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A new pipoid frog (Anura, Pipimorpha) from the Paleogene of Patagonia. Paleobiogeographical implications

Une nouvelle grenouille pipoïde (Anoures, Pipimorpha) du Paléogène de Patagonie. Implications paléobiogéographiques

Alexis M. Aranciaga Rolando[a,*], Federico L. Agnolin[a,b], Julián Corsolini[c]

[a] *Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Consejo Nacional de Investigaciones Científicas y Técnicas - CONICET, Buenos Aires, Argentina*
[b] *Fundación de Historia Natural 'Félix de Azara', Universidad Maimónides, Buenos Aires, Argentina*
[c] *Museo de Geología y Paleontología del Lago Gutierrez "Dr. Rosendo Pascual", Calle Bosque Petrificado 367, Villa Los Coihues, Lago Gutiérrez, R8405ZAB San Carlos de Bariloche, Río Negro, Argentina*

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ABSTRACT

The aim of the present contribution is to describe a new genus and species of Pipoidea from the Huitrera Formation (Eocene) from Patagonia, Argentina. The new genus shows a unique combination of characters indicating that it is a valid taxon different from other pipimorphs, including the coeval *Llankibatrachus truebae*. The phylogenetic analysis resulted in the nesting of the new taxon within a previously unrecognized endemic clade of South American aglossans. This new clade turns out to be the sister-group of crown-group Pipidae. This phylogenetic proposal reinforces the hypothesis sustaining the dispersal of pipids between Africa and South America through an island chain or a continental bridge across the Atlantic Ocean by Early Tertiary times.

RÉSUMÉ

Le but de cet article est de décrire de nouveaux genre et espèce de Pipioidea de la formation Huitrera (Éocène) de Patagonie, Argentine. Le nouveau genre montre une combinaison unique de caractères indiquant que c'est un taxon valide, différent des autres pipimorphes incluant *Llankibatrachus truebae*, contemporain. L'analyse phylogénétique résulte en la nidification du nouveau taxon au sein d'un clade endémique, auparavant non reconnu, d'aglosses d'Amérique du Sud. Il en résulte que le nouveau clade est le groupe frère du groupe couronne des Pipidae. Cette proposition phylogénétique renforce l'hypothèse en faveur d'une dispersion des pipidés entre l'Afrique et l'Amérique du Sud au moyen d'une chaîne insulaire ou d'un pont continental à travers l'Océan atlantique au Tertiaire inférieur.

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* Corresponding author.
E-mail address: Mauro.a_guido@hotmail.com (A.M.A. Rolando).

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1. Introduction

The fossil record of South American anurans is strongly biased, having scarce representation of most neobatrachian groups (Agnolín, 2012; Báez, 2000; Cione and Báez, 2007). Exceptions to this record constitute the clades Calyptocephalellidae and Pipidae, which have a relatively extensive record since Late Cretaceous times (Báez, 1987; Báez et al., 2000; Cione and Báez, 2007; Muzzopappa and Báez, 2009).

Pipids are fully aquatic frogs represented by five living genera distributed in tropical South America and sub-Saharan Africa (Cannatella, 2015, Gómez, 2016). The fossil record of pipids is extensive, especially in South America, where it consists of several genera and species ranging from the Late Cretaceous to the Pleistocene (Báez, 1987; Báez et al., 2000, 2009). During the Paleogene in Patagonia, pipids appear to be especially diverse, being represented by abundant fossils and more than three different taxa (Báez, 2000; Báez and Trueb, 1997; Báez and Púgener, 1998, 2003; Casamiquela, 1960, 1965).

The aim of the present contribution is to describe a nearly complete skeleton of a new genus and species of pipoid coming from the middle Eocene (Wilf et al., 2005) Huitrera Formation, at Río Negro province, Argentina. This new specimen invites us to review some points on the phylogeny of South American pipoids, and also sheds light on some aspects of the paleobiogeography of the clade.

1.1. Materials and methods

The material here described is housed at the Museo del Lago Gutierrez “Dr. Rosendo Pascual”, Villa Los Coihues, San Carlos de Bariloche, Río Negro province, Argentina (MLG).

For descriptive purposes, we follow the anatomical terminology provided by Báez and Púgener (2003) and the taxonomic nomenclature employed by Frost et al. (2006) and Frost (2015), as modified by Gómez (2016). General nomenclatural acts follow the terms of the ICZN and phylogenetic nomenclature, for new names. However, some comparisons with juvenile specimens are tentative as not enough immature specimens are known for the moment.

The diagnoses of the newly named clades are deduced from the phylogenetic analysis. With the aim to explain the identity of the resulting synapomorphies, we include each character and state numbers between brackets on each diagnosis.

In order to assess the phylogenetic relationships of the new taxon among pipoids, we follow the osteological characters following Cannatella and Trueb (1988), Báez and Trueb (1997), and Gómez (2016).

