Cretaceous Research 175 (2025) 106150

Contents lists available at ScienceDirect

Cretaceous Research

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

New records of frogs (Anura, Lissamphibia) from the Late Cretaceous Bauru Group of Brazil and its paleobiogeographic implications

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ARTICLE INFO

Article history:
Received 7 December 2024
Received in revised form
17 March 2025
Accepted in revised form 22 April 2025
Available online 30 April 2025

Keywords:
Anura
Bauru Group
Neobatrachia
Provincialism
South America
Late Cretaceous

ABSTRACT

South America hosts one of the largest diversities of living frogs in the world, but our knowledge of the group during the Mesozoic Era is still limited. The Upper Cretaceous Bauru Group, in the south-central region of Brazil, has yielded a variety of vertebrate groups. Frog records are rare and restricted to a few well-preserved skeletons and fragmentary material. Nevertheless, they have offered important clues about the early diversification and distribution of frogs, especially among the speciose clade Neobatrachia. Here, we report new records of frogs from the Adamantina and Serra da Galga formations. The described specimens expand the geographical range of frogs in the Bauru Group and corroborate the hypothesis of a widespread distribution of neobatrachians in Gondwana landmasses by the Late Cretaceous. The discovery of the first putative *Calyptocephalella*-like form from a northern region in South America sheds light on the proposed biogeographic provincialism of frog faunas in South America by the Late Cretaceous.

1. Introduction

Anurans (toads, frogs, treefrogs, and related forms) are among the most speciose and widespread groups of living vertebrates, with over 7650 extant species (AmphibiaWeb, 2024; Frost, 2024). More than one-third of these species are found in South America, a region widely known for hosting some of the most important biodiversity hotspots on the planet (Vasconcelos et al., 2019). Yet, this diversity is far from being well represented in the fossil record of the continent.

The Mesozoic fossil record of frogs in South America is mainly composed of a limited number of occurrences from the Cretaceous of Brazil and Argentina (see review by Barcelos and Santos, 2023). Although scarce, they document two significant events: 1) the early diversification of Pipidae, the only "archaeobatrachian" group known to inhabit South America (e.g., Gómez, 2016), and 2) the origin and early diversification of Neobatrachia (e.g., Báez et al., 2009, 2012a; Báez and Gómez, 2018; Agnolin et al., 2020; Moura et al., 2021), a cosmopolite clade that accounts for nearly 95 % of living species (AmphibiaWeb, 2024). Both events have been intimately tied to the fragmentation of the Gondwanan landmasses, especially the separation between Africa and South America (Frazão et al., 2015; Feng et al., 2017).

Our understanding of the South American batrachofaunas during the Cretaceous has significantly improved in recent years with the report of new fossils, ranging from well-preserved, articulated, and nearly complete specimens, some exhibiting soft tissue preservation (Carvalho et al., 2019; Agnolin et al., 2020; Moura et al., 2021; Muzzopappa et al., 2022; Santos et al., 2023), to isolated and fragmentary material (Novas et al., 2019; Moyano-Paz et al., 2022; Suazo-Lara and Gómez, 2022; Sterli et al., 2022; Freitas et al., 2023). Here, we report new Late Cretaceous records of frogs

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https://doi.org/10.1016/j.cretres.2025.106150
0195-6671/

from five localities in the south-central region of Brazil. The described specimens include the northernmost record of frogs for the Bauru Group and a cf. Calyptocephalellidae reported from a northern region in South America. These findings contribute to our understanding of the paleobiogeographic patterns of anuran faunas in South America during the Late Cretaceous.

2. Geological settings

The Cretaceous deposits of the Bauru Basin are widely distributed in the south-central region of Brazil (Fernandes and Coimbra, 1996). They have been traditionally divided into the Caiuá and Bauru groups (Fernandes and Coimbra, 1996; Fernandes and Coimbra, 2000; Batezelli et al., 2005). The Bauru Group comprises aeolian, lacustrine, alluvial, and fluvial deposits formed during the Late Cretaceous (e.g., Batezelli, 2015; Menegazzo et al., 2016; Soares et al., 2020). The unit has been dated as Campanian-Maastrichtian in age based on palynology and vertebrate fauna (Martinelli and Teixeira, 2015; Langer et al., 2022; Arai and Fernandes, 2023; Gobbo and Bertini, 2023). There is currently no consensus on the lithostratigraphic classification of the Bauru Group (e.g., Fernandes and Coimbra, 1996; Batezelli et al., 2005; Paula e Silva et al., 2005; Menegazzo et al., 2016). Most proposals agree with the validity of the Araçatuba, Marília, and Uberaba formations but mainly differ in the acceptance of subdivisions within the Adamantina Formation (Vale do Rio do Peixe, Presidente Prudente, São José do Rio Preto formations) (see discussion in Langer et al., 2022; Delcourt et al., 2024). Recently, the outcrops previously attributed to the Marília Formation in the Uberaba territory (i.e., the traditional Serra da Galga and Ponto Alta members) were reinterpreted as belonging to a new lithostratigraphic unit, the Serra da Galga Formation, based on its lithological, stratigraphic, paleopedological, biostratigraphic, and genetic characteristics (Martinelli et al., 2019; Soares et al., 2020; Basilici et al., 2024).

Three fossil anuran specimens here reported (LPITB-PV 04 to 06) were found in a newly discovered fossiliferous outcrop at the Serra do Corpo Seco locality in the Ituiutaba municipality, Minas Gerais State (19°01′55.1″S, 49°28′51.1″W; fig. 1 in Giaretta et al., 2024). This outcrop comprises a succession of sandstone beds intercalated with a fossiliferous pebbly channel facies from the Adamantina Formation. Several isolated specimens have been recovered from this channel-hostel bonebed, including theropods (Giaretta et al., 2024), but only those attributed to anurans are described herein. A possible lungfish burrow has been described for one of the paleosol layers in the locality (Rangel et al., 2022).

Specimen MPMA 04-0021-10 was discovered in Santa Rita Farm (21°15′17.7″S, 48°33′29.9″W), in the Monte Alto municipality, São Paulo State. It was found in a reddish, massive sandstone from the Adamantina Formation. Near this locality, several undescribed crocodyliform eggs and eggshells have been collected (TSF unpubl.). The Monte Alto region has yielded a relatively rich vertebrate fauna that includes snakes, turtles, crocodyliforms, and dinosaurs (e.g., Iori and Campos, 2016; Fachini et al., 2020; Iori et al., 2021; Langer et al., 2022; Fachini et al., 2023). The presence of frogs in this assemblage is reported here for the first time.

The remaining specimens come from three localities of the Serra da Galga Formation in the Uberaba Municipality, Minas Gerais State. The Uberaba region has been extensively studied over decades and preserves a well-known fossil assemblage that includes all major vertebrate groups in continental settings (e.g., Candeiro et al., 2006; Martinelli and Teixeira, 2015). Specimens CPPLIP 1428, CPPLIP 621, and CPPLIP 473 were found in the "Ponto 1 do Price" (19°43′26.93″S, 47°44′46.87″W), an important locality that has yielded type specimens of turtles, crocodyliforms, titanosaur dinosaurs, and the neobatrachian *Uberabatrachus carvalhoi* (Báez et al., 2012a; Martinelli and Teixeira, 2015; Martinelli et al., 2019). Specimen CPPLIP 173 was collected in the "Ponto 2 do Price" (19°43′13″S, 47°45′06″W), which has produced remains of turtles, crocodyliforms, and dinosaurs (Martinelli and Teixeira, 2015; Martinelli et al., 2019). The specimens CPPLIP 1855–1859, and CPPLIP 1887 were found in the road cut km 153 of the highway BR-050 (19°35′33″S, 48°01′42″W), from where the titanosaur *Uberabatitan ribeiroi* and numerous isolated and fragmentary specimens representing a variety of fishes have been collected (Martinelli and Teixeira, 2015).

3. Material and methods

The described material (Fig. 1) comes from five localities exposing rocks of the Adamantina and Serra da Galga formations (Bauru Group) in Minas Gerais and São Paulo states. Specimens are housed in the following institutions: CPPLIP, Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price", Universidade Federal do Triângulo Mineiro, Peirópolis, Uberaba, Brazil; MPMA, Museu de Paleontologia "Prof. Antonio Celso de Arruda Campos, Monte Alto, Brazil; and LPITB-PV, Laboratório de Paleontologia, Universidade do Estado de Minas Gerais, Unidade Ituiutaba, Ituiutaba, Brazil.

General osteological terminology mainly follows Trueb (1973) and Sanchiz (1998); terminology referring to the ilium follows Gómez and Turazzini (2016). Identified parts are listed in Fig 1.

