AMEGHINIANA
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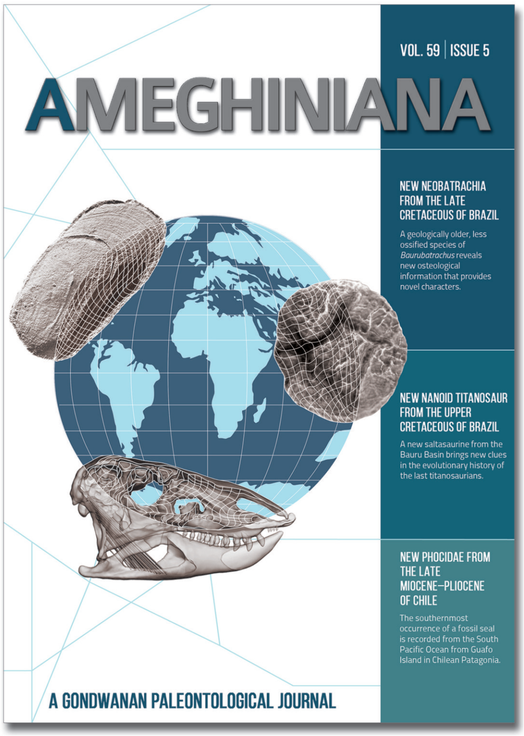

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AMEGHINIANA

NEW NEOBATRACHIA FROM THE LATE CRETACEOUS OF BRAZIL

A geologically older, less ossified species of *Baurubatrachus* reveals new osteological information that provides novel characters.

NEW NANOID TITANOSAUR FROM THE UPPER CRETACEOUS OF BRAZIL

A new saltasaurine from the Bauru Basin brings new clues in the evolutionary history of the last titanosaurians.

NEW PHOCIDAE FROM THE LATE MIOCENE–PLIOCENE OF CHILE

The southernmost occurrence of a fossil seal is recorded from the South Pacific Ocean from Guafo Island in Chilean Patagonia.

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A NEW SPECIES OF *BAURUBATRACHUS* (ANURA, NEOBATRACHIA) FROM THE LATE CRETACEOUS ADAMANTINA FORMATION OF BRAZIL FURNISHES EVIDENCE ON THE DIVERSITY OF THIS BIZARRE GENUS

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Abstract. In the present paper, we report new anuran remains recovered from strata referred to the Adamantina Formation (Upper Cretaceous) cropping out near Catanduva city, São Paulo, Brazil. The remains represent two individuals, one of which bears a set of peculiar characteristics, both cranial and postcranial, that allows us to assign them to the already known genus *Baurubatrachus*. To date, the genus was only represented by the holotype of *Baurubatrachus pricei*, recovered from the Upper Cretaceous Serra da Galga Formation (which is younger than the Adamantina Formation), near Peirópolis (Minas Gerais, Brazil), 200 km north of Catanduva City. The lesser ossification as well as the slender configuration of the scapula and ilia of the new remains, relative to *B. pricei*, points to the identification of a new species, *Baurubatrachus santosdoroi* sp. nov. The detailed study of the peculiar anatomy of these specimens provides new osteological features for the genus, such as the presence of a subtympanic foramen, as well as new character states for other traits to be considered in future systematic studies.

Key words. Neobatrachia. Calyptocephalellidae. Mesozoic. Gondwana. Bauru Basin. Osteology.

Resumen. UNA NUEVA ESPECIE DE *BAURUBATRACHUS* (ANURA, NEOBATRACHIA) DEL CRETÁCICO SUPERIOR DE LA FORMACIÓN ADAMANTINA DE BRASIL PROPORCIONA EVIDENCIA SOBRE LA DIVERSIDAD DE ESTE GÉNERO ESTRAFALARIO. El presente trabajo reporta nuevos restos de anuros hallados en estratos referidos a la Formación Adamantina (Cretácico Superior) aflorantes en las proximidades de la ciudad de Catanduva, San Pablo, Brasil. Los restos representan dos individuos, uno de ellos portador de una cantidad de características particulares, cranianas y postcranianas que permite asignarlo al género ya conocido *Baurubatrachus*. Hasta la fecha, el género estaba únicamente representado por el holotipo de *Baurubatrachus pricei,* recuperado de la Formación Serra da Galga del Cretácico Superior (que es más joven que la Formación Adamantina), cerca de la ciudad de Peirópolis (Minas Gerais, Brasil), 200 km al norte de la ciudad de Catanduva. La menor osificación, así como la condición más esbelta de las cinturas pectoral y pélvica de estos restos respecto de *B. pricei*, indica la presencia de una especie diferente, *Baurubatrachus santosdoroi* sp. nov. El estudio detallado de la anatomía particular de estos especímenes permitió identificar nuevos caracteres como la presencia de un foramen subtimpánico y, a su vez, nuevos estados de carácter para otras características, las cuales son plausibles de ser utilizadas en futuros estudios sistemáticos.

Palabras clave. Neobatrachia. Calyptocephalellidae. Mesozoico. Gondwana. Cuenca de Bauru. Osteología.

NEOBATRACHIA, the so-called "modern frogs", constitutes a diverse monophyletic group that is distributed worldwide except for extreme latitudes (including Antarctica) and most oceanic islands (including New Zealand) (Frost *et al.*, 2006). The list of the hitherto known Early to Late Cretaceous neobatrachians reveals a relatively high abundance in northern South America and an almost exclusive distribution in countries of the southern hemisphere, which was used to infer this region as the area of origin and radiation of the group (*e.g.*, Feng *et al.*, 2017). However, although the fossil record of Neobatrachia is profuse during the Cenozoic (*e.g.*, Tihen, 1962; Roček *et al.*, 2011; Laloy *et* *al.*, 2013; Otero *et al.*, 2014; Nicoli, 2017; Pérez-Ben *et al.*, 2019; Carlini *et al.*, 2021; Lemierre *et al.*, 2021), it is sparse during the Mesozoic. Only a few species are recorded from the Early and Late Cretaceous: *Arariphrynus placidoi* (Leal *et al.*, 2007; Báez *et al.*, 2009), *Eurycephalella alcinae* (Báez *et al.*, 2009), *Cratia gracilis* (Báez *et al.*, 2009), *Primaevorana cratensis* (Moura *et al.*, 2021), *Kururubatrachus gondwanicus* (Agnolin *et al.*, 2020), *Baurubatrachus pricei* (Báez & Perí, 1989; Báez & Gómez, 2018) and *Uberabatrachus carvalhoi* (Báez *et al.*, 2012) from Brazil; *Hungarobatrachus szukacsi* from Hungary (Szentesi & Venczel, 2010; Venczel *et al.*, 2021); *Indobatrachus pusillus* from India (Noble, 1930; Špinar & Hodrová, 1985); and *Beelzebufo ampinga* from Madagascar (Evans *et al.*, 2008). Additional Cretaceous neobatrachian records come from Chile and Argentina (calyptocephalellid neobatrachians, Báez, 1987; Martinelli & Forasiepi, 2004; Agnolin, 2012; Novas *et al.*, 2019; Sterli *et al.*, 2021; Moyano-Paz *et al.*, 2022; Suazo-Lara & Gómez, 2022), from Sudan (neobatrachian indet., Báez & Werner, 1996) and Niger (neobatrachian indet., de Broin *et al.*, 1974). It is noteworthy that the systematic position of the aforementioned extinct species remains blurred despite attempts to include them in phylogenetic studies. This might be explained in part by the incompleteness of the fossilized skeletons and the limited nature of the information provided by such specimens, which are limited to skeletal characters only (Moura *et al.*, 2021). The high homoplasy levels retrieved in large-scale anuran phylogenies (Báez & Gómez, 2018) and the lack of a broad-scale osteological analysis in the search for new characters may also account for this problem, as highlighted by Moura *et al.* (2021). Already pointed out in several sources (*e.g.*, Nicoli *et al.*, 2009; Nicoli, 2017; Báez & Gómez, 2018; Moura *et al.*, 2021; Sterli *et al.*, 2021), the current understanding of the evolutionary history of Anura is based mostly on molecular characters (*e.g.*, San Mauro *et al.*, 2005; Frost *et al.*, 2006; Pyron & Wiens, 2011; Irisarri *et al.*, 2012; Pyron, 2014; Jetz & Pyron, 2018), and osteological information is lacking for most of sampled species. The recent systematic studies that attempt to place the Cretaceous neobatrachians in an evolutionary context hardly include the discussion of new osteological characters (Agnolin *et al.*, 2020; Moura *et al.*, 2021), and perform different analyses of the resulting matrix with varying parameters, especially to deal with homoplasy (Báez & Gómez, 2018; Agnolin *et al.*, 2020; Moura *et al.*, 2021). The phylogenetic position of these fossils is usually poorly supported, and the resulting trees retrieve spurious clades. *Baurubatrachus pricei* was one of the first described species of neobatrachian for the Cretaceous (Báez & Perí, 1989). The relatively well-preserved and complete specimen was collected in two pieces of sandstone of the Serra da Galga Formation (previously, the Serra da Galga Member of the Marília Formation) near Peirópolis (Uberaba, Minas Gerais State, Brazil; Báez & Gómez, 2018; Fig. 1). The Serra da Galga Formation was deposited during the Maastrichtian in the Bauru Basin (Fernandes & Coimbra, 2000). Additional osteological details were recently revealed by subsequent preparation of the type specimen, which allowed an updated perspective on the anatomy and relationships of this taxon (Báez *et al.*, 2005; Báez & Gómez, 2018).

In this contribution, we describe a new species of *Baurubatrachus* based on two specimens recovered from an outcrop referred to the Adamantina Formation (Bauru Group), in Catanduva city, São Paulo State, Brazil (200 km south of Peirópolis; Fig. 1). The specimens were discovered in 2011 by Edvaldo Fabiano dos Santos, Laércio Fernando Doro and one of us (FVI) in two isolated blocks collected near the "Mario Paludeto" Bridge. These findings extend the stratigraphic range of *Baurubatrachus* from the Serra da Galga Formation to the underlying Adamantina Formation, while also providing evidence for a more southern distribution of this genus. New osteological data, including some new traits, is discussed in detail, which we believe should be considered in future systematic analyses.

Institutional Abbreviations. DNPM, Departamento Nacional da Produção Mineral, Secção Paleontologia, Rio de Janeiro, Brazil; **KU,** Museum of Natural History, University of Kansas, Lawrence, KS, USA; **MACN-HE,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Herpetological Collection), Ciudad Autónoma de Buenos Aires, Argentina; **MPEF-PV,** Museo Paleontológico Egidio Feruglio (Paleovertebrate Collection), Trelew, Chubut, Argentina; **MPMA,** Museu de Paleontologia "Prof. Antonio Celso de Arruda Campos", Monte Alto, São Paulo State, Brazil; **MPPC,** Museu de Paleontologia Pedro Candolo, Uchôa, São Paulo State, Brazil.

GEOLOGICAL AND PALEONTOLOGICAL CONTEXT

The Bauru Basin (Fig. 1) is an intracratonic basin (*e.g.*, Fernandes & Coimbra, 1992, 1996, 2000; Fernandes, 1998, 2004; Batezelli *et al.*, 2006; Menegazzo *et al.*, 2016) that extends approximately 370,000 km^2 over the northwest of Paraná, west of São Paulo and Minas Gerais, northeast of Mato Grosso do Sul, and south of Goiás states of Brazil (Fernandes & Coimbra, 1996). It was loaded by continental deposits during the Cretaceous (Fernandes & Coimbra, 2000); from bottom to top, the sedimentary column is

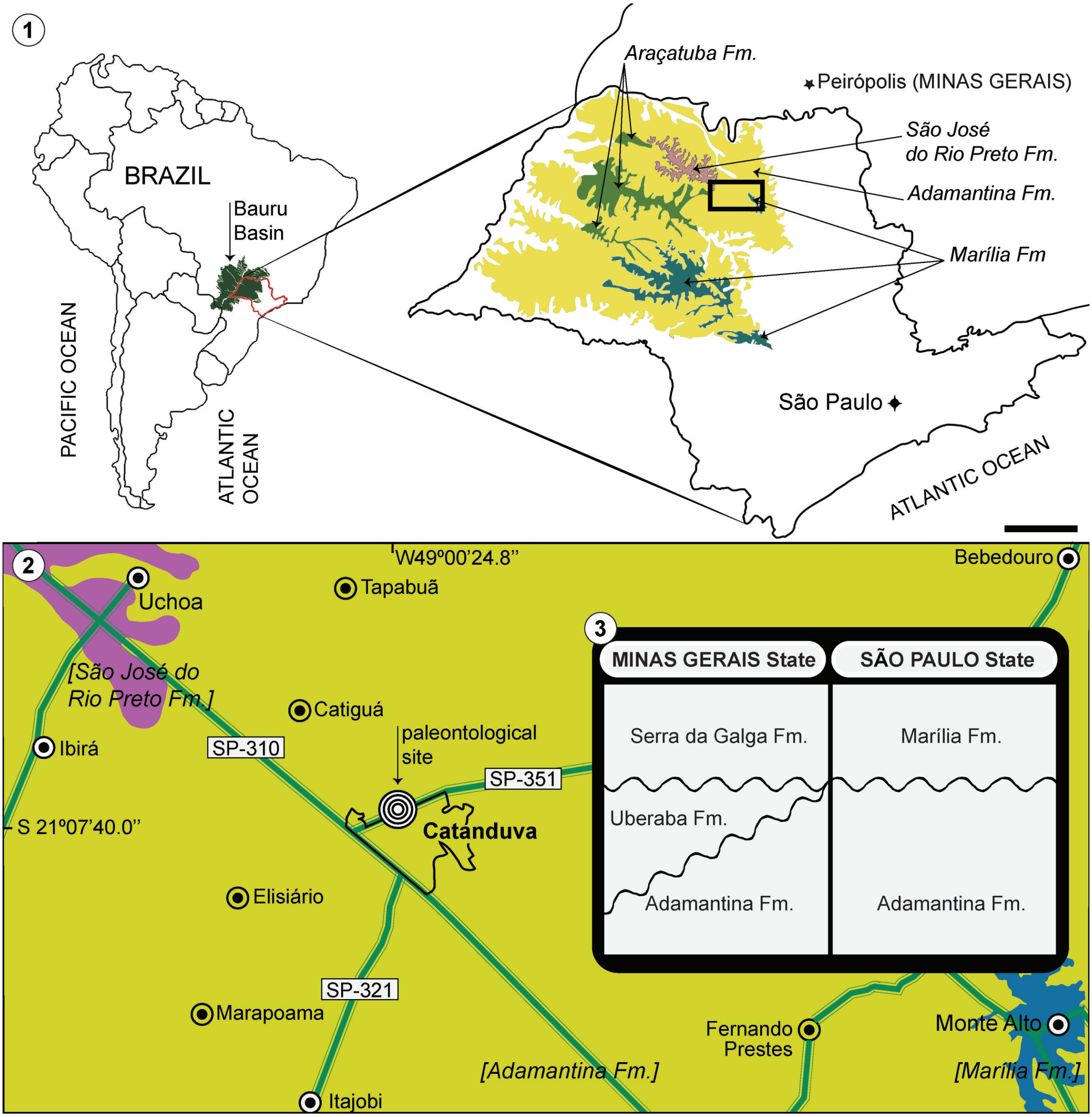

Figure 1.1, geographic boundary of the Bauru Basin in Brazil, with details of the outcrops of different formations in the São Paulo State. The type locality for *Baurubatrachus pricei*, Peirópolis, is indicated with a black star. **2,** detail of the paleontological site near Catanduva city, where the fossils here studied were collected. **3,** summarized schematic diagram showing the relative occurrence of mentioned litostratigraphic units of Bauru Group, as they outcrop in Minas Gerais and São Paulo States. Scale bar equals 100 km.

usually divided into the Caiuá and Bauru groups. The Caiuá Group includes the Goio Erê, Río Paraná and Santo Anastácio formations (Fernandes, 2004; Batezelli *et al.*, 2006). Regarding the Bauru Group, there is no consensus about the stratigraphic units included in it. One scheme includes the Araçatuba, Adamantina (~Vale do Rio do Peixe Formation; Fernandes & Coimbra, 2000), Uberaba, Serra da Galga and Marília formations (*e.g.*, Soares *et al.*, 1980; Batezelli *et al.*, 2006; see also the modifications of Soares *et al.*, 2021). In other studies, the group is comprised of a larger number of lithostratigraphic units represented by the Caiuá, Pirapozinho, Araçatuba, Santo Anastácio, Birigui, São José do Rio Preto, Uberaba, Adamantina, Marília (including the Serra da Galga Formation, sensu Soares *et al.*, 2021) and Itaqueri formations (Menegazzo *et al.*, 2016).

Specimens MPMA 68-0002/11 and MPPC 11-001 were discovered during the broadening of the state route SP-351 between kilometers 216 and 217 in Catanduva city (Fig. 2). The excavation of the sides of the road exposed a considerable number of rocks referred to the Adamantina Formation. In the same area, several fragmentary fossil remains were discovered in the removed rocks and also *in situ*, including freshwater bivalves, fishes, turtles, notosuchian crocodyliforms (the sphagesaurid *Caipirasuchus* sp. and an indeterminate peirosaurid; Iori *et al.*, 2011, 2016), and titanosaur and theropod dinosaur remains. The fossil-bearing level to which the anuran blocks belonged was inferred based on the lithological aspects of the blocks.

The age of the Adamantina Formation is certainly referred to the upper portion of the Late Cretaceous, but due to the lack of absolute dating in almost all outcrops (including those at Catanduva) and the lack of a clear lateral correlation among them, dating is indirect. The only high-precision U-Pb dating is based on samples from the Fazenda Buriti outcrop, in General Salgado, west of São Paulo state, which provides a post-Turonian maximal age for the Adamantina Formation, suggesting a late Coniacian–late Maastrichtian temporal constraint (Castro *et al.*, 2018).

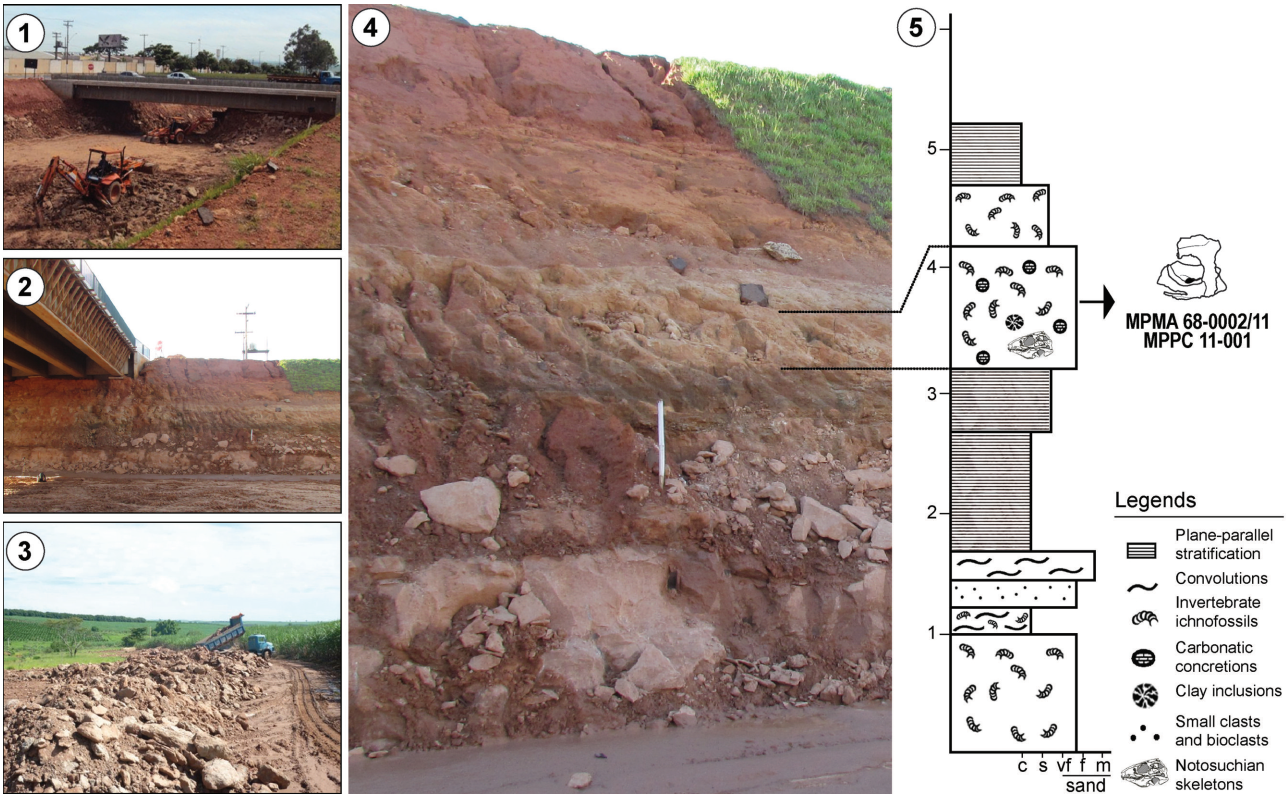

Figure 2. 1–4, pictures taken during the removal of Cretaceous rocks and exploration at the fossil-bearing Catanduva Paleontological Site on State Road SP-351, near to the "Mário Paludeto" Bridge (Catanduva, São Paulo State, Brazil). **5,** schematic stratigraphy section in the studied area.

According to the paleontological data, the Adamantina Formation is considered either Turonian to Santonian after the presence of charophytes and ostracods (Dias-Brito *et al.*, 2001) or Campanian–Maastrichtian based on ostracods (Gobbo-Rodrigues *et al.*, 1999). The tetrapod fossil record includes diverse notosuchian mesoeucrocodylians and titanosaur dinosaurs, which also suggests a Campanian to early Maastrichtian age for the unit (*e.g.*, Bertini *et al.*, 1993; Santucci & Bertini, 2001; Montefeltro *et al.*, 2011; Martinelli & Teixeira, 2015; Martinelli *et al.*, 2018; Iori *et al.*, 2021), being not older than Santonian.

The holotype of *Baurubatrachus pricei* comes from the Serra da Galga Formation, a formation that overlies the Uberaba Formation, the latter laterally correlated to the Adamantina Formation (Soares *et al.*, 2021) (see Fig. 1.3).

Taphonomic remarks

The preservation of the specimens referred to the new taxon is remarkable, especially when compared to other frogs from the Bauru Group. To date, the scarce frog remains from the Bauru Group indicated two distant taphonomic pathways for the fossil preservation: a rapid burial of the carcasses, according to the well-preserved and largely articulated *Baurubatrachus pricei*, *Uberabatrachus carvalhoi*, and an unnamed neobatrachian (Carvalho, 2006); and a prolonged exposure to biostratinomic processes that led to the preservation of isolated skeletal elements (Bertini *et al.*, 1993). However, the specimens of the current work represent an intermediate taphonomic pathway, which preserved cranial and postcranial elements in close association but, at the same time, fully disarticulated (except for the pelvic girdle). It is inferred that the individuals were buried only after reaching the last stages of decomposition. In experimental studies, significant disarticulation of frog skeletons is achieved after 45 days of decay in aquatic settings (Dodson, 1973) or after 30 days on sediment (Iniesto *et al.*, 2017). However, it is expected that frog carcasses in natural conditions would disarticulate in a shorter period because of additional disturbance factors, such as scavenging and hydraulic flows (Henrici & Fiorillo, 1993). A brief period of subaerial exposure before burial is supported by the well-preserved surface of the bones and lack of weathering marks (Behrensmeyer, 1978).

From the sedimentological and taphonomic aspects, some features suggest a flooding event that rapidly buried the skeletal remains. This scenario is consistent with the horizontal and vertical distribution of the specimens throughout the sediment. The length of interaction between the elements and the hydraulic flow was short based on the absence of abrasion signs (Aslan & Behrensmeyer, 1996; Fernández-Jalvo & Andrews, 2003; Van Orden & Behrensmeyer, 2010) and the presence of bones with distinct dispersal potentials (Dodson, 1973). Also, a group of disarticulated small bones would tend to be highly dispersed over time under sustained hydraulic flows (Rogers & Brady, 2010), and not concentrated as in the present case. After the burial, the deposit was exposed to pedogenesis, probably in a floodplain context, as indicated by the fossiliferous bed represented by massive sandstone with calcareous concretions, mottling and bioturbation (Iori *et al.*, 2011).

The Adamantina Formation comprises sediments deposited in an alluvial system associated with meandering and/or braided rivers under hot arid to semi-arid conditions (Soares *et al.*, 1980; Goldberg & García, 2000; Batezelli *et al.*, 2006; Marsola *et al.*, 2016). The climate was pronouncedly seasonal with long dry periods alternated with periods of intense rains and flooding (Goldberg & García, 2000; Vasconcellos & Carvalho, 2010). The proposed taphonomic scenario is coherent with the paleoenvironmental conditions of the Adamantina Formation, and it is possible that the burial of the remains occurred during the more humid season. The stressful drier periods might have elevated the mortality of many groups and increased the input of skeletal remains in the depositional environments.

MATERIAL AND METHODS

Specimens MPMA 68-0002/11 and MPPC 11-001 were mechanically prepared with needles under a stereomicroscope and Paraloid B-72 was used to stiffen the weak portions of the fossil and prevent damage.

The anatomical terminology follows Bolkay (1919) and Trueb (1973), except for terms indicated in the text. The features of the pelvic girdle are named according to Gómez and Turazzini (2015), except for the pubis. Owing to the calcified instead of bony condition of the ventral portion of the pelvic girdle in MPMA 68-0002/11, we considered it as the calcified remnants of the puboisquiadic plate and not the pubis (which might have its own ossification center).

Hence, we follow Gaupp and Ecker (1896), who named this after cartilago remanens. The systematic terminology follows Frost *et al.* (2006) and the anuran taxonomy is updated according to Frost (2021).

SYSTEMATIC PALEONTOLOGY

ANURA Fischer, 1813
NEOBATRACHIA Reig, 1958

Genus ***Baurubatrachus*** Báez and Perí, 1989

Type species. *Baurubatrachus pricei* Báez and Perí, 1989.

Revised diagnosis (based on Báez & Gómez, 2018). Neobatrachian frog diagnosed by the combination of the following features: large size; heavily ossified skeleton with a moderately depressed skull; dermal roofing skull bones bearing sculpture consisting of tubercles and rounded pits that nearly reach the ventral margin of the maxillary arcade; high pars facialis throughout the length of the maxilla and the quadratojugal (the latter according to *B. santosdoroi* sp. nov. ambiguous in *B. pricei*); nasals in broad contact with one another along the midline; discrete triangular palatines (neopalatines of Trueb, 1993) tapering medially and well separated medially from one another; massive pterygoid with anterior ramus bearing a conspicuous ventral flange and medial ramus broadly sutured with the corresponding parasphenoid ala; parasphenoid alae lacking ventral keels; squamosal having an extensive lamella alaris in contact with the maxilla by means of the zygomatic ramus (the latter according to *B. santosdoroi*; ambiguous in *B. pricei*); round opening in the temporal area of the skull made by the lamella alaris of the squamosal and the pars facialis of the quadratojugal (according to *B. santosdoroi*; ambiguous in *B. pricei*); lamella alaris and ventral ramus of the squamosal in tight contact; ventral ramus of the squamosal fused to the posterior ramus of the pterygoid and the pars facialis of the quadratojugal (the latter according to *B. santosdoroi*; ambiguous in *B. pricei*); subtympanic foramen resulting from the fusion of ventral ramus of the squamosal and the quadratojugal; extensive sphenethmoidal ossification extending into the septum nasi anteriorly and the planum antorbitale laterally, and roofing the cavum cranii posteriorly; lower jaw articulation well posterior to the occiput; eight discrete presacral vertebrae; high atlantal neural spine partially fused to succeeding neural arch; transverse processes of Vertebrae III and IV expanded distally and reaching farther laterally than the moderately expanded sacral diapophyses; moderately long scapula bearing a crest deflected ventrally to form a deep basin on its leading edge; well-ossified, large cleithrum with anterior branch and plate-like posterior portion; robust clavicle strongly bowed anteriorly; ilium with well-developed dorsal crest and an elongated dorsal protuberance obliquely oriented and strongly projected laterally but barely projecting from iliac outline in acetabular view; ventral acetabular expansion and iliac shaft forming an angle of nearly 70°; ischium bearing a large posterodorsal expansion; cartilago remanens heavily calcified in adults; femur bearing a ventral crest.

Holotype of the type species. DNPM 1412-R A and B, an incomplete, partially articulated skeleton preserved within two pieces of sandstone, lacking part of the skull and anterior and posterior autopodia.

Diagnosis of *Baurubatrachus pricei*. Hyperossification extended to the coossification of dermal and chondral elements of the skull, mineralization of the medial half of the planum antorbitale, and the obliteration of sutures among different elements of the pectoral and pelvic girdles; rounded cross-section of the shelf-like pars palatina anterior to the orbit, dorsoventrally flattened against the pars facialis at the level of the orbit.

Type locality and horizon. Rodovia Site, on the Road BR-262, east to Peirópolis town, Uberaba Municipality, Minas Gerais State, Brazil. Serra da Galga Formation (previously, the Serra da Galga Member of the Marília Formation), Bauru Group, Maastrichtian (Late Cretaceous).

Baurubatrachus santosdoroi sp. nov.

Figures 3–4

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Etymology. The specific name is a tribute to the discoverers of the fossils, the late Edvaldo Fabiano dos Santos and Laércio Fernando Doro.

Holotype. MPMA 68-0002/11, associated cranial and postcranial elements preserved in a single sandstone block.

Referred specimen. MPPC 11-001, fragment of maxilla and fragments of indeterminate bones.

Locality, horizon and age. Catanduva Paleontological Site, State Road SP-351, between kilometers 216 and 217, near the "Mario Paludeto" Bridge, Municipality of Catanduva, São Paulo State, Brazil. Adamantina Formation, Bauru Group, Bauru Basin; Campanian–Maastrichtian, Late Cretaceous.

Diagnosis. It differs from *B. pricei* by a lesser ossification of the skeleton, lack of coossification of dermal and chondral elements, rounded cross-section of the shelf-like pars palatina throughout the length of the maxilla; slenderer scapular shaft and a longer ilial shaft with respect to the ilial body, approximately by 10%.

Description. The specimen MPMA 68-0002/11 consists of few associated, though disarticulated, cranial and postcranial elements contained within a block of sandstone; some of the bones are preserved in their full extent. The preservational quality of the fossil is exquisite as it retains many details, but it is simultaneously very fragile, a fact that limited the mechanical preparation of some bones. The fragmentary condition of the specimen prevents us to establish a definitive snout-vent length (**SVL**). However, comparison with equivalent elements in the holotype of *Baurubatrachus pricei* allows us to suggest a similar SVL for the mentioned holotype (*i.e.*, approximately 110 mm). Cranial remains include the two maxillae with partial dentition (Fig. 3.1), the right squamosal, the right quadratojugal and fragments of the right pterygoid (Fig. 3.2–3.3). The postcranial skeleton is represented by one presacral vertebra (Fig. 4.1), most of the pectoral girdle (scapula, clavicle, and coracoid, Fig. 4.2, 4.4), parts of the forelimb (humerus and radioulna, Fig. 4.5–4.6), the complete pelvic girdle (Fig. 4.7), and parts of the hindlimbs (femur, tibiofibula, and some autopodial elements, Fig. 4.8–4.9). According to the ossification degree of the elements, the skeleton belongs to an adult, probably a fully grown individual.

Dermal skull-roof elements show hyperossification in the ways of sculpturing (exostosis) and wide extension of some bones (casquing) (following Trueb, 1973). The sculpturing consists mostly of rounded pits, which are well-marked

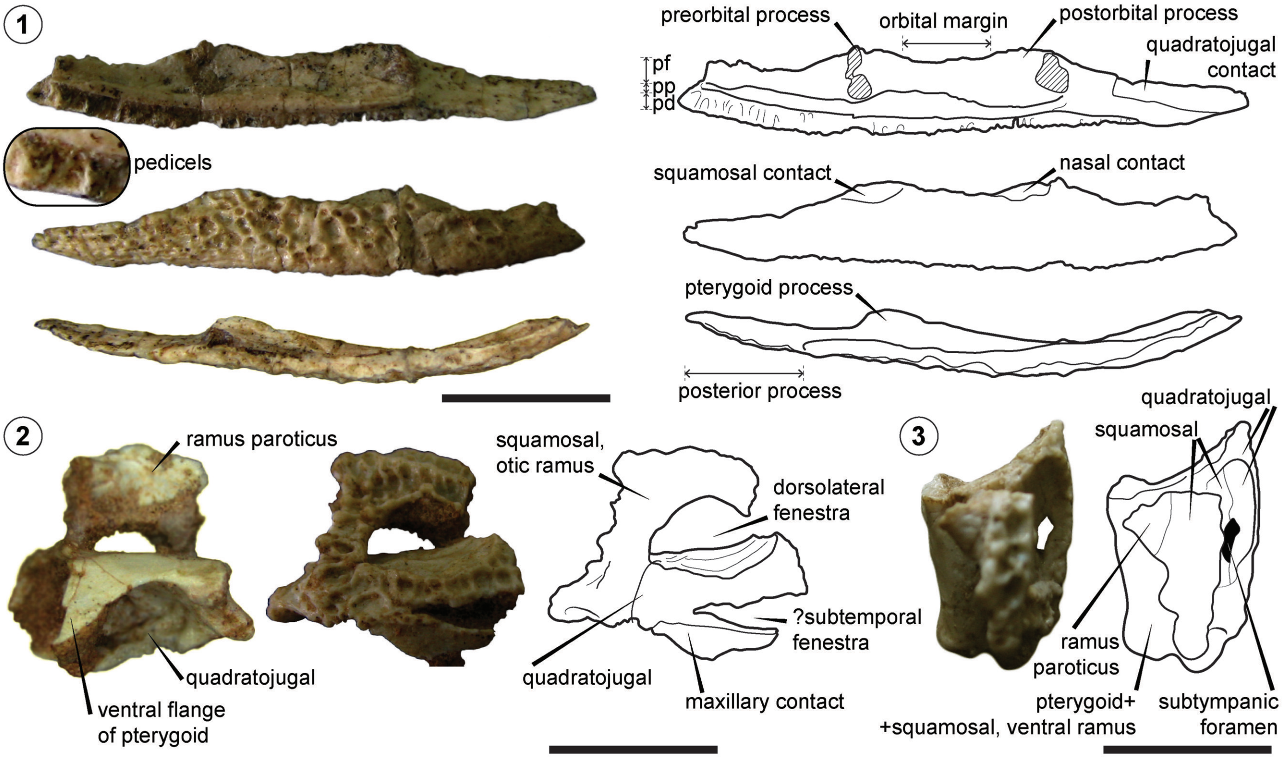
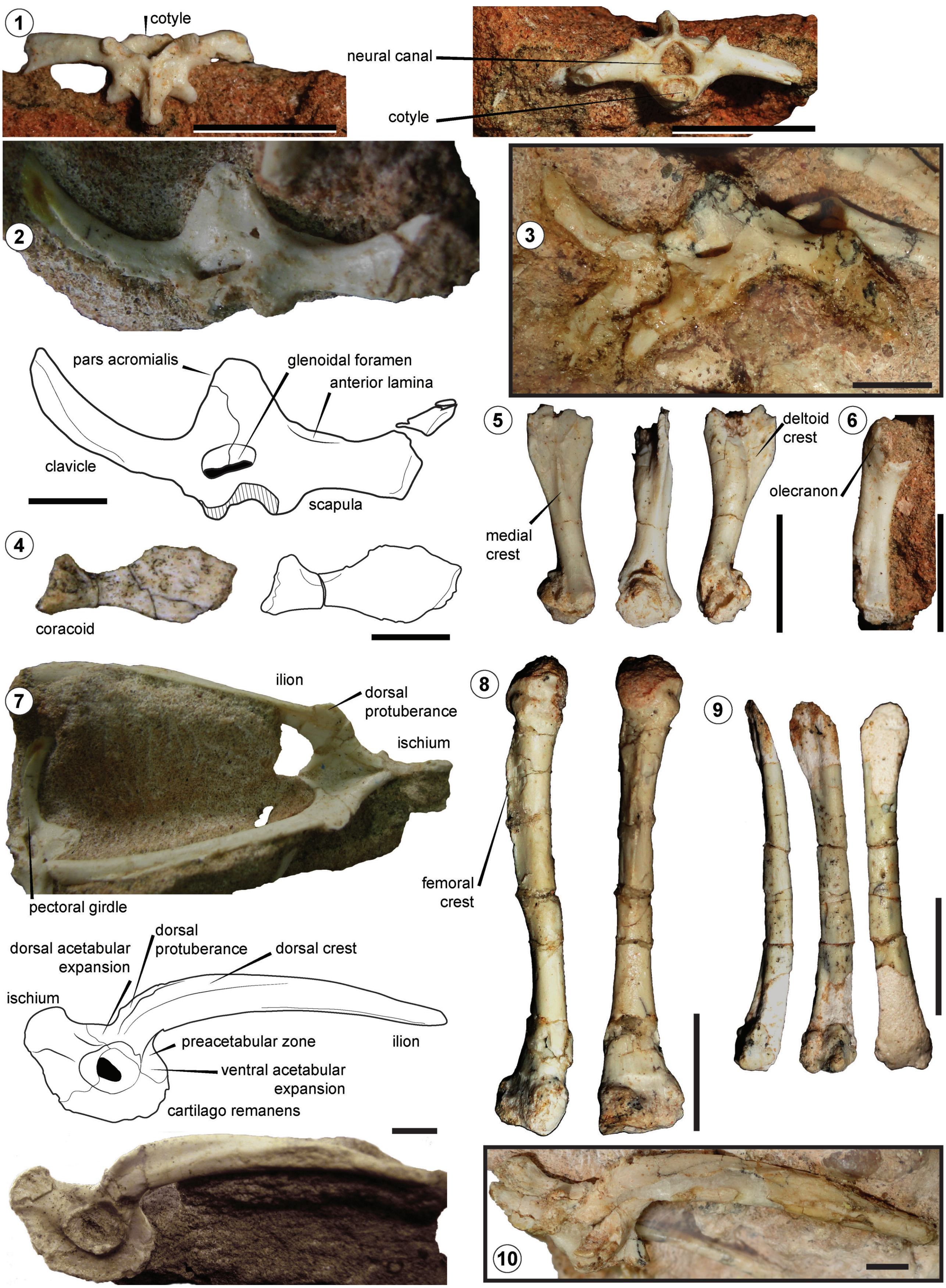


Figure 3. ***Baurubatrachus santosdoroi*** sp. nov., **MPMA** 68-0002/11; **1,** right maxilla in internal, external and dorsal views, with their corresponding interpretive drawings, and detailed pedicels on pars dentalis; **2,** posterior portion of the skull, block of fused quadratojugal, squamosal, and pterygoid in internal and lateral views, with interpretive drawing of the lateral view; **3,** block of fused quadratojugal, squamosal, and pterygoid in dorsal view with corresponding interpretive drawing. Abbreviations: **pf,** pars facialis; **pd,** pars dentalis; **pp,** pars palatina. Scale bars equal 10 mm.


1
cotyle
neural canal
cotyle
2
3
pars acromialis
glenoidal foramen
anterior lamina
clavicle
scapula
4
coracoid
5
medial crest
deltoid crest
6
olecranon
7
ilion
dorsal protuberance
ischium
pectoral girdle
dorsal acetabular expansion
dorsal protuberance
dorsal crest
ischium
preacetabular zone
ilion
ventral acetabular expansion
cartilago remanens
8
femoral crest
9
10

in the squamosal and quadratojugal and subtler in maxillae; some tubercles are also evident on some regions of these bones. Noteworthy, sculpturing differs on left maxilla where pits are oblong and radiate from the orbital margin. Both right and left maxillae are almost complete; the inner side is visible on the right side where all three partes (pars facialis, pars palatina and pars dentalis) are well-defined (Fig. 3.1). The anterior margin of the maxilla is oblique, the pars dentalis extending beyond the limits of the pars facialis; according to the terminology of Báez and Gómez (2018), no anterodorsal process is present. Posteriorly, the maxilla is tapering, composed only of the pars facialis which makes the posterior process. The pars facialis is high all along its length, but higher at the central portion. The latter is limited by very subtle, triangular pre and postorbital processes; on the outer surface of the two aforementioned processes, a lack of sculpturing suggests the places where the nasal and the zygomatic ramus of the squamosal established contact with the maxilla. The pars palatina is distinct though not prominent, orthogonal to the pars facialis and rounded in cross-section all along its length but for the posterior pterygoid process, which is horizontally flat. It extends from the anterior end of the maxilla up to the posterior end of the postorbital process, where the posterior pterygoid process is placed. Posterior to this, the pars palatina steeply diminishes and disappears. The pars dentalis bears the barrs to accommodate pedicelate teeth. The preservation of the internal portion of the pars dentalis is poor; however, in the right maxilla at least two pedicels remain intact, preserving a hollow at their bases (Fig. 3.1). Teeth were evidently large anteriorly and very small posteriorly to the level of the pterygoid process; several of them are still in their natural place on the left maxilla. According to the few complete crowns, teeth are conical, slightly curved posterolingually, and bicuspid; the second cusp, however, is so faint that it is difficult to perceive.

The posterior portion of the skull is represented by a consolidated block of bones consisting of portions of the quadratojugal, the squamosal and the pterygoid (Fig. 3.2–3.3); this tight arrangement of the elements, with discernible sutures, indicates some synostotic fusion. A remarkable aspect of this block is that bones form the margins of a circular opening, called dorsolateral fenestra by Báez *et al.* (2012), which most likely surrounded the tympanic membrane as suggested previously by Báez and Perí (1989) and Báez and Gómez (2018) (see Discussion). The sculpturing on the margins of this circular opening changes to some tubercles set over the borders of the pits. The quadratojugal is represented by its posterior portion; it has a clear ventral area for the articulation with the maxilla (maxillary contact) and it expands dorsally into a high pars facialis, which makes the ventral and part of the anterior margins of the opening for the tympanic membrane. Although incomplete, the preservation of the quadratojugal provides evidence that the maxillary arcade was complete. The gap between the pars facialis and the maxillary contact of the quadratojugal might represent the subtemporal fenestra. The squamosal is represented by the otic and ventral rami. The former, part of a probably larger lamela alaris (*sensu* Roček, 1980), lays on the lateral margin of crista parotica by means of a small, triangular ramus paroticus (*sensu* Roček, 2003) and extends posteriorly and ventrally in an almost vertical plane. The lamela alaris makes the dosal, posterior and probably part of the anterior margins of the aforementioned circular opening. The squamosal lamela alaris is continuous with the posterior end of the pars facialis of the quadratojugal and simultaneously lays on the squamosal ventral ramus. The latter is fused with the posterior ramus of the pterygoid, according to the evident ventral flange preserved on the medial side of the block, which corresponds to the anterior ramus of the pterygoid. The posterior ramus of pterygoid and the ventral ramus of squamosal are horizontally oriented and project far beyond the level of the tympanic membrane, thus it indicates that the mandibular articula-

Figure 4. 1–2, 4–9, ***Baurubatrachus santosdoroi*** sp. nov., **MPMA** 68-0002/11; **1,** presacral vertebra in dorsal and anterior views; **2,** right scapula and clavicle in dorsal view with corresponding interpretive drawing; **4,** left coracoid in dorsal view with corresponding interpretive drawing; **5,** left humerus in medial, ventral and lateral views; **6,** radioulna in ventral view; **7,** pelvic girdle in dorsal and lateral (acetabular) views, with interpretive drawing of the lateral view; **8,** femur in lateral and ventral views; **9,** tibiofibula in lateral, ventral, and dorsal views. **3, 10,** ***Baurubatrachus pricei***, **DNPM** 1412-R A and B; **3,** right pectoral girdle in dorsal view; **10,** right side of the pelvic girdle in lateral (acetabular) view (pictures from one of the authors, PM). Scale bars equal 5 mm.

tion was posterior to the level of the occiput. Also, the ventral ramus of the squamosal is fused to the inner side of the quadratojugal; a small subtympanic foramen remains between them (Fig. 3.3; see Discussion).

Only one procoelous presacral vertebra has been recovered from the block (Fig. 4.1). According to the anteroventral projection and the robustness of the transverse processes, it most likely represents the PV II. The vertebral body is rather cylindrical; it bears anteriorly a suboval, slightly depressed cotyle, indicating that it was not fused to the atlas. Although the transverse processes are distally incomplete, some traces on the rock show that they were long, more than twice the width of the neural arch; the ventral curvature plus the length of the transverse processes made them reach the level of the vertebral body. The neural arch is quadrangular and bears a high dorsal spine projected well posterodorsally, probably overlapping the succeeding vertebra. From an anterior view, the neural canal is clearly triangular and tall, taller than the vertebral body. The prezygapophyses make an acute angle (approximately 45°) with the vertical line.

The pectoral girdle is represented by the right scapula and clavicle and the left coracoid. The scapula and clavicle are exposed in dorsal view (Fig. 4.2); they retain their relative position, seemingly fused to each other. The glenoidal foramen, delimited in bone by the two elements, is roughly rectangular with the largest axis mediolaterally oriented. The scapula has a cylindrical, slender shaft which slightly expands and flattens towards the supraescapula. The lateral (dorsal) end of the scapula is triangular-shaped, the anterior margin more extended than the posterior one. The shaft bears a small, ventrally bent anterior lamina along its mid portion. The pars acromialis is triangular, notably projected anteriorly, while the pars glenoidalis is shorter; the glenoid cavity seemingly faced posteroventrally. The clavicle is curved, its medial and lateral margins reaching the same level. The head of the clavicle abuts the pars acromialis of the scapula along all its length, thus, the clavicle is also notably projected anteriorly. The coracoid (Fig. 4.4), when in a natural position, reaches the medial level of the corresponding clavicle. The glenoidal end of the coracoid is quadrangular and the medial end is flat. Although slightly incomplete, it is evident that the medial end was widely expanded. The anterior margin of the coracoid is more concave than the posterior one, indicating an asymmetrical expansion towards the anterior end.

The humerus (herein interpreted as the left one) is incomplete (Fig. 4.5). The shaft is straight in dorsal/ventral view and recurved dorsally when observed in lateral/medial aspect. The proximal end is missing. The diaphysis bears the distal part of what was a notably high and well-defined deltoid crest, which is slightly shifted medially. The medial surface of the diaphysis has a very subtle accessory crest (medial or parietal crest) at the level of the distal part of the deltoid crest. The distal end of the humerus is lateromedially expanded if observed in dorsal/ventral aspect. In opposition to most other elements of the skeleton, the distal epiphysis is subossified, denoting a cartilaginous condition of the eminentia capitata as well as its more distal portion; it might be suggested that the missing head of the humerus is also a consequence of subossification. The lateral epicondyle is broken off; the medial epicondyle is incomplete due to subossification, but the ossified portion indicates it was moderately expanded. One of the radioulnae is mostly preserved and probably represents the right one (Fig. 4.6). It bears a pronounced, well-ossified olecranon process, which has a right-angled outline in medial/lateral view. The natural sulcus that separates the fused radio and ulna is rather shallow on both medial and lateral surfaces. Half of the distal end of the ulnar portion of radioulna is missing, but the radial portion shows an ossified epiphysis which exposes a flat surface on the interpreted medial side, thus indicating that carpal rotation occurred in this species.

The pelvic girdle is complete (Fig. 4.7). Ilia and ischia, both right and left, remain articulated as in life. The pelvis is well ossified and its components well bounded; the cartilago remanens is mineralized, thus, the corpus has a ventral, extensive portion other than the ilial and ischiatic components. The acetabulum is rounded to semioval, with well-demarcated rims; the anteroventral being the most protruding. As a consequence of the profuse mineralization, the acetabulum is completely circumscribed by bone and mineralized cartilage. Only the bottom of the acetabular fossa remained cartilaginous, leaving a semi-oval opening in the fossilized specimen. Each ilial body has a rather small triangular dorsal acetabular expansion and an also triangular ventral acetabular expansion, more protuberant than the former and with rounded margins. The preacetabular zone is narrow, but evident, in acetabular aspect. The ilial shaft has a subtle dorsoventral curvature and establishes a right to an acute angle with the ilial body; it is mediolaterally depressed posteriorly and turns circular in cross-section at its anterior end. The ilial shaft bears a high, dorsally projecting dorsal crest along four-fifths of its length; the posteriormost two-fifths are the highest and then it diminishes in height towards the anterior end. The dorsal protuberance is elongated; it outlines the base of the dorsal crest and extends from the level of the anterior margin of the acetabulum to the level of the anterior tip of the ilial body. From a dorsal aspect, it is clear that the dorsal protuberance is laterally projected. Whether there is a dorsal prominence is not possible to discern, owing to the presence of the well-developed dorsal crest. The ischium is large, barely rectangular with its major axis oriented posterodorsally. As stated before, the cartilago remanens is strongly mineralized, thus allowing to describe a wide ventral portion of the puboischiadic cartilage. The hindlimbs are represented by a complete femur and a partial tibiofibula. The femur (Fig. 4.8), probably the right one, is straight in dorsal view, but sigmoid when exposed laterally. From the lateral view, a well-defined, small femoral crest is visible, extending longitudinally along the proximal half of the ventral surface of the element. Both proximal and distal epiphyses are well ossified. The condition of the tibiofibula does not allow to refer it either to the right or to the left side of the body, but shows a well-ossified epiphysis at one end (Fig. 4.9). The femur is notably longer than the tibiofibula.

Specimen MPPC 11-001 does not provide further data on the cranial anatomy of *B. santosdoroi*. The maxilla is similar to that of the holotype and thus is considered a second specimen for the new species.

DISCUSSION

As Báez and Gómez (2018) pointed out, there is a set of very peculiar anatomical features in *Baurubatrachus pricei* (whether they are autapomorphic or not) that makes this a bizarre taxon. The posterolateral architecture of the skull, with a conspicuous round opening that draws attention at a first glance, is one of them (Fig. 5.1). This outstanding feature was already described by Báez and Perí (1989) when the species was erected and was interpreted as a way to provide an osseous support to the round tympanic membrane (Báez & Perí, 1989; Báez & Gómez, 2018). Additional remarkable features present in *B. pricei* are the high pars facialis along all of the length of the maxilla, the presence of a ventral flange in the anterior ramus of the pterygoid, the deflected anterior lamina (tenuitas cristaeformis) of the scapula, the shape and projection of the dorsal protuberance of the ilium, and the angle made between the ilial corpus and ilial shaft (**VSA**). Specimen MPMA 68-0002/11 shares with *B. pricei* all the cited features; furthermore, the similarities extend to other items not highlighted by Báez and Gómez (2018): the posterior ramus of the pterygoid and the ventral ramus of the squamosal are fused, the latter being also fused to the lamella alaris of the squamosal and the quadratojugal, leaving a subtympanic foramen between the quadratojugal and squamosal below the opening for the tympanic membrane (Fig. 5.2). Other traits are also the development of a pars facialis of the quadratojugal (suggested by Báez & Perí, 1989; but not mentioned by Báez & Gómez, 2018); the coracoidal morphology with a concave anterior border and a straighter posterior one; and the humerus concave in lateral/medial views but straight in dorsal/ventral views. From the above, MPMA 68-0002/11 can be clearly assigned to the genus *Baurubatrachus*.

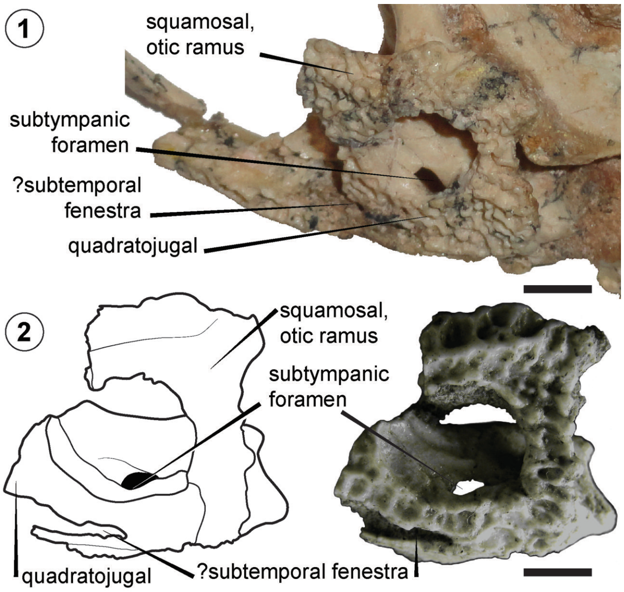


Figure 5. 1, ***Baurubatrachus pricei***, **DNPM** 1412-R A and B, posterior portion of the left side of the skull, showing the equivalent preserved portion of *B. santosdoroi* (pictures from one of the authors, PM). **2,** ***Baurubatrachus santosdoroi*** sp. nov., **MPMA** 68-0002/11, posterior portion of the skull, block of fused quadratojugal, squamosal, and pterygoid in dorsolateral view with corresponding interpretive drawing. Flipped for comparative purposes. Scale bars equal 5 mm.

There are, however, differences that allow the recognition of MPMA 68-0002/11 as a separate species, *B. santosdoroi*. The evenly rounded, shelf-like aspect of the pars palatina of the maxilla contrasts with the flattened condition below the orbit described by Báez and Gómez (2018) for *B. pricei*. Noteworthy, an analogous morphological characteristic separates taxonomically the australobatrachian *Calyptocephalella canqueli* from the other species of the genus (Muzzopappa & Báez, 2009). The girdles (pectoral and pelvic) of MPMA 68-0002/11 and that of *B. pricei* are notably alike (see Fig. 4.2–4.3, 4.7, 4.10), but they differ in their proportions, providing additional taxonomical separation among them: the scapula is slender in MPMA 68-0002/11 and the ilial shaft, referred to the length of the body, is larger in MPMA 68-0002/11 than in the holotype of *B. pricei*. Other features vary in both species, but they may not be taxonomically informative, and may rather reflect polymorphism. The clearest polymorphic trait refers to the differences in the pattern of sculpturing in the maxilla, as observed in the right and the left maxillae of the same specimen, MPMA 68-0002/11 (see above). The presence of this intraindividual variation indicates that the taxonomic use of subtle differences in the sculpturing details of dermal roofing bones should be considered with caution. Another example of possible polymorphism of osteological features is the degree of development of the anterior lamina of the scapula. When comparing MPMA 68-0002/11 with *B. pricei*, the scapula has a less conspicuous anterior lamina in the former than in the latter. Differences of this kind were observed within the spectrum of variations for the neobatrachian *Telmatobius oxycephalus* (Barrionuevo, 2013); although phylogenetically not related, the case of *T. oxycephalus* illustrates that this trait can be variable.

MPMA 68-0002/11 further differs from *B. pricei* in the degree of ossification. It is worth mentioning that the size of equivalent skeletal elements is similar in both MPMA 68-0002/11 and the holotype of *B. pricei* (DNPM 1412-R A and B). Skeletal elements, such as ilia and femora, are equally ossified, indicating that these two individuals were adults that had attained a similar developmental degree. Notwithstanding the above, MPMA 68-0002/11 is notably less ossified than *B. pricei*. This is especially evident in the subossification of the humeral ball, clearly cartilaginous in the specimen studied herein, but well-ossified in *B. pricei* (Báez & Gómez, 2018, fig. 6B). This milder ossification is also expressed in the lack of synostotic fusion between the ilia and isquia and between the scapula and clavicle, in the isolated condition of the maxillae (not fused to any other element of the skull), and in the lack of coossification of dermal and condrocranial bones represented by the detachment of the ramus paroticus of the squamosal from the crista parotica. In *B. pricei*, the coosification of dermal and chondral elements is suggested in roofing and palatal bones of the skull (Báez & Gómez, 2018). Particularly, the limits of the ramus paroticus were not discernible from the crista parotica, according to Báez and Gómez (2018); they appraise these unclear boundaries might result either from the poor development of the ramus paroticus or its fusion to the crista parotica. Considering that a noticeable ramus paroticus is evident in MPMA 68-0002/11, the most likely option for *B. pricei* is the fusion of the squamosal to the chondral element by means of the ramus paroticus. The above differences regarding ossification denote different ontogenetic trajectories for the two *Baurubatrachus* species.

The lesser ossification of *Baurubatrachus santosdoroi* provides some morphological details that are ambiguous in *B. pricei*. The similarity in the anatomy of both species allows to hypothesize that the following features observed in *B. santosdoroi* might also occur in *B. pricei*. One of special interest is the maxilla making the lateral part of the orbit; in the recent restudy of *B. pricei*, Báez and Gómez (2018) explained that, owing to the extreme ossification of the skull as well as the preservation of the specimen, they were not able to completely ascertain the contribution of the maxilla to the orbit, something that is clearly established for *B. santosdoroi*. It is also clearly established for the new species that the pars facialis of the maxilla has no anterodorsal process (scored as dubious from the holotype of *B. pricei*; Báez & Gómez, 2018, their ch. 51), as well as a lack of contribution of the maxilla to the tympanic osseous opening in the posterior region of the skull; instead, the latter is made by the pars facialis of the quadratojugal and the lamella alaris of the squamosal. The disarticulated preservation of the maxilla also allows to assess the hollowed condition of the pedicels, which denotes they had no surrounding bone at their bases as observed in Ceratophryidae species (see Fig. 3.1 and Báez & Gómez, 2018, fig. 8). Regarding the girdles, the clear suture observed in *B. santosdoroi* between scapula and clavicle shows the latter abuts the scapula only medially, while the clear suture among the ilium and ischium allows to recover completely their morphology. The good preservation of the pelvic girdle makes evident the extent of calcification of the cartilago remanens in adult specimens of the new species. Considering that even the less mineralized *B. santosdoroi* has a fully mineralized cartilago remanens, the same condition is expected for *B. pricei*.

As mentioned above, the posterolateral portion of the skull in *Baurubatrachus* is noteworthy. The big, round opening on the temporal area that putatively provides an osseous support to the tympanic membrane (Báez & Perí, 1989; Báez & Gómez, 2018) is singular. Báez and Gómez (2018) pointed out that the bufonid *Peltophryne empusa* bears an opening of the kind surrounding the tympanic membrane in the squamosal (Pregill, 1981; Pramuk, 2002). Other species of the genus *Peltophryne* (*e.g.*, *P. guentheri*, *P. peltocephala*, *P. lemur*) have a squamosal surrounding the tympanic membrane, too, although incompletely (Pregill, 1981; Pramuk, 2002). The fact that the sculpturing on the squamosal of *B. santosdoroi* changes towards the margins of this circular opening supports the idea proposed by Báez and Perí (1998) that the squamosal braces the tympanic membrane.