In order to determine the age of the fossil individual, MLG 2630 was compared with the ontogenetic stages of *Xenopus laevis* (Trueb and Hanken, 1992).

1.1.1. Phylogenetic analysis

A phylogenetic analysis was conducted to assess the phylogenetic relationships of specimen MLG 2630 with other pipoids. The present phylogeny is based on the extensive analysis published by Gómez (2016) with the addition of characters 166–176, based on personal observations and newly published contributions (S1). The coding of character 39 was modified and state 1 was split into two different states (S1). We added a state 2 to character 99 (S1). The coding of several character states of *Saltenia ibanezi* was modified from that of previous authors based on newly collected specimens (MAS-P/2; Scanferla et al., 2011) (see S2). Characters 18, 19, 32, 33, 36, 38, 39, 50, 59, 62, 74, 75, 82, 93, 94, 98, 101, 109, 115, 124, 125, 126, 135, 137, 158 and 168 were treated as ordered.

These modifications resulted in a data matrix composed of 176 characters scored for 38 taxa (S3).

The phylogenetic analysis was performed using TNT 1.1 (Goloboff et al., 2008). All characters were equally weighted and treated as unordered. Heuristic searches were performed after 1,000 pseudoreplicates of WAG + TBR search strategy, with 10 random addition sequences after each search, and 100 trees were saved at each replicate. Bremer Support and absolute bootstrap frequencies were calculated with the aim to test the robustness of tree branches (Fig. 4).

1.1.2. Locality and horizon

The specimen was collected at Río Pichilefú fossiliferous locality, (41°09’ 26.06” S, 70° 49’ 57.11” W), about 60 km east from San Carlos de Bariloche, Río Negro, Argentina (Fig. 1).

As mentioned by Wilf et al. (2005), the Río Pichileufú fossil-bearing strata pertain to the Huitrera Formation (early to middle Eocene, 47.46 ± 0.05 Ma; Melendi et al., 2003; Wilf et al., 2005). The sediments are dated by the ^{39}Ar/^{40}Ar technique; this dating method has been carried out on sanidine phenocrystals from stratigraphically related tuffs (Wilf et al., 2005).

The paleoclimatic scenario of the Huitrera Formation corresponds, initially, to warm and humid conditions (Wilf et al., 2005; Ramírez et al., 2016), showing abundant subtropical vegetation and insects, but turning temperate or cold-temperate through its end (Ramírez et al., 2016). The flora of the Huitrera Formation includes numerous records of gymnosperm clades, some of them already present in Patagonia, like Ginkgoaceae, Cycadaceae, Podocarpaceae, and Aracauriaceae (Wilf et al., 2005, 2010) and a rich and diverse angiosperm record including families such as Asteraceae, Celtidaceae, Lauraceae, Malvaceae, Myrtaceae, Proteaceae, and probably Salicaceae (Barreda et al., 2010; Wilf et al., 2005, 2010). The faunistic association is far less diverse and comprises insects (e.g., frenguellids, formicids, passandrids, siricids; Wilf et al., 2005), fishes and pipoid frogs (Casamiquela, 1961; Wilf et al., 2005).

1.2. Systematic paleontology

Anura Rafinesque, 1815
Pipoidea Fitzinger, 1843
Panpipidae nomen novum.

Diagnosis. The anuran clade is diagnosed based on the following synapomorphies: 1) anterior ramus of pterygoid dorsally located with respect to the maxilla (23-1); 2) straight distal margin of sacral diapophyses (99-1); 3) cleithrum covering posterior edge of suprascapular cartilage (114-1); 4) interiliac scar ample both ventrally and