The specimen MPMA 04-0021-10 was CT-scanned to better assess the potential for hidden bones inside the block and to visualize the elements without risking further damage. The

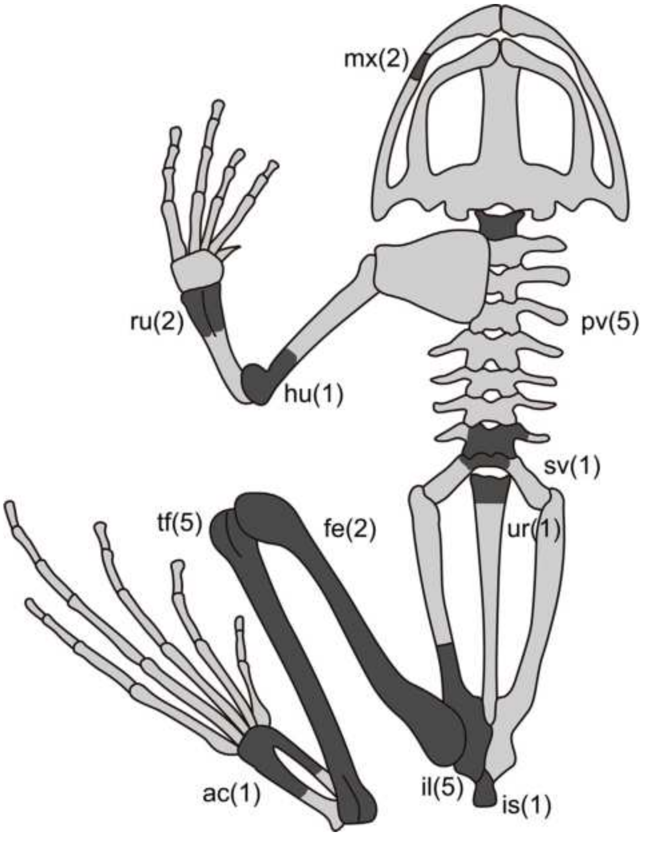

Fig. 1. Schematic drawing of an anuran skeleton in dorsal view exhibiting the location and number of elements described in this work. The right and left sides are not differentiated in the drawing. Abbreviations: ac, astragalus-calcaneum; fe, femur; hu, humerus; il, ilium; is, ischium; mx, maxilla; pv, presacral vertebra; ru, radioulna; sv, sacral vertebra; tf, tibiofibula; ur, urostyle.

scanning was acquired using the micro-CT scanning GE Phoenix V|tome|x S240 available at the "Centro para Documentação da Biodiversidade", Universidade de São Paulo (Ribeirão Preto). The following parameters were used: 1000 projections, exposure time of 0.3s, voltage of 130 kV, and a current of 150 μA, with a voxel size of 25.8 μM. Bones were segmented and rendered in 3D using Avizo (v. 7.0.0).

4. Systematic paleontology

Lissamphibia Haeckel, 1866
Anura Duméril, 1805
Neobatrachia Reig, 1958
Baurubatrachus Báez and Perí, 1989
Baurubatrachus sp.

Material. CPPLIP 1428, right maxilla fragment.

Horizon and Locality. Serra da Galga Formation, Bauru Group; "Ponto 1 do Price", Uberaba municipality, Minas Gerais state.

Description. The maxilla is incomplete, with the anteriormost and posterior portions broken away (Fig. 2A, B). The labial surface of the bone is ornamented by rounded pits and ridges (Fig. 2A). The pits covering the pars facialis are irregularly distributed, varying greatly in size. At the level of the pars palatina, the ventral borders of different pits merge to form a continuous ridge (Fig. 2A). From this point to the ventral margin of the pars dentalis, the ornamentation changes markedly as the pits become significantly smaller and shallower. In lingual view, the pars facialis is high and bears an anterodorsally directed projection, which is tentatively interpreted as the broken base of the processus palatinus (Fig. 2B). The pars palatina is prominent, rounded in cross-section, and perpendicular in relation to the pars facialis. The pars dentalis is moderately shallow in the preserved portion, being shorter or as high as the pars palatina (Fig. 2B). The interdental septa and the bases of several teeth are preserved. Still, their state of preservation precludes further details on tooth morphology and implantation.

Remarks. The maxilla CPPLIP 1428 differs from the Early Cretaceous neobatrachian taxa described from the Crato Formation (Báez et al., 2009; Agnolin et al., 2020), as well as from *Uberabatrachus carvalhoi* (Báez et al., 2012a), and *Mariliabatrachus navai* (Santos et al., 2023), by its ornamented external surface. It shares with *Baurubatrachus* and *Calyptocephalella*-like calyptocephalellids a high pars facialis, a shelf-like pars palatina, and an external ornamentation composed of pits and ridges (e.g., Muzzopappa and Báez, 2009; Agnolin, 2012; Báez and Gómez, 2018; Muzzopappa et al., 2022; Nicoli et al., 2022). However, it differs from *Calyptocephalella*-like forms, in which the pars dentalis is higher and the pits are more uniform in size and distribution (Agnolin, 2012; Moyano-Paz et al., 2022; Nicoli et al., 2022; Sterli et al., 2022). CPPLIP 1428 further resembles *Baurubatrachus* in the following features: 1) ornamentation pattern composed by irregularly distributed pits; 2) pits varying in size, some being distinctively large (diameter larger than the pars palatina height); and 3) pars dentalis relatively short (at least in *B. santosdoroi*) (see Báez and Peri, 1989; Báez and Gómez, 2018; Muzzopappa et al., 2022). Báez and Gómez (2018) inferred that the surface sculpture of the pars facialis overlapped that of the pars dentalis in *Baurubatrachus pricei* (Báez and Peri, 1989), which differs from the condition present in CPPLIP 1428 and *Baurubatrachus*

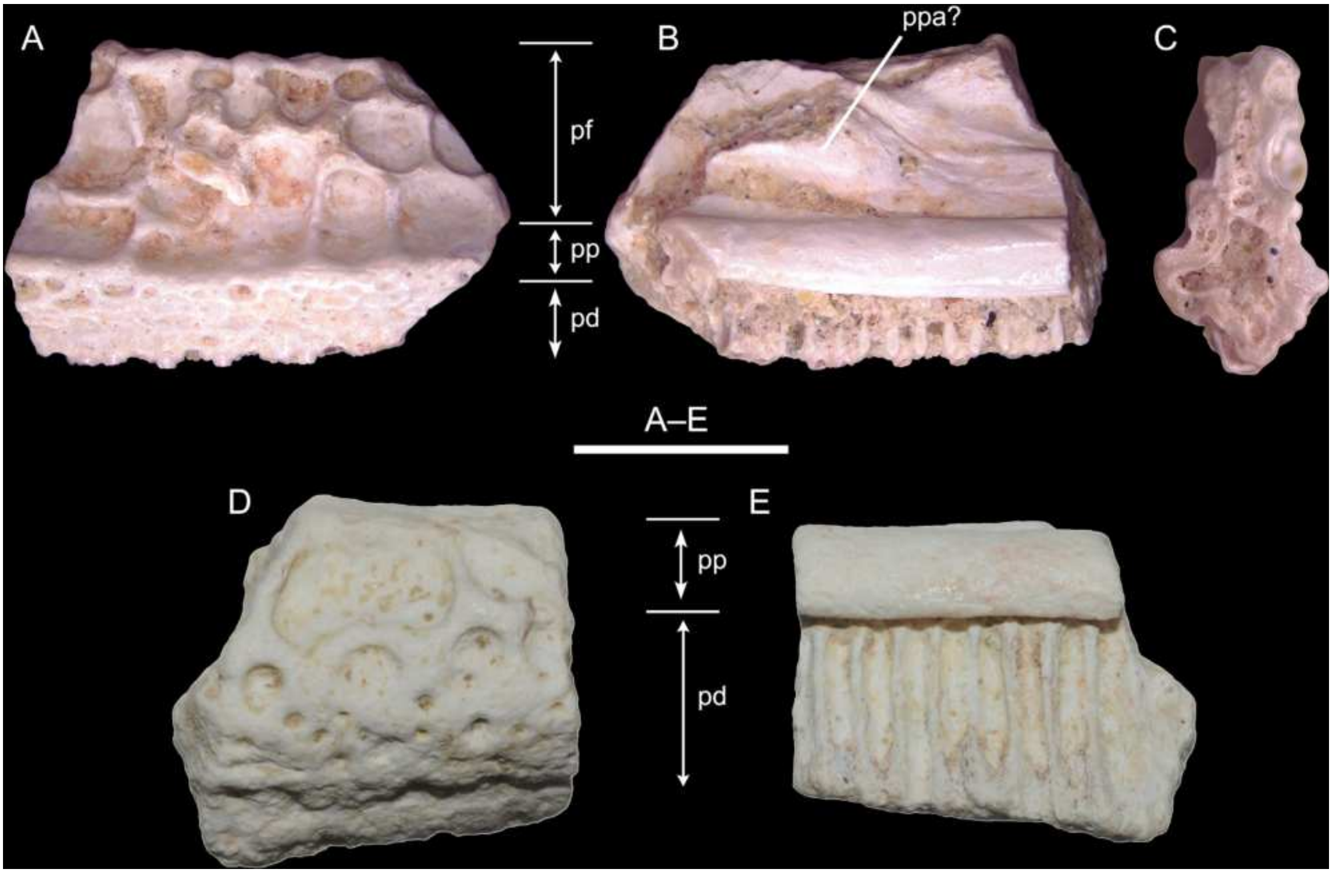

Fig. 2. Neobatrachians from the Serra da Galga Formation at the Uberaba municipality, Minas Gerais state, Brazil. A–C, *Baurubatrachus* sp., photograph of right maxilla fragment (CPPLIP 1428) in A, labial; B, lingual; and C, posterior views. D–E, cf. Calyptocephalellidae, photograph of maxilla fragment (CPPLIP 1887) in D, labial; and E, lingual views. Abbreviations: pd, pars dentalis; pf, pars facialis; pp, pars palatina; ppa, processus palatinus. Scale bar equals 5 mm.

