



Early Cretaceous neobatrachian frog (Anura) from Brazil sheds light on the origin of modern anurans

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ABSTRACT

The fossil record of anurans in South America is scarce, especially for Mesozoic-aged beds. The aim of the present paper is to describe a new neobatrachian anuran coming from the Early Cretaceous (Aptian) Crato Formation from Brazil. The specimen, represented by a nearly complete skeleton is reminiscent to the extant clade Hyloidea. In contrast with recent claims, this finding, together with previously known fossils from South America indicates that modern frog clades were present and well-diversified by 40 million years before the K/T boundary. In the same sense, the analysis of Mesozoic and Paleogene anuran record in South America contradicts the hypothesis of massive anuran extinction at the K/T boundary.

1. Introduction

The fossil record of Mesozoic anurans in South America is strongly biased. Basal anurans of the clade Pipoidea have been recorded from diverse Early-to Late Cretaceous sites in Brazil and Argentina (see Báez, 1987, 1996; Martinelli and Forasiepi, 2004; Gómez, 2016; Carvalho et al., 2019). In contrast, the finding of modern anurans (i.e., neobatrachians) in Mesozoic beds is far scarcer than that of pipoids. In fact, informative and complete specimens have been only recorded from the Early and Late Cretaceous beds of Brazil (e.g., Báez and Peri, 1989; Báez et al., 2009, 2012; Báez and Gómez, 2017). Further, abundant remains in Maastrichtian sites from Argentina were referred to calyptocephalellids of the extant genus *Calyptocephalella* (Báez, 1987; De La Fuente et al., 2007; Agnolin, 2012). This brief picture clearly shows the incomplete nature of the neobatrachian fossil record in the Mesozoic of South America.

In Brazil, the Crato Formation (Early Cretaceous, Aptian) has yielded a diverse assemblage of plants and animals, including dinosaurs, birds, lepidosaurs, fishes, and anurans (Martill et al., 2007). Among anurans, both pipoids and neobatrachians have been reported

(Báez et al., 2009; Carvalho et al., 2019). Pipoids are represented by *Cratopipa novaolindensis* (Carvalho et al., 2019) and innominate specimens (Báez et al., 2009; see also Martill et al., 2007), whereas neobatrachians are more diverse, being represented by at least three different genera (Báez et al., 2009). Leal and Brito (2006) were the first authors that describe anuran remains from Crato Formation; they nominate the new taxon *Arariphrynus placidoi* and considered it belonged to the Leptodactylidae. Posteriorly, Báez et al. (2009) concluded that the hypodigm of *Arariphrynus* included several new taxa belonging to disparate neobatrachian groups. In this way, Crato neobatrachians were probably highly diversified, being represented by at least 3 genera and species (Báez et al., 2009) in addition to several new taxa that remain innominate and undescribed (see as for example Martill et al., 2007).

The aim of the present contribution is to describe a nearly complete skeleton of a new neobatrachian genus and species from the Crato Formation (Fig. 1). This new specimen is very well preserved, and its skeletal anatomy indicates that it belongs to neobatrachians. This record constitutes one of the oldest known for the clade and has a great importance for the knowledge of the early radiation of modern frogs.

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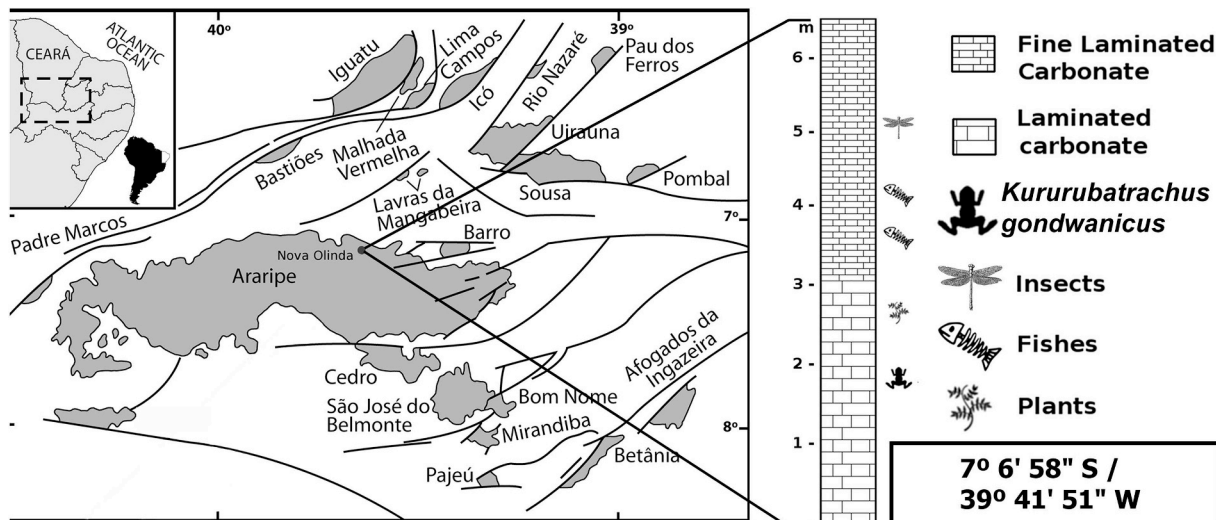