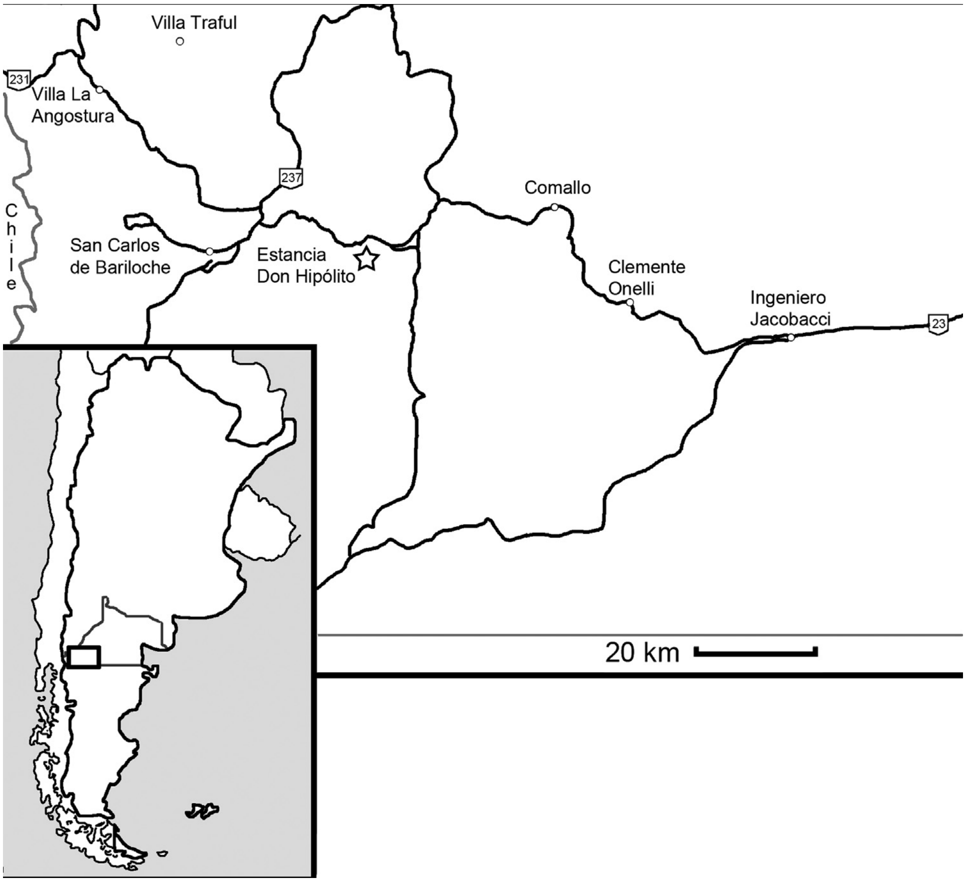

Fig. 1. Map indicating fossiliferous locality. The fossil site is indicated by a star.

Fig. 1. Carte indiquant la localité fossilifère, marquée d'une étoile.

dorsally (149-2); and 5) presence of a poorly-developed lateral flange on pterygoid (167-1).

Definition. Stem-based clade consisting of *Patagopipa* and all species that share a more common ancestor with *Shelania laurenti*, *Pipa*, and *Xenopus laevis* than with *Vulcanobatrachus mandelai*, *Avitabatrachus uliana*, *Cordicephalus gracilis*, or *Paleobatrachus grandipes*.

Remarks. The clade Panpipidae is here coined with the aim to include the crown-group Pipidae, Shelaniinae, and another stem pipids. We follow previous authors (Gómez, 2016; Ford and Cannatella, 1993) in the restriction of Pipidae to crown group taxa; this is Pipinae + Xenopodinae.

Shelaniinae nomen novum.

Diagnosis. This clade is diagnosed based on the following synapomorphies: 1) anterior ramus of pterygoid reaching the antorbital plane (24-1); 2) eight presacral vertebrae (82-1); 3) presacral vertebrae I–II not fused but imbricated medially (88-1); 4) marked forward orientation of the transverse process of presacra vertebrae IV (94-2); 5) cross-section of distal iliac shaft flattened, dorsoventrally compressed (137-2); 6) second pair of ribs anterolaterally oriented (174-1).

Definition. The stem-based clade consisting of *Patagopipa* and all species that share a more common ancestor with *Shelania laurenti* than with *Pipa, Silurana, Xenopus*, or *Eoxenopoides*.

Included taxa. *Shelania pascuali* Casamiquela, 1960; *Saltenia ibanezi* Reig, 1959; *Kuruleufenia xenopoides* Gómez, 2016; *Patagopipa corsolinii* nov.

Temporal distribution. From Late Cretaceous to Eocene (probably Pleistocene; Báez et al., 2007) times.

Patagopipa nov. gen.

Diagnosis. Small pipoid frog diagnosable based on the following combination of characters (autapomorphies marked by an asterisk): 1) elongate and transversely narrow pterygoids, with poorly expanded proximal flanges*; 2) frontoparietal dorsally flat with rounded anterior and posterior margins; 3) frontoparietal lacking interorbital constriction; and 4) notably robust and stout radioulna and humerus*.

Etymology. *Patago*, from Patagonia the region of Argentina in which the holotype specimen was found; *Pipa*, the type genus of the Pipidae family.

Type species. *Patagopipa corsolinii* nov. sp.

Patagopipa corsolinii nov. sp. (Figs. 2, 3)

Diagnosis. The same as for genus by monotypy.