santosdoroi (Muzzopappa et al., 2022). However, the assessment of this feature in *B. pricei* is affected by the dorsoventral crush of the skull (Báez and Gómez, 2018). The pars facialis ornamentation on the anterior half of the maxilla of *B. santosdoroi* seems to be less sculptured ventrally compared to CPPLIP 1428 (Muzzopappa et al., 2022; Fig. 3). Although there are potentially minor ornamentation differences between the described specimen and the two known species of *Baurubatrachus*, they may simply reflect intraspecific variation. Bone ornamentation patterns can vary according to ontogeny and sexual dimorphism (e.g., Georgalis et al., 2023) and even in the same individual (e.g., Muzzopappa et al., 2022). Due to the incomplete nature of our specimen, it is only referred to *Baurubatrachus* sp. here.

Calyptocephallidae Reig, 1960
cf. Calyptocephallidae

Material. CPPLIP 1887, maxilla fragment.

Horizon and locality. Serra da Galga Formation, Bauru Group; BR-050 km 153 locality, Uberaba municipality, Minas Gerais state.

Description. CPPLIP 1887 is a fragment of a large maxilla (Fig. 2D, E). The pars facialis is largely missing, except for a small part of its ventral margin. In lingual view, the pars palatina is well-projected medially, perpendicular to the pars facialis, and has a rounded cross-section. The pars dentalis is distinctively deep, roughly two times higher than the pars palatina, and bears vertical septa for pedicellate teeth (Fig. 2E). In labial view, the maxilla is convex, and its surface is ornamented by pits and ridges (Fig. 2D). The ornamentation changes dorsoventrally, with the pits becoming increasingly smaller towards the ventral margin of the pars dentalis, where the surface is relatively smooth.

Remarks. The maxilla CPPLIP 1887 differs from the Early Cretaceous neobatrachians from the Crato Formation (Báez et al., 2009; Agnolin et al., 2020), *U. carvalhoi* (Báez et al., 2012a), and *M. navai* (Santos et al., 2023) in having an ornamented external surface. It resembles *Baurubatrachus* and *Calyptocephalella*-like calyptocephalellids by having a shelf-like pars palatina and a surface ornamentation of pits and ridges (e.g., Muzzopappa and Báez, 2009; Agnolin, 2012; Báez and Gómez, 2018; Muzzopappa et al., 2022; Nicoli et al., 2022). It differs from *Baurubatrachus* in having a larger size, higher pars dentalis, and by details of the ornamentation. The relative height of the pars dentalis in *B. pricei* is unknown because the articulated lower jaws obscure the lingual portions of the maxillae. However, in *B. santosdoroi*, the almost complete right maxilla shows that the pars dentalis is relatively short. There are also some minor differences in the ornamentation patterns between *Baurubatrachus* and CPPLIP 1887. The ornamentation in *Baurubatrachus* is highly variable. At the level of the pars dentalis, their external surface might be locally smooth, wrinkled (posterior region), or bear irregularly distributed oval or oblong pits (Báez and Gómez, 2018; Muzzopappa et al., 2022). In CPPLIP 1887, however, the ornamentation consists of numerous pits that decrease in size towards the ventral margin of the pars dentalis, which is relatively smooth. CPPLIP 1887 further resembles *Calyptocephalella*-like calyptocephalellids by having a distinctively high pars dentalis (Muzzoppapa and Báez, 2009; Agnolin, 2012; Nicoli et al., 2022). Although *Calyptocephalella* representatives are sometimes described as having a smooth alveolar margin (e.g., Agnolin, 2012), thus differing from the condition on CPPLIP 1887, this feature apparently varies interspecifically. The alveolar margin of fossil *Calyptocephallela* can have low ridges (e.g., Fernicola and Albino, 2012; Muzzopappa, 2019; Nicoli et al., 2022) or pits of different sizes (e.g., Nicoli et al., 2022; Vizcaino et al., 2022). Fragmented maxillae from the Late Cretaceous of Argentina associated with *Calyptocephallela* include specimens in which the alveolar margin is ornamented with pits that may or may not reach the ventral margin of the bone (Agnolin, 2012; Moyano-Paz et al., 2022; Sterli et al., 2022), similar to the condition seen in CPPLIP 1887. The foregoing comparisons demonstrate that the anatomy of CPPLIP 1887 does not resemble any of the maxillae so far described for the Bauru Group and is most consistent with those of *Calyptocephalella.* Unfortunately, the incompleteness of the specimen prevents the evaluation of other typical calyptocephalellid features in the material (e.g., maxilla contributing to the orbital margin, high laminar ascending postorbital process; Nicoli et al., 2022; Muzzopappa et al., 2025) and hinders more detailed comparisons with other representatives of the group. Thus, the specimen is identified as cf. Calyptocephalellidae until more informative specimens become available.

Partially articulated specimen from Monte Alto, São Paulo state, Adamantina Formation

Neobatrachia Reig, 1958
Neobatrachia indet.

Material. MPMA 04-0021-10, incomplete and partially articulated post-cranium skeleton that includes remains of both femora, both tibiofibula, right tibiale-fibulare, right humerus, and parts of the pelvic girdle and axial skeleton.

Horizon and locality. Adamantina Formation, Bauru Group; Santa Rita Farm, Monte Alto Municipality, São Paulo State.

Description. The specimen is poorly preserved and only partially articulated (Fig. 3). The right femur is articulated to the remnants of the right ilium and the right tibiofibula. The left femur and left ilium are severely crushed. Both ilia are articulated and parts of the ischia are exposed dorsally. The right humerus is the only forelimb bone preserved. The skull and most of the axial elements are absent.

Pelvic girdle. The ilia lack their ilial shafts and the dorsal portion of the ilial bodies (Fig. 3A, B). The medial wall of the right ilium is better preserved and articulates with the contralateral ilium to form the interilial symphysis. The shape and size of this contact suggest the interiliac tubercle was not significantly developed. Because the ischia are eroded, it is not possible to identify the suture between them and the ilia.

Hindlimbs. The right femur is the most complete hindlimb element (Fig. 3B). It is slightly sigmoid and bears a short, eroded expansion along its proximal half that probably corresponds to a femoral crest. Both proximal and distal epiphyses are well-ossified. The left femur is largely eroded. Only the proximal region of the right tibiofibular and the distal region of the left tibiofibular are preserved. They bear the sulcus proximalis and distalis, respectively, which mark the fusion of the tibia and fibula. The preservation condition of the tibiale-fibulare (astragalus-calcaneum) does not allow to unequivocally refer it either to the right or left side of the body, although its closer proximity to the right femur and tibiofibula might suggest it belongs to the right hindlimb. The tibiale and fibulare are separated from one another at their midpoint, forming a lenticular space. They are apparently fused distally, while the proximal condition is unknown because it is broken.

Humerus. The right humerus is partially preserved, lacking part of its diaphysis and proximal epiphysis (Fig. 3C-E). Its distal end is robust, well ossified, and bears a large humeral condyle (eminentia capitata) that occupies more than half of the maximum distal width of the bone. The humeral condyle is roughly aligned to the main axis of the diaphysis and is bordered by distinct medial and lateral epicondyles. The medial epicondyle is more developed and projected than the lateral epicondyle. A distinct but small ventral fossa is present above the humeral condyle. A transversal slice of the diaphysis shows that the medullary space is wide with a relatively thin cortical region (Fig. 3F).

Presacral vertebrae. The preserved presacral vertebrae are very incomplete and comprise three articulated centra (Fig. 3G). Parts of

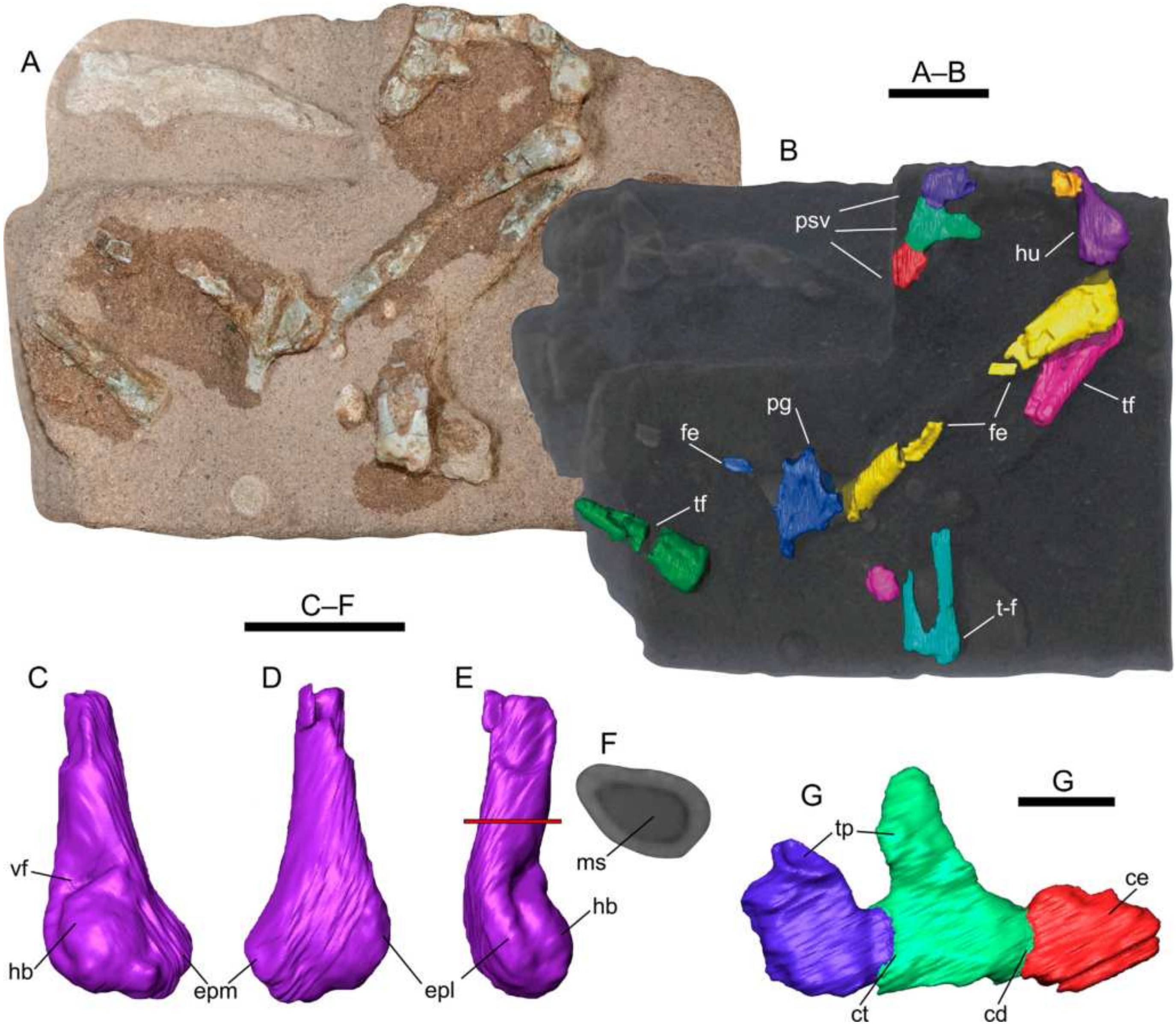

Fig. 3. Indeterminate neobatrachian (MPMA 04-0021-10) from the Adamantina Formation, Monte Alto municipality, São Paulo state. A–B, photograph (A) and CT-scan reconstruction image (B) of the block containing the fossil specimen. C–E, right humerus in C, ventral; D, dorsal; and E, lateral views. F, diaphyseal cross section of the right humerus. G, three incomplete, articulated presacral vertebrae in dorsal view. Abbreviations: cd, condyle; ce, centrum; ct, cotyle; epl, lateral epicondyle; epm, medial epicondyle; fe, femur; hb, humeral ball; hu, humerus; ms, medullary space; pg, pelvic girdle; psv, presacral vertebra; tf, tibiofibular; t-f, tibiale-fibulare; tp, transverse process; vf, ventral fossa. The scale bar equals 10 mm for A-B and 5 mm for C-G.

the right transverse processes of the two most anterior vertebrae are preserved. The condyle is probably at the posterior end of the centrum, and a cotyle is at its anterior end (i.e., procoelous condition).

Remarks. The material can be confidently attributed to Anura based on the following traits: the presence of a large and rounded humeral condyle (eminentia capitata); elongated, sigmoid, and largely featureless femur; compound radioulna and tibiofibula; and elongated tarsal elements (tibiale-fibulare) (Duellman and Trueb, 1986; Holman, 2003; Sigurdsen and Bolt, 2009). Although most of these bones are characteristic of frogs, they are rather uniform in morphology and, thus, provide little taxonomic information. The humerus, ilium, and vertebrae have a combination of features that differentiate them from the pipimorphs, the only South American "archaeobatrachian" group, thus suggesting an affinity to neobatrachians. The reported humerus has a large humeral condyle that is bordered by unequally developed epicondyles, which contrasts with the typical condition in Pipimorpha where the humeral condyle is small and flanked by similarly well-developed epicondyles (Báez et al., 2012b; Rage et al., 2013; Gómez, 2016). The broad medullary cavity of the preserved humerus further distinguishes it from the humeri of pipids, in which the medullary cavities are narrow and indicative of aquatic habits (Canoville and Laurin, 2009; Gómez, 2016). Although the preserved ilia are only exposed in dorsal view, the morphology of the contact between both bones suggests that the interiliac tubercle was poorly developed. By contrast, in Pipimorpha (especially in Pipidae), the interiliac tubercle is much more developed and may occupy most of the medial side of the ilial body (Báez et al., 2012b; Gómez and Turazzini, 2016). The suggested procoelous condition of the preserved presacral vertebrae also differs from the specimens from Pipimorpha, which usually have opisthocoelous vertebrae (Gómez, 2016). Among Neobatrachia, the recovered humerus differs from those of *Calyptocephalella*-like calyptocephalellids by having the medial and lateral epicondyles unevenly developed (e.g., Báez, 1987; Agnolin, 2012; Muzzopappa et al., 2016). Given the lack of more diagnostic features in the incomplete material, the specimen is regarded as an indeterminate neobatrachian.

Isolated specimens from the Serra da Galga Formation, Uberaba, Minas Gerais state

Neobatrachia Reig, 1958
Neobatrachia indet.

Material and Provenance. Isolated specimens from the Serra da Galga Formation, Uberaba Municipality, Minas Gerais State. BR-050 km 153 locality: CPPLIP 1856 (atlas), CPPLIP 1857 (presacral vertebra), CPPLIP 1858 (sacral vertebra), and CPPLIP 1859 (urostyle). “Ponto 1 do Price” locality: CPPLIP 473 (left ilium). “Ponto 2 do Price” locality: CPPLIP 173 (left ilium). CPPLIP 1187 (left ilium) originates from an unknown locality within the region.

Description. The specimen CPPLIP 1856 is an incomplete atlas (Fig. 4A-D). The bone consists of an eroded centrum and the broken bases of the neural arch. The centrum is ventrally flat and expands anteriorly where it bears the cervical cotyles. Although the cervical cotyles are only partially preserved, the right one being severely eroded, they were probably not widely separated from one another and differ from type I atlas as proposed by Lynch (1971). The transverse processes are absent, which suggests the atlas was unfused to the second presacral vertebra. Posteriorly, a partially complete condyle is preserved, indicating a procoelous condition.

Specimen CPPLIP 1857 is an isolated and partially complete presacral vertebra (Fig. 4E-H). The centrum is robust and slightly depressed dorsoventrally, being oval in cross-section. In ventral view, it is smooth and as wide as long. The neural canal is oval in shape and taller than the centrum. The neural arch is thick and bears only the base of the neural spine, which extends from the posterior margin to the anterior part up to the level of the prezygapophyses. In dorsal view, the neural arch lamina is wider than long. The right prezygapophysis and both postzygapophyses are preserved and have broad, oval articular surfaces with the main axes inclined dorsoventrally. The vertebra retains only the proximal portion of the right transverse process, which is posterolaterally projected. The posterior condyle and anterior cotyle indicate that the vertebra belonged to a column with procoelous vertebrae.