Fig. 1. Locality and horizon that yielded the holotype specimen of *Kururubatrachus gondwanicus* nov. gen. et sp.

2. Materials and methods

General osteological terminology used in this paper mostly follows that of Trueb (1973), terminology concerning carpal and tarsal elements is that of Fabrezi and Alberch (1996) and Fabrezi (1993).

Locality and horizon. The type specimen comes from Pedra Branca Mine, Nova Olinda County, Ceará State, Brazil (7° 6' 58" S/39° 41' 51" W; Fig. 1). The specimen was found in strata belonging to the Crato Formation, Early Cretaceous (Aptian; Carvalho et al., 2019) (Figs. 2–4).

The Araripe Basin is a Northeastern Brazilian interior basin, developed during a phase of mechanical subsidence in a rift system (Matos, 1992). The lithostratigraphy of this basin has been discussed by many authors (see Assine, 2007). The new fossil anuran was collected in beds belonging to the Crato Formation, dated as late Aptian (119–113 My; Rios-Netto et al., 2012). The Crato Formation is considered a fossil Lagerstätte (see Maisey, 1991; Martill et al., 2007). It comprises a 60-m-thick succession of metric-scale laminated carbonate units interlayered with equally thick successions of green shales and fine-to-coarse sandstones deposited during a hot and arid climate (Carvalho, 2000).

Phylogenetic analysis. In order to estimate the phylogenetic position of the new taxon, a maximum parsimony analysis based on a matrix made up of 77 characters, and 34 taxa originally employed by Báez (2013) and modified by Xing et al. (2018) (Appendix 1–2). Terminal taxa included species representing major lineages within Anura according to current hypotheses of anuran relationships primarily based on molecular and paleontological data (Frost et al., 2006; Báez et al., 2009; Pyron and Wiens, 2011; Báez, 2013; Xing et al., 2018). To this matrix we added the new taxon, 6 new taxa representing diverse hylids, and the new characters 73–77 (see Appendix 1–2).

The data matrix was analyzed under equally weighted parsimony using TNT 1.1 (Goloboff et al., 2008). A heuristic search of 100 replications of Wagner trees (with random addition sequence) followed by TBR branch swapping (holding 10 trees per replicate) was performed. The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches among all of the recovered MPTs were collapsed (i.e. rule 1 of Coddington and Scharff, 1994).

The analysis recovered 10 most parsimonious trees (MPTs) of 294 steps with a consistency index (CI) of 0.36 and a retention index (RI) of 0.63 (Fig. 5).

As a branch support measure, Bremer support was calculated, and as a measure of branch stability, a bootstrap resampling analysis was conducted, performing 10,000 pseudoreplicates. Bremer support was calculated after searching for suboptimal trees and not with the script

that accompanies the program. Both absolute and GC bootstrap frequencies are reported (Fig. 6).

2.1. Systematic paleontology

Anura Fischer von Waldheim, 1813

Neobatrachia Reig, 1958.

Kururubatrachus nov. gen.

Etymology. *Kururu*, is the common name of a living species of South American toad (*Rhinella schneideri*) but also, according a legend of the tupí-guaraní culture, is the animal that brings the fire to humans during the creation of the world; *batrachus* is the Latin word for “toad”.

Diagnosis. Neobatrachian anuran diagnosable on the basis of the following combination of characters (autapomorphies marked by an asterisk*): 1- transversely elongate premaxilla with pars facialis not reaching the medial margin of the bone; 2- frontoparietal bone with extensive lateral processes*; 3- proximally expanded humerus and deltoid crest*; 4- proximally expanded scapula with a proximally narrow blade that exhibits a fan-shaped and expanded distal end; and 5- prominent and strongly dorsally convex dorsal iliac crest (Figs. 2–4).