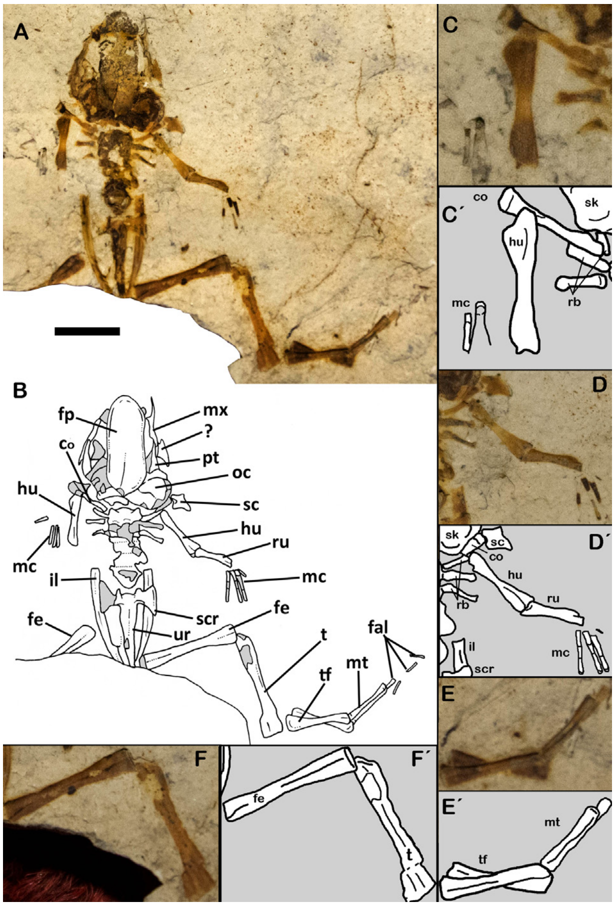

Fig. 2. Holotype specimen of *Patagopipa corsolini* (MLG 2630) in dorsal view. A: Slab showing actual specimen; B: interpretative drawing; C: close-up of the left arm; C': interpretative drawing of the latter; D: close-up of the right arm; D': interpretative drawing of the latter; E: close-up of the right hindlimb; E': interpretative drawing of the latter; F: close-up of the right pes; F': interpretative drawing of the latter. Abbreviations: **co**: coracoid; **fal**: falanges; **fe**: femur; **fp**: frontoparietal; **hu**: humerus; **il**: ilium; **mc**: metacarpal; **mt**: metatarsal; **mx**: maxilla, **oc**: occipital; **pt**: pterygoid; **rb**: ribs; **ru**: radioulna; **sc**: scapula; **scr**: sacrum; **sk**: skull; **t**: tibiofibula; **tf**: tibiale and fibulare; **ur**: urostyle. The parts in grey represent molds of elements (because they are broken or incompletely ossified). Scale bar: 5 mm.

Fig. 2. Spécimen holotype de *Patagopipa corsolini* (MLG 2630) en vue dorsale. A : Plaque montrant le spécimen actuel ; B : dessin interprétatif ; C : bras gauche replié ; C' dessin interprétatif de ce dernier ; D : bras droit replié ; D' : dessin interprétatif de ce dernier ; E : membre arrière replié ; E' dessin interprétatif de ce dernier ; F : pied droit replié ; F' : dessin interprétatif de ce dernier. Abréviations : **co** : coracoïde ; **fal** : phalanges ; **fe** : fémur ; **fp** : frontopariétal ; **hu** : humérus ; **il** : ilium ; **mc** : métacarpien ; **mt** : métatarsien ; **mx** : maxillaire ; **oc** : occipital ; **pt** : ptérigoïde ; **rb** : côtes ; **ru** : radioulna ; **sc** : scapula ; **scr** : sacrum ; **sk** : crâne ; **t** : tibiofibule ; **tf** : tibia et fibule ; **ur** : urostyle. Les parties grisées représentent les moulages des éléments (parce qu'ils sont cassés ou incomplètement ossifiés). Barre d'échelle : 5 mm.

Holotype. MLG 2630, a single slab containing a nearly complete skeleton having partially disarticulated skull, incomplete vertebral column, and nearly complete right fore- and hindlimbs. Left forelimb is poorly preserved, and left hindlimb is only represented by the proximal end of the femur.

Etymology. The specific epithet honors Rodolfo Corsolini, director of the MLG Museum.

1.3. Nomenclatural acts

This article conforms to the requirements of the amended International Code of Zoological Nomenclature–except for the new names, which are defined by the phylogenetic nomenclature. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID for this publication is: urn:lsid:zoobank.org:pub:2CF53EA3-50C6-48C0-9665-9A29D8F01931.

2. Description and comparisons

The size of the *Patagopipa corsolinii* holotype is comparable to that of the stage 66 of paleobatrachid tadpoles, but it is larger than the stage 63 of the latter and the same stage of *Xenopus*.

Skull. The skull is subrectangular to roughly subtriangular in contour when viewed dorsally. The zygomatic arcade is incomplete, and a quadratojugal is absent, a condition shared with most pipoids (Báez and Trueb, 1997).