The sacral vertebra (CPPLIP 1858) is incomplete, with both diapophyses missing (Fig. 4I-L). The bone is robust and has a

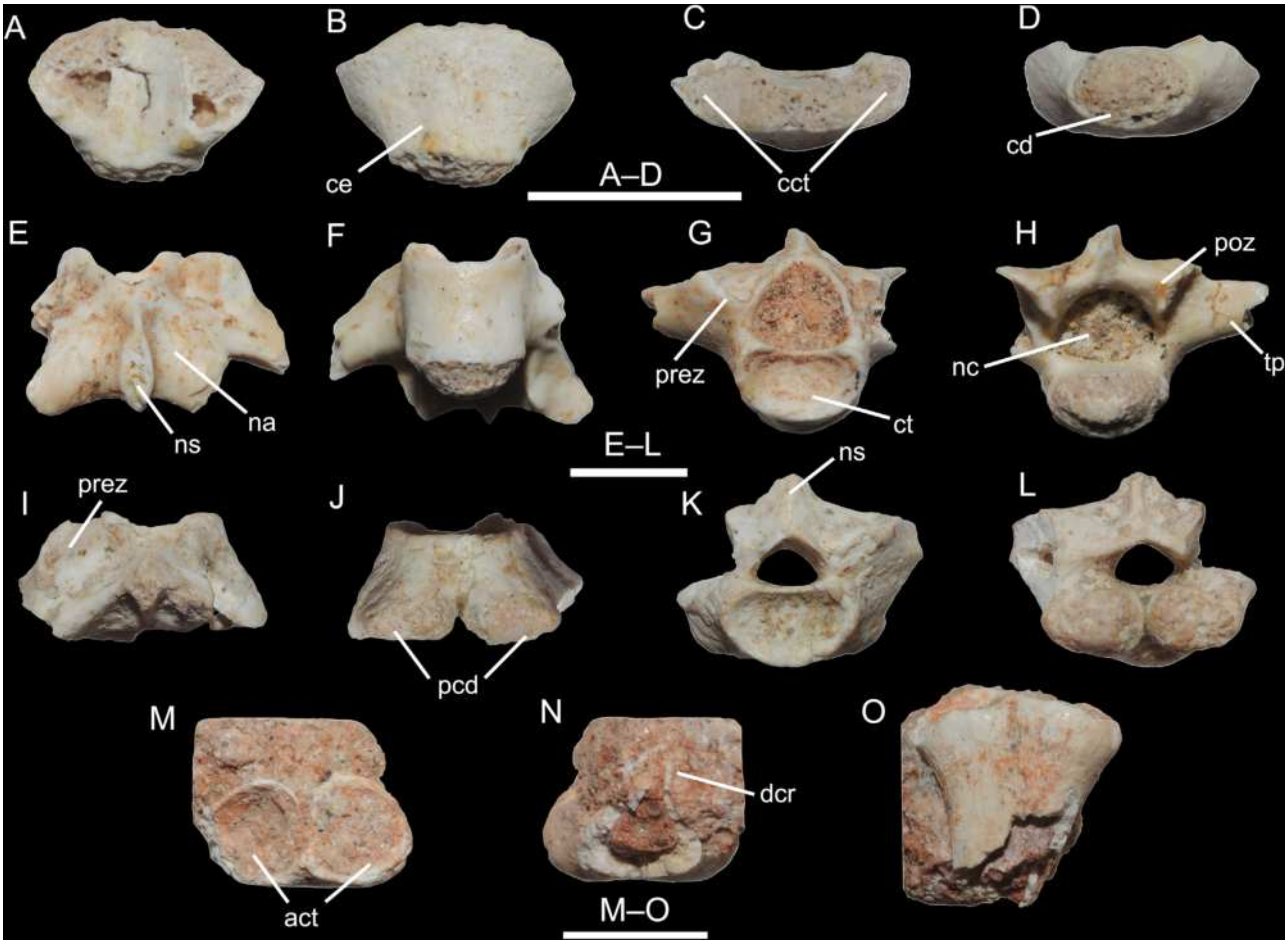

Fig. 4. Indeterminate neobatrachians from the Serra da Galga Formation, Uberaba municipality, Minas Gerais state. A–D, photograph of incomplete atlas (CPPLIP 1856) in A, dorsal; B, ventral; C, anterior; and D, posterior views. E–H, photograph of presacral vertebra (CPPLIP 1857) in E, dorsal; F, ventral; G, anterior; and H, posterior views. I–L, photograph sacral vertebra (CPPLIP 1858) in I, dorsal; J, ventral; K, anterior; and L, posterior views. M–O, photograph of incomplete urostyle (CPPLIP 1859) in M, anterior; N, posterior; O, ventral views. Abbreviations: act, anterior cotyles; cct, cervical cotyles; cd, condyle; ce, centrum; ct, cotyle; dcr, dorsal crest; na, neural arch; nc, neural canal; ns, neural spine; pcd, posterior condyles; poz, postzygapophysis; prez, prezygapophysis; tp, transverse process. Scale bars equal 5 mm.

distinctively small and rounded neural canal. The centrum has an anterior cotyle and bears two well-developed posterior condyles for a bicondylar articulation with the urostyle. The neural arch has a neural spine, which is confluent with a low and thickened ridge that extends laterally above the neural canal in posterior view. The preserved left prezygapophysis is broad, oval, posterolaterally directed, and does not project prominently from the neural arch lamina. Although the left diapophysis is broken at the level of the lateral neural arch wall, the preserved broken surface suggests that the former was projected posterolaterally.

Specimen CPPLIP 1859 is the anterior portion of a urostyle that lacks lateral processes and has a bicotylar anterior surface (Fig. 4M–O). In anterior view, the cotyles are nearly rounded in shape and partially separated by a V-shaped groove. Although the dorsal area of the urostyle is covered by sediment, it is clear from the posterior view that it bears a distinct crest, at least along the more anterior part of the bone.

The three fossil ilia are incomplete and lack most of the ilial shaft, as well as different portions of the ilial bodies (Fig. 5). The posterior portion of the ilial shaft is moderately compressed mediolaterally in all specimens. The dorsal prominence is elongated, slightly projected laterally, and continuous with a well-developed dorsal crest (condition poorly preserved in CPPLIP 1187). The posterior slope of the dorsal prominence in CPPLIP 173 is anteriorly oriented (Fig. 5D), while it is steeper in CPPLIP 473 (Fig. 5A). Although the dorsal prominence of the former specimens has a prominent thickened area, it is not clearly delimited as a dorsal protuberance. The ilial area of the acetabular fossa is round, bordered by a shallow dorsal margin and protruding anterior and anteroventral margins. The dorsal acetabular expansion is moderately broad (lost in CPPLIP 173). The ventral acetabular expansion is broken in CPPLIP 173 and 473 but is moderately developed in CPPLIP 1187 (Fig. 5G). In this specimen, the anterior margin of the ventral acetabular expansion forms an obtuse angle with the ventral margin of the ilial shaft. A preacetabular zone is discernible in all specimens (Fig. 5B, E, H). Although incomplete, the medial wall of the ilial body is straight, which indicates it was not medially projected to form a developed interiliac tubercle in any specimen.

Remarks. Procoelous presacral vertebrae are found within palaeobatrachids, basal pipimorphs, pelodytids, pelobatoids, and neobatrachians (Jones et al., 2003; Prasad and Rage, 2004; Rocek, 2013; Gao and Chen, 2017). The Pipimorpha is the only “archaeobatrachian” group recorded in South America, and given that its representatives during the Late Cretaceous had opisthocoelous vertebrae, it is inferred that the specimens CPPLIP 1856–1858 belong to neobatrachians. Conversely, the presence of a bicondylar sacral vertebra with presumably slightly expanded sacral diapophyses (CPPLIP 1858) and a bicotylar urostyle lacking transverse processes (CPPLIP 1859) are consistent with assignment to Neobatrachia (Báez et al., 2012a; Evans et al., 2014). The morphology of these bones differs from what is observed in fossil and living adult Pipidae, in which the urostyle is firmly fused to a sacral vertebra

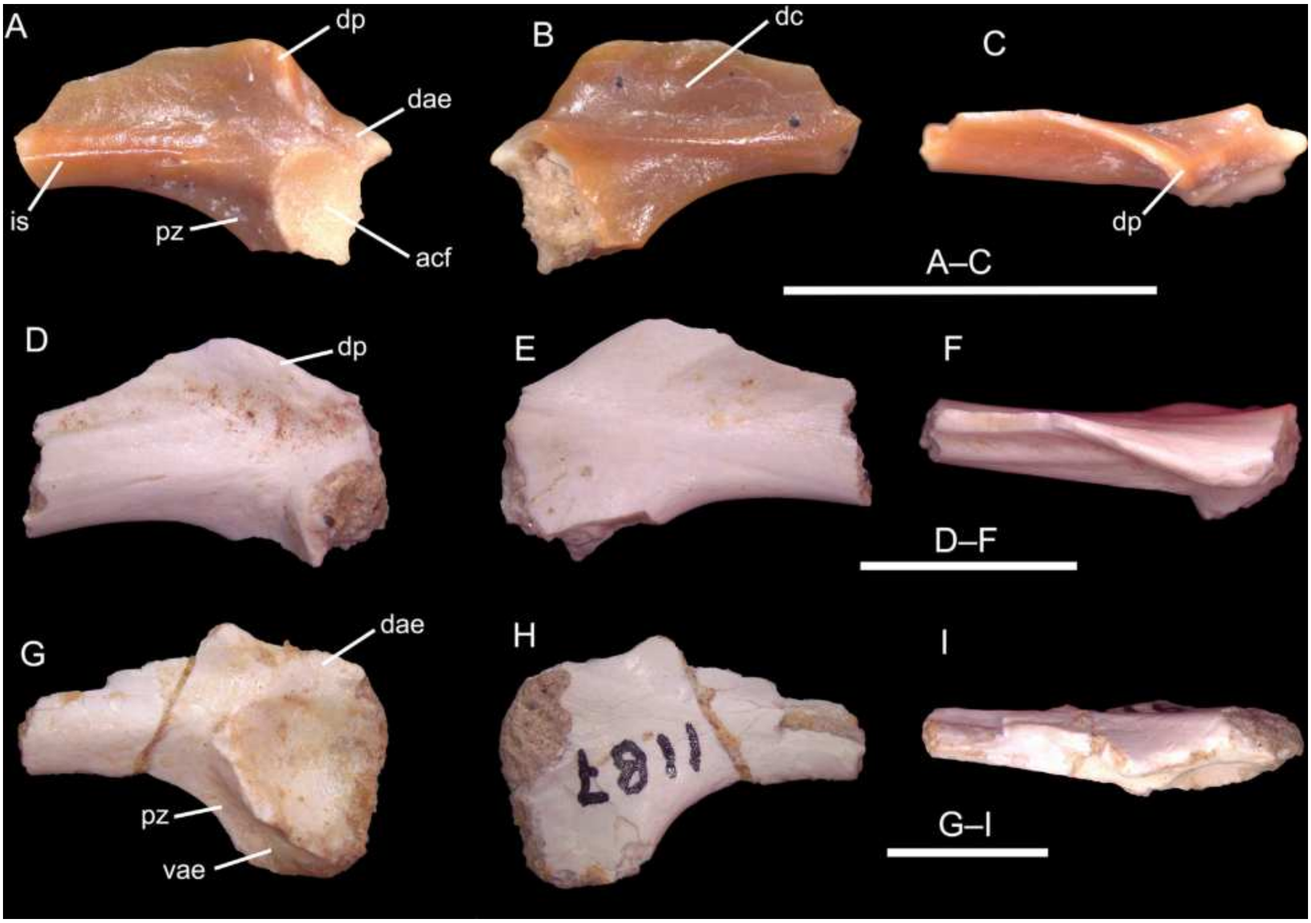

Fig. 5. Indeterminate neobatrachians from the Serra da Galga Formation, Uberaba municipality, Minas Gerais state. A–C, photograph of left ilium (CPPLIP 473) in A, lateral; B, medial; and C, dorsal views. D–F, photograph of left ilium (CPPLIP 173) in D, lateral; E, medial; and F, dorsal views. G–I, photograph of left ilium (CPPLIP 1187) in G, lateral; H, medial; and I, dorsal views. Abbreviations: acf, acetabular fossa; dae, dorsal acetabular expansion; dc, dorsal crest; dp, dorsal prominence; is, ilial shaft; pz, preacetabular zone; vae, ventral acetabular expansion. Scale bars equal 5 mm.

with widely expanded diapophyses (Trueb and Cannatella, 1986; Cannatella and Trueb, 1988; Báez et al., 2000; Báez, 2013).

Further comparisons of the isolated vertebrae described here with Cretaceous neobatrachians from South America are hindered by their incomplete preservation and lack of diagnostic features. The Early Cretaceous taxa from the Crato Formation are typically preserved in a two-dimensional mode, with many elements covered by sediment or lost to weathering. Although specimens from the Bauru Group are more three-dimensionally preserved, they face similar limitations. The atlas CPPLIP 1856 differs from *Arariphrynus placidoi* (Báez et al., 2009) and *M. navai* in having narrowly separated cervical cotyles (Báez et al., 2009; Santos et al., 2023), resembling the condition in *Baurubatrachus* (Báez and Gómez, 2018), *U. carvalhoi* (Báez et al., 2012), and *Calyptocephalella satan* (Agnolin, 2012). The presacral vertebra CPPLIP 1857 is distinct from *U. carvalhoi* and *M. navai* due to its robust and ventrally protuberant centrum, which is more similar to that of *Baurubatrachus* (Muzzopappa et al., 2022). Although incomplete, the preserved portion of the sacral vertebra CPPLIP 1858 indicates that the sacral diapophyses were moderately expanded, slightly dorsoventrally flattened, and posteriorly directed, differing from other known sacral vertebrae. It differs from *B. pricei*, which has laterally projected sacral diapophyses (Báez and Gómez, 2018); *M. navai* and *U. carvalhoi*, which have sacral diapophyses that appear rounded proximally (Báez et al., 2012; Santos et al., 2023); and *C. satan*, which exhibits greatly expanded sacral diapophyses (Agnolin, 2012). Collectively, the isolated vertebrae show morphological features that could suggest they belong to distinct taxa, though additional material is needed for a more precise taxonomic assessment.

The fossil ilia differ from Pipimorpha by having a dorsal prominence confluent with the dorsal crest, moderately developed dorsal and ventral acetabular expansions, a distinct preacetabular zone, and an inconspicuous interiliac tubercle (Trueb and Cannatella, 1986; Báez and Pugener, 2003; Báez et al., 2012b; Rage et al., 2013). They resemble the ilia of the neobatrachians *Baurubatrachus* and *Mariliabatrachus*, also from the Bauru Group, and extinct and extant representatives of *Calyptocephalella* in having an elongated dorsal prominence that is continuous with the posterior margin of a well-developed dorsal crest (Muzzopappa and Báez, 2009; Báez and Gómez, 2018; Muzzopappa et al., 2022; Nicoli et al., 2022; Santos et al., 2023). However, the specimens differ from *Baurubatrachus* and *Mariliabatrachus*, in which a well-delimited and laterally projected dorsal protuberance is present (Báez and Gómez, 2018; Muzzopappa et al., 2022; Santos et al., 2023). They further differ from *Baurubatrachus* because its ilial shaft is notably recurved dorsoventrally near the contact with the ilial body, forming an acute angle with the ventral acetabular expansion (Muzopappa et al., 2022; Fig. 4). In the studied specimens, the same area of the ilial shaft is only slightly flexed and in CPPLIP 1187 forms an obtuse angle with the ventral acetabular expansion. The material does not resemble the ilia of *Calyptocephalella*-like forms in several features. The dorsal prominence of CPPLIP 473 is steeper compared to that of CPPLIP 173 and *Calyptocephalella* (Muzzopappa and Báez, 2009; Nicoli et al., 2022). In *Calyptocephalella*, the posterior end of the dorsal prominence obliquely extends across the dorsal acetabular expansion and, thus, is hidden in medial view (Muzopappa and Báez, 2009; Nicoli et al., 2022). However, the dorsal prominence of the studied ilia does not cross the dorsal acetabular expansion. Also, in *Calyptocephalella*, the dorsal acetabular expansion is distinctively inclined dorso-posteriorly roughly starting at the level of the anterior margin of the acetabulum, which results in a well-developed and triangular structure (Báez and Nicoli, 2004; Nicoli et al., 2022). By contrast, the dorsal acetabular expansion of the analyzed specimens does not show a marked dorso-posterior slope (poorly preserved in CPPLIP 173). Comparison with *Uberabatrachus carvalhoi* is hampered because only the anterior portion of the ilia is preserved in the specimen. However, considering the size of these fragments and their nearly cylindrical shape in cross section (Báez et al., 2012a), a considerable portion of the ilial shaft lacked a conspicuous dorsal crest. Thus, it is very unlikely that *U. carvalhoi* possessed a well-developed dorsal crest posteriorly such as in the examined material. The foregoing comparisons demonstrate that the studied specimens have a distinct morphology and indicate a higher diversity of neobatrachians in the Bauru Group.

Anura indet.

Material. Adamantina Formation, Minas Gerais state, Ituiutaba municipality, Serra do Corpo Seco locality: LPITB-PV 04, LPITB-PV 05, tibiofibulae; LPITB-PV 06, radioulna. Serra da Galga Formation, Minas Gerais state, Uberaba municipality, BR-050 locality: CPPLIP 1855, radioulna. “Ponto 1 do Price” locality: CPPLIP 621, left tibiofibula.

Description. The incomplete preservation of most specimens prevents referring to them as from the right or left side (Fig. 6). The radioulnae (LPITB-PV 06, CPPLIP 1855; Figs. 6F, G) are represented by their distal portions. The distal ends, although damaged, are expanded and bear a shallow sulcus longitudinalis that indicates the area of fusion of the radius and ulna. The size of CPPLIP 1855 indicates a remarkably large individual. The tibiofibulae fragments (LPITB-PV 04, LPITB-PV 05, CPPLIP 621; Figs. 6A, C, E) are straight, elongated, and preserve part of the sulcus that marks the median fusion of the tibia and fibula. The compound origin of these fragments is clearly visible in cross-section (Fig. 6D). The characteristic foramen nutritium was preserved in LPITB-PV 04 (Fig. 6D).

Remarks. The radioulna and tibiofibula are characteristic bones of frogs, but as previously mentioned, they provide little taxonomic information for further identification.

5. Discussion

The understanding of the Late Cretaceous record of South American frogs is currently limited by poor sampling and phylogenetic uncertainty of some fossil taxa (Table S1). The Pipimorpha is the only “archaeobatrachian” group with extant and fossil representatives known in South America, being represented by fossil specimens from Argentina (e.g., Báez, 1981, 1987; Báez et al., 2000; Gómez, 2016; Báez et al., 2022; Moyano-Paz et al., 2022; Suazo-Lara and Gómez, 2022) and Chile (Suazo-Lara and Gómez, 2022). Neobatrachians from Brazil include well-preserved, articulated, and relatively complete forms (Báez and Perí, 1989; Carvalho, 2006; Báez et al., 2012a; Muzzopappa et al., 2022; Santos et al., 2023). Their phylogenetic placement within Neobatrachia is still enigmatic, although some taxa are interpreted as stem hyloids under specific analytical conditions (see discussion in Báez and Gómez, 2018). The fossil record of neobatrachians in Argentina and Chile consists primarily of isolated and fragmentary remains that have been assigned to *Calyptocephalella* or referred as indeterminate calyptocephalellids (Báez, 1987; de la Fuente et al., 2007; Agnolin, 2012; Novas et al., 2019; Moyano-Paz et al., 2022; Suazo-Lara and Gómez, 2022; Sterli et al., 2022). Additional isolated materials recovered in Brazil and Argentina have been simply considered as indeterminate neobatrachians (e.g., Muzzopappa and Varela, 2014; Sterli et al., 2022; Freitas et al., 2023). Poorly diagnostic remains attributed to indeterminate frogs have been recovered in Bolivia, Brazil, and Argentina (e.g., Bertini et al., 1993; Gayet et al., 2001; Martinelli and Forasiepi, 2004; Casal et al., 2016; Novas et al., 2019; Sterli et al., 2022).

All fossil frogs from the Late Cretaceous of Brazil come from the Bauru Group. Two neobatrachian species are known from the Serra

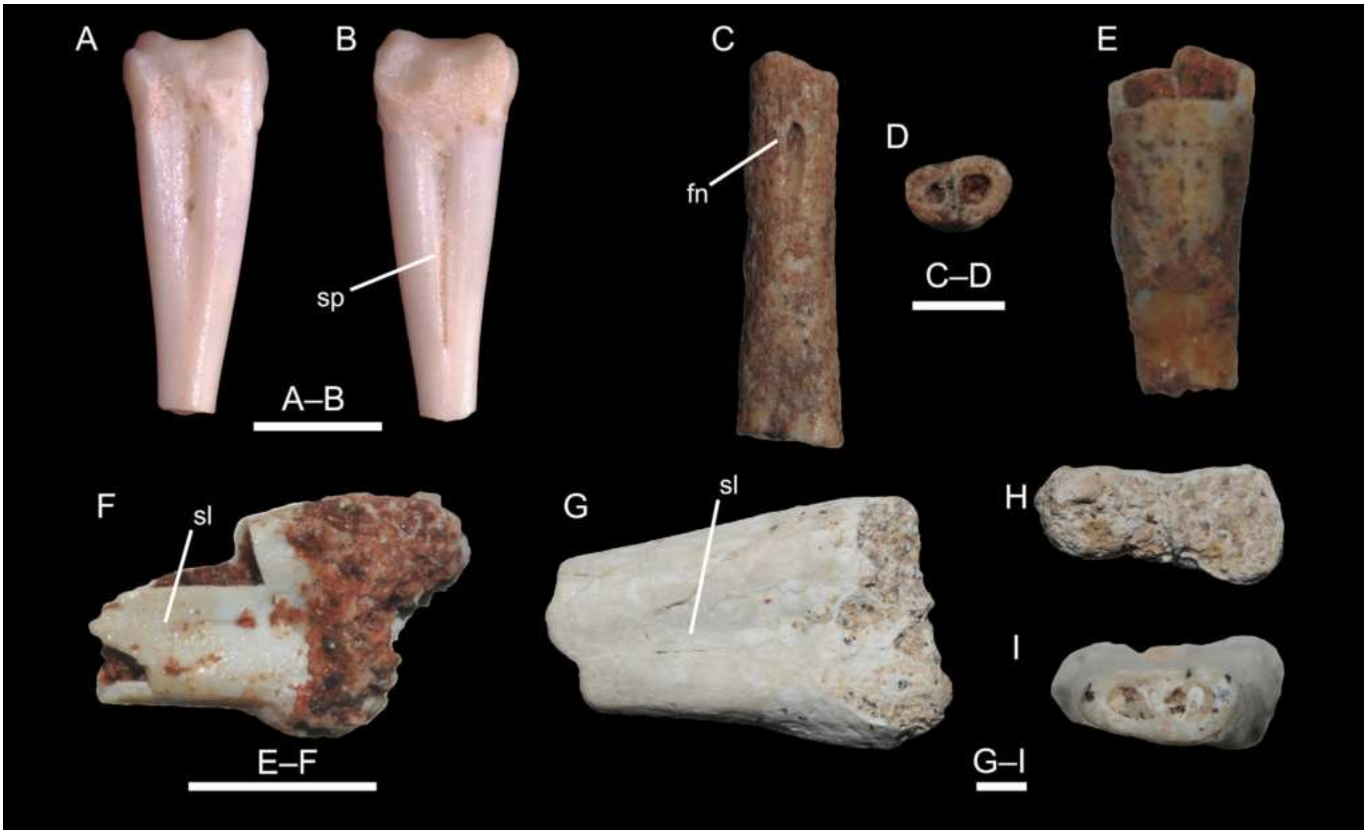

Fig. 6. Indeterminate frogs from the Adamantina and Serra da Galga formations, Minas Gerais state. A—B, photograph of left tibiofibula (CPPLIP 621) in lateral (A) and medial (B) views. C—D, photograph of fragmentary tibiofibular (LPITB-PV 04) in lateral view (C) and cross section (D). E, photograph of fragmentary tibiofibular (LPITB-PV 05). F, photograph of fragmentary radioulna (LPITB-PV 06). G—I, photograph of fragmentary radioulna (CPPLIP 1855), in anterior (H) and posterior (I) views. Abbreviations: fn, foramen nutritium; sl, sulcus longitudinalis; sp, sulcus proximalis. Scale bars equal 2 mm.

da Galga Formation (sensu Soares et al., 2020), *Baurubatrachus pricei* (Báez and Perí, 1989) and *Uberabatrachus carvalhoi* (Báez et al., 2012a). The Adamantina Formation has also yielded remains of frogs, which include the recently described neobatrachians *Baurubatrachus santosdoroi* (Muzzopappa et al., 2022) and *Mariliabatrachus navai* (Carvalho, 2006; Santos et al., 2023), but also isolated material attributed to indeterminate neobatrachians (Freitas et al., 2023; this study) and indeterminate frogs (Bertini et al., 1993; this study). The recent growth in the number of neobatrachian occurrences being reported in the Bauru Group (Muzzopappa et al., 2022; Freitas et al., 2023; this study) is in accordance with the hypothesis that this group was already widespread and diversified in Gondwana landmasses during the Late Cretaceous (Báez et al., 2012a; Venczel et al., 2021; Lemierre and Blackburn, 2022).

Some level of provincialism has been suggested for South American batrachofaunas during the Late Cretaceous (Agnolin, 2012; Báez et al., 2012a; Fig. 7). In the southern regions of the continent, the anuran fossil record is dominated by pipimorphs and *Calyptocephalella*-like calyptocephalellids. By contrast, no pipimorph has been reported from northern South America, where the neobatrachian fossils have been historically assigned to non-*Calyptocephalella* representatives. Similar compositional differences between these northern and southern faunas have been suggested for other taxa, including turtles, dinosaurs, and mammals (Martinelli and Forasiepi, 2004; Novas et al., 2013; Novas et al., 2019; Lamanna et al., 2020; Rougier et al., 2021; Agnolín et al., 2022; Suazo-Lara and Gómez, 2022; Delcourt et al., 2024). However, differences between the northern and southern regions may be more complex than previously assumed, involving not only differences in the distribution of taxa (presence or absence) but also differences in the relative abundance of taxa found in both regions. Moreover, the current understanding of this provincialism remains sensitive to sampling and taphonomic biases and might substantially change depending on a few discoveries.

The putative presence of a *Calyptocephalella*-like specimen in the Bauru Group represents one more potential case of shared taxa between South America northern and southern faunas. However, its apparent rarity in the Bauru Group suggests it was probably a minor component of the neobatrachian fauna if this taxonomic assignment is confirmed. Comparable cases occur with turtles and theropod assemblages. Podocnemidoid turtles have a dominant presence in the northern region but are less abundant in the southern parts, where chelids are the predominant component of turtle assemblages (e.g., Maniel et al., 2021). Regarding the theropod faunas, megaraptorids are a dominant component in the southern regions, while abelisaurids become more prevalent at more northerly latitudes (Novas et al., 2013; Lamanna et al., 2020; Delcourt et al., 2024). Nevertheless, there is evidence that megaraptorids might have been present in the Bauru Group as a smaller component of the fauna (e.g., Méndez et al., 2012; Martinelli et al., 2013).

Today, calyptocephalellids are represented by *Telmatobufo* and *Calyptocephalella*, both with a restricted distribution in central and southern Chile (Frost, 2024). The fossil record indicates that they were present in the Antarctic Peninsula during the Eocene (Mörs et al., 2020) and widespread in the Argentinean Patagonia from the Late Cretaceous to the Miocene (Tauber, 1999; Muzzopappa and

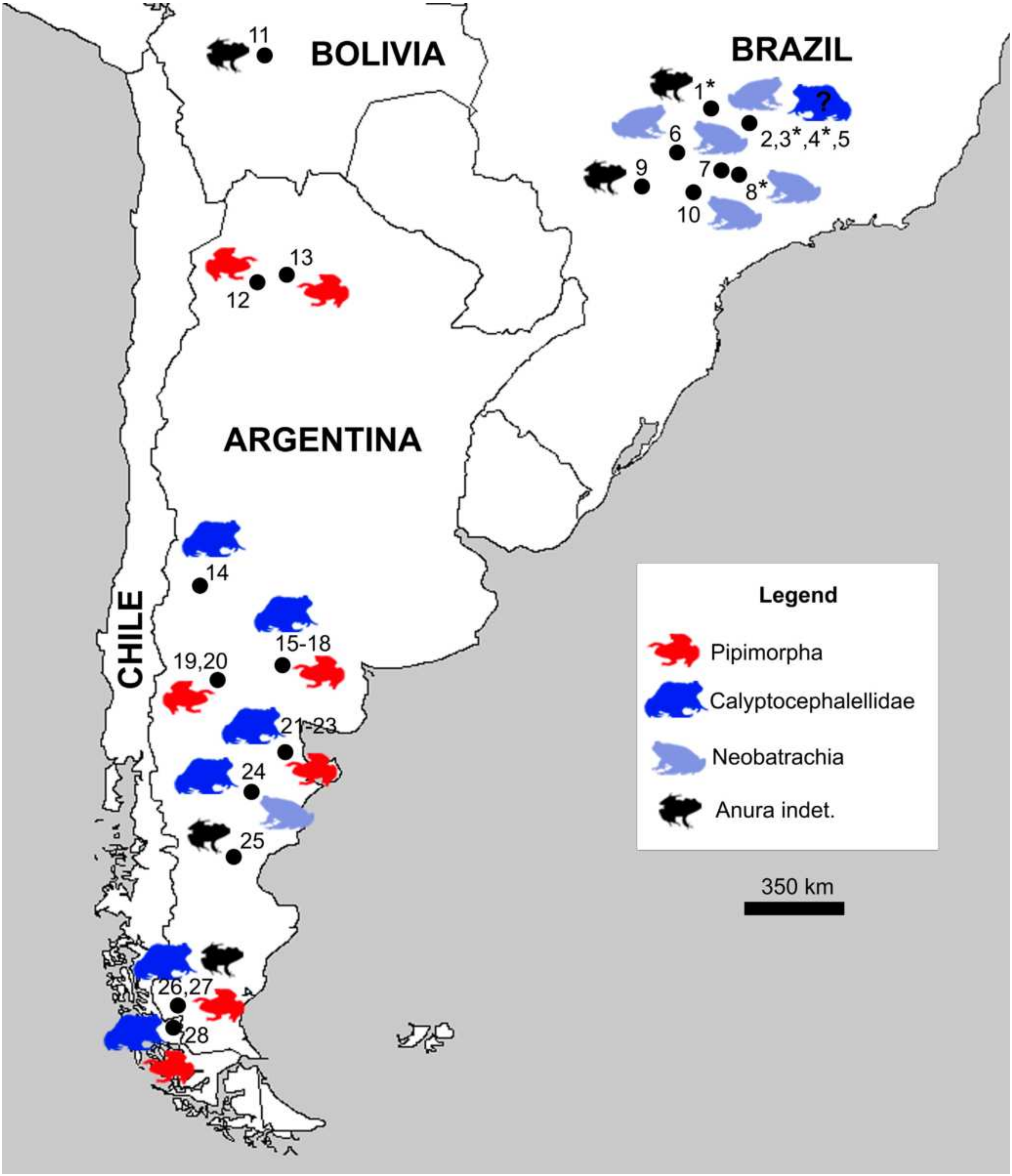

Fig. 7. Map showing occurrences of Late Cretaceous frogs in South America. Localities marked with an asterisk (*) indicate sites where frog remains are described for the first time. Localities and units: 1, 6, 7–10, Adamantina Formation, Brazil; 2–5, Serra da Galga Formation, Brazil; 11, El Molino Formation, Bolivia; 13, 13, Las Curtiembres Formation, Argentina; 14, Loncoche Formation, Argentina; 15–18, Allen Formation, Argentina; 19, 20, Candeleros Formation, Argentina; 21–23, Los Alamitos Formation, Argentina; 24, La Colonia Formation, Argentina; 25, Bajo Barreal Formation, Argentina; 26, 27, Chorrillo Formation, Argentina; 28, Dorotea Formation, Chile. References and more details are in Table S1.

Báez, 2009; Nicoli et al., 2016; Muzzopappa, 2019; Nicoli et al., 2022; Barcelos and Santos, 2023; Muzzopappa et al., 2025). The living pipimorphs in South America are currently represented only by the aquatic *Pipa*, which are mainly distributed in northern South America (Trueb and Cannatella, 1986; Fouquet et al., 2022; Frost, 2024). Although pipids are currently absent in southern South America, they were widely distributed in this region during the Late Cretaceous, with the last representatives being recovered in the Pleistocene of the Pampean region (Báez et al., 2008; Báez et al., 2012b; Barcelos and Santos, 2023). The extinction of calyptocephalellids and pipimorphs from southern regions is generally linked to the post-Miocene progressive aridification and climatic cooling (Báez et al., 2008; Muzzopappa and Báez, 2009; Gómez et al., 2011; Agnolin, 2012; Báez et al., 2012b; Nicoli et al., 2022; Muzzopappa et al., 2025).

Considering that living pipimorphs and *Calyptocephalella* are highly aquatic frogs (Cei, 1962; Trueb, 2003) and their regional extinction has been linked to aridification processes, the absence of pipimorphs and potential rarity of *Calyptocephalella*-like forms in the Bauru Group might reflect a genuine biogeographic signal. Arid to semi-arid conditions during the Late Cretaceous of the Bauru Group are inferred based on the presence of aeolian deposits, pedogenetic carbonates, palygorskite-bearing paleosols, and other lithological features (Batezelli, 2015; Fernandes and Ribeiro, 2015; Basilici et al., 2016; Batezelli et al., 2019). Water bodies might have been more restricted and ephemeral, thus much less favorable for these aquatic frogs. Additionally, the absence of these taxa could also be partially explained by taphonomic biases, as warm, shallow waters are apparently more conducive to early disarticulation and loss of completeness in small vertebrates (Brand et al., 2003; Falk et al., 2022). Continued collecting and taxonomic refinement of fossil frogs from South America will allow more robust testing of these hypotheses. Luckily, due to more diagnostic features throughout the skeleton, pipimorphs and *Calyptocephalella*-like forms are relatively “easier” to identify than others. So, even localities that only provide isolated and fragmentary material might be helpful in inferring past biogeographical processes.

6. Conclusions

The described anuran specimens represent new records for the Bauru Group and expand their known geographical range within the unit. The recent reports on the anuran content of the Bauru Group, including the additional neobatrachian remains described herein, are congruent with previous hypotheses of a widespread distribution of neobatrachians in Gondwanan landmasses by the Late Cretaceous. The potential presence of a *Calyptocephallela*-like calyptocephalellid in the Bauru Group significantly expands the geographical distribution of the group and provides new insights into the idea of provincialism of anuran faunas in South America during the Late Cretaceous.

CRediT authorship contribution statement

Fellipe Muniz: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Ariovaldo Giaretta:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Thiago S. Fachini:** Writing – review & editing, Writing – original draft, Methodology. **Thiago da Silva Marinho:** Writing – review & editing, Writing – original draft. **Pedro Buck:** Writing – review & editing, Writing – original draft. **Sabrina Rodrigues:** Writing – review & editing, Writing – original draft. **Agustín G. Martinelli:** Writing – review & editing, Writing – original draft, Supervision, Investigation.

Declaration of competing interest

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.

Acknowledgments

This research was supported by the São Paulo Research Foundation (FAPESP No. 2020/07997-4 and No. 2024/03599-5 to FPM), the National Council for Technologic and Scientific Development (306138/2023-9 to AAG; 308900/2021-9 to TSM) and the Coordination for the Improvement of Higher Education Personnel (CAPES). PVB thanks Universidade do Estado de Minas Gerais for the Edital PQ/UEMG Nº 06/2023 grant. The authors thank the support provided by Centro para Documentação da Biodiversidade, Universidade de São Paulo, Brazil, regarding the use of the CT-scan machine. Sandra Tavares kindly allowed access to the holotype of *B. santosdoroi* in the Museu de Paleontologia Prof. Antonio Celso de Arruda Campos. Finally, we thank the Editor-in-Chief, Maria Rose Petrizzo, and the reviewers (A. Lemierre and an anonymous one) for their suggestions that improved the manuscript.

During the preparation of this work the authors used ChatGPT from OpenAI and Grammarly in order to revise the grammar of the manuscript. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2025.106150.