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FOSSIL FROGS FROM THE UPPER MIOCENE OF SOUTHWESTERN BRAZILIAN AMAZONIA (SOLIMÕES FORMATION, ACRE BASIN)

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ABSTRACT—Much of what we know about late Miocene vertebrates from the Brazilian Amazonia is based on the fossil record from several sites in the Solimões Formation. The Talismã site, one of the most important for vertebrate fossils in the formation, has produced an abundant and diverse fauna dominated by crocodylians, mammals, and turtles, but small vertebrates are still underrepresented. We report some isolated bones recovered from this site, providing the first Neogene records of anurans in Brazil. Two taxa are recognized, a distinct species of *Pipa*, and an unidentified species of the *Rhinella* clade, both of which are members of the extant Amazonian batrachofauna. These new fossils expand our knowledge of the late Miocene anuran assemblages from the region and contribute to the paleoenvironmental reconstruction of the site.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

The late Miocene was an important interval of landscape change in western Amazonia triggered by the Andean orogeny. The lacustrine system that dominated the region during most of the Miocene transitioned to a fluvial environment, called the “Acre system,” similar to the present-day Pantanal biome (Hoorn et al., 2010; Latrubesse et al., 2010). The drainage patterns of the Amazon basin shifted dramatically and the modern transcontinental Amazon river system was probably established at the end of the Miocene (Figueiredo et al., 2009; Hoorn et al., 2017). These large-scale paleoenvironmental modifications coincided with a substantial diversification of the biota and the extinction of some typical Miocene forms at the end of the epoch, which probably played a role in shaping the current Amazonian biodiversity (e.g., Hoorn et al., 2010; Schley et al., 2018; Cidade et al., 2019).

Deposits of the Solimões Formation in the Acre Basin have yielded a great deal of information about the paleontological history of the southwestern Brazilian Amazonia during the late Miocene (Cozzuol, 2006; Latrubesse et al., 2007, 2010). The vertebrate fossil record of the unit is rich and abundant, composed mainly of reptiles and mammals (Cozzuol, 2006; Ribeiro et al., 2013; Bissaro-Júnior et al., 2019). It includes some of the most remarkable and iconic mega-sized crocodylians (e.g., *Purusaurus*, *Mourasuchus*, *Gryposuchus*) and side-necked turtles (*Stupendemys*) (Riff et al., 2010). Nevertheless, there are still significant gaps in our knowledge of the small vertebrate fauna,

which hinders more robust paleoecological and paleoenvironmental reconstructions.

Here we describe an anuran fossil assemblage from the Talismã site, consisting of isolated bones referable to two extant genera, *Pipa* and *Rhinella*. The new findings represent the first records of anurans from the Solimões Formation and enhance our understanding of the regional late Miocene herpetofauna.

GEOLOGICAL SETTING

The fossils were discovered in the rocks of the Solimões Formation cropping out at the Talismã site (UTM 19L 510475 E/ 9029741 S, datum WGS84), situated on the right bank of the upper Purus River, in the south of Amazonas state, near the border with Acre state, Brazil (Fig. 1). The Solimões Formation, located in the southwestern region of the Brazilian Amazonia, consists mainly of variously colored sandstones, siltstones, and mudstones, with gypsum veins and calcareous concretions, deposited in a fluvio-lacustrine environment (Hoorn, 1993; Latrubesse et al., 2007, 2010). It is dated as late Miocene (Huayquerian-Mesopotamian SALMA, 9–6.5 Ma) on the basis of palynological and faunal correlations (Cozzuol, 2006; Latrubesse et al., 2007). Recent U-Pb dating of detrital zircons from two fossiliferous sites has yielded concordant ages of 8.5 Ma and 10.9 Ma as maximum deposition ages, in the Tortonian stage (Bissaro-Júnior et al., 2019).

The Talismã site is one of the most important bonebeds of the Solimões Formation. An abundant and diverse vertebrate fauna has been discovered of fishes, crocodylians, turtles, snakes, lizard, birds, and mammals (e.g., Barbosa and Benchimol, 1993; Bergqvist et al., 1998; Negri, 2004; Cozzuol, 2006; Hsiou and Albino,

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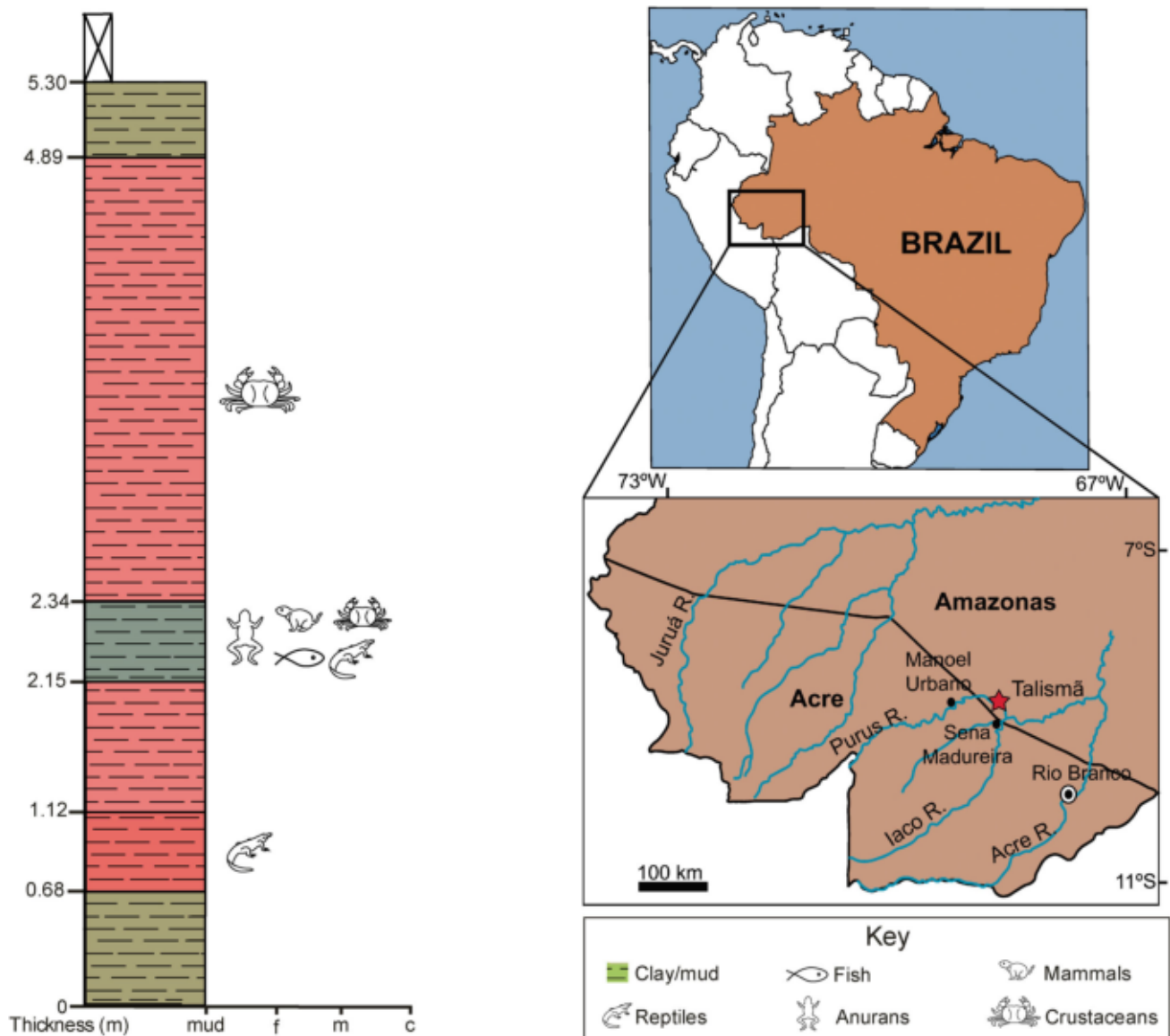


FIGURE 1. Stratigraphic column of the studied area showing fossiliferous horizons (modified from Bissaro-Júnior et al., 2018) and map of Acre and Amazonas states showing location of Talismã site (star). (Color figure available online.)

2009, 2010; Hsiou et al., 2009; Fortier et al., 2014; Souza-Filho and Guilherme, 2015; Kerber et al., 2017; Souza-Filho et al., 2020; Muniz et al., 2021). The section is dominated by fine sediments (clays and silts), lacking lamination or other recognizable structures, all of which indicate deposition in lacustrine/swampy settings. Gypsum and calcite veins are present and are possibly diagenetic in origin (Cozzuol, 2006). The entire exposed section is 5.30 m in height and contains three fossiliferous layers (Fig. 1). Although we were not able to determine the precise stratigraphic levels from which part of the anuran material was derived, all anuran specimens recovered during fieldwork carried out in 2015 and 2016 were collected from the middle fossiliferous layer.

MATERIALS AND METHODS

The material studied herein is housed at the Coleção de Paleovertebrados do Laboratório de Pesquisas Paleontológicas (UFAC, Rio Branco, Brazil). The anuran remains consist of

disarticulated elements collected carefully through excavation and screen-washing at the Talismã site. Anatomical comparisons were made with available dry skeletons housed at the CHRP (Coleção Herpetológica de Ribeirão Preto, Universidade de São Paulo, Brazil) and CT-scanned specimens of extant anurans accessed on MorphoSource.org (Appendix 1) and data from the literature. Osteological terminology mainly follows Holman (2003), Báez and Pugener (2003), Báez et al. (2012), and Gómez and Turazzini (2016). To investigate the phylogenetic position of the fossil pipid within Pipoidea, we scored the specimens into an existing morphological data matrix published by Gómez (2016) and modified by Carvalho et al. (2019). We made the following scoring changes to *Cratopipa* based on a recent redescription of the taxon by Báez et al. (2021): character 32 (?→1), character 34 (1→0), character 65 (0→?), character 82 (2→1), character 88 (3→2), and character 104 (3→?). Coding of character 104 (3→?) has been changed for *Avitabatrachus* based on comments by Báez et al. (2022). We removed from the matrix three characters proposed by Carvalho et al. (2019).

Characters 167 and 176 were excluded because they are likely non-independent relative to other characters. Character 172 is considered not applicable. The resulting matrix consists of 173 characters for a total of 38 taxa (Supplementary Data). The parsimony analysis was performed using the heuristic search mode of TNT v. 1. 5 (Goloboff et al., 2008), with 1000 replications and 10 trees saved per replication. Characters were unordered and equally weighted, and the branch-swapping algorithm used was tree-bisection-reconnection (TBR). *Ascaphus truei* was set as the outgroup. Bremer support values were calculated in TNT using the 'Bremer.run' script to estimate clade robustness.

SYSTEMATIC PALEONTOLOGY

ANURA Fischer, 1813
XENOANURA Savage, 1973
PIPIDAE Gray, 1825
PIPA Laurenti, 1768
PIPA sp.
(Figs. 2A–D, I–N, 3A–B)

Referred Material—One atlas (UFAC 6475), three incomplete left humeri (UFAC 1766, Ufac 6983, Ufac 6984), two incomplete right humeri (UFAC 2853, Ufac 6459), two incomplete humeri (side unknown; Ufac 2852, Ufac 6461), one incomplete right ilium (UFAC 6457).

Locality and Horizon—Talismã site, southern Amazonas state, Brazil; Solimões Formation, upper Miocene.

Description

UFAC 6475 is a composite element (herein called atlas) formed by the fusion of presacral vertebrae I and II. This is indicated by the presence of well-developed transverse processes and the presence of minute foramina on the ventral side of the transverse processes, interpreted as the exit for spinal nerves I and II. The reduced size of the fused elements, which form a distinctively short bone, and the absence of a visible suture can be explained by the synchondrosis of vertebrae I and II early in development (Trueb et al., 2000; Pugener et al., 2003). The atlas is incomplete, lacking most of the transverse processes and the anterior margin of the neural arch (Fig. 2A–D). The centrum is strongly compressed dorsoventrally and has a broad, smooth ventral surface. It bears a posterior cotyle, indicating that the first trunk vertebra bore an anterior condyle and was opisthocoelous. In the absence of other evidence, it is assumed that all trunk presacral vertebrae were opisthocoelous. The posterior cotyle lack well developed dorsal and ventral rims, but it is well delimited laterally. Anteriorly, the atlas possesses two articular facets (cervical cotyles) that articulated with the occipital condyles. The cervical cotyles are wide and oval, positioned ventrolateral to the neural canal, and with the main axis slightly inclined dorsomedially; ventrally, these are well separated by a long intercotylar area that is shallowly convex anteriorly in ventral outline. The neural arch lamina is smooth in dorsal view and bears a low, thick neural spine that extends from the posterior margin to the anterior part, although its full extent cannot be determined because the anterior terminus of the anterior margin is not preserved. In this same view, the neural arch is wider than long. The atlas retains only the base of the right transverse process and the proximal portion of the left one. The latter is oval in cross-section and posterolaterally directed. Dorsally, the posterior margin of the neural arch displays a wide and short V-shape indentation. In posterior view, the neural canal has an oval shape and the neural arch bears zygosphenes-like, robust lateral pedicels.