The frontoparietals form an azygous bone, as observed in other pipoids (Báez and Púgener, 2003; Gómez, 2016). This bone is oval and anteroposteriorly long, being almost three times longer than wide, a ratio also observed in *Eoxenopoides* and *Shelania laurenti* (Báez and Púgener, 1998; Estes, 1977). The anterior and posterior margins are rounded, resembling *Saltenia* and *Eoxenopoides*, while in other pipids the anterior margin is usually pointed (Báez and Trueb, 1997; Báez and Púgener, 1998). This condition could be related with the postmetamorphic condition of the specimen. The lateral margins of the frontoparietal are slightly convex, lacking an interorbital constriction observed in most panpipids. Interestingly, *Saltenia*, '*Shelania*' *laurenti* and *Eoxenopoides* lack these constrictions (Báez and Trueb, 1997). The frontoparietal is flat, lacking any sign of parasagittal crests, in contrast to *Llankibatrachus*, *Shelania pascuali* and *Paleobatrachus* (Báez and Trueb, 1997; Báez and Púgener, 1998).

Some authors noted that tadpoles of pipids (e.g., *Llankibatrachus*, *Xenopus;* Báez and Trueb, 1997; Henrici and Báez, 2001) show an ovoid frontoparietal lacking interorbital constriction and parasagittal crests, features that are present in post-metamorphic specimens.

The maxilla is long and its posterior end is acuminate and does not form a closed zygomatic arcade. The pars facialis is notably long anteriorly, as in *Shelania pascuali* and '*Shelania*' *laurenti*, but not as long as in *Saltenia* (Báez, 1981; Báez and Púgener, 1998; Casamiquela, 1961). The pars facialis probably overlapped the alary process of the premaxilla, as occurs in most pipimorphans (Gómez, 2016). The maxilla shows a short antorbital process, a feature shared with *Llankibatrachus*, *Saltenia*, *Shelania pascuali*, and '*Shelania*' *laurenti*. Furthermore, in *Patagopipa* the antorbital process is located on the anterior third of the maxilla, as occurs in *Llankibatrachus*, '*S.*' *laurenti* and *S. pascuali*, while in *Saltenia* it is located almost at mid-length of the

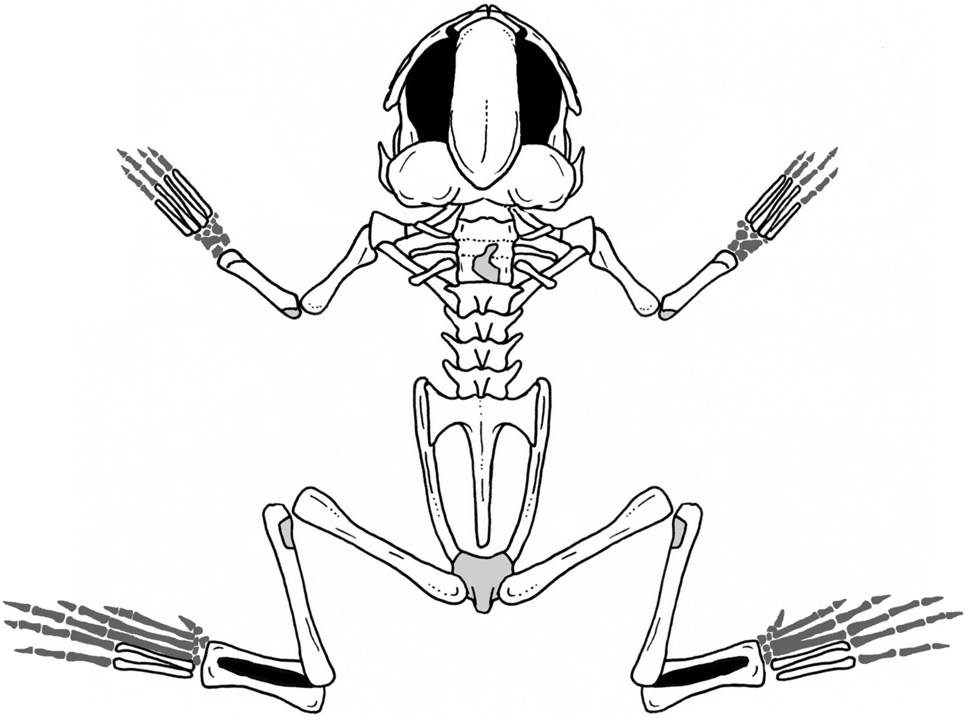

Fig. 3. Skeletal reconstruction of *Patagopipa corsolini*. The bones in grey represent missing elements.

Fig. 3. Reconstitution du squelette de *Patagopipa corsolini*. Les parties grisées représentent les éléments osseux manquants.

bone (Báez, 1981). In *Patagopipa* and *Saltenia*, the antorbital process is thin and is not in contact with the braincase; in contrast, in *Llankibatrachus* and *Shelania*, the process is thick and well developed (Báez and Trueb, 1997; Báez and Púgener, 2003).

