

# A new pipid frog from the Upper Cretaceous of Patagonia and early evolution of crown-group Pipidae



Raúl O. Gómez

CONICET-IGEBBA-Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, 1428 Buenos Aires, Argentina

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## ABSTRACT

Pipid frogs are fully aquatic frogs that today inhabit freshwater environments of southern continents on both sides of the Atlantic Ocean, with a fairly good fossil record dating back to the Cretaceous. Here I report on fossils from the Allen Formation (upper Campanian–lower Maastrichtian), Río Negro Province, Argentina, that are ascribed to a new genus and species of pipid. In order to assess the evolutionary relationships of the new taxon, which is represented by sphenethmoids, otic capsules, ilia, humeri, and vertebrae, cladistic analyses of a data matrix of 165 osteological characters scored for 36 taxa were performed. The results are congruent with previous hypotheses of pipoid interrelationships and consistently place the new taxon as part of the lineage today represented by the African xenopodines. Temporal calibration of the phylogenetic tree based on the fossil record imply that the origin and early diversification of crown-group Pipidae might have occurred during the Early Cretaceous, prior to the final breakup of western Gondwana. This study highlights the importance of including fossils, even fragmentary ones, directly in phylogenetic analyses in order to disentangling how, when, and where pipid frogs diversified.

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## 1. Introduction

Pipids are fully aquatic frogs well represented in the fossil record, which documents greater taxonomic diversity and wider geographic distribution during Cretaceous and Paleogene times (Báez, 1996; Báez and Púgener, 2003) than today. To date, the family Pipidae includes 41 extant species arranged in four or five monophyletic genera (Frost, 2015). These genera, in turn, form three groups: *Pipa*, from tropical South America east of the Andes, and Xenopodinae (*Silurana* + *Xenopus*) and Hymenochirini (*Hymenochirus* + *Pseudhymenochirus*), both from sub-Saharan Africa (Báez et al., 2012; Bewick et al., 2012). Even though the monophyly of the crown-group Pipidae and their three major constituent clades are now well-corroborated, the interrelationships of these lineages are still debated (Frost et al., 2006; Pyron and Wiens, 2011; Báez et al., 2012; Bewick et al., 2012; Cannatella, 2015). Because this is a three-taxon problem, the relationships among these groups depend entirely on the placement of the root of Pipidae (Bewick et al., 2012). In this scenario, the

inclusion of fossil pipids in quantitative phylogenetic analysis might help in stabilizing the placement of the root.

The Cretaceous fossil record of pipimorphs comes mainly from formerly Gondwanan landmasses and includes non-pipid pipimorphs and crown-group pipids of uncertain affinities (e.g., Báez, 1996, 2013; Báez and Rage, 1998; Báez et al., 2000; Trueb et al., 2005; Rage and Dutheil, 2008). In South America, the oldest records date back to the mid-Cretaceous of Patagonia (Cenomanian–Turonian Candeleros Formation; Báez et al., 2000) and Brazil (Aptian–Albian Crato Formation; Báez et al., 2009) and consist of non-pipid pipimorphs. Purported crown-group pipids in the continent appear only later in the Upper Cretaceous (Campanian–Maastrichtian) in rocks of Las Curtiembres, Los Alamitos, and Allen formations of Argentina (Báez, 1981, 1987; Martinelli and Forasiepi, 2004). The records from Las Curtiembres Formation (Campanian) of northwestern Argentina consist of several specimens corresponding to metamorphic and post-metamorphic individuals that represent a single taxon, *Saltenia ibanezi* (Reig, 1959; Báez, 1981). Despite many specimens being recorded, preservational issues have limited the interpretation of numerous features of *Saltenia* (Báez, 1996), which could explain in part disparate results regarding its phylogenetic placement among pipids, even

E-mail address: [raulgomez@gl.fcen.uba.ar](mailto:raulgomez@gl.fcen.uba.ar).

outside the crown group (Báez, 1981; Báez and Trueb, 1997; Báez and Pügener, 2003; Báez et al., 2012). The known records of pipids from Los Alamitos and Allen formations (Campanian–Maastrichtian) of Patagonia consist of a few isolated remains (Báez, 1987; Martinelli and Forasiepi, 2004), of which those from Los Alamitos were thought to be closely allied to extant *Xenopus* (Báez, 1987). This hypothesis, which would have clear implications on palaeobiogeographical aspects and on divergence-time estimates of xenopodines and even pipids as a whole, has not been tested so far.

Recent fieldwork led by Guillermo Rougier (University of Louisville) at outcrops of the Allen Formation, near the Trapalcó and Santa Rosa depressions, Río Negro Province, have yielded a rich collection of small vertebrates obtained through screen-washing techniques (Gómez et al., 2008; Rougier et al., 2009; Gómez, 2011). Among these are pipid frog remains that, together with those already known from the same levels (Martinelli and Forasiepi, 2004), are here recognized as a new genus and species. This new pipid taxon is represented by well-preserved cranial and postcranial remains that provide new data to elucidate their systematic relationships. With this aim, I performed a phylogenetic analysis using several osteological characters that were not included in previous studies of fossil pipoids. I also discuss the results in the context of previous hypotheses of pipid interrelationships, palaeobiogeography, and divergence-time estimates, highlighting the importance of including fossils, even fragmentary ones, directly in phylogenies.

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York, USA; CPBA-V, Palaeontología, Vertebrados, Departamento de Ciencias Geológicas, Universidad de Buenos Aires, Buenos Aires, Argentina; DGM, Dirección de Geología e Minería, Río de Janeiro, Brazil; FCEN, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; FML, Instituto de Herpetología de la Fundación Miguel Lillo, Tucumán, Argentina; KU, Natural History Museum, University of Kansas, Lawrence, Kansas, U.S.A.; MACN-HE, Colección de Herpetología del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; MACN-PV RN, Colección Río Negro, Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; MCN, Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; MLP, Museo de La Plata, La Plata, Argentina; MML-PV, Paleontología de Vertebrados, Museo Municipal de Lamarque, Lamarque, Argentina; MNCN, Museo Nacional de Ciencias Naturales de Madrid, Madrid, España; MPEF-PV, Paleontología de Vertebrados, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MUCPv, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Sección Paleontología de Vertebrados, Neuquén, Argentina; SAM, Iziko South African Museum, Cape Town, South Africa.

## 2. Geological and paleontological framework

The remains described herein were discovered at several paleontological localities near Salinas de Trapalcó and Salitral de Santa Rosa, which are located about 120 km south-west of Lamarque, Río Negro province, Argentina (Fig. 1). The fossil bearing rocks belong to the Allen Formation, which was interpreted as representing a nearshore-to-restricted-marine environment at the initial stage of the transgressive cycle that ended with the entrance of the Maastrichtian Sea (Uliana and Dellapé, 1981).

The lowermost levels of the Allen Formation, from which the fossils were collected, are extensively exposed at the study area and comprise an alternation of tabular layers of siltstones and fine-

grained sandstones with intercalated conglomerates that were interpreted as deposited in a meandriform fluvial system (Artabe et al., 2004). The fossil-bearing beds consists of friable, yellowish, fine-grained sandstone enclosed between siltstone layers (Fig. 1) and have yielded abundant and taxonomically-diverse vertebrate remains, including those of chondrichthyan and osteichthyan fishes, frogs, mammals, turtles, rhynchocephalians, snakes, and dinosaurs (Martinelli and Forasiepi, 2004; Gómez et al., 2008; Rougier et al., 2009; Bogan et al., 2011; Gómez, 2011).