The seven humeri are incomplete specimens that preserve the distal epiphyses, but lack most of their proximal portions, including the parietal crest and the proximal epiphyses (Fig. 2I–N). The humeri are well ossified and have a remarkably straight shaft. The humeral ball (eminencia capitata) is comparatively small, with a transverse diameter that is nearly half the maximum width of the humerus distal extremity. It is flanked by two conspicuous epicondyles with similar sizes, giving an almost symmetric appearance to the distal end of the humerus. Both epicondyles are directed distally and their extremities are separated from the humeral ball by a shallow notch, which is wider between the medial epicondyle (ulnar epicondyle) and the humeral ball. The ventral fossa (fossa cubitalis) is wide, deep, and extends anteriorly, forming a triangular shape. In the better-preserved specimens (UFAC 1766, Ufac 6983; Fig. 2K, M), a small ridge arises from the ventral surface of the medial epicondyle and passes proximally, presumably joining the most distal portion of the deltoid crest (crista ventralis). The olecranon scar is distinct, large, and medially positioned. The cross sections of the broken humeri reveal that the medullary space is narrow in relation to the cortical bone.

UFAC 6457 (Fig. 3A–B) is an incomplete right ilium lacking most of the ilial shaft. The specimen is well ossified and most likely belonged to an adult individual. The morphology of the posterior extremity indicates that the ilium was not fused to the ischium or pubis. The posterior portion of the preserved ilial shaft is straight, mediolaterally flattened, and bears the most posterior part of the dorsal crest. In lateral view, the dorsal acetabular expansion is narrow and the ventral acetabular expansion is inconspicuous. The ilial portion of the acetabular fossa is large, shallow, and anteroposteriorly elongated; it is surrounded by a subtle dorsal margin, and by a strongly projected anteroventral margin. The dorsal prominence is wide-based and moderately high, extending from near the posterior extremity of the dorsal acetabular expansion to the level of the anterior margin of the acetabular fossa. In lateral view, the anterior and posterior sides of the dorsal prominence arise more or less sharply from the ilial body near the midline and create an almost symmetrical, bell-shaped outline. In this same view, the anterior portion of the dorsal prominence bears a dorsal protuberance that is low and rounded. In dorsal view, the dorsal prominence is narrow and not angled laterally or medially. The ilium lacks a lateral oblique ridge near the anterior margin of the acetabular fossa, as well as a medial oblique ridge on the proximal portion of the medial face of the bone. The medial portion of the ilial body bears a thick and wide interiliac tuberosity.

Remarks

The atlantal, humeral, and ilial specimens show a combination of features that is known only in the total group of Pipidae: vertebra with opisthocoelous centrum; humerus with a small humeral ball and similarly developed medial and lateral epicondyles; ilium with a well-developed dorsal prominence, reduced dorsal and ventral acetabular expansions; and a large interiliac tuberosity (Trueb and Cannatella, 1986; Báez and Pugener, 2003; Báez et al., 2012; Rage et al., 2013). The atlas from Talismã is presumably formed by the synchondrotical fusion of vertebrae I and II and bears well-separated anterior cotyles. This combination of features is seen among pipids in crown Pipinae (*Hymenochirus*, *Pipa*) and closely related taxa (*Singidella*, *Pachycentrata*) (Báez et al., 2012; Gómez, 2016; Carvalho et al., 2019). Similarly, the ilium has a combination of features that occurs together among pipids only in some members of Pipinae: proximal portion of the ilial shaft flattened; dorsal prominence moderately high, symmetrical, and with its apex