The prootic is poorly preserved. It constitutes the major part of the otic capsule in dorsal aspect. Its dorsal surface is smooth without crests but with epiotic prominences on its medial margin. The exoccipital seems fused with the prootics, forming the posteromedial part of the otic capsule and the occipital condyles. The otic capsules are notably large and posteriorly surpass the level of the occipital condyles.

The pterygoids are very elongate and transversely narrow, when compared to other pipimorphans (e.g., *Shelania*, *Llankibatrachus*, *Pipa*) and shows an extensive lateral flange of bone at its base. This is reminiscent of the condition present in pterygoids of *Saltenia* and *Xenopus* (Báez, 1981; Trueb and Hanken, 1992), but in *Patagopipa* the lateral flange is more reduced than in any known pipoid. This condition is here interpreted as a possible autapomorphy of this genus.

Axial skeleton. Only the first four vertebrae can be clearly observed, and the total number of vertebrae cannot be estimated. The neural arches of the second to fourth presacral vertebrae are strongly anteroposteriorly compressed, its width being approximately three times its length, a ratio similar to that of *Saltenia* and tadpoles of pipimorphans (Báez and Púgener, 2003), whereas in postmetamorphic individuals (e.g., *Shelania, Llankibatrachus, Kuruleufenia, Pipa, Xenopus*, among others) the vertebrae are sub-quadrangular in contour, being almost as long as wide (Báez and Trueb, 1997). The sacrum and urostyle are fused, a condition diagnostic of pipids (Báez and Trueb, 1997; Báez and Púgener, 2003). The sacrum lacks webs of bone between the urostyle and the sacral diapophyses, indicating that this element is separated from the urostyle. The urostyle is incompletely preserved, but is subequal in length to the vertebral column. The sacral diapophyses are relatively short and show well-developed and fan-shaped lateral expansions. As described above, this feature is probably the result of the immature stage of the specimen. The maximum anteroposterior expansion of the sacral diapophyses duplicates the transverse width of proximal end of urostyle. Poorly expanded sacral diapophyses are shared with basal pipimorphans (e.g., *Thoraciliacus, Cordicephalus, Paleobatrachus, Vulcanobatrachus, Eoxenopoides, Saltenia*; Báez, 1981; Estes, 1977; Trueb, 1999; Trueb et al., 2005; Trueb and Báez, 2006). This degree of expansion is notably low when compared with non-shelaniine pipids (e.g., *Pipa, Xenopus*; Báez, 1977) in which the diapophyses are at least five times the proximal width of the urostyle. Interestingly, in the latter taxa the strong development of the sacral diapophyses is observed, not only on adult individuals, but also in postmetamorphic tadpoles (Báez and Púgener, 2003). In *Patagopipa*, the sacral expansion is asymmetrical, having a well-developed posterior process, a condition observed in *Saltenia* (Báez, 1981), but contrasting with non-shelaniine pipids that show symmetrically expanded diapophyses. The lateral margin of the diapophyses is gently concave, a condition observed in *Saltenia* (Báez, 1981).

Three pairs of free ribs are observed in association with presacrals 2 to 4. The first pair of ribs is anterolaterally oriented, the second pair is slightly posterolaterally oriented, and the third pair is strongly posterolaterally projected. *Saltenia* and *Shelania* share with *Patagopipa* anterolaterally directed processes at the second sacral vertebra (Báez, 1981; Báez and Trueb, 1997). The ribs are thin rods that lack distal expansions.

Pectoral girdle. Only three elements have been preserved: right and left coracoids and right scapula. The scapula is free and there is no trace of the clavicle; until adult specimens of this species come to light, we cannot know if this feature persists in the adult. The scapula is subquadrangular in shape with concave anterior and posterior margins; the latter exhibits a round posterior process. The lateral margin is slightly wider than the medial one. The pars glenoidalis is round and large, representing less than the half of the total length of the scapula, a condition also observed in ‘*Shelania*’ *laurenti, Xenopus*, and *Silurana* (Báez and Trueb, 1997; Báez and Púgener, 1998). The coracoids are elongate, straight, and show moderately expanded ends (because of its preservation, it is difficult to infer if it is exposed on medial or lateral views), a condition shared with basal pipimorphans as *Shelania, Saltenia, Llankibatrachus, Paleobatrachus, Thoraciliacus* and *Eoxenopoides* (Báez and Púgener, 2003; Báez and Trueb, 1997; Estes, 1977; Trueb, 1999; Rócek, 2003), whereas basal anurans (e.g., *Discoglossus*) and more derived pipids show notably stout and short coracoids (Cannatella and Trueb, 1988; Báez and Trueb, 1997; Trueb and Massemin, 2001). In spite of its immature condition, both ends of coracoid of *Patagopipa* seem subequal in size, as is observed in basal pipimorphans, whereas derived members of Pipidae (e.g., *Pipa,* hymenochrynids, rhynophrynids) have coracoids with the sternal end much more expanded than its counterpart (Báez and Trueb, 1997; Cannatella and Trueb, 1988; Trueb and Massemin, 2001).

Forelimb. The humerus is long and robust, with well-developed and expanded proximal and distal ends. The humeral shaft is straight, a condition similar to the case of other panpipids (Gómez, 2016). The deltoid crest is long and robust, and extends along the proximal third of the bone, a morphology shared with pipids with the exception of *Llankibatrachus* (Báez and Púgener, 2003; Gómez, 2016). The distal end of the bone has a wide medial epicondyle and a much narrower lateral one, a condition also present in *Llankibatrachus* (Báez and Púgener, 2003).

Only the right radioulna is preserved. It is a notably short element, its length representing only 2/3 the total length of the humerus. The shaft of this bone is nearly straight, with transversely narrow shaft at mid-length, and transversely expanded proximal and distal. This morphology is shared with basal pipimorphans and basal Panpipidae (e.g., *Llankibatrachus, Saltenia*; Báez, 1981). In contrast, more derived pipids (e.g., *Pipa*; Trueb et al., 2000) show a notably stout radioulna; its shaft is almost subequal in width through the length of the bone. Proximally, the radioulna shows a well-developed olecranon process, whereas distally it shows a longitudinal groove representing the limit between fused radius and ulna. No carpal bones have been recovered. On both left and right sides of the specimen, four slender metacarpals are observed, of which the third is the longest. Metacarpals are not completely ossified, resembling the 66 stage of some paleobatrachid tadpoles (Rócek, 2003). This condition also applies for the metatarsals.

Pelvic girdle. The ilia have long and narrow shafts. Both halves form a U-shaped contour, a condition observed in pipimorphans as *Saltenia, Paleobatrachus*, *Llankibatrachus, Xenopus*, and *Pipa*, whereas in other taxa the ilia are V-shaped in outline (e.g., *Cordicephapus, Thoraciliacus, Shelania,* hymenochirines) (Báez, 1981; Báez and Trueb, 1997; Báez and Púgener, 2003; Cannatella and Trueb, 1988). The iliac shaft is rod-like posteriorly, with a dorsoventrally oriented major axis. Anteriorly it becomes dorsoventrally compressed. A long dorsolateral crest is observed on the anterior two-thirds of the iliac shaft.

Hindlimb. The femur is robust, straight and is slightly expanded at its proximal and distal ends. This bone is shorter than the tibiofibula, but the latter is relatively straight. The tarsals are notably long, a condition shared with most pipids (Báez and Trueb, 1997). Only two metatarsals have been preserved, but these are incompletely ossified (see above). These elements are relatively long and narrow.

2.1. Ontogenetic notes about Patagopipa corsolinii

The *Patagopipa corsolinii* holotype shows a combination of characters that indicates that it was at a juvenile stage. It has a completely ossified humerus, radio-ulnae, femora, tibio-fibulae, ilia, and pedal phalanges. Trueb and Hanken (1992) indicate that in *Xenopus* all these bones ossify during stages 57–58 of Nieuwkoop and Faber (1956). Metacarpals, and coracoid epiphyses are not completely ossified, traits that in X*enopus* (Trueb and Hanken, 1992) occur between the stages 58 and 60. Regarding the ribs, in X*enopus* these ossify at stage 58 (Trueb and Hanken, 1992), but the transverse processes of all presacral vertebrae ossify at stage 64. *Patagopipa* shows well-developed ossified ribs, but these are not connected to vertebrae. In *Patagopipa,* the sacral diapophyses seem not completely ossified because they are smaller and poorly laterally expanded and do not form the straight (or nearly straight) lateral margin typical of pipids; interestingly, in *Xenopus* the diapophyses start to ossify at stage 63. Interestingly, in paleobatrachid tadpoles (Rócek, 2003), the sacral diapophyses in stage 63 are only weakly ossified, but in stage 66 the osseous part is much notorious, and even, shows a similar contour with those of *P. corsolinii*. The urostyle is formed by the fusion of the postsacral vertebrae with the hypocord (Trueb and Hanken, 1992), which occurs in Stage 66; this condition is already present in *Patagopipa*. Finally, *P. corsilinii* lacks distal tarsals, carpals and phalanges of the hand, which in *Xenopus* (Trueb and Hanken, 1992) ossify during stage 60 or after. For these reasons, the stage of the present specimen probably corresponds to stage 66.

3. Discussion

3.1. Phylogenetic results

The phylogenetic analysis recovered 14 most parsimonious trees (MPTs) that resulted in a strict consensus tree of 592 steps in length, having a consistency index of 0.40, and a retention index of 0.71. Most nodes have low Bremer Support values, in agreement with previous analyses made based on this data matrix (e.g., Gómez, 2016; Fig. 4).

The strict consensus tree differs from previous analyses in the position of some taxa (e.g., Báez and Trueb, 1997; Báez and Púgener, 2003; Gómez, 2016; Trueb and Báez, 2006). As indicated above, probably the most important innovation is that a new clade (Shelaniinae) is coined with the aim to include South American aglossans previously regarded as basal pipids (*Saltenia*) or basal xenopodinomorphans (*Kuruleufenia, Shelania*). In this sense, after the phylogenetic analysis the interrelationships of these clades are modified, including the relationships between Pipinae and Xenopodinae. In this sense, Shelaniinae turn out to be the sister group of crown Pipidae (= Pipidae *sensu stricto*; Pipinae + Xenopodinae; Báez and Trueb, 1997; Báez and Púgener, 2003; Gómez, 2016), and both clades constitute Panpipidae (see diagnoses above). As in previous works, *Vulcanobatrachus* turns out to be a basal pipoid (Gómez, 2016; Trueb et al., 2005), being nested here as a stem-Panpipidae. *Llankibatrachus*, '*Xenopus*' *romeri* and '*Shelania*' *laurenti* were considered xenopodinomorphans by previous authors (Báez and Trueb, 1997; Báez and Púgener, 2003). In this analysis, these taxa are more derived than Shelaniinae, being the successive sister groups of the clade Pipinae + Xenopodinae. *Llankibatrachus* resemble pipids, and differ from shelaniines, by the presence of three unambiguous synapomorphies, namely strongly expanded sacral diapophyses (98-2), clavicle fused to scapula (108-2), and anterior half of iliac shafts subparallel to each other (175-0). This combination of characters is absent in most shelaniines, including *Patagopipa*. Further, '*Xenopus*' *romeri* and '*Shelania*' *laurenti* share with crown pipids a rounded posterior margin of the frontoparietal bone (166-0), and posterior margin of otic capsules at the same level as or anterior to occipital condyles (168-0). Both features are different from the condition observed in Late Cretaceous and Paleogene pipoids from South America, including *Llankibatrachus, Saltenia* and *Shelania*, for example. Finally, the extinct genus *Oumtkoutia* from the early Late Cretaceous of Morocco (Rage and Dutheil, 2008) is excluded from its original position among Xenopodinae and is nested as stem-Pipinae. This result rests on weak evidence; *Oumtkoutia* shares with Pipinae a single unambiguous derived feature: poorly-developed basal processes on the otic capsules. Because of this, and because of the low statistical support of the phylogenetic position of *Oumtkoutia*, we regard this taxon as of uncertain phylogenetic position. Furthermore, because of the presence of several plesiomorphic traits of the braincase (see Rage and Dutheil, 2008) it is also possible that this genus may be better nested among basal pipoids. The phylogenetic position of this taxon should be resolved when more complete specimens become available. In sum, the new results here performed indicate that interrelationships among Pipimorpha are far from robust and well-established.

Patagopipa belongs to Panpipidae based on the presence of several derived features, namely the presence of a large azygous frontoparietal bone, large otic capsules, fused sacrum and urostyle, and strongly expanded sacral diapophyses (Báez, 1981; Báez and Trueb, 1997; Estes, 1975; Estes and Reig, 1973; Trueb and Báez, 2006).

Patagopipa shares these characters with shelaniines: anterior ramus of pterygoid reaching the antorbital plane, marked forward orientation of the transverse process of presacral vertebrae IV, second pair of ribs anterolaterally oriented, and distal iliac shaft dorsoventrally flattened in cross section. In addition to these synapomorphies, *Patagopipa* shares with shelaniines such as *Shelania* and *Saltenia* common anatomical traits, including: short anterior nasal process, presence of a well-developed and acute antorbital process of the maxilla (39-2), and posteriorly expanded otic capsules that surpass the posterior level of occipital condyles (168-1) (see Casamiquela, 1960, 1961; Báez, 1981; Báez and Trueb, 1997; Báez and Púgener, 1998).

Among shelaniines, the present phylogenetic analysis indicates that *Patagopipa* constitutes the sister group of the genus *Saltenia*. Both genera are united by the derived presence of rounded anterior margin of frontoparietal bone (169-1), and frontoparietal lacking interorbital constriction (170-1). Furthermore, *Saltenia* and *Patagopipa* lack derived features present at the clade conformed by *Kuruleufenia* + *Shelania*, including neural arch lamina of sacrum nearly as long as wide (101-1), and vertebrae that are subrectangular in contour when viewed dorsally (172-1).

Llankibatrachus truebae was found in beds near those that yielded *Patagopipa corsolinii* (Báez and Púgener, 2003), and thus, detailed comparisons between both taxa are necessary. In the present phylogenetic analysis, *Llankibatrachus* nests outside Shelaniinae (lacking all the synapomorphies of the clade), as the sister group of the Pipidae clade. In this sense, *Llankibatrachus* lