007; Sertich and O'Connor 2014). However, in *Titanochampsia iorii*, the meatal chamber ends anteriorly in a reduced surface, limited ventrally by the dorsal tip of the lateral temporal fenestra and dorsally by the lateral shelves of the postorbital and squamosal expanding from the skull roof. The configuration present in *Titanochampsia iorii* is similar to that of eusuchians, including extant forms such as *Caiman* spp. and *Crocodylus* spp. The poorly developed posterolateral process of the squamosal, which is projected horizontally at the same level of the skull in *Titanochampsia iorii*, is similar to that of eusuchians, whereas peirosaurids possess an elongated, thin, and posteriorly directed posterolateral process. The squamosal and the postorbital of *Titanochampsia iorii* have parallel lateral margins, resembling the condition of Neosuchia and *Barreirosuchus franciscoi*, whereas these margins diverge posteriorly in other peirosaurids.

Neosuchian traits of *Titanochampsia iorii*

Although *Titanochampsia iorii* does not preserve any of the synapomorphies of Eusuchia and/or Crocodylia recovered in our phylogenetic analyses; it exhibits some features shared with members of Neosuchia. The rectangular skull table of *Titanochampsia iorii* resembles that of peirosaurids, as well as of the neosuchians *Pholidosaurus purbeckensis* and *Sarcosuchus imperator*, whereas baurusuchids and eusuchians have trapezoidal skull tables. The squamosal of *Titanochampsia iorii* lacks a supratemporal fossa on the lateral border of the supratemporal fenestra. This condition is present in almost all neosuchians analysed here, except for *Crocodylus* spp. and *Alligator mississippiensis*, diverging from a fenestra bordered entirely by the supratemporal fossa found in Notosuchia. *Titanochampsia iorii*, peirosaurids, and neosuchians have smooth supratemporal rims, contrasting with the raised and hypertrophied rims observed in several notosuchians, such as Baurusuchidae, Mahajangasuchidae, Sebecidae, *Simosuchus clarki*, *Yacarerani boliviensis*, and *Caipirasuchus paulistanus* (Turner and Buckley 2008; Kley et al. 2010; Montefeltro et al. 2011; Pol et al. 2014). Finally, *Titanochampsia iorii* bears the supratemporal fenestrae occupying almost the entire area of the supratemporal fossa, as also seen in *Pholidosaurus purbeckensis*, *Eosuchus minor*, *Argochampsia krebsi*, and *Gavialis gangeticus*, whereas most notosuchians have small, anterolaterally oriented supratemporal fenestrae.

In this context, the recent description of *Burkesuchus mallingrandensis* (Novas et al. 2021), a possible neosuchian from the Late Jurassic of Chile, represents an interesting base for comparison with *Titanochampsia iorii*, given that both South American taxa have a somehow ambiguous taxonomy. Both specimens are fragmentary, but there is important anatomical overlap between them. Specifically, although both *Titanochampsia iorii* and *Burkesuchus mallingrandensis* preserve most of their cranial roofs, they only share two conspicuous features: a rod-like descending process of the postorbital; and a single subtympenic foramen. On the other hand, *Burkesuchus mallingrandensis* differs from *Titanochampsia iorii* by possessing a heavily ornamented skull roof, a frontal bearing a longitudinal ridge (which is also present in some notosuchians and neosuchians), small supratemporal fenestrae and foramina (shared with most notosuchians);

a squamosal strongly flexed posteroventrally, forming an expanded wing that partially covers the meatal chamber, in addition to an external auditory meatus, deeply sunk and mostly covered laterally by the wing of the squamosal (also observed in eunotosuchians). Therefore, even though *Burkesuchus mallingrandensis* was not included along with *Titanochampsia iorii* in our phylogenetic analyses, the many differences between these two South American early neosuchians would likely imply in different positions in the mesoeucrocodylian tree.

Body size of *Titanochampsia iorii* and its palaeobiological implications

After comparisons with other mesoeucrocodylians, we coarsely estimated the dorsal cranial length (DCL) of *Titanochampsia iorii* to be constrained between 37.01 and 74.43 cm. Given the significant difference between the higher and upper limits of this estimation, we did not use the mean value of DCL to apply the equations of Hurlburt et al. (2003), and instead used maximum and minimum DCL values. This resulted in a total body length (TL) of *Titanochampsia iorii* ranging from 2.98 to 5.88 metres.

Even though we do not expect our body size estimation to be very accurate, given the fragmentary nature of MPMA 02-0005/87 and the varied body proportions of different crocodyliform subgroups, these results suggest that *Titanochampsia iorii* possibly surpassed three metres in total body length. Baurusuchids were the notosuchian apex predators of the Bauru Group (Riff and Kellner 2011; Godoy et al. 2014; Bandeira et al. 2018; Montefeltro et al. 2020), ranging from about two to four metres in total length, they represent some of the largest crocodylomorphs with a fully terrestrial lifestyle (Godoy et al. 2014; 2016; 2019). In comparison, the aforementioned total body length range recovered to the *Titanochampsia iorii*, place it in the large-size end of the spectrum of body size variation seen among the Bauru Group mesoeucrocodylians and of terrestrial crocodylomorphs in general (Godoy et al. 2019).