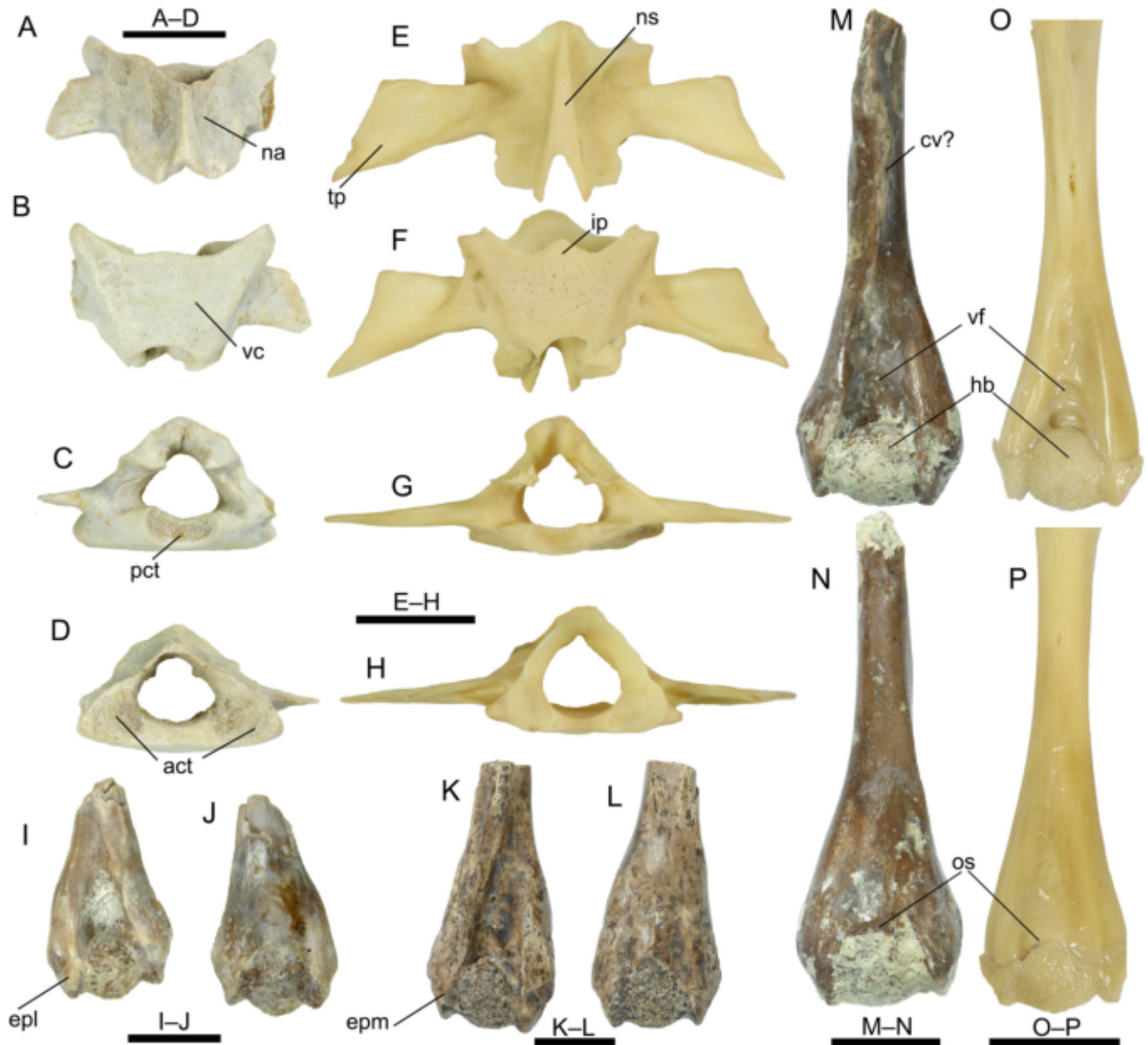


FIGURE 2. Atlantal and humeral comparison between fossil specimens of *Pipa* sp. and extant *Pipa pipa*. Atlas of *Pipa* sp. (UFAC 6475) in **A**, dorsal, **B**, ventral, **C**, posterior, and **D**, anterior views. Atlas of *P. pipa* (CHRP 2170) in **E**, dorsal, **F**, ventral, **G**, posterior, and **H**, anterior views. Right humerus (UFAC 6459, I–J) and two left humeri (UFAC 1766, K–L; UFAC 6983, M–N) of *Pipa* sp., in **I**, **K**, **M**, ventral and **J**, **L**, **N**, dorsal views. Left humerus of *P. pipa* (CHRP 2170) in **O**, ventral, and **P**, dorsal views. **Abbreviations:** act, anterior cotyle; cv, crista ventralis; epl, lateral epicondyle; epm, medial epicondyle; hb, humeral ball; ip, intercotylar process; na, neural arch; ns, neural spine; os, olecranon scar; pct, posterior cotyle; tp, transverse process; vc, vertebral centrum; vf, ventral fossa. Scale bars equal 5 mm. (Color figure available online.)

positioned posterior to the anterior margin of the acetabular fossa; distinct dorsal protuberance; very reduced dorsal acetabular expansion; and an interiliac scar that is broad both dorsally and ventrally (Báez et al., 2012; Gómez, 2016). The humeral morphology of pipids has not been studied in detail, and currently there are no diagnostic features that allow for a designation at the generic or specific level. The fossil humeri show a combination of features that is typical for many pipids: straight shaft; relatively small humeral ball; similarly developed medial and lateral epicondyles; and wide, triangular-shaped ventral fossa (Gómez, 2016).

Among pipines, the atlas UFAC 6475 differs from *Pseudhymenochirus* by the more widely separated cervical cotyles (Gómez, 2016) and the absence of a pointed intercotylar process

(Cannatella and Trueb, 1988b:fig. 3). It also differs from *Hymenochirus*, in which the intercotylar area is notched (Cannatella and Trueb, 1988b). Features of the ilium UFAC 6457 also rule out an affinity with *Pseudhymenochirus* or *Hymenochirus*. Ili of *Hymenochirus* differ from the Talismã ilium in having a dorso-laterally oriented globose dorsal protuberance and a very high dorsal prominence whose apex is located approximately at the same level as the anterior margin of the acetabular fossa (Báez et al., 2012; Gómez, 2016). In contrast, UFAC 6457 has a laterally projected dorsal protuberance that is low and rounded, and a moderately high dorsal prominence whose apex lies posterior to the level of the anterior margin of the acetabular fossa. Also, the fossil ilium was presumably not fused to the ischium, in contrast to the fused condition in *Hymenochirus* (except for