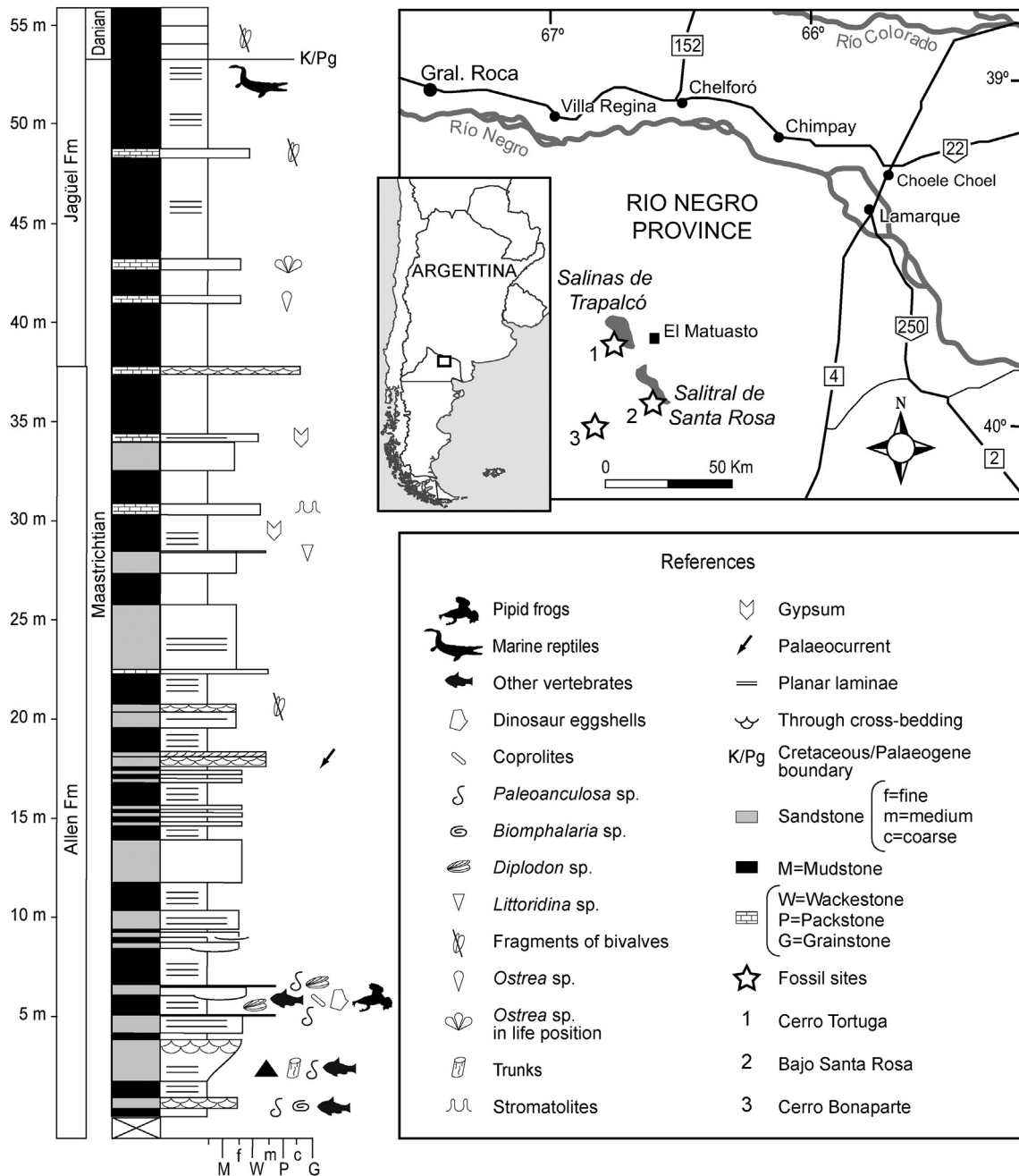
The stage assignment of the Allen sequence is bracketed between the lower Campanian Anacleto Formation (Hugo and Leanza, 2001) and the upper Maastrichtian–Danian Jagüel Formation (Uliana and Dellapé, 1981), where the Cretaceous/Palaeogene boundary was identified based on foraminiferal associations (Concheyro et al., 2002; Fig. 1). Additionally, early Maastrichtian microfossils were described from the top of the Allen Formation (Ballent, 1980). Thus, the available evidence points to a late Campanian–early Maastrichtian age for the fossils described herein.

## 3. Materials and methods

The fossil material consists of isolated, tridimensionally preserved elements, which are housed at the vertebrate palaeontological collections of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' (MACN-PV RN) Buenos Aires, and Museo Municipal de Lamarque (MML-PV), Río Negro province, Argentina. Photographs were made using a Nikon D3200 digital camera equipped with a macro lens. Anatomical comparisons were made with a relatively wide sample of dry or cleared and stained skeletons of extant pipoids, as well as to several extinct pipimorph taxa, based on direct observation of fossil specimens whenever possible (see [Supplementary material](#)).

Anatomical terminology mainly follows that of Báez and Pügener (2003) with additional terms for the ilium from Báez et al. (2012) and Gómez and Turazzini (2015). Systematic nomenclature mainly follows that of Frost et al. (2006) and Frost (2015), but with some minor changes: *Silurana* is here recognized as a genus distinct from *Xenopus* based on morphological, genetic, and temporal grounds (e.g., Cannatella and Trueb, 1988; Henrici and Báez, 2001; Evans et al., 2004; Bewick et al., 2012; Evans et al., 2015) and commonly used high-rank-group names such as pipoids (e.g., Báez and Pügener, 2003) are used throughout the paper together with formal names from Frost et al. (2006).

In order to assess the phylogenetic relationships of the new taxon among pipoids I perform a Parsimony analysis based on osteological characters mainly using those published by Cannatella and Trueb (1988), Báez and Pügener (2003), Báez et al. (2009, 2012), and Báez (2013). However, several additional characters were considered (labeled with G throughout the text), particularly regarding the morphology of the braincase and otic capsules, presacral vertebrae, sacrum, and humerus (see [Supplementary material](#)). Also, many character statements were modified from previous analyses in order to complete their syntaxes, provide more detail, and/or to separate neomorphic and transformational patterns (Serenó, 2007). Some characters entail variation that is continuous and were discretized in the least possible number of states. The cut-offs of this variation was based on cluster analyses of the respective quantitative data performed in the statistical package PAST (Hammer et al., 2001), where large clusters separated by large distances from one another were considered as separate discrete states. Highly disparate values that often resulted in additional small clusters were merged to the most similar state. When commenting particular character and character states, these are noted throughout the text between brackets with their respective numbers separated by a colon.



**Fig. 1.** Stratigraphic column showing the fossiliferous level and map showing the fossil sites from which the pipid materials were recovered (modified from Gómez et al., 2008). Geographic coordinates: Cerro Tortuga (39° 47' S, 66° 42' W), Bajo Santa Rosa (39° 59' S, 66° 40' W), Cerro Bonaparte (40° 03' S, 66° 48' W).

The taxon sampling includes all the taxa of the recently published dataset of Báez et al. (2012) plus three outgroup taxa included in recent morphological cladistic analyses (Báez, 2013) and, besides *Kuruleufenia*, 11 additional pipoid species (see Supplementary material). Most of the latter are fossil taxa that were considered in different previous analyses (Báez et al., 2007; Báez, 2013), including several non-pipid pipimorphs. Of particular relevance for their pre-Campanian Cretaceous age are the African *Pachycentrata taqueti* (Coniacian–Santonian of Niger; Báez & Rage, 1998) and *Oumtkoutia anae* (Cenomanian of Morocco; Rage and Dutheil, 2008); the latter being included here for the first time in a cladistic analysis. The resultant data matrix consists of 165 characters scored for 36 terminal taxa (Supplementary material).

The dataset was analyzed using the heuristic search of TNT v. 1.1 (Goloboff et al., 2008) under weighting regimes against homoplasy, using implied weighting, and under equal weights. Sensitivity of the results to variations in the strength of the weighting function was assessed with integer values of the concavity constant ( $k = 1–20$ ). The tree search consisted of 1000 replicates of Wagner trees with random addition sequence of taxa followed by Tree Bisection and Reconnection (TBR) branch swapping, holding ten trees per replication, and collapsing branches of zero length after tree search, with the resulting trees subjected to a final round of TBR branch swapping. Multistate characters were treated as unordered during the tree search. Most-parsimonious trees (MPTs) were rooted with *Ascapthus truei*. Node support was assessed using

absolute frequencies under jackknifing with 1000 pseudo-replicates and the Bremer index, both calculated in TNT.

The topology obtained under equal weights was time-calibrated following the approach of Marjanović and Laurin (2014) and using the fossil ages considered by Cannatella (2015).

**Anatomical abbreviations:** acf, acetabular fossa; cc, cortical compacta; cd, condyle; cee, crest on epiotic eminence; cp, crista parotica; cqf, cranio-quadrata foramen; cty, cavum tympani; dae, dorsal acetabular expansion; dpm, dorsal prominence; dpt, dorsal protuberance; ec, Eustachian canal; epl, lateral epicondyle; epm, medial epicondyle; fm, foramen magnum; fpf, frontoparietal fenestra; fps, frontoparietal scar; hb, humeral ball; hsd, horizontal semicircular duct; iec, inner ear cavity; ier, inner ear region; iis, interiliac scar; ij, ilioischial junction; ipf, inferior perilymphatic foramen; ish, iliac shaft; it, interiliac tubercle; jf, jugular foramen; lor, lateral oblique ridge; mec, medial epicondylar crest; mog, medial oblique groove; ms, medullary space; nal, neural arch lamina; nap, neural arch pedicel; ns, neural spine; oc, occipital condyle; onf, orbitonasal foramen; opf, optic foramen; os, olecranon scar; pc, parietal crest; prz, prezygapophysis; psp, parasphenoid; pss, parasphenoid scar; ptz, postzygapophysis; pvp, posteroventral process of otic capsule; sd, sacral diapophysis; sf, spinal foramen; sn, septum nasi; tn, tectum nasi; tp, transverse process; ur, urostyle; vae, ventral acetabular expansion; vf, ventral fossa; vlot, ventrolateral otic ledge; vp, ventral process; VSA, angle between the ventral acetabular expansion margin and the iliac shaft.

#### 4. Systematic palaeontology

Anura Fischer Von Waldheim, 1813

Xenoanura Savage, 1973 (=Pipoidea Ford & Cannatella, 1993)

Pipimorpha Ford and Cannatella, 1993

Pipidae Gray, 1825

***Kuruleufenia* gen. nov.**

**Derivation of name.** From the Mapudungun (Araucanian) Kuru Leufu, which means Río Negro, for the provenance of the fossils.

**Type species:** *Kuruleufenia xenopoides* gen. et sp. nov.

**Diagnosis.** As for the only known species.

***Kuruleufenia xenopoides* gen et sp. nov.**

(Figs. 2–4)

**Derivation of name.** From *Xenopus* and the Greek suffix *-oides*, for its overall resemblance to extant xenopodine pipids.

**Holotype.** MACN-PV RN 1064, an almost complete sphenethmoid.

**Hypodigm.** The type; MACN-PV RN 1065 (sphenethmoid), 1066 (almost complete right humerus); MML-PV 1042 (two incomplete humeri), 1047 (?fifth presacral vertebra and two incomplete presacrals), 1057–1058 (two otic capsules), 1059 (incomplete sacro-urostyle), 1060–1061 (incomplete ilia), 1062–1063 (incomplete presacrals).

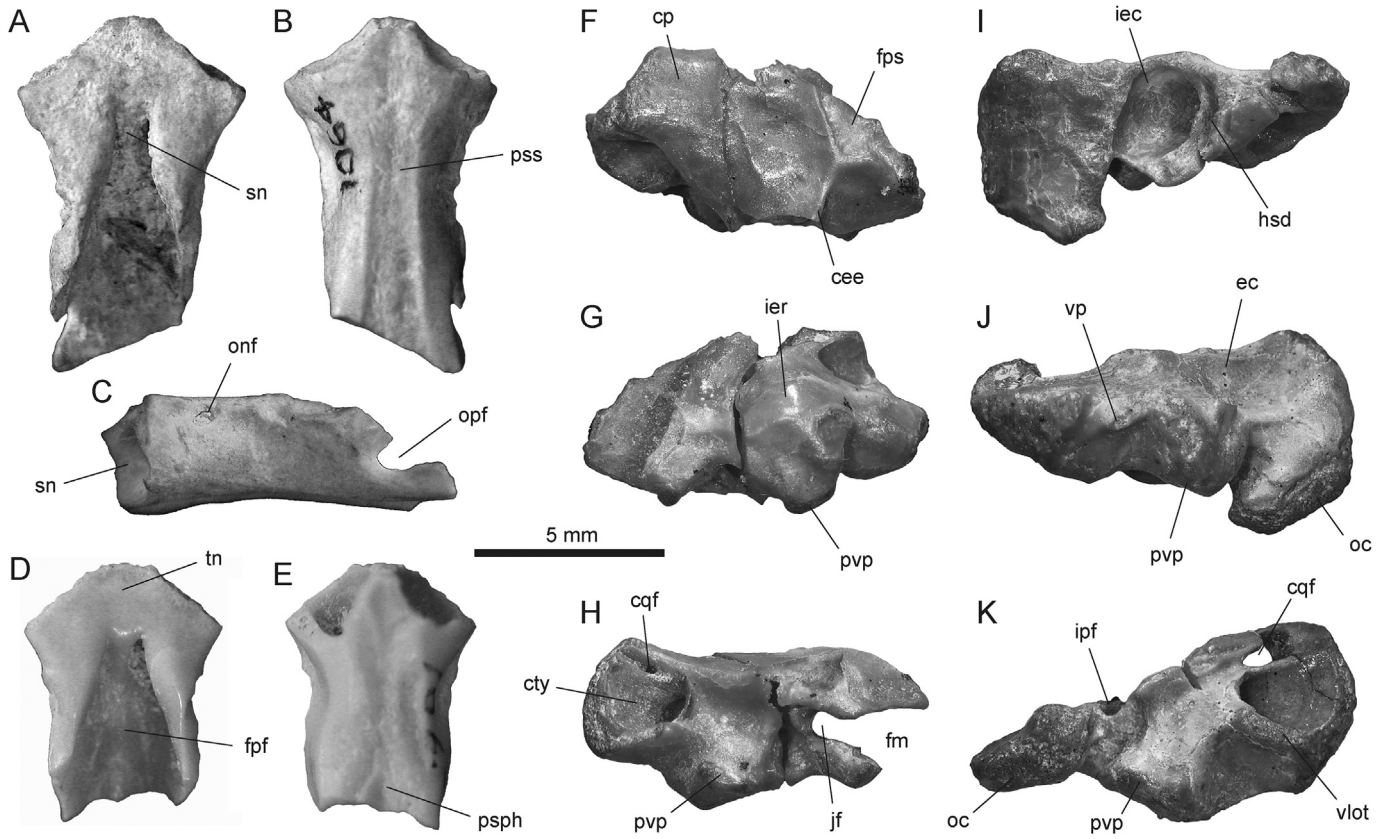
**Horizon and locality.** Microvertebrate layer (Rougier et al., 2009), lower member of the Allen Formation (upper Campanian–lower Maastrichtian; Hugo and Leanza, 2001); several paleontological localities nearby Trapalcó and Santa Rosa depressions (Cerro Tortuga, Bajo Santa Rosa, Cerro Bonaparte), about 120 km south-west of Lamarque, Río Negro province, Argentina (Fig. 1).

**Diagnosis.** Well-ossified pipid frog of moderately large size, similar to small adults of *Xenopus laevis*, with sphenethmoid surrounding the optic foramen (synapomorphy of Pipidae; state 55:1) and a frontoparietal fenestra extending anteriorly through a tapering embayment up to the tectum nasi (autapomorphic; state G46:1). Sphenethmoid transversely constricted at a level just posterior to that of the orbitonasal foramina. Otic capsule with a deep furrow

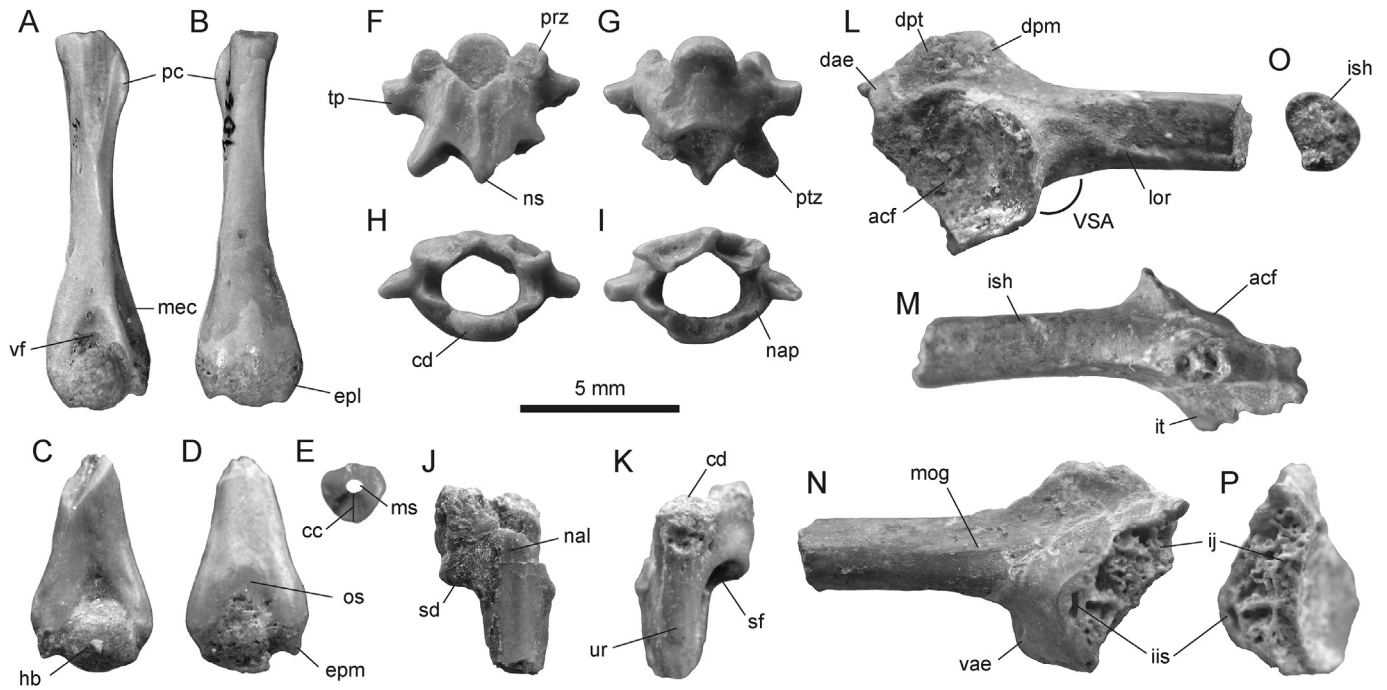


**Fig. 2.** *Kuruleufenia xenopoides* gen. et sp. nov. Partial reconstruction of the skeleton (in grey) and parts represented by fossil specimens (in white) in dorsal view. The skeletal reconstruction, which is based on that of *Shelania pascuali* (Báez and Trueb, 1997), is superimposed on the body outline of an adult *Xenopus laevis* (in black).

for Eustachian canal (synapomorphy of Pipidae plus *Avitabatrachus*; state 58:1), a large inferior perilymphatic foramen that open extracranially posterior to the jugular foramen (plesiomorphic for pipoids; state 62:1), a large posteroventral process ventrolateral to condyloid fossa (putatively for the m. intertransversarius capitis inferior; synapomorphy of Xenopodinomorpha or a less inclusive clade; state G67:1), and a cranio-quadrata passage with an exit foramen completely bound in bone (autapomorphic; state G70:1). Opisthocoelus presacral vertebrae (synapomorphy of an unnamed clade of pipimorphs; state 96:1) with flat centra, neural arch lamina deeply indented anteriorly and pointed posteriorly with a ridge-like neural spine (synapomorphy of Xenopodinomorpha or a less inclusive clade; state 90:1) flanked by a pair of faint ridges, and flat prezygapophyseal articular surfaces (plesiomorphic for pipoids; state 84:0). Sacral neural arch lamina squared-shaped (synapomorphy of Xenopodinomorpha or a less inclusive clade; state G101:1) and lacking a medial ridge or crest (plesiomorphic for pipoids; state 102:0; pipinomorphs show state 102:1). Humerus with a straight shaft (synapomorphy of Pipimorpha; state 123:0), small humeral ball (a putative synapomorphy of Pipidae plus *Avitabatrachus*; state G124:0), relatively short deltoid crest (synapomorphy of Pipimorpha; state G126:0), well-developed parietal crest (plesiomorphic for pipoids; state G127:1), and medial epicondylar crest (autapomorphic; state G128:1). Ilium not fused to ischium (plesiomorphic for pipoids; state 152:0), interiliac scar ample both ventrally and dorsally (synapomorphy of Xenopodinomorpha or a less inclusive clade; state 149:2), ilial shaft lacking a dorsal crest (at least on its proximal part; plesiomorphic at this level; states 145:0 or 146:0) and with a circular proximal cross-section (synapomorphy of an unnamed clade of xenopodinomorphs; state 136:0), bell-shape dorsal prominence well



**Fig. 3.** *Kuruleufenia xenopoides* gen. et sp. nov. A–C, Holotype (MACN-PV RN 1064), sphenethmoid in A, dorsal, B, ventral, and C, left lateral views. D–E, Sphenethmoid (MACN-PV RN 1065) in D, dorsal and E, ventral views. F–H, Left otic capsule (MML-PV 1058) in F, dorsal, G, ventral, and H, posterior views. I–K, Right otic capsule (MML-PV 1057) in I, dorsal, J, ventral, and K, posterior views.



**Fig. 4.** *Kuruleufenia xenopoides* gen. et sp. nov. A–B, Right humerus (MACN-PV RN 1066) in A, ventral and B, dorsal views. C–E, Distal portion of left humerus (MML-PV 1042) in C, ventral, D, dorsal, and E, proximal (cross-section of the diaphysis) views. F–I, Posterior (?V) presacral vertebra (MML-PV 1047) in F, dorsal, G, ventral, H, anterior, and I, posterior views. J–K, Sacro-urostyle (MML-PV 1059) in J, dorsal and K, ventral views. L–P, Right ilium (MML-PV 1060) in L, acetabular, M, dorsal, N, medial, O, distal (cross-section of the shaft), and P, posterior views.

developed (plesiomorphic for pipoids; state 139:0), lateral oblique ridge (a putative synapomorphy of Pipidae plus *Avitabatrachus*; state 148:1) and medial oblique groove present.

**Description and comparisons.** Here I describe new remains of pipids from the Allen Formation and redescribed those previously documented from the same unit (Martinelli and Forasiepi, 2004). All specimens are three-dimensionally preserved and show fine anatomical detail. Although these elements were found through screen-washing, their relative size and consistent morphology suggest that the entire pipid material represent a single taxon (Fig. 2), here ascribed to a new genus and species, *Kuruleufenia xenopoides*. The different elements are in general extensively ossified and their size is consistent with mature individuals of some of the largest extant pipid species (e.g., *Xenopus laevis*; Fig. 2).

**Sphenethmoid.** This element is represented by two nearly complete specimens, the holotype MACN-PV RN 1064 (Fig. 3A–C) and MACN-PV RN 1065 (Fig. 3D, E) from Bajo Santa Rosa, previously described and ascribed to Pipidae by Martinelli and Forasiepi (2004). The following description is fundamentally based on the holotype and does not disagree with that of the latter authors, but gives some additional details. This single bone is extensively ossified, forming most of the lateral wall of the braincase and enclosing the orbitonasal foramina anteriorly and the optic foramina posteriorly (as is evident on the left side of MACN-PV RN 1064; Fig. 3C); the latter condition is considered synapomorphic of Pipidae (Cannatella and Trueb, 1988; Báez and Pügener, 2003). Along the orbital region this element is relatively narrow with nearly parallel lateral walls and ventrally rounded, but visibly widens anteriorly at the level of the orbitonasal foramina, extending into the most proximal part of the antorbital plane, and is transversely constricted (discernible only in ventral view; Fig. 3B, E) at a level just posterior to that of the orbitonasal foramina. The bone also encompasses part of the nasal capsules, including the posterior portion of the tectum nasi, solum nasi, and septum nasi. At both sides of the septum, opening into the nasal cavity, a pair of round, large olfactory foramina are neatly demarcated by bony tissue, which contrasts with the condition in extant xenopodines (Báez and Pügener, 1998:fig. 7c). In anterior view, the sphenethmoid has the shape of a relatively low isosceles trapezoid, with the ossified tectum nasi around twice as wide as the ossified solum nasi and bearing a shallow depression towards the mid-line on the otherwise flat tectum nasi. In dorsal view, the sphenethmoid delimits the anterior and lateral margins of the frontoparietal fenestra, which extends anteriorly through a tapering embayment up to the tectum nasi, where the posterior part of the septum nasi becomes noticeable in this same view (Fig. 3A, D). A pair of faint impressions on the anterior part of the ossified tectum nasi represents the scars left by the nasals, indicating that the latter had convex posterior margins and were not fused with one another or with the underlying sphenethmoid at this level. As preserved, it is clear that the sphenethmoid was not fused to the frontoparietal. Ventrally, a distinct, narrow impression that extends all along the bone (Fig. 3B), indicates that a long cultriform process of the parasphenoid surpassed anteriorly the level of the antorbital plane and was not fused to the braincase in the orbital region. This is also evident from the remnants of parasphenoid preserved in MACN-PV RN 1065 (Fig. 3E).

**Otic capsule.** MML-PV 1057 is a right otic capsule lacking most of its roof (Fig. 3I–K), whereas MML-PV 1058 is a left one lacking part of its anterior wall (Fig. 3F–H), both coming from Cerro Tortuga. Each otic capsule is formed by a single bone, the otoccipital, resultant from the fusion of prootic and exoccipital. As preserved, the ventromedial edge of MML-PV 1057 and the dorsomedial edge of MML-PV 1058 suggest that contralateral otic capsules were not

fused to one another. The crista parotica has a convex dorsal surface and lacks dorsal crests like those of species of *Pipa* and *Hymenochirus*, suggesting that the pars externa of the m. depressor mandibulae might have originated on a fascia covering the crista parotica as in extant xenopodines and non-pipid frogs (Cannatella and Trueb, 1988). Above the epiotic eminence there is a sharp crest that is confluent anteriorly with the posterolateral angled corner of the frontoparietal, which has not been preserved as bone but left a flat and deep impression on the otic capsule (Fig. 3F); the latter appear to have not reached the foramen magnum. Ventrally, the prootic region shows a deep furrow that lies anteriorly to the bulged inner ear region that represents the Eustachian canal (Fig. 3J), which likely housed the Eustachian tube in life as in all extant pipids. The presence of a pterygoid knob could not be ascertained since this region is not preserved in any specimen.

The occipital condyle, which is well preserved in MML-PV 1057, is convex and reniform in posterior view as in most anurans, but not in species of *Pipa*, and is oriented at a relatively low angle with respect to the horizontal, outlining the ventrolateral margin of the foramen magnum (Fig. 3K). The dorsal margin of the latter, as preserved in MML-PV 1058, is almost straight and low-angled with respect to the horizontal. Considering the complementary evidence from the two specimens, the restored foramen magnum appears as having the shape of a relatively low and wide rhomboid, a configuration distinct from that of most compared species, but that has been documented in an indeterminate pipid from the Cretaceous of Niger (Báez and Rage, 1998:fig. 3k). Lateral to the occipital condyle, a large inferior perilymphatic foramen, of which only its ventral margin is preserved in MML-PV 1057, opens extracranially on a shallow and poorly-demarcated condyloid fossa on the posteromedial wall of the inner-ear capsule lateral to the jugular foramen (Fig. 3K). The medial wall of the otic capsule, preserved in MML-PV 1058, lacks a superior perilymphatic foramen, but shows an oval excavated area where the acoustic foramina likely opened. The combined presence of inferior perilymphatic foramen and absence of superior perilymphatic foramen has only been recognized in extant xenopodines as well as in the Paleogene *'Xenopus' romeri* and *'Shelania' laurenti* (Estes, 1975; Báez and Pügener, 1998).

Clearly visible in posterior and ventral views of both specimens, a large, bulging process projects from the posteroventral edge of each otic capsule (Fig. 3G, H, J, K). This projection, here referred to as the posteroventral process of the otic capsule, and although it has been rarely reported in anurans (Paterson, 1946:fig. 2) is present in several pipids, including extant species of *Silurana*, *Xenopus*, and *Hymenochirus*, as well as the Paleogene *Shelania pascuali* (Báez and Trueb, 1997:fig. 5), *'Xenopus' romeri* (Estes, 1975:fig. 1), and *'Xenopus' stromeri* (Rage, 2008:fig. 3a). Examination of dissected material of *Xenopus laevis* shows that the m. intertransversarius capitis inferior inserts on the posteroventral process of the otic capsule and further that it originates on the transverse process of the vertebra II (Grobbeelaar, 1924; Ryke, 1953). Asymmetric contraction of this muscle could be related with lateral bending of the head (Haas et al., 2006), but otherwise the muscle might only have a postural function in fixing the position of the head relative to the trunk as occurs in other amphibians (Wake, 1993). In addition, anteroventral to this process and adjacent to the posterior margin of the Eustachian canal there is a small projection pointing ventrally (Fig. 3J), which has not been observed in other pipids. Among frogs, a similar projection has only been detected in the aquatic hyliid *Pseudis*, which interestingly is, to my knowledge, the only anuran taxon outside Pipidae that also shows a posteroventral process of the otic capsule. The presence of both processes in the distantly related *Pseudis* suggests a functional significance related to an aquatic lifestyle, though their exact role is not clear at present.

The laterally oriented fenestra ovalis deeply lies at the bottom of the funnel-shape middle ear space formed by the prootic. The latter bone is extensively ossified, being the ventrolateral otic ledge and anterior wall of the cavum tympani, which is entirely formed in bony tissue (Fig. 3H, K). On the anterior wall of the prootic, the cranioquadrate passage, through which typically run the internal jugular vein and the hyomandibular branch of the facial (VII) nerve, lies in a closed canal formed by the anteroventral extension of the crista parotica as in extant pipids (Paterson, 1946). This passage opens into the tympanum through a foramen that is completely bound by the prootic; a condition that contrasts with that of most other pipids examined, as well as other anurans, in which this foramen is only partially delimited by bone or lies completely in cartilage.

**Presacral vertebrae.** Only a few postatlantal presacral elements were recovered and housed under the numbers MML-PV 1047, 1062, and 1063, of which only one vertebra from Cerro Tortuga is almost complete; the following description is mainly based on this specimen (Fig. 4F–I). The vertebral centrum is opisthocoelus and markedly flattened dorsoventrally, with a generally smooth ventral surface only pitted by a few nutrient foramina. Both condyle and cotyle are low, but are as wide as the centrum; a condition that contrasts to that of species of *Pipa* in which the condyle is visibly narrower than the centrum. The cotyle is shallow around the midline, but laterally it is well demarcated by posteroventral projections of the pedicels of the neural arch that also contribute to the cotyle surface, as also occur in extant xenopodines. The relative contribution of the pedicels and the centrum in the formation of the vertebral body is particularly evident in a few fragmentary specimens from Cerro Tortuga and Bajo Santa Rosa by the distinct coloration of each component part. The bases of these pedicels are oriented at a low angle from the horizontal and show wide depressions on their anterior and posterior margins (Fig. 4H, I), which reflect the passage of the spinal nerves. Dorsally, the neural arch is nearly as long as it is wide and bears a pair of rounded, narrow, posterolaterally oriented transverse processes, of which only their proximal parts are preserved. The morphology of the transverse processes indicates that the vertebra represents a posterior presacral (V or a more posterior one) and their orientation is, among pipids, only consistent with those of a fifth presacral of some fossil pipids (e.g., *Llankibatrachus truebae*; Báez and Púgener, 2003). In dorsal aspect, the lamina of the neural arch is smooth, but bears a low and ridge-like neural spine and a pair of low ridges flanking the most dorsal part of the neural arch (Fig. 4F). In this same view, the anterior margin of the dorsal lamina of the neural arch, which does not extend further anteriorly than the posterior limit of the prezygapophyses, has a deep V-shape indentation, so that the anterior half of the centrum is visible. Conversely, the posterior margin of the dorsal lamina is triangular, in which the neural spine strongly projected posteriorly in a medial point far beyond the posterior end of the centrum. This configuration, plus the fact that the neural arch is a little lower anteriorly than posteriorly, indicates that the neural arches of the presacral vertebrae in this region of the column were, at least, partly overlapped at the midline. In posterior view, the neural arch is relatively thick and bears a pair of excavations at both sides of the protruding neural spine, well demarcated dorsoventrally by the edges of the lamina and laterally by the marked buttress of each postzygapophyses (Fig. 4I). Both prezygapophyses and postzygapophyses have flat articular surfaces (Fig. 4F, G), without any sulcus or ridge, oriented at a low angle with respect to the horizontal, and thus differing from the condition in extant xenopodines, as well as from that in hymenochirines. In dorsal view the prezygapophyseal articular surfaces are almost round, but those of the postzygapophyses are narrow and elongated with their main axis directed posterolaterally.

**Sacro-urostyle.** Although MML-PV 1059 from Cerro Tortuga is badly preserved, it is informative regarding some features of systematic value. A single sacral vertebra is completely fused to the urostyle to form a sacro-urostyle complex (Fig. 4J, K), as in all known extant and fossil pipids. The sacro-urostyle bears an anterior condyle for articulation with the last presacral vertebra; this condyle, although it is damaged, appears to be less depressed and much more round than that of the preserved presacrals. The sacral vertebra of the complex has widely expanded diapophyses (partly preserved on the left side), the broad bases of which merge with the lateral webs of bone of the urostyle delimiting a pair of broad spinal foramina that opens posterolaterally (Fig. 4K). Dorsally, the lamina of the neural arch of the sacro-urostyle is smooth and nearly flat, being only slightly raised medially along the preserved portion of the bone (Fig. 4J), but there is no hint of a distinct neural spine, ridge or crest. The minimum length of this dorsal lamina is clearly smaller than the (estimated) maximum external interzygapophyseal width. Only the left prezygapophysis remains and is poorly preserved, but it appears to have a relatively small, flat articular surface (Fig. 4J), which is consistent with the morphology of the known presacral vertebra.

**Humerus.** A fairly complete right humerus from Bajo de Santa Rosa (MACN-PV RN 1066; Fig. 4A, B) only lacking its proximal epiphysis and most of its deltoid crest, which Martinelli and Forasiepi (2004) tentatively ascribed to 'Leptodactylidae,' and two distal portions of humeri from Cerro Tortuga (MML-PV 1042), one left (Fig. 4C–E) and one right, and are here considered as showing distinct pipid traits. As has been previously acknowledged, humeral morphology of anurans has not been thoroughly documented for most anurans groups (Martinelli and Forasiepi, 2004), thus, I discuss the features that point to the pipid affinities of the fossil humeri and provide synonyms for some anatomical terms in order to minimize potential misunderstandings regarding humeral morphology. The referral to Pipidae is supported by the strikingly straight shaft that regularly widens distally throughout most of its length (Fig. 4A, B), the relatively small humeral ball (=eminencia capitata = capitulum), whose transverse diameter is a little more than half (0.55) the maximum width of the distal end of the humerus (Fig. 4A, C), the large, moderately deep and triangular-shaped ventral fossa (=fossa cubitalis; Fig. 4A, C), the relatively short deltoid crest (=crista ventralis) extending for about the proximal third of the diaphysis, and the well-developed parietal crest (=crista paraventralis) running medially on the proximal third of the diaphysis (Fig. 4A, B). Many of these features are atypical of most anurans and to some extent recall those of salamanders, but their combination characterizes the humerus of several extant and extinct pipids (Báez, 1987; Báez and Rage, 1998; Báez and Púgener, 2003; Rage, 2008). Additionally, both epicondyles are well ossified and similarly expanded transversely giving the distal portion of the humerus a roughly symmetrical aspect (Fig. 4C), which is also typical of many pipids (though some variation exists; Báez and Púgener, 2003). In the three available specimens the medial epicondyle (=radial epicondyle = entepicondyle) is pointed distally and its tip is separated from the humeral ball by a shallow groove, whereas the lateral epicondyle (=ulnar epicondyle = ectepicondyle), though similarly developed, is less distinct from the humeral ball distally. There is a fine, well-developed medial epicondylar crest (=crista medialis) along the distal fourth of the diaphysis in MACN-PV RN 1066 (Fig. 4A), which is less distinct in the other specimens. The olecranon scar is large and pointed, being particularly well preserved in MACN-PV RN 1066 (Fig. 4B). In the incomplete right humerus (MML-PV 1042) the cross-section of the shaft is neatly exposed at approximately its mid-length, showing a very narrow medullary space with a thick cortical compacta (Fig. 4E). This configuration has been

shown to be typical of aquatic amphibians, and particularly pipids among frogs, and markedly contrasts to that of other anurans in which this type of data is available (Canoville and Laurin, 2009).

*Ilium*. The pelvic girdle is only represented by two more or less incomplete, though well preserved, right ilia from Cerro Tortuga (MML-PV 1060; Fig. 4L–P) and one very incomplete right ilium from Cerro Bonaparte (MML-PV 1061). The three specimens preserve the ilial body as well as the proximal part of the shaft. They are well ossified, but, as preserved, indicate that the ilium was not fused to the ischium. The proximal portion of the ilial shaft is nearly round in cross section, being slightly flattened laterally (Fig. 4O). A dorsal crest is absent along the preserved portion of the shaft (Fig. 4L–N). A faint lateral oblique ridge extends from near the mid-height of the anterior margin of the acetabular fossa to the ventrolateral edge of the shaft (Fig. 4L). There is also a wide, shallow medial oblique groove on the medial side of the ilial body, extending diagonally towards, but not reaching, the ventral margin of the shaft (Fig. 4N); however, a medial oblique ridge is lacking. The well-developed dorsal prominence has a very broad base, extending along the dorsal margin of the ilial body from near the posterodorsal tip of the dorsal acetabular expansion to approximately the anterior level of the acetabular fossa (Fig. 4L). In acetabular view, the dorsal prominence is moderately high with respect to the acetabular fossa and bell-shape (i.e., almost symmetrical), with anterior and posterior slopes smoothly merging with the ilial body. In dorsal aspect, the dorsal prominence is thin, lying in the same plane as the acetabular fossa (i.e., it is neither tilted laterally nor medially; Fig. 4M). On its lateral surface, the dorsal prominence bears a subtle, round dorsal protuberance located on its posterior half (Fig. 4L). The dorsal acetabular expansion is relatively narrow in acetabular view, whereas the ventral acetabular expansion is almost completely concealed in this same view. The acetabular fossa is wide and shallow, having an extruded and roughly square anteroventral rim, but an even dorsal margin. As in all known pipids, the ilioischial junction is transversely broad (Fig. 4P) and the interiliac tubercle is large, with a broad articular surface for the contralateral ilium comprising most of the medial face of the ilial body (Fig. 4N).

## 5. Phylogenetic relationships

The evolutionary relationships of *Kuruleufenia xenopoides* gen et sp. nov. were tested cladistically under different weighting schemes. The analysis under equal weights yielded nine MPTs of 517 steps (CI = 0.433, RI = 0.738), and the strict consensus is relatively well resolved (Fig. 5), whereas those under implied weighting schemes with values of  $k$  between 6 and 20 always yielded a single MPT (CI = 0.433, RI = 0.738) with the same topology (Fig. 6), whereas with values of  $k$  between 1 and 5 the topology was also invariant and very similar to the one reported. The main previously recognized groups and relationships obtained in these analyses reflect previous phylogenetic hypotheses of anuran, and particularly pipoid, interrelationships (e.g., Trueb et al., 2005; Báez et al., 2007; Báez, 2013). In this regard, the main anuran clades Costata (discoglossoids), Acosmanura, Anomocoela (pelobatoids), and Xenoanura (pipoids), as well as their alleged interrelationships based on molecular data (e.g., Pyron and Wiens, 2011) were consistently recovered. Among pipoids, the analysis also mirrors previous hypotheses in recovering several well-recognized clades (Figs. 5, 6), including Pipidae, Xenopodinae, and Hymenochirini, as well as the sister-group relationship of hymenochirines and *Pipa* constituting the clade Pipinae, which has previously been obtained using morphological and/or molecular

data (Báez and Púgener, 2003; Evans et al., 2004; Trueb et al., 2005; Báez et al., 2012; Bewick et al., 2012; Evans et al., 2015).

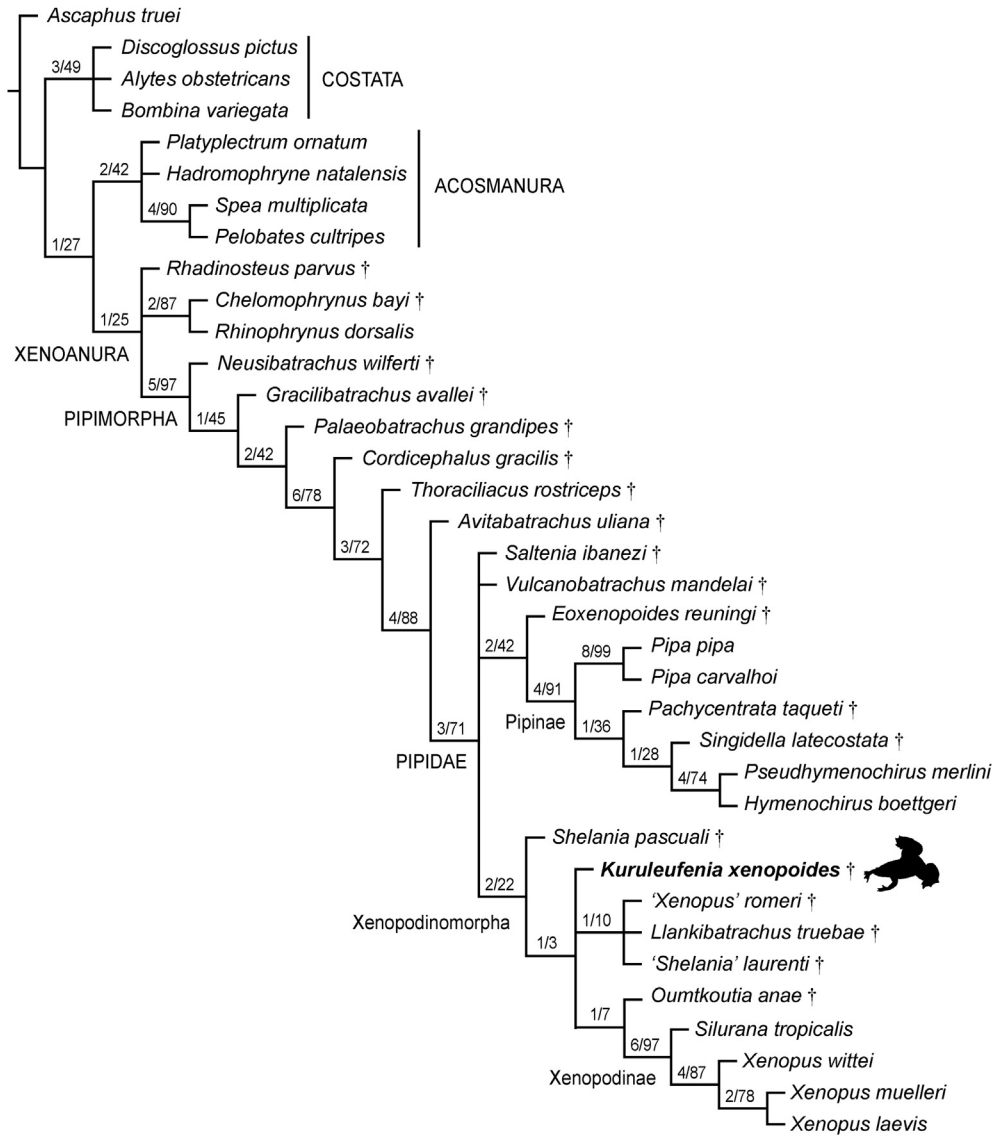
Additionally, the arrangement and content of Xenoanura and the stem-group based clades Pipimorpha, Xenopodinomorpha, and Pipinomorpha are largely consistent with previous hypotheses based on combined molecular and morphological data or morphological data alone, including the position of *Avitabatrachus* outside crown-group Pipidae, the sister-group relation of *Eoxenopoides* to Pipinae, and the placement of Paleogene South American pipids within Xenopodinomorpha (Báez and Púgener, 2003; Báez et al., 2007, 2012; Cannatella, 2015). It has to be noted that a few taxa, namely *Rhadinosteus*, *Saltenia*, and *Vulcanobatrachus*, take alternative positions among MPTs under equal weights, some of which draw away from previous hypotheses; yet this was expected either based on the disparate published results regarding their relationships and/or on their poor preservation (Báez, 1981, 1996; Báez and Trueb, 1997; Henrici, 1998; Báez and Púgener, 2003; Trueb et al., 2005; Báez et al., 2012). In this regard, in one third of the MPTs *Rhadinosteus* is recovered as sister group of Xenoanura, which contrasts with the almost unanimous agreement that this taxon is part of crown-group pipoids and more closely related to rhinophrynids than to pipids (Henrici, 1998; Roček, 2000; Báez, 2013; Marjanović and Laurin, 2014); the latter position is recovered in the other two thirds of the MPTs. The Cretaceous taxa *Saltenia* and *Vulcanobatrachus* alternate their basal positions within xenopodinomorphs, but *Vulcanobatrachus* also appears as the sister group of Pipidae in part of the MPTs, mirroring the position of *Saltenia* in a few earlier studies (Báez, 1981; Báez and Trueb, 1997). Interestingly, the enigmatic *Oumtkoutia* from the mid-Cretaceous of northern Africa, which phylogenetic relationships have not been tested previously, is recovered here as the sister group of Xenopodinae (Figs. 5, 6).