However, the comparative morphology of *Titanochampsia iorii*, as well as our phylogenetic results, suggests a closer relation to neosuchians, which are predominantly semiaquatic/freshwater crocodyliforms (Wilberg et al. 2019). As other stratigraphic units of the Bauru Group, the lithology of the Marília Formation suggests a fluvial depositional environment, in semiarid context (Garcia et al. 2005; Basilici et al. 2016; Mineiro et al. 2017; Batezelli 2019; Soares et al. 2020). Therefore, a semiaquatic lifestyle cannot be ruled out for *Titanochampsia iorii*. In this case, the size of this taxon would be compatible with that of medium-sized aquatic crocodylomorphs, which are consistently larger than their terrestrial counterparts, due to physiological constraints (Godoy et al. 2019; Gearty and Payne 2020; Godoy and Turner 2020).

Paleoenvironmental and ecological implications of *Titanochampsia iorii*

In a recent study of Soares et al. (2020), the former Serra da Galga and Ponte Alta Member of the Marília Formation were elevated to the Formation rank. Those authors argue that the Serra da Galga Formation was deposited in proximal-medial distributive fluvial systems (Basilici et al. 2016; Mineiro et al. 2017; Soares et al. 2020), whereas the Echaporã Member of the Marília Formation (which yielded *Titanochampsia iorii*) represents the distal portion of such systems, with occasional unconfined flows, in a semiarid to arid environment with well-drained periods. Such environmental differences would also be evidenced by the fossil record, with the Serra da Galga Formation revealing a vast diversity of invertebrates

and vertebrates, including several notosuchian crocodyliforms (Carvalho et al. 2004; Campos et al. 2005; Kellner et al. 2005; 2011; Novas et al. 2005; 2008; Salgado and Carvalho 2008; Báez et al. 2012; Martinelli et al. 2013; Martinelli and Teixeira 2015) and the Marília Formation yielding much fewer fossils (Bertini et al. 2001; Méndez et al. 2014; Iori and De Arruda-Campos 2016; Mineiro et al. 2017). Among these, *Titanochampsia iorii* is the first crocodyliform described for the Marília Formation, as redefined by Soares et al. (2020).

The discovery of *Titanochampsia iorii* in deposits of the Echaporã Member suggests that this taxon, with possible neosuchian affinities, would inhabit an arid to semiarid environment, where ephemeral water bodies were common. Its large internal supratemporal fenestra indicates the presence of bulk adductor muscles of the lower jaw (Busbey 1989), suggesting a strong bite (Iordansky 1964; Walmsley et al. 2013). In contrast, most notosuchians have smaller internal supratemporal fenestrae, which might help explaining the surprisingly weak bite estimated for baurusuchids (Montefeltro et al. 2020). Both the large size of *Titanochampsia iorii* and its inferred strong bite are compatible with an amphibian lifestyle, including ambushing behaviour, as seen in most crocodiles nowadays and matching its possible affinity to Eusuchia. This inferred behaviour strongly departs from that of most crocodylians recorded in the older Adamantina Formation, which are predominantly terrestrial, with more diverse feeding habits. Although the record of a single specimen provides no strong basis for bold statements, the prevalence of crocodylians such as *Titanochampsia iorii* may be an outcome of the increase in humidity seen in the last phases of the Bauru Basin deposition, which includes the Echaporã Member (Fernandes and Ribeiro 2015).

Conclusions

The comparative description of *Titanochampsia iorii* reveals its uniqueness among mesoeucrocodylians, differing from notosuchians by lacking typical traits of the group, such as a meatal chamber closed anteriorly by a flange of the posterior process of the postorbital and posteriorly by the ventrally deflected lateral margin of the squamosal. Our phylogenetic analyses recover *Titanochampsia iorii* nested within Neosuchia, although almost all key-features of the group are not preserved in the rather incomplete specimen. Nevertheless, the skull roof of *Titanochampsia iorii* resembles that of neosuchians by the anterior extension of the meatal chamber covered by the squamosal, the constricted flange of the posterior process of the postorbital, and the poorly developed posterolateral process of squamosal. Perhaps most importantly, the material is well-preserved enough to confidently rule out its inclusion within Baurusuchidae, and less clearly within Peirosauridae. The more than three metres long *Titanochampsia iorii* is the only crocodyliform presently known for the Marília Formation and its inferred ecology matches the climatic conditions prevalent at the time.

Acknowledgments

We thank both Dr. Sandra Tavares, curator of the “Museu de Paleontologia Prof. Antonio Celso de Arruda Campos”, and Dr. Fabiano Iori for the loan of the specimen. TSF was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant number 165031/2018-2). PLG was supported by the National Science Foundation (NSF DEB 1754596). JCAM and PLG were supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES grant numbers 8887.572782/2020-00 and 88887.583087/2020-00). JCAM and MCL were supported by the São Paulo Research Foundation (FAPESP grant

numbers 2021/1456-4 and 2020/07997-4). FCM was supported by Program 162 (Projetos De Cooperação em Pesquisa Entre o Brasil e a Alemanha - CAPES/DAAD -PROBRAL). TNT is made freely available through the Willi Henning Society.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 165031/2018-2), National Science Foundation (NSF DEB 1754596), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES 8887.572782/2020-00 and 88887.583087/2020-00), and São Paulo Research Foundation (FAPESP 2021/1456-4 and 2020/07997-4).

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