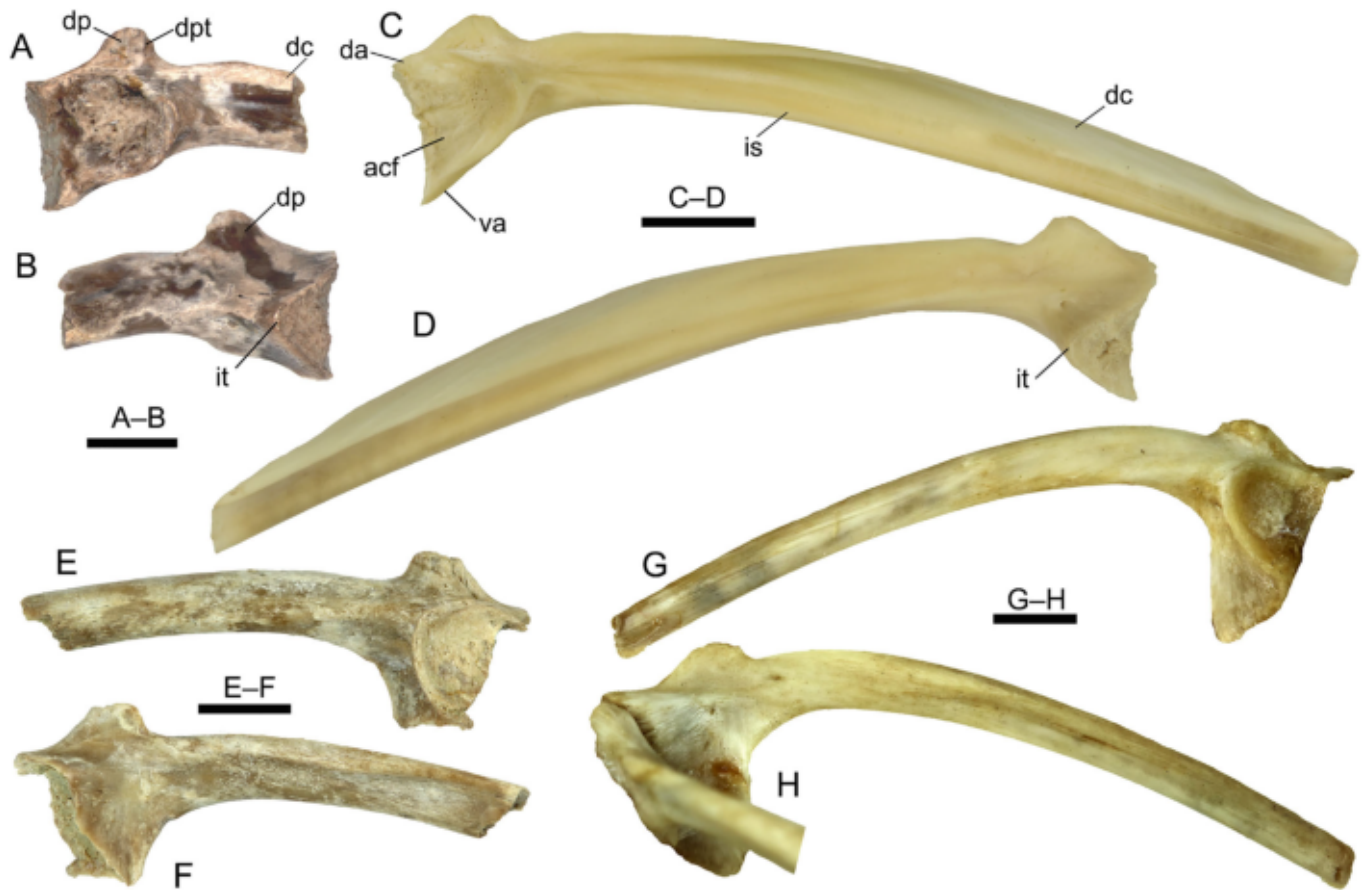


FIGURE 3. Ilial morphology of fossil *Pipa* sp., extant *Pipa pipa*, fossil cf. *Rhinella*, and extant *Rhinella diptycha*. Right ilium of *Pipa* sp. (UFAC 6457) in **A**, lateral, and **B**, medial views. Right ilium of *P. pipa* (CHRP 2170) in **C**, lateral, and **D**, medial views. Left ilium of cf. *Rhinella* (UFAC 6474) in **E**, lateral, and **F**, medial views. Left ilium of *R. diptycha* (CHRP 2171) in **G**, lateral, and **H**, medial views. **Abbreviations:** acf, acetabular fossa; dae, dorsal acetabular expansion; dc, dorsal crest; dpm, dorsal prominence; dpt, dorsal protuberance; is, ilial shaft; it, interiliac tuberosity; vae, ventral acetabular expansion. Scale bars equal 5 mm. (Color figure available online.)

H. curtipes) and *Pseudhymenochirus* (Cannatella and Trueb, 1988b; Gómez and Pérez-Ben, 2019). The fossil atlas and ilium also show a combination of characters that only occurs in *Pipa*, the only extant South American pipid genus: well-separated anterior cotyles in the atlas; intercotylar area not notched; dorsal prominence moderately high, with its apex located posterior to the level of the anterior margin of the acetabular fossa; dorsal protuberance rounded and projected dorso-laterally; and unfused ilium (Báez et al., 2012; Gómez, 2016).

Among the seven living species of *Pipa*, the atlas UFAC 6475 can be distinguished from those of *P. myersi* by its broad paramedial processes. By contrast, in *P. myersi* the neural arches bear spinose paramedial processes (Trueb and Cannatella, 1986). This condition was also reported for *P. parva* (Trueb and Cannatella, 1986), however, the atlas of a specimen available to us (UF-Herp. 37924) does not show evidence of distinct spinose paramedial processes, although these are present in posterior vertebrae. Interestingly, the atlas of *P. pipa* is described as bearing broad paramedial processes ((Trueb and Cannatella, 1986) as in the fossil, but the specimen shown here (Fig. 2E) has spinose processes. It seems that this feature varies considerably intraspecifically and may be of little taxonomic use. The fossil atlas shares with *P. pipa*, *P. carvalhoi*, and *P. arrabali* a relatively straight intercotylar area (Trueb and Cannatella, 1986; Trueb et al., 2000). This condition is different from that of *P. snethlageae*, *P. myersi*, and *P. parva*, in which the intercotylar area of the atlas

bears a well-developed process (Trueb and Cannatella, 1986). It also differs from *P. aspera*, in which the intercotylar area is concave (Trueb and Massemin, 2001). It should be noted that although *P. pipa* has been described as having a relatively straight intercotylar area (Trueb and Cannatella, 1986; Cannatella and Trueb, 1988b; Trueb et al., 2000), one of the specimens available for this study exhibits a distinct process between the cotyles (Fig. 2F), indicating an intraspecific variation of this feature. The proximal portion of the left transverse process of the fossil atlas is straight (Fig. 2A), similar to that of *P. pipa* (Fig. 2E) and *P. aspera* (Trueb, 2001:fig. 4B). By contrast, *P. parva* (UF-Herp. 37924), *P. myersi* (Trueb and Cannatella, 1986:fig. 11C, D), *P. snethlageae* (Trueb and Cannatella, 1986:fig. 11E, F), and *P. carvalhoi* (Báez et al., 2022:fig. 5J) show a constriction in the proximal portion of their transverse processes, giving the atlas a ‘bow tie’ shape in dorsal view.

The fossil ilium UFAC 6457 shares with all living species of *Pipa* the following features: proximal cross section compressed mediolaterally; dorsal prominence low to moderately developed, bell-shaped, vertically oriented, and with its apex lying posterior to the level of the anterior margin of the acetabular fossa; and dorsal and ventral acetabular expansions distinctively reduced (see matrix in Gómez and Pérez-Ben, 2019; Trueb and Cannatella, 1986). The fossil ilium resembles those of *P. pipa* and *P. snethlageae* in having a relatively low and broad dorsal prominence. By contrast, in the remaining species of *Pipa*, the dorsal