Either under equal or implied weights ( $k = 1$  to 30), *Kuruleufenia* appears as a crown-group pipid more related to xenopodines than to pipines (Figs. 5, 6), and its removal from Pipidae requires four additional steps. Every optimal topology recovered under equal weights and most under implied weights ( $k = 6$ –20) depicts *Kuruleufenia* nested within Xenopodinomorpha in a more crown-ward position than *Saltenia*, *Vulcanobatrachus*, and *Shelania pascuali*, a position that is supported by cranial and postcranial characters (see Discussion). In these trees *Kuruleufenia* always forms a polytomy with Xenopodinae and a clade formed by '*Shelania*' *laurenti*, *Llan-kibatrachus truebae*, and '*Xenopus*' *romeri* (18/30). This latter Palaeogene South American clade, which has also been recovered previously (Báez and Púgener, 2003; Báez et al., 2007), is here supported by four unambiguous synapomorphies. Among the latter, only the ventral position of the inferior perilymphatic foramina has been previously recognized as a potential synapomorphy of this group (Báez and Púgener, 2003). The other three synapomorphies refer to vertebral character states that were not considered in previous analyses of pipid interrelationships, namely the posteromedial margin of neural arch with irregular projections (90:3), transverse processes of presacral VI oriented moderately forward (94:1), and sacral neural arch lamina of transversely rectangular shape (G101:0).

## 6. Discussion

The phylogenetic analyses performed herein unequivocally recovered *Kuruleufenia xenopoides* as a member of crown-group Pipidae, in agreement with previous interpretations based on part of the material here ascribed to this new taxon (Martinelli and Forasiepi, 2004). This is substantiated by a few features that can be confidently assessed in *Kuruleufenia*, including an optic foramen completely bound in bone (55:1) and symmetrical development of





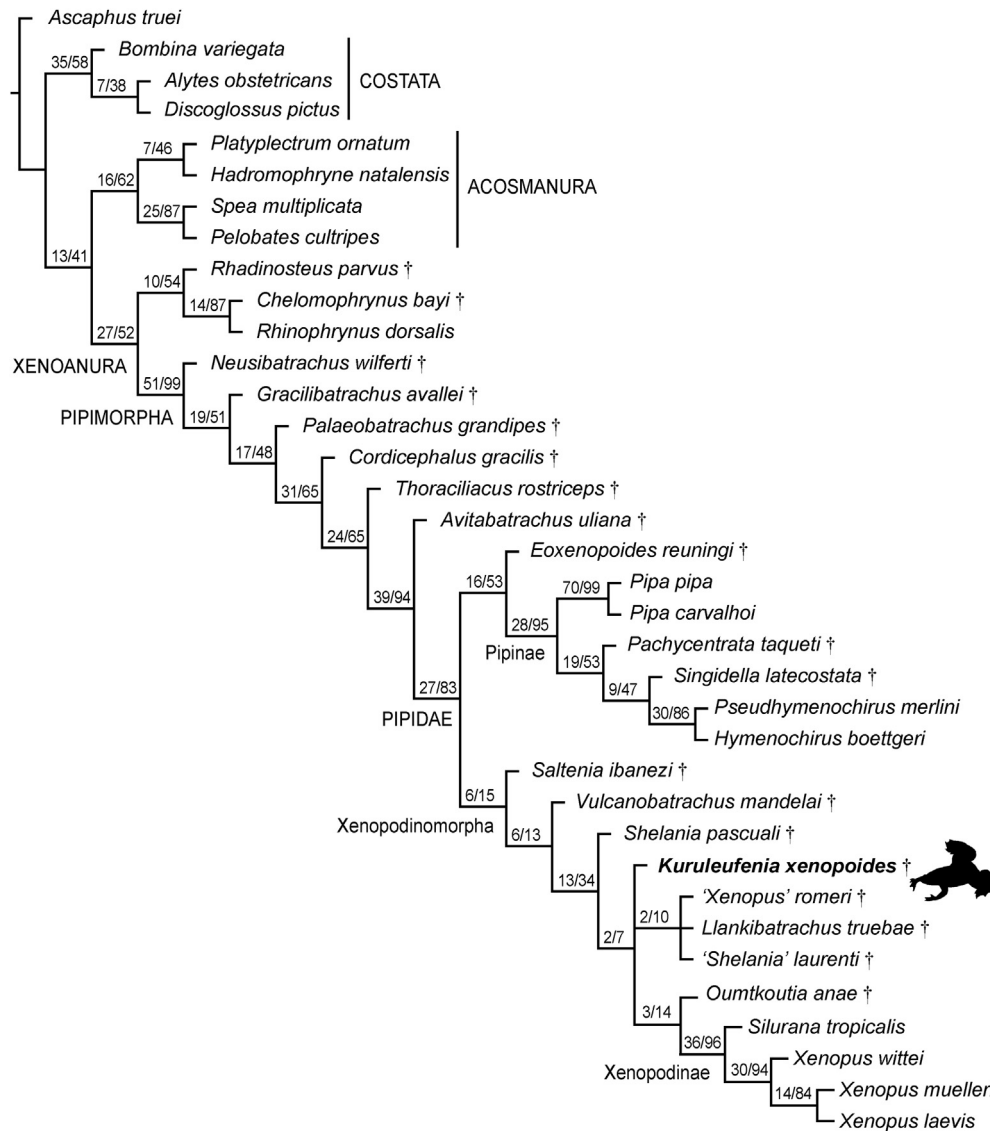
**Fig. 5.** Strict consensus of nine MPTs of 517 steps obtained under equal weights showing the phylogenetic position of *Kuruleufenia xenopoides* gen. et sp. nov. Fossil taxa are denoted with a †. Node support is indicated above the branches with Bremer support to the left and Jackknifing absolute frequencies to the right.

medial and lateral epicondyles of the humerus (G125:2); these features have traditionally been considered as pipid fingerprints (Báez, 1987; Báez and Trueb, 1997) and are here consistently recovered as pipid synapomorphies. *Kuruleufenia* also exhibits some traits that concur with its pipid affinities, namely a deep Eustachian canal (58:1), contact area for palatoquadrate facing completely ventrally (G60:1), cranio-quadrate passage housed in a bony canal (G69:1), and a sacrum fused to the urostyle (104:3), but that optimized in the analyses either as ambiguous or unambiguous synapomorphies of a clade a little more inclusive that also comprises *Avitabatrachus*.

Furthermore, *Kuruleufenia* always emerges in the analyses as part of Xenopodinomorpha and crown-ward to *Vulcanobatrachus* and *Saltenia*, taxa which, however, were not always recovered as part of this lineage or even as crown-group pipids (Báez, 1981; Báez and Trueb, 1997; Trueb et al., 2005; this study). The xenopodinomorph affinities of *Kuruleufenia* are supported by several putative synapomorphies of Xenopodinomorpha or less inclusive clades that can be assessed in the fossils: superior perilymphatic foramina absent (63:1), posteroventral process of otic capsule

present (G67:1), posterior presacrals with a well-developed neural spine projected posteriorly (90:1), sacral neural arch lamina of roughly square shape (G101:1), and ilium with broad interiliac scar (149:2). This makes *Kuruleufenia* a certain relative of the lineage today represented by *Silurana* and *Xenopus*, but also one of the oldest known crown-group pipids from South America (Fig. 7). The position of *Saltenia*, which comes from Campanian rocks that apparently predates those of the Allen Formation, is far less certain and must be revised considering unpublished additional materials. Fossils from the Campanian–Maastrichtian Los Alamos Formation, which have also been related to xenopodinomorphs, were originally described as cf. *Xenopus* (Báez, 1987), but their systematic position has not been tested in a cladistic framework so far. Preliminary comparisons of the latter to the pene-contemporaneous *Kuruleufenia* suggests that they might represent the same taxon, but a thorough revision of these and additional pipid fossils from this unit is still needed in order to properly test this hypothesis.

The inferred evolutionary relationships for *Kuruleufenia*, as well as for the older *Pachycentrata* and *Oumtkoutia*, indicate that crown-group pipids were well diversified in the Late Cretaceous (around

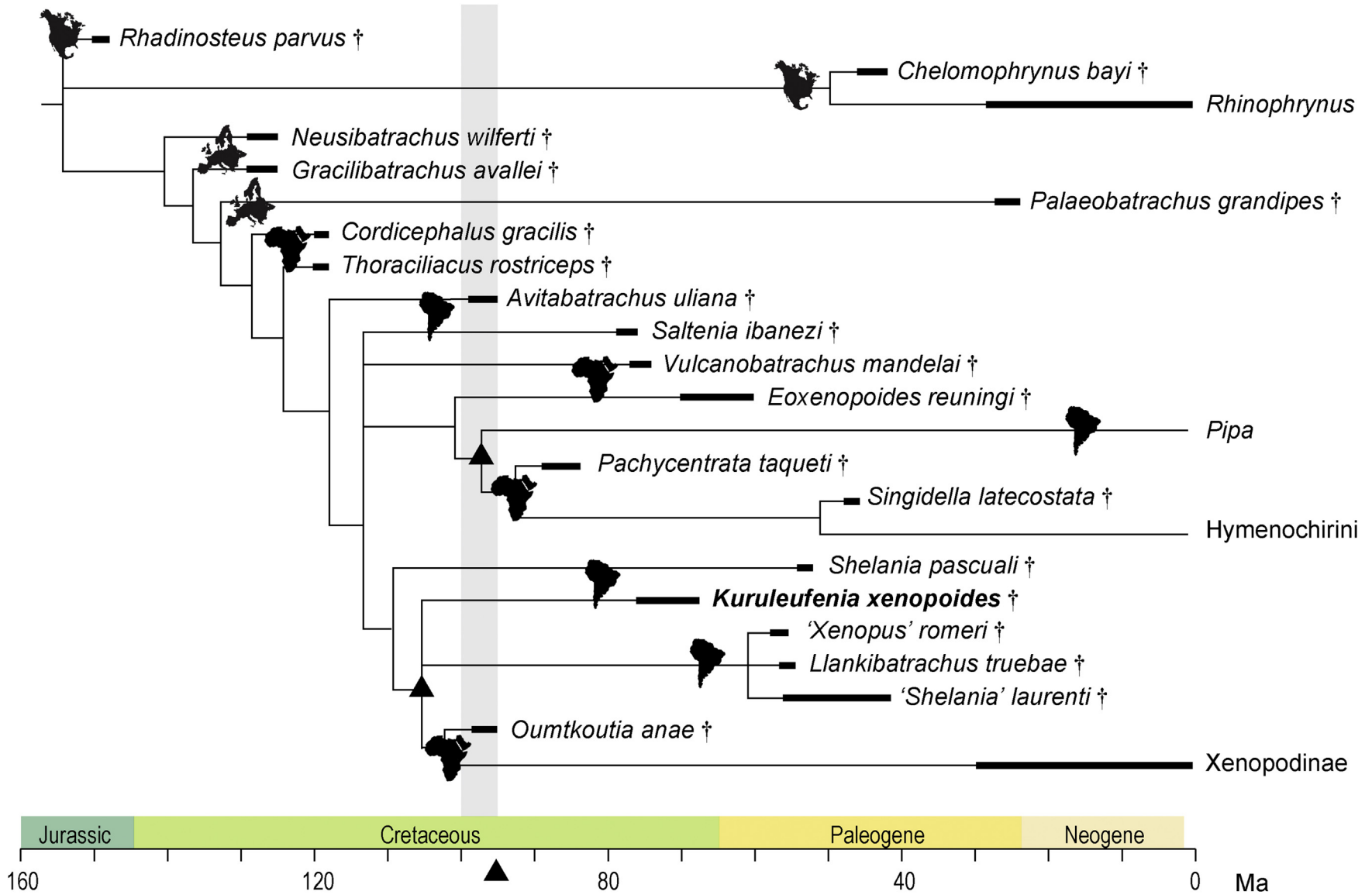


**Fig. 6.** Single MPT obtained under implied weights with  $k$  from 6 to 20 showing the phylogenetic position of *Kuruleufenia xenopoides* gen. et sp. nov.  $\text{Fit}=(\text{for } k = 7)$ . Fossil taxa are denoted with a †. Node support (calculated under implied weights with  $k = 7$ ) is indicated above branches with Bremer support in units of  $\text{fit} \times 100$  to the left and Jackknifing absolute frequencies to the right.

100 Ma), and imply that the three major lineages of extant pipids had already diverged by that time (Fig. 7). This is consistent with time estimates based on molecular clock methods that posit this divergence between 150 Ma and 100 Ma (Evans et al., 2004; Bewick et al., 2012; Cannatella, 2015). Further, the topological arrangement obtained both under equal and implied weights ( $k = 6-20$ ), in which *Kuruleufenia* appears in a polytomy with a clade formed by *Oumtkoutia* plus Xenopodinae, implies that this African lineage might have diverged from South American xenopodinomorphs at least by the mid-Cretaceous around 100 Ma (Fig. 7). Similarly, the position of *Pachycentrata* as more related to hymenochirines than to *Pipa* date the divergence of South American from African lineages prior to the Coniacian. This evolutionary scenario is largely congruent with the purported role that the complete opening of the South Atlantic Ocean around 95–100 Ma (Veevers, 2004; Granot and Dymont, 2015) played in triggering the diversification of crown-group pipids (Bewick et al., 2012).

Recently, it has been argued that overwater dispersal rather than vicariance would be the best explanation both for the

presence of xenopodines in Africa and pipines in South America (Cannatella, 2015). However, the phylogenetic relationships here recovered for some Cretaceous pipid taxa, including *Kuruleufenia* and *Oumtkoutia* deeply nested within Xenopodinomorpha and *Pachycentrata* nested within Pipinomorpha, suggest a palaeobiogeographic pattern that does not need to invoke overwater dispersal. This also agrees with the widespread geographical distribution throughout Western Gondwana of non-pipid pipimorphs and xenopodinomorphs during mid- to Late Cretaceous times (Báez, 1996; Báez et al., 2000; Rage and Dutheil, 2008). Considering all the available evidence, it becomes evident that the origin and early divergence of crown-group Pipidae might have occurred during the Early Cretaceous, prior to the complete separation of Africa from South America (Evans et al., 2004; Bewick et al., 2012; Fig. 7). This study shows that the inclusion in phylogenetic analyses of extinct taxa only known by disarticulated but well preserved fossil materials, though challenging, is promising in disentangling how, when, and where pipid frogs diversify.



**Fig. 7.** Time-calibrated tree of pipoids based on the strict consensus of the analysis under equal weights. Black bars over the branches indicate known fossil record. Grey column crossing the tree represents the complete opening of the South Atlantic Ocean around 95–100 Ma. Continent of distribution or provenance of the terminal taxa is indicated by black silhouettes of Africa plus Arabian Peninsula; Europe; North America; South America. Black triangles indicate putative vicariant events.

## 7. Concluding remarks

The described anuran remains from the Upper Cretaceous Allen Formation represent a new genus and species of pipid frog, *Kuruleufenia xenopoides*. The phylogenetic analyses performed herein unequivocally recovered the new taxon as a member of crown-group Pipidae and more closely related to xenopodines than to pipines. These evolutionary relationships were supported by cranial and postcranial characters states. The temporal calibration of the pipoid tree indicates that the main lineages of crown-group pipids have already diverged when Africa and South America set apart around 95–100 Ma and refutes recent proposals of more recent over-water dispersal of pipids across the South Atlantic Ocean.

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## Appendix A. Supplementary material

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2016.02.006>.