Among Crato anurans, *Kururubatrachus* nov. gen. differs from previously named taxa in a unique combination of traits: elongate skull that is more anteroposteriorly long than wide (shared with *Cratia*; *Arariphrynus* shows subequal length and width; *Eurycephalella* skull is much wider than long), relatively low premaxilla with the *pars facialis* located at mid-length of the bone (in *Eurycephalella* the *pars facialis* of the premaxilla is notably robust and is laterally placed; in *Cratia* the premaxilla is notably low and dorsally concave, with a very narrow *pars facialis* narrow frontoparietal bones that do not expand anteriorly (in contrast to the wide frontoparietals shown by *Arariphrynus* and *Eurycephalella*, the anteriorly divergent frontoparietal margins of *Arariphrynus*, and the strongly constricted frontoparietal of *Cratia*), elongate scapular blade (in *Arariphrynus*, *Cratia*, and *Eurycephalella* the glenoid is nearly one third the length of the entire element, whereas in *Kururubatrachus* nov. gen. is much smaller; further in *Cratia* the scapular blade is notably shortened) elongate tibiale and fibulare that are half the length of the tibia (one third tibial length in *Arariphrynus* and *Eurycephalella*), terminal phalanges lacking distal protuberances (present in *Arariphrynus*) (Báez et al., 2009).

Type and only included species. *Kururubatrachus gondwanicus* nov. sp.

Kururubatrachus gondwanicus nov. sp.

Holotype. UFRJ-DG 08 A (Universidade Federal do Rio de Janeiro, Departamento de Geologia collection), a nearly complete and

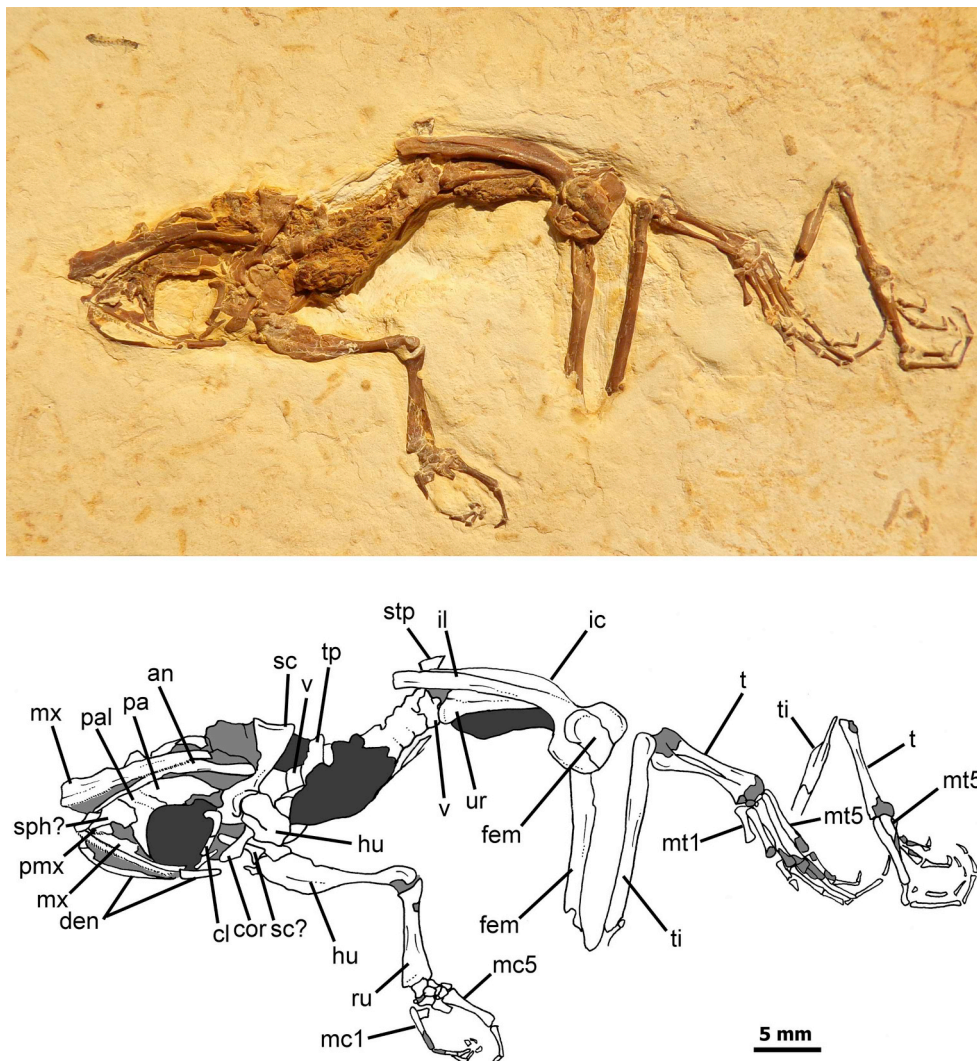


Fig. 2. Holotype of *Kururubatrachus gondwanicus* nov. gen. et sp. (UFRJ-DG 08 A). **References.** an, angular; cl, clavicle; cor, coracoid; fem, femur; hu, humerus; ic, iliac crest; il, ilium; mc1, first metacarpal; mc5, fifth metacarpal; mt1, first metatarsal; mt5, fifth metatarsal; mx, maxilla; pa, parasphenoid; pal, neopalatine; pmx, premaxilla; ru, right radioulna; sc, scapula; sph?, possible portion of sphenetmoid; stp, sacral transverse process; t, tibiale; ti, tibiofibula; tp, transverse process; ur, urostyle; v, vertebra. Broken areas and sediment shaded in grey.

articulated skeleton, lacking most of the right half of the skeleton (Figs. 2–4). The skull and trunk are exposed in ventral view, and the sacrum and hindlimbs are viewed from the left side.

Locality and horizon. The type specimen comes from Pedra Branca Mine, Nova Olinda County, Ceará State, Brazil (7° 6' 58" S/39° 41' 51" W; Fig. 1). The specimen was found in strata belonging to the Crato Formation, Early Cretaceous (Aptian; Carvalho et al., 2019).

Diagnosis. The same as for genus by monotypy.

Etymology. The species name, *gondwanicus*, comes from the Gondwanan context of the Araripe Basin.

2.2. Description

The specimen is relatively well preserved, but several bones are dorsoventrally crushed (Fig. 2). The skull is relatively elongate, much longer than transversely wide (Figs. 3–4). The skull bones lack any sign of ornamentation.

The premaxilla is transversely long and shows at least 15 teeth. The pars facialis is smooth and subtriangular in contour, is separated from the medial edge of the bone. The articulation with the maxilla was not preserved. The maxilla is notably elongate and low (including the orbital portion) and shows a smooth outer surface. It shows more than 40

teeth. The zygomatic process is low. The palatine process is very poorly developed and shelf-like along all its length, forming a small and barely defined pterygoid process. The posterior process is rod-like, subcircular in cross-section. Frontoparietals are fused on a single bone and lack supraorbital shelf. The apparently complete roofing of the *cavum cranii* suggests that a complete tectum parietale was already present. Sphenetmoid is well-ossified; however, strong distortion obscures several anatomical details. Parasphenoid is represented by an incomplete but transversely expanded scale-like bone. The palatines are free (= neopalatines *sensu* Trueb, 1993) and subtriangular in contour. Regrettably most of the braincase is not preserved or heavily distorted, precluding the description of anatomical details.

They are not well preserved and its total number is uncertain, but at least 8 elements are preserved. Their incomplete and highly distorted nature precludes a clear description and analysis of anatomical details. The vertebral centra are procoelous. The first two vertebrae are not fused to each other. The last presacral shows two condyles that articulate with the two proximal cotyles of the urostyle. The sacrum shows reduced transverse processes with poorly expanded distal ends. The urostyle length is less than that of femur.

The pectoral girdle shows a very deep and well defined glenoid, with prominent lips. The scapula shows a plate-like proximal end. It

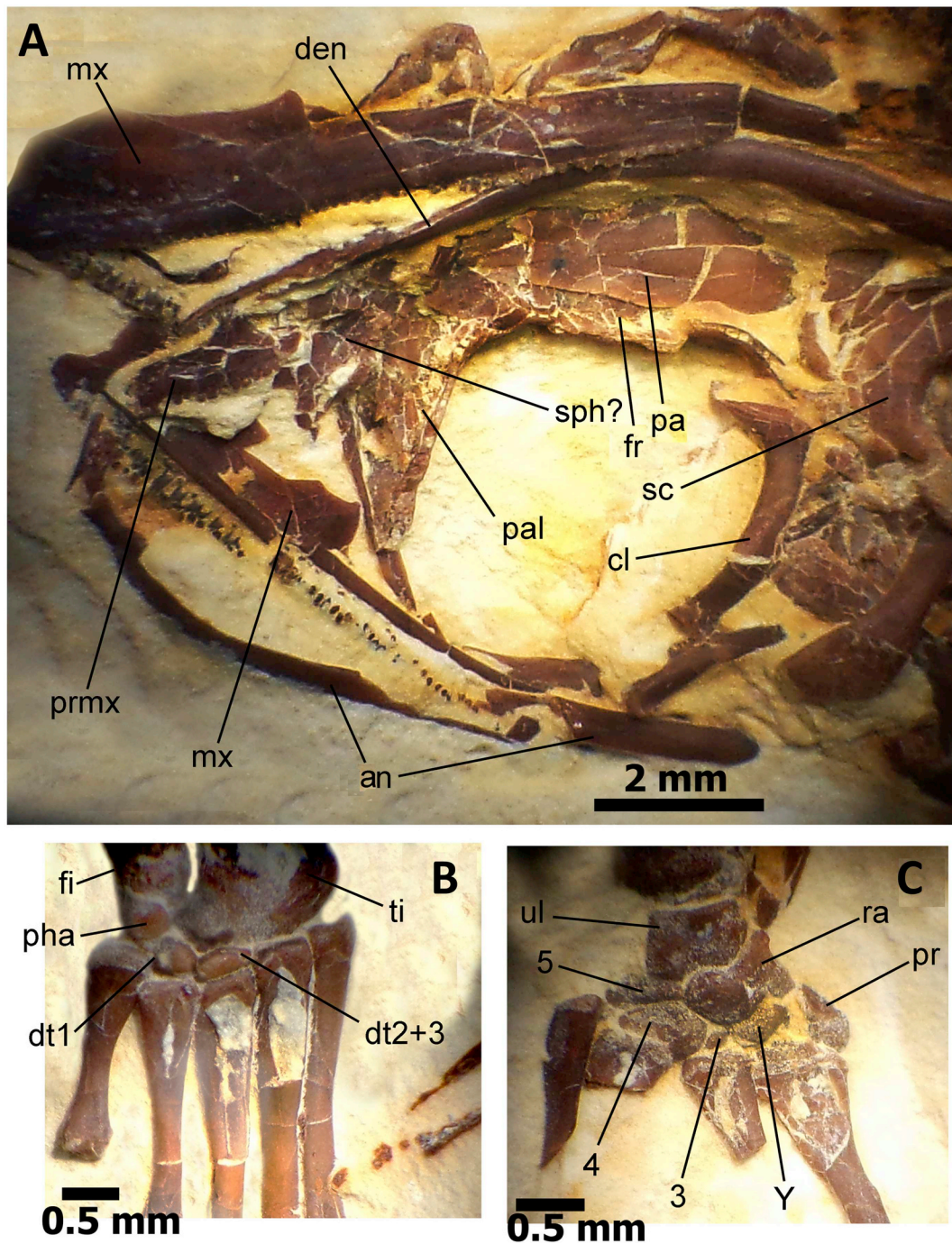


Fig. 3. Selected elements of holotype specimen of *Kururubatrachus gondwanicus* nov. gen. et sp. (UFRJ-DG 08 A). A, dissarticulated skull; B, left foot in plantar view; C, right hand in palmar view. **References.** an, angular; cl, clavicle; dt1, first distal tarsal; dt2+3, second plus third distal tarsal; fi, fibulare; fr, frontoparietal; mx, maxilar; pha, prehallical element; pa, parasphenoid; pal, neopalatine; pr, prepollex basal component; prm, premaxilar; ra, radiale; sc, scapula; sph?, sphenethmoid?; ti, tibiale; ul, ulnare; Y, “Y” element; 3,4,5, distal carpal elements.

shows a very narrow base of scapular blade that exhibits a fan-shaped distal end with a nearly straight distal edge. The coracoid is represented by flange of bone that is probably fused with the scapula. The humerus is notably proximally expanded and shows a large deltoid crest that extends more than half of its total length. The radioulna is relatively narrow and shows a small olecranon process.

Carpal bones are well-preserved (Fig. 3). Seven discrete elements are identified and are arranged in two rows. The ulnar and radial carpals are large and interlocked. The radial contacts the radius on its proximomedial corner. Remaining carpals are disc or beam shaped. Distal carpal 5 is small and tightly appressed to the ulnar. The second

row of elements is composed by distal carpals 4 and 3, the “Y” element (sensu Fabrezi and Alberch, 1996) and prepollex basal component.

The ilium is robust and curved in side view, and shows a high and dorsally convex dorsal crest that reaches the anterior tip of the bone. Dorsal protuberance and acetabular expansion are absent. Ventral acetabular expansion is narrow. Pubis is strongly fused, and ischium is strongly dorsally extended.

The femur and tibiofibula are elongate and nearly straight. The tibiofibula is notably elongate and duplicates the length of the tibiale. Tibiale and fibulare are fused at both ends. There are 4 discrete distal tarsal elements (Fig. 3). Prehallical element is relatively large; distal

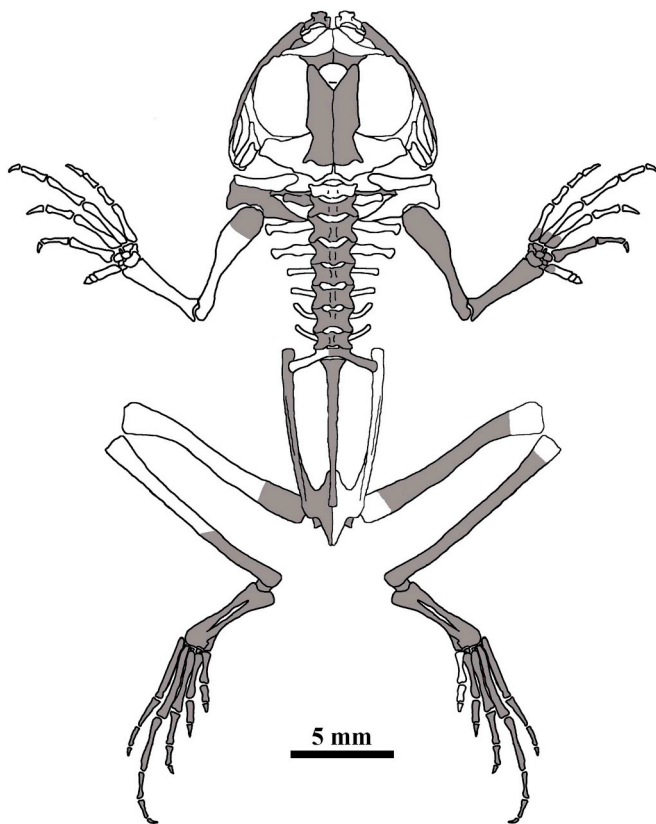


Fig. 4. Skeletal reconstruction of *Kururubatrachus gondwanicus* nov. gen. et sp. (UFRJ-DG 08 A). Shaded areas indicate preserved bones of the holotype specimen.

tarsals 1 and 2 + 3 are disc-shaped. Terminal phalanges are sub-triangular in contour and acute, with lateral processes at their bases. Digit size: 1 < 2 < 5 < 3 < 4.

Measurements. Snout to vent length: 45.9 mm; maximum maxilla length: 15.8 mm; maximum scapular length: 8.17 mm; maximum humeral length: 13.78 mm; maximum radioulna length: 8.21 mm; maximum urostyle length: 13.7 mm (as preserved); maximum iliac length: 14.4 mm; maximum femoral length: 18.71 mm (as preserved); maximum tibiofibula length: 18.6 mm (as preserved); maximum tibial length: 9.6 mm; maximum metatarsal V length: 6.2 mm.

3. Discussion

Present phylogenetic analysis resulted in the inclusion of *Kururubatrachus* nov. gen., well-nested among the Neobatrachia clade, in a polytomy together with members of the Hyloidea (Fig. 5). The analysis here carried out is based on Báez (2013), with the modifications by Xing et al. (2018), and the addition of 5 characters and seven new taxa. In spite that neobatrachians lack exclusive synapomorphies, *Kururubatrachus* nov. gen. shows occurrence of features diagnostic for this clade as a whole, including presence of neopalatines, holochordal procoelous vertebral centra, narrow sacral diapophyses that are sub-circular in cross-section at its base, absence of free ribs, bicondylar articulation between sacrum and urostyle, scapula lacking anterior lamina and with a proportionally long shaft, fused distal tarsals 2 + 3, and modified terminal phalanges of foot (Reig, 1958; Muzzopappa and Báez, 2009; Báez et al., 2009). Most internal nodes within Neobatrachia lack osteological synapomorphies, which lead to uncertain position of many extinct taxa (Báez et al., 2009). In agreement with the lack of unambiguous synapomorphies of different clades within neobatrachians, present phylogenetic analysis resulted in a polytomy at the base of that clade that includes *Kururubatrachus*, hyloids and ranoids. A more accurate phylogenetic position for *Kururubatrachus* is not possible

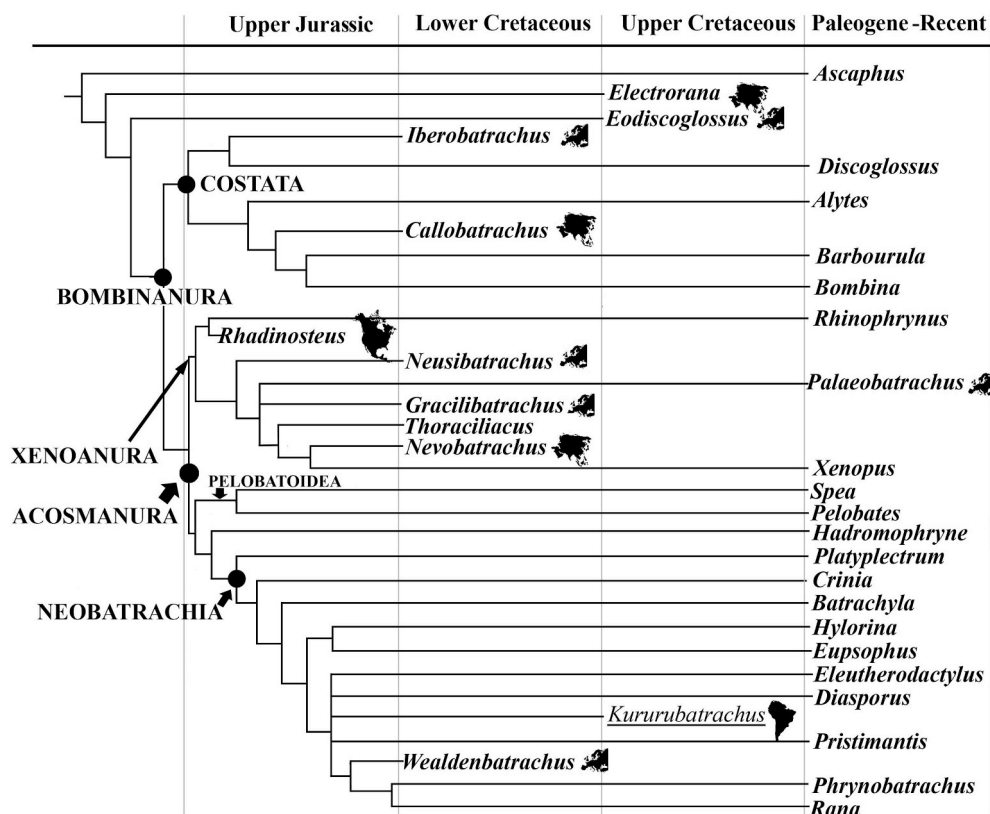


Fig. 5. Phylogenetic relationships of *Kururubatrachus gondwanicus* nov. gen. et sp. among anurans. Numbers indicate Bremer support value for each tree node. Fossil taxa include continental silhouettes indicating its geographical origin.



Fig. 6. Phylogenetic relationships of *Kururubatrachus gondwanicus* nov. gen. et sp. Numbers above branches indicate Bremer support values, and absolute and GC bootstrap frequencies.

under present phylogenetic analysis. Notwithstanding the foregoing, several features present in *Kururubatrachus* nov. gen. are shared with Hyloidea (in contrast to Archaeobatrachia and Ranoidea) including distally expanded and flange-like transverse process of sacral vertebra, and anterior presacral vertebrae with elongate transverse processes, whereas posterior presacral transverse processes are shortened (Lynch, 1971; Báez and Peri, 1989).

The fossil record has the potential to constitute an unambiguous reference of the presence of a certain lineage in at a given point in the history of Earth. Anurans do not escape to this general rule. In a recent contribution, Feng et al. (2017) using dataset of unprecedented size and 20 fossil-based calibrations arrived to a novel phylogenetic tree of frogs. This tree constitutes an important effort for constituting a robust timescale for frog evolution.

The main conclusion of Feng et al. (2017) dataset is that three species-rich clades (Hyloidea, Microhylidae, and Natatanura) had a simultaneous and rapid diversification at the K/T boundary. This contrasts with traditional divergence-time estimates which indicate that the origin of that clades ranges from Late Jurassic to Early Cretaceous times (Biju and Bossuyt, 2003; Roelants et al., 2007; Frazão et al., 2015).

In spite that, the paper by Feng et al. (2017) constitutes a benchmark and probably a breaking-point contribution, important fossils with deep implications on the calibration and timescale of frog tree were omitted. As for example, Feng et al. (2017) calibrate the node Myobatrachoidea based on the Eocene species *Calyptocephalella pichileufensis* (Gómez et al., 2011). However, several *Calyptocephalella* specimens were described from older deposits, including the Late Cretaceous (Campanian-Maastrichtian) Patagonian species *Calyptocephalella satan* (Agnolin, 2012). This species is more than 20 My older than *C. pichileufensis*. Further, the presence of *Calyptocephalella* at the Eocene of Chile, at beds that are nearly coeval to those that yielded *Calyptocephalella pichileufensis* (Otero et al., 2014), indicates that at least two species of this genus were present by Eocene times in Argentina and Chile. This suggests that *Calyptocephalella* was probably highly diversified by that time, in agreement with the finding of Cretaceous remains ascribed to this genus (Agnolin, 2012).

One of the main conclusions by Feng et al. (2017) is that the Hyloidea clade originated and diversified near the K/T boundary. However, the Early Cretaceous (Aptian) derived neobatrachians *Cratia*, *Arariphrynus* and *Eurycephalella* from Brazil (Báez et al., 2009), known by nearly complete and informative skeletons, were not included in the analysis. Further, Báez and Gómez (2017), based on an extensive phylogenetic analysis reinforced the position of Early Cretaceous *Cratia*

and *Arariphrynus* within Ranoidea, and *Eurycephalella* well-nested among Hyloidea. To these taxa we add here the derived neobatrachian *Kururubatrachus* nov. gen. The presence of at least three different ranoid and hyloid-related taxa by Early Cretaceous times contradicts the hypothesis sustaining a recent origin of most anuran clades.

Because Feng et al. (2017) do not include the Cretaceous records of *Calyptocephalella* nor the Early Cretaceous neobatrachians *Cratia*, *Arariphrynus* and *Eurycephalella*, we think that these calibration flaws may have important impact on anuran timescale, since the choice of calibration points has significant consequences on divergence time estimations.

Feng et al. (2017) also argue that frogs experienced a major extinction at the K/T. However, this pattern is not so clear in the fossil record from South America, at least. In spite of the sketchy fossil record, by Late Cretaceous times, members of Pipoidae and Calyptocephalellidae are well represented in Patagonia, and constitute the main anuran lineages recorded for that period (Báez, 1987; De La Fuente et al., 2007; Agnolin, 2012; Gómez, 2016). Pipoids and calyptocephalellids continue as the more diversified and abundant anuran clades during the Paleogene of Patagonia (Báez, 1996; Agnolin, 2012). In the case of Brazil, the Cretaceous record indicates diversified hyloids and nobleobatrachians, as well as pipoids (Báez et al., 2009, 2012; Carvalho et al., 2019), whereas by early Paleocene times that clades were still present and diversified (Estes and Reig, 1973; Estes, 1975). In this way, the anuran faunas in Patagonia, and probably also Brazil, appear not to be strongly affected by the K/T boundary extinctions. Although this pattern cannot be extrapolated to other faunas of Gondwana, the lack of deep changes in fossil anuran record before and after the K/T should be taken in consideration.

4. Conclusions

We describe here the new fossil and species of anuran *Kururubatrachus gondwanicus* nov. gen. et sp., coming from the Early Cretaceous (Aptian) Crato Formation from Brazil. The specimen, represented by a nearly complete and articulated skeleton belongs to Neobatrachia, and it is reminiscent to the extant clade Hyloidea. Further, a brief overview on the fossil record of anurans indicate that several relevant reports have been overlooked by previous literature (e.g., Báez and Gómez, 2017; Báez et al., 2009, 2012; Agnolin, 2012). These, reinforce previous ideas of an old diversification of neobatrachians deep in the Cretaceous period. As for example, in spite of the poor fossil record in Patagonia, members of Calyptocephalellidae appear to be abundant and well-diversified in the Maastrichtian. Further,

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