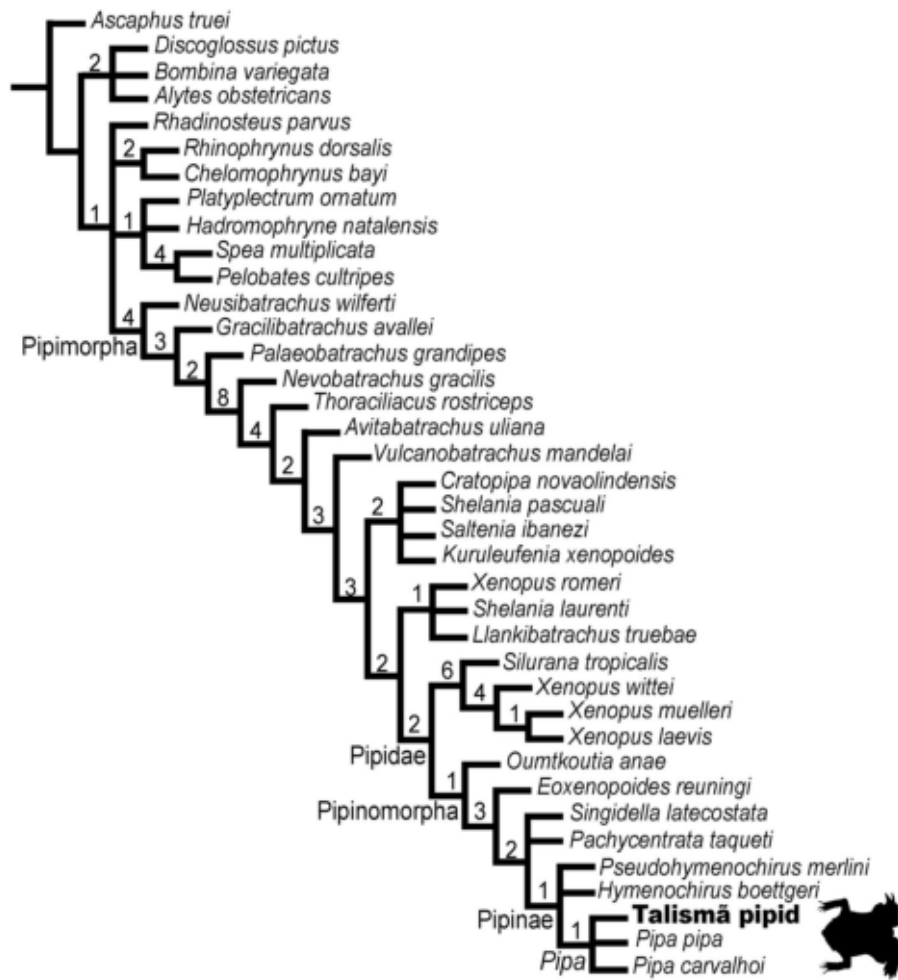


FIGURE 4. Strict consensus of 36 MPTs of 573 steps showing the phylogenetic position of the pipid from Talismã within Pipidae. Bremer support values are shown above branches.

prominence is more distinct and triangular in lateral view (Trueb and Cannatella, 1986; Cannatella and Trueb, 1988a). Other ilial features that vary interspecifically (e.g., the shape of the distal cross section of the ilial shaft, and the extension and orientation of the dorsal crest; Trueb and Cannatella, 1986; Gómez and Pérez-Ben, 2019) cannot be assessed in the fossil ilium because most of the distal portion of the bone is missing.

Despite the above-noted similarities between the fossil atlas and ilium with those of *Pipa pipa*, they differ in four features. In *P. pipa* there is a small depression between the lateral border of the atlas and the lateral margin of the anterior cotyle. This depressed area is absent in the fossil, because the lateral border of the vertebra is greatly reduced in this portion (Fig. 2A, B vs. 2E, F). The dorsal prominence of the fossil ilium is relatively higher and with steeper anterior and posterior slopes compared with that of *P. pipa* (Fig. 3A vs. 3C). Also, the fossil atlas lacks accessory intervertebral articulations located on both sides of the posterior cotyle. Although this feature has not been well studied, it has been reported for *P. pipa* (Fig. 2B vs. 2F) and other *Pipa* species (Cannatella, 1985; Báez et al., 2021). Lastly, the fossil ilium does not have a lateral oblique ridge anterior to the acetabulum, unlike all living *Pipa* species (Gómez and Pérez-Ben, 2019). The foregoing comparisons demonstrate that the fossil from Talismã represents a new taxon of *Pipa*. However, due to the incompleteness of the material we refrain from erecting a new species, and, instead,

conservatively identify the specimens as *Pipa* sp. until more diagnostically informative specimens become available.

We assessed the phylogenetic relationships of the Talismã pipid in the context of the major relationships within Pipidae. The analysis resulted in 36 MPTs of 573 steps. While the strict consensus tree (CI = 0.410, RI = 0.720) shown in figure 4 is less resolved than that of Gómez (2016) and Carvalho et al. (2019), several major clades within Pipimorpha were recovered. Our topology resembles that of Carvalho et al. (2019) in placing many fossil pipimorphs outside crown-group Pipidae. We recovered the Talismã pipid as a member of crown Pipinae in a polytomy together with *P. pipa* and *P. carvalhoi*. Because only two of the seven living *Pipa* species were included in the data matrix, it provides little information concerning the position of the fossil within the clade. Nevertheless, both parsimony analysis and the previous morphological comparisons indicate that the fossil pipid represents a species of *Pipa*. The specimens exhibit only two putative synapomorphies of Pipinomorpha or a less inclusive clade: proximal cross section of the ilium compressed (136:1) and vertebra I synchondrotically fused to vertebra II (88:4). The clade formed by the Talismã pipid and the species of *Pipa* is only supported by one synapomorphy, sharing an unfused ilium and ischium (152:0).

The fossil record of pipimorphs is rich and comes mainly from Gondwanan landmasses (Africa and South America), ranging from the Early Cretaceous to the Quaternary (e.g., Estes et al.,

1978; Báez et al., 2000; Trueb et al., 2005; Rage and Dutheil, 2008; Báez et al., 2008; Gardner and Rage, 2016; Gómez, 2016; Carvalho et al., 2019). In South America, the post-Paleogene record is scarce and only three fossils have been assigned to the living *Pipa*. A complete skull from the Holocene or Pleistocene of Rio das Velhas in Brazil was reported by Liais (1872), but not described or figured. It was identified as *Pipa bimaculata*, an invalid name that is not listed by Frost (2021) as a synonym to any of the *Pipa* species. The same skull was mentioned as *Pipa* sp. by Sanchiz (1998). The other two records consist of fused sacra and urostyles from the late Miocene and late Pliocene of Venezuela that have been identified as cf. *Pipa* sp. (Delfino and Sánchez-Villagra, 2018; Carrillo-Briceño et al., 2021). Thus, the specimens reported herein help to fill the gap in the fossil record of pipines in the Miocene and suggest a greater diversity within *Pipa* during the Cenozoic.

All living pipids are fully aquatic frogs that are found in permanent and temporary water bodies, such as swamps, lakes, floodplains, and rivers (Trueb, 2003). The species of *Pipa* are known to frequently inhabit stagnant and turbid waters (Souza, 2009). Currently, most species of *Pipa* occur in areas within the Amazon and Orinoco drainage basins (Trueb and Cannatella, 1986; Frost, 2021). Other species occur in different drainages in Panamá and Colombia (*P. myersi*), Maracaibo Lake in Venezuela (*P. parva*), and waters in the dry Caatinga and Atlantic Forest biomes in Brazil (*P. carvalhoi*) (Trueb and Cannatella, 1986; Silva et al., 2010; Frost, 2021). Four species of *Pipa* are found in Brazil (*P. arrabali*, *P. carvalhoi*, *P. pipa*, and *P. snethlageae*), and the genus is part of the current Amazonian batrachofauna that inhabits the region where the fossils were found (Venâncio and Souza, 2016).

NEOBATRACHIA Reig, 1958
 BUFONIDAE Gray, 1825
 cf. *RHINELLA* sp. Fitzinger, 1826
 (Fig. 3E, F)

Referred Material—One incomplete left ilium (UFAC 6474).
Locality and Horizon—Talismã site, southern Amazonas state, Brazil; Solimões Formation, upper Miocene.

Description

The specimen consists of a well ossified and incomplete left ilium (Fig. 3E, F). The distal portion of the ilial shaft is not preserved, and part of the ventral acetabular expansion and acetabular fossa are broken. The preserved posterior and middle portions of the ilial shaft are moderately compressed mediolaterally, lacking a distinct dorsal crest. The dorsal acetabular expansion is poorly developed in lateral view. The preserved portion of the ventral acetabular expansion is relatively more developed and has an expanded preacetabular zone, forming an obtuse angle with respect to the ilial shaft. The preacetabular zone has a shallow preacetabular fossa pierced by a small foramen. The anteroventral margin of the ventral acetabular expansion is not preserved. The acetabular fossa is deep, round, and bordered by a shallow dorsal margin and sharply projected anterior and ventral margins. The dorsal prominence is robust, long, moderately high, and with a nearly flat dorsal margin. It is projected dorsally and positioned relatively posteriorly, with about two-thirds of its length lying above the acetabular fossa. The anterior slope of the dorsal prominence is steeper than the posterior slope, resulting in an asymmetric shape in lateral or medial views. The apex of the dorsal prominence bears a dorsal protuberance that is broad, bulky and with rounded protruding margins. The posterior portion of the ilial body is also broken in medial view, however the ilioischial juncture is very thin and indicates there was no developed interiliac tubercle.

Remarks

UFAC 6474 is assigned to Bufonidae based on the following combination of features: posterior portion of the ilial shaft without a dorsal crest; dorsal acetabular expansion poorly developed; dorsal prominence present and dorsally projecting; and interiliac tubercle absent (Rage, 2003). Unfortunately, detailed comparisons among clades are hindered by the lack of substantial data on the ilia of extant species. Nevertheless, the specimen differs from all bufonid clades that occur in South America (*Amazophrynella*, *Atelopus*, *Dendrophryniscus*, *Frostius*, *Incilius*, *Melanophryniscus*, *Metaphryniscus*, *Nannophryne*, *Oreophrynella*, *Osornophryne*, *Truebella*), except for *Rhinella* and *Rhaebo*, by its robustness and larger size (e.g., Duellman and Ochoa, 1991; Señaris et al., 1994; Graybeal and Cannatella, 1995; De la Riva et al., 2005; Señaris et al., 2005; Carvalho-e-Silva et al., 2010; Mendelson and Mulcahy, 2010; Juncá et al., 2012; Mueses-Cisneros et al. 2012; Páez-Moscoso and Guayasamin, 2012; Costa-Campos and Carvalho, 2018; Rojas et al., 2018; Deforel et al., 2021). The absence of a distinct calamita ridge or a homologous structure on the lateral surface of the fossil ilial shaft, further distinguishes it from *Melanophryniscus* and *Nannophryne* (at least *N. variegata*) (Gómez and Turazzini, 2016; F.P.M., pers. observ.). The size of the fossil ilium is consistent with those of *Rhaebo*, but we could not directly compare the fossil material with most of the species of this clade. This is due to the unavailability of specimens for this study and the lack of osteological information in the literature. However, at least *Rhaebo guttatus* and *Rhaebo blomeri* differ from the fossil specimen in having a more developed dorsal acetabular expansion and lower dorsal prominence (Přikryl et al., 2009:fig. 7–2; F.P.M., pers. observ.). The size and general morphology (e.g., relatively high dorsal prominence, minimally developed dorsal acetabular expansion; Fig. 3E, F) of the fossil ilium are most consistent with those of living species of *Rhinella* (Fig. 3G, H; Pramuk, 2006:fig. 10; Araújo-Júnior and Moura, 2014:figs. 2, 4). Due to the incompleteness and the fragmentary state of the fossil material, it is not possible to infer the phylogenetic relationships of the fossil within the clade. Most osteological characters used in phylogenetic analyses of *Rhinella* are from the skull (Pramuk, 2006; Maciel et al., 2010) and very few of them refer to the ilium (four out of 83 morphological characters used by Pramuk, 2006). Thus, we tentatively identify our specimen as cf. *Rhinella*, pending the discovery of additional and more diagnostically informative material.

Bufonids are one of the most speciose and widespread groups of frogs (Pramuk et al., 2008). To date, around 630 living species have been described, naturally inhabiting most regions of the world except Madagascar, Antarctic, and parts of Oceania (Pramuk et al., 2008; Frost, 2021). The South American fossil record of the group is scarce and mainly represented by fragmentary and isolated bones. Fossil specimens have been reported from Argentina, Bolivia, Brazil, Colombia, and Peru, spanning in age from the Paleocene?–early Eocene to the Pleistocene–Holocene. They have been identified as belonging to living or indeterminate species of *Rhinella*, or as indeterminate bufonids (Tihen, 1962; Estes and Wassersug, 1963; Casamiquela, 1967; Vergnaud-Grazzini, 1968; Estes, 1970; Gasparini and Báez, 1975; Frailey and Campbell, 1980; Báez and Nicoli, 2004; Tomasini et al., 2013; Araújo and Moura, 2014; Pérez-Ben et al., 2014, 2019a, 2019b; Cruz et al., 2018; Barcelos and Verdade, 2020; Guevara et al., 2022). The exceptions are *Rhinella loba* and *Rhinella xerophylla*, which are the only valid extinct species of bufonids from South America (Pérez-Ben et al., 2019a; Ponssa et al., 2022). The Brazilian fossil record of bufonids is restricted to putative extant species from the Paleocene?–lower Eocene of Itaboraí (Estes, 1970) and from the Quaternary of Itapipoca (Araújo and Moura, 2014). Thus, our report of cf. *Rhinella*

from the Miocene of Acre represents the first record of a bufonid for the Neogene of Brazil.

Currently, *Rhinella* consists of 89 extant species with a Neotropical distribution. They are naturally found from southern Texas (USA) and Mexico, through Central America to southern South America, occupying a diverse range of habitats, such as tropical forests, savannas, coastal environments, and disturbed areas (Gilda and Carnaval, 2004; Frost, 2021).

DISCUSSION AND CONCLUSIONS

The fossil atlas, humeri, and ilia reported here from the Talismã site represent the first Neogene record of anurans for Brazil. At least two species are present: a distinct pipid species, belonging to the extant *Pipa*, and an unidentified bufonid species belonging to or closely related to the *Rhinella* clade.