Another remarkable feature of the temporal architecture of *Baurubatrachus* is the small opening inside the middle ear area. This opening is neither the postemporal nor the subtemporal fenestra (*sensu* Lynch, 1971), nor even remnants of the adductor chamber. Instead, it consists of a small foramen below the tympanic annulus and between the internal border of the quadratojugal and the posterior ramus of the squamosal (Fig. 5). Although not reported or named in the literature, this subtympanic foramen can be observed in some phylogenetically distant casque-headed anurans such as the microhylid *Mantophryne menziesi* (Morphosource M105026, as *Pherohapsis menziesi*), and several species of the bufonid genus *Peltophryne* (*e.g.*, *P. lemur* [Morphosource M105025, KU:KUH288691]; *P. guentheri* [Morphosource M11380, UF:HERP 104862]; *P. fustiger* [M42232, usnm: amphibians & reptiles:51864]) (Fig. 6); in contrast, it is absent in other casque-headed species whose casquing is not especially referred to the squamosal (Trueb, 1970), such as *Triprion petasatus* (Morphosource M14971 UF:HERP 98441), *Trachycephalus jordanis* (Morphosource M165517 UF:HERP 98302), *Gastrotheca peruana* (Morphosource M16448 UF:HERP 65783), and also absent in casque-headed species whose casquing does imply well-developed squamosals, such as *Calyptocephalella gayi* (MACN-HE 45743-45748; Reinbach, 1939), the extinct *C. canqueli* (Muzzopappa & Báez, 2009) or any of the Ceratophryinae species (Lynch, 1971; Perí, 1993; Nicoli, 2019). The subtympanic foramen results from the articulation of the lamella alaris and the ventral ramus of the squamosal, in some cases involving also the quadratojugal (as ocurrs in *P. fustiger* and in *Baurubatrachus*). Although the articulation was already described by Pregill (1981, as an extensive ossification of the zygomatic ramus) and Pramuk (2002), they did not

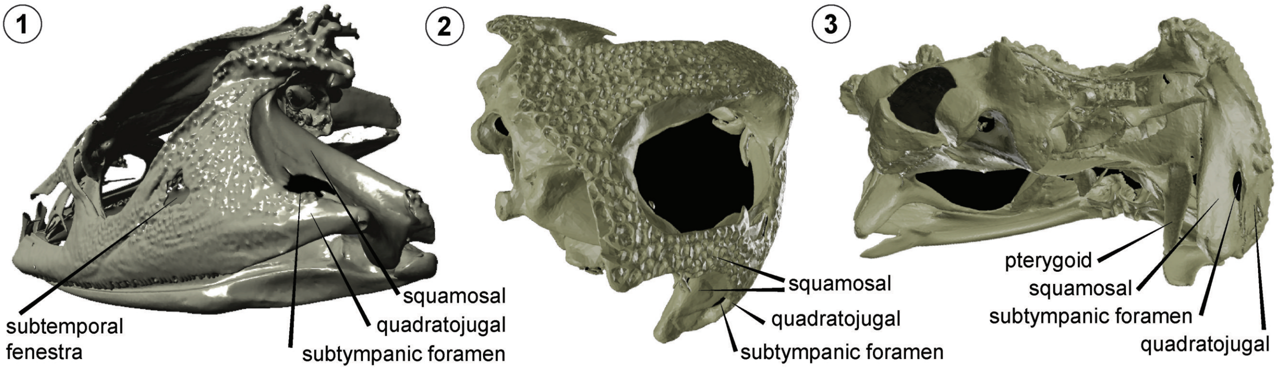


Figure 6. Skulls of hyperossified taxa, showing the presence of a subtympanic foramen within the tympanic region. **1,** ***Cornufer guentheri***, Morphosource M000037445, uf:herp:80585. **2,** ***Mantophryne menziesi***, Morphosource M105026, amnh:herpetology:a-84449. **3,** ***Peltophryne lemur***, Morphosource M105025, KU:KUH288691. No scale availble.

mention any related foramen. No muscles—neither adductor mandibulae, depressor mandibulae nor hyoid musculature—are expected to go through this opening (*e.g.*, Limeses, 1965; Starrett, 1968; Carroll & Holmes, 1980; Barrionuevo, 2016; Roček *et al.*, 2016; Kunisch *et al.*, 2021). Instead, this subtympanic foramen most likely constitutes the trace left by the passage of the mandibular arch of the trigeminal nerve (V3) on its way to the mandible (see Starrett, 1968; Lynch, 1986; Johnston, 2011; Grant & Bolívar-G, 2014).

Baurubatrachus and calyptocephalellid traits

Previously proposed ceratophryid affinities for *Baurubatrachus pricei* (Báez & Perí, 1989; Evans *et al.*, 2008) were rejected in the recent restudy of the anatomy and systematic of the taxon (Báez & Gómez, 2018), in agreement with the hypothesis suggested by Báez *et al.* (2005). Instead, this Cretaceous species is retrieved as the sister taxon of *Calyptocephalella gayi* in most of the several analyses performed by Báez and Gómez (2018). However, owing to the low support of the *B. pricei-C. gayi* clade, Báez and Gómez (2018) refrained from considering *Baurubatrachus* as a calyptocephalellid, but stressed the recovery of *B. pricei* among Neobatrachia, being probably a hyloid. It is noteworthy that the clade Calyptocephalellidae (*Calyptocephalella* + *Telmatobufo*, both genera scored for the analysis) was not recovered in any of the trees. The characters that ultimately unite *B. pricei* and *C. gayi*, as discussed by Báez and Gómez (2018), are the presence of a supraorbital flange in the frontoparietal, an extensive contact of pterygoid and parasphenoid, a markedly posterior lower jaw articulation, and a high iliac dorsal crest. Of these, only the latter two characters could be evaluated and assessed for *B. santosdoroi*.

Owing to the sustained recovery of the sister taxon relationship of *Baurubatrachus pricei* and *Calyptocephalella gayi*, we thought it convenient to discuss some features, paying particular attention to *C. gayi* but including other australobatrachians whenever possible. Certainly, the discussion of characters, character states, and the addition of new ones to the data matrices will enhance future analyses and, hopefully, result in better-supported nodes containing fossil frogs.

The skulls of *Baurubatrachus* and *Calyptocephalella* species are highly exostosed and their skull roof elements are notably expanded although by different means. As stated elsewhere, the hyperossification in frogs is a highly homoplasic condition attained independently in many branches of the anuran tree (*e.g.*, Báez & Gómez, 2018; Paluh *et al.*, 2020). After analysing the distribution of hyperossification in the anuran tree, Paluh *et al.* (2020:3) concluded that "phylogenetic relatedness does not explain variation in the skull" by considering that several lineages convergently evolve similar extreme shapes related to their hyperossified skulls. These same homoplastic characters, however, are phylogenetically informative at lower hierarchical levels, especially when using different analytical strategies (*e.g.*, Vidal-García & Keogh, 2017; Báez & Gómez, 2018). The current broad-scale anuran phylogenetic trees are mostly based on molecular sequences and, hence, most nodes are devoid of osteological characters (*e.g.*, Pyron & Wiens, 2011; Pyron, 2014; Jetz & Pyron, 2018). When dealing with scarce fossil frog remains, the lack of osteological synapomorphies for tree nodes and the considerable homoplasy in skull characters obscure their taxonomy.

The neurocranium is seldom recovered in the fossil record, especially because it is regularly chondral in most of its extension (*e.g.*, Trueb, 1973; Duellman & Trueb, 1994). In *Baurubatrachus pricei*, however, it is well ossified and nicely preserved; the anterior sphenethmoid was described as narrow and extensively ossified (Báez & Gómez, 2018), while the posterior cristae paroticae are long and slim, according to Báez and Perí (1989), but "distally expanded" according to Báez and Gómez (2018). The orbital portion of the sphenethmoid of *B. pricei* was not described and, thus, not considered as a character in the matrix by Báez and Gómez (2018). It is barely triangular in dorsal aspect and its margins converge posteriorly (Fig. 7.1). This feature contrasts with that of calyptocephalellids, whose sphenethmoids have parallel margins in dorsal aspect in the same region (Fig. 7.2-7.4; Reinbach, 1939; Formas *et al.*, 2001; Morphosource M105294 ku:kuh 161438). This condition is also observed in many other australobatrachian species (Lynch, 1971, figs. 55, 60–72; Davies, 1984, 1989), such as *Limnodynastes peronii* (Fig. 7.5), *Lechriodus melanopyga* (Fig. 7.6), *Philoria frosti* (Fig. 7.7). By contrast, the sphenethmoid of *Adelotus brevis* (Fig. 7.8) and *Mixophyes fasciolatus* is more similar to that of *B. pricei* (Lynch, 1971, figs. 53, 58–59;

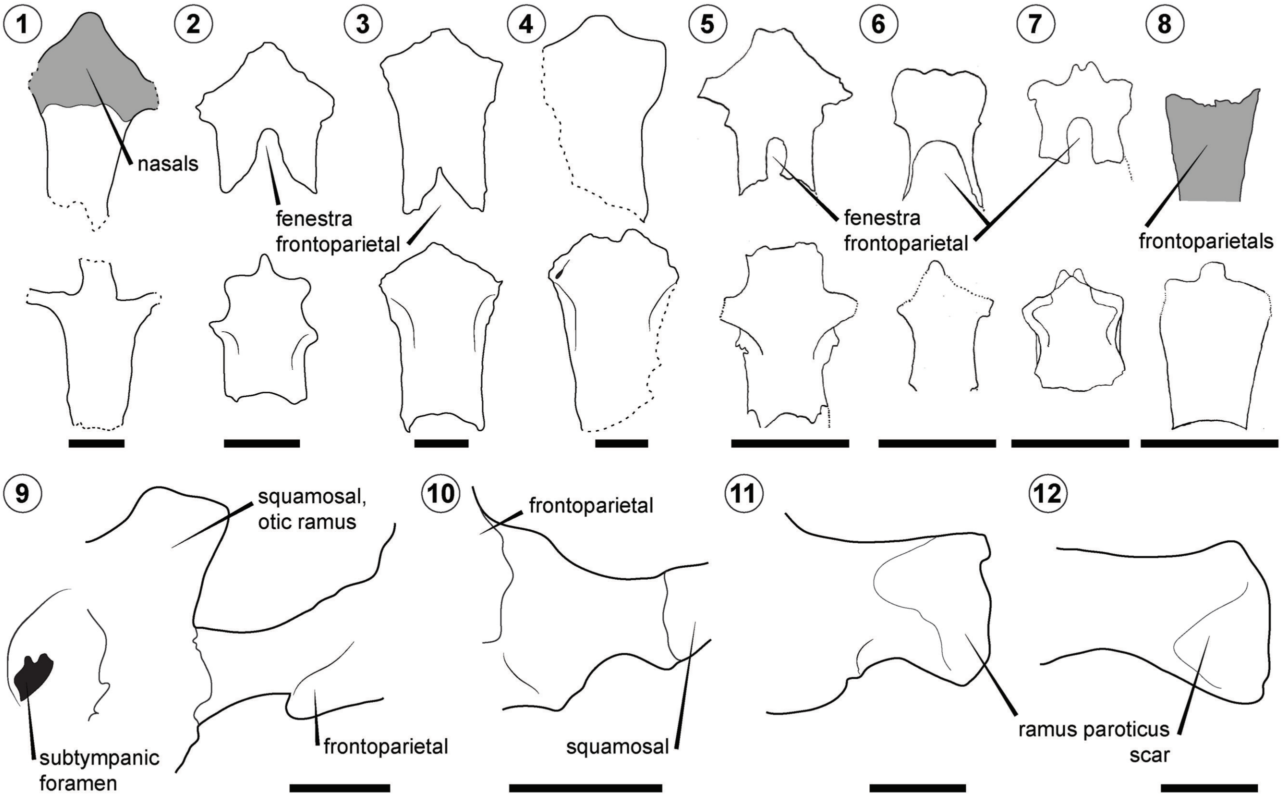


Figure 7. 1–8, Schematic outlines of sphenethmoids in dorsal (upper) and ventral (lower) views; **1, *Baurubatrachus pricei***, **DNPM** 1412-R A; **2, *Telmatobufo venustus***, **KU** 161439; **3, *Calyptocephalella gayi***, **MACN-HE** 45745; **4, *C. canqueli***, **MPEF-PV** 1882; **5, *Limnodynastes peronii***, **KU** 179939; **6, *Lechriodus melanopyga***, **KU** 133626; **7, *Philoria frosti***, **KU** 186907; **8, *Adelotus brevis***, **KU** 186773. **9–12,** schematic outlines of cristae paroticae of otoccipital in dorsal view; **9, *Baurubatrachus pricei***, **DNPM** 1412-R A, left side of the skull; **10, *Telmatobufo venustus***, **KU** 161439, right side of the skull; **11, *Calyptocephalella gayi***, **MACN-HE** 45745; **12, *C. canqueli***, **MPEF-PV** 1881a. Scale bars equal 5 mm.

Vidal-García & Keogh, 2017). Regarding the cristae paroticae, the distal expansion of *B. pricei* (Fig. 7.9) is much less extensive (Báez & Perí, 1989; Báez & Gómez, 2018; PM, pers. obs.) than the observed in the distal cartilagious portion of *Telmatobufo venustus* (Fig. 7.10; Morphosource M105294 ku:kuh 161438) and in *Calyptocephalella* species (Fig. 7.11–12), all of them equally scored by Báez and Gómez (2018, ch. 39). Additionally, the overlapping of the squamosal to the crista parotica is lateral in both *Baurubatrachus* species but dorsal in calyptocephalellids (Fig 7.10–7.12; Morphosource M105294 ku:kuh 161438). It is noteworthy that the contact of these two elements was treated differently by Báez and Gómez (2018, their ch. 9), who analyzed the overlapping as reduced or absent; small, overlapping the most lateral portion of the crista parotica; or extensive, overlapping the prootic. The condition in *B. pricei* was scored as dubious, in *T. venustus* as small-overlapping crista parotica and in *C. gayi* as extensive-overlapping prootic (Báez & Gómez, 2018, Supplemental material). However, according to our observations, in both *C. gayi* and *T. venustus* the overlapping of the lamela alaris/otic ramus is restricted to the crista parotica; although more extensive in the former than in the latter, it does not invade the otic region and thus the prootic in *C. gayi.* The cartilaginous lateral end of the crista parotica in *T. venustus*, in opposition to that of adults of *C. gayi*, bears no trace of the squamosal overlapping.

Since the best-preserved skull roof element for the two *Baurubatrachus* species is the maxilla, only this dermal element is analyzed below in detail. Several differences can be pointed out between the maxillae of *B. pricei* and *B. santosdoroi* and calyptocephalellids, some of them not considered in the matrix of the systematic analysis performed by Báez and Gómez (2018). The lack of the anterodorsal process of the pars facialis is a condition herein confirmed for *B. santosdoroi*, which is shared with the species of *Telmatobufo* (Morphosource M105294 ku:kuh 161438; Formas *et al.*, 2001) but not with those of *Calyptocephalella* (Muzzopappa & Báez, 2009, fig. 3.1–3.4). Still regarding the pars facialis, it is evident from the complete and disarticulated maxillae of *B. santosdoroi* that the orbital region is higher than the preorbital portion, a feature that contrasts with the condition in calyptocephalellid species, in which the orbital region is, aside from the posterior process, the lowest. A shared condition of these two hyperossified genera (*Baurubatrachus* and *Calyptocephalella*, but not *Telmatobufo*) is the tight contact among nasals and maxillae, and squamosals and maxillae. However, the pre and postorbital processes of the maxillae, through which those contacts are established, are small and triangular in *B. santosdoroi* but rather extensive and straight in *Calyptocepalella* species (see Muzzopappa, 2019, fig. 3.5). Finally, as mentioned above, the pars palatina in *B. santosdoroi* is rounded and bears a posterior pterygoid process whose posterior margin is steep in dorsal view. In contrast, in calyptocephalellids the pars palatina is flat and the posterior margin of the pterygoid process is concave in dorsal view (see Muzzopappa, 2019, fig. 3.1).

The last feature to be mentioned is in the humerus, which in *Baurubatrachus* is dorsally concave (a regular condition for anurans, *e.g.*, Vidal-García & Keogh, 2017; Keeffe & Blackburn, 2020) and straight in dorsal/ventral views. This feature was not translated into a character in the cladistic analysis of Báez and Gómez (2018), whose only character related to the humerus was their ch. 116 “Humerus, ventral condyle, diameter relative to total distal width at epicondyle level”. In calyptocephalellids the humerus is laterally curved (Fig. 8.1–8.3; Muzzopappa & Báez, 2009; Otero *et al.*, 2014; Suazo-Lara & Gómez, 2022), a state also observed for forward-burrowing frogs, including the myobatrachid *Myobatrachus gouldi* (Keeffe & Blackburn, 2020). However, the regular condition for myobatrachids is rather the opposite, *i.e.*, a columnar humerus in dorsal/ventral views (Fig. 8.4–8.8).

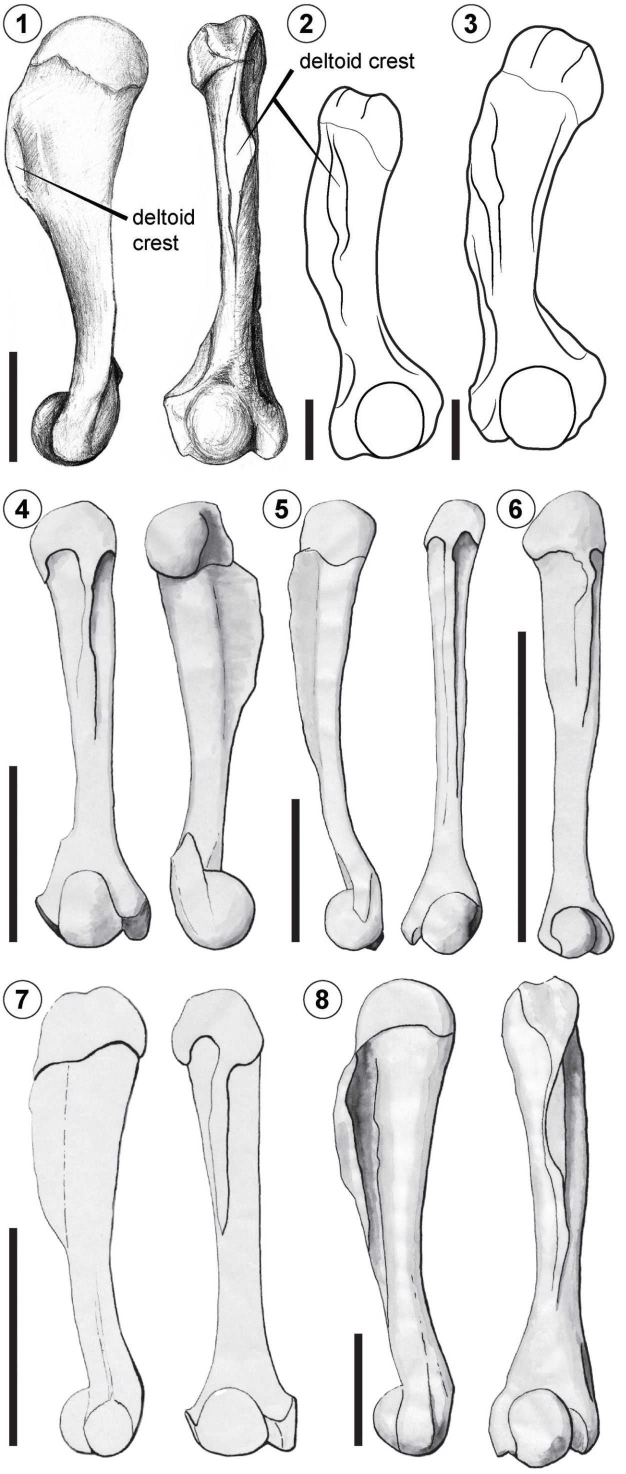


Figure 8. Humerus of Calyptocephalellidae and Myobatrachoidea taxa. **1,** ***Telmatobufo venustus***, **KU** 161439, lateral and ventral views. **2,** ***Calyptocephalella gayi***, **MACN-HE** 45745, ventral view. **3,** ***C. canqueli***, **MPEF-PV** 1884, ventral view. **4,** ***Philoria frosti***, **KU** 186907, ventral and lateral views. **5,** ***Lechriodus melanopyga***, **KU** 133626, lateral and ventral views. **6,** ***Limnodynastes peronii***, **KU** 179939, ventral view. **7,** ***Adelotus brevis***, **KU** 186773, lateral and ventral views. **8,** ***Mixophyes iteratus***, **KU** 1779963, lateral and ventral views. Scale bars equal 5 mm.

CONCLUSION

The new remains recovered from the proximities to Catanduva city provide evidence of an older, less ossified species of the genus *Baurubatrachus*, presented herein as *B. santosdoroi*. The peculiar morphology of the temporal region makes this and the younger *B. pricei* two bizarre species, the systematic of which remains blurred. Considering *Baurubatrachus* is one of the oldest neoabatrachian found so far, the resolution of the systematic relationships of this genus could give clues to the early evolution of the diverse neobatrachians frog clade. The latter implies that the resolution of the placement of *Baurubatrachus* within the anuran tree needs and merits further analysis of osteological characters. The knowledge of the environment in which *Baurubatrachus* occurred along with a better understanding of the evolution of the characters that are so intriguing in this genus might provide some clues regarding the evolutionary forces that drove this lineage to be so singular.

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