Our findings of *Pipa* from the late Miocene of Talismã and a previous report from the late Miocene of Venezuela (Delfino and Sánchez-Villagra, 2018) represent the oldest fossils attributable to the group. While they help fill a gap in the history of South American pipines, there is a discrepancy between the fossil record and estimates of their divergence times. Recent estimates suggest that *Pipa* probably appeared at the start of the Eocene (~55 Ma, Pyron, 2014; Gómez and Pérez-Ben, 2019), thus indicating an interval of 45–50 My of unsampled history of the group in South America. Although also sparse, the fossil record of *Rhinella* includes more occurrences, ranging from the Paleogene to the Quaternary (e.g., Báez and Nicoli, 2004; Araújo and Moura, 2014). Molecular age estimates indicate that the group originated in the Oligocene (~30 Ma; Pyron, 2014) or earlier, between the Eocene and Oligocene (~44–31 Ma; Pramuk et al., 2008). If the fossil remains from the Paleocene?–lower Eocene of Itaboraí are referable to species of *Rhinella* (Estes, 1970), they would indicate an older origin for the group, contrasting with the molecular estimates. Our record of *Rhinella* in the late Miocene of Brazil falls comfortably within the range of both estimated origin times for the clade (Pramuk et al., 2008; Pyron, 2014).

The paleoenvironment of the Solimões Formation is interpreted as a complex fluvio-lacustrine system containing a mosaic of fluvial belts, lakes, and swamps, surrounded by closed forests and open herbaceous areas (Latrubesse et al., 2010). Taphonomic features and the taxonomic composition of the fossiliferous layer where most of the specimens studied herein were recovered indicate a deposition under a low energy aquatic environment (Muniz et al., 2021). The discovery of the remains of pipids, a group of highly aquatic frogs that are frequently found in stagnant water bodies, is in accordance with the interpreted depositional environment. Furthermore, the preference of pipids for aquatic habitats could account for their higher abundance in the fossil assemblage. By contrast, living *Rhinella* inhabit a wider range of habitats and are less dependent on water bodies, though these are visited for reproduction and necessary for the development of tadpoles (Gilda and Carnaval, 2004; Crump, 2015; Frost, 2021).

Pipa and *Rhinella* can be found today living in the region of the Talismã locality (Miranda et al., 2014; Venâncio and Souza, 2016). Other fossil findings from Colombia (Estes and Wassersug, 1963) and Venezuela (Delfino and Sánchez-Villagra, 2018) provide further evidence that at least these two groups have been components of the Amazonian batrachofauna since the Miocene.

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APPENDIX 1. Specimens examined.

Institutional Abbreviations—**CAS-Herp**, California Academy of Sciences, San Francisco, California, U.S.A.; **CHRP**, Coleção Herpetológica de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; **IRSNB**, Institut Royal des Sciences Naturelles del Belgique, Brussels, Belgium; **KU**, Herpetology Collection, Biodiversity Institute, University of Kansas, Lawrence, Kansas, U.S.A.; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **NHMUK-Zoo**, Natural History Museum, London, U.K.; **NCSM-Herp**, North Carolina State Museum, Raleigh, North Carolina, U.S.A.; **UF-Herp**, University of Florida, Florida Museum of Natural History, Herpetology, Gainesville, Florida, U.S.A.; **UFAC**, Coleção de Paleovertebrados do Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Rio Branco, Brazil; **USNM**, National Museum of Natural History, Smithsonian Institution,

Washington, DC, U.S.A.; **ZUEC**, Museu de Zoologia da Universidade Estadual de Campinas, Campinas, Brazil.

Abbreviations—**DS**, dry skeleton; **F**, fossil; **MS**, skeleton accessed through Morphosource (morphosource.org).

Specimens Examined

- Amazophrynella*: *A. manaos* IRSNB 15817 (MS; ARK ID: ark:/87602/m4/M98122)
- Atelopus*: *A. ignescens* IRSNB 425.C (MS; ARK ID: ark:/87602/m4/M98142); *A. hoogmoedi* IRSNB 17145 (MS; ARK ID: ark:/87602/m4/M98137); *A. oxyrhynchus* UF-Herp. 93190 (MS; ARK ID: ark:/87602/m4/M11363)
- Dendrophryniscus*: *D. brevipollicatus* IRSNB 57.C (MS; ARK ID: ark:/87602/m4/M98135)
- Frostius*: *F. erythrophthalmus* ZUEC 16631 (MS; ARK ID: ark:/87602/m4/M98143); *F. pernambucensis* USNM 565102 (MS; ARK ID: ark:/87602/m4/M32526)
- Melanophryniscus*: *M. moreirae* ISNM 207760 (MS; ARK ID: ark:/87602/m4/M98144); *M. stelzneri* UF-Herp 63183 (MS; ARK ID: ark:/87602/m4/M12431)
- Metaphryniscus*: *M. sosai* USNM 550143 (MS; ARK ID: ark:/87602/m4/M98156)
- Nannophryne*: *N. variegata* IRSNB 12826 (MS; ARK ID: ark:/87602/m4/M98210)
- Oreophrynella*: *O. vasquezi* IRSNB 14395 (MS; ARK ID: ark:/87602/m4/M98249); *O. seegobini* IRSNB 1980 (MS; ARK ID: ark:/87602/m4/M98245); *O. nigra* IRSNB 14388 (MS; ARK ID: ark:/87602/m4/M98241); *O. quelchii* IRSNB 17140 (MS; ARK ID: ark:/87602/m4/M98242); *O. macconnelli* IRSNB 14364 (MS; ARK ID: ark:/87602/m4/M98235); *O. cryptica* IRSNB 17133 (MS; ARK ID: ark:/87602/m4/M98214); *O. huberi* IRSNB 17135 (MS; ARK ID: ark:/87602/m4/M98212)
- Osornophryne*: *O. bufoniformis* USNM 193540 (MS; ARK ID: ark:/87602/m4/M98136)
- Pipa*: *P. pipa* MNHN 1882-462, 1888-103 (DS), CHRP 2170 (DS); *P. parva* UF-Herp. 37924 (MS; ARK ID: ark:/87602/m4/M12417); *Pipa* sp. UFAC 2853, 2852, 1766, 6457, 6459, 6461, 6475 (F)
- Rhaebo*: *R. blomeri* UF-Herp 104602 (MS; ARK ID: ark:/87602/m4/M42667)
- Rhinella*: *R. diptycha* CHRP 2171 (DS); *R. beebei* IRSNB 17147 (MS; ARK ID: ark:/87602/m4/M98145); cf. *Rhinella* UFAC 6474 (F)
- Truebella*: *T. skoptes* KU-Kuh 196839 (MS; ARK ID: ark:/87602/m4/M39601); *T. tothastes* KU-Kuh 196599 (MS; ARK ID: ark:/87602/m4/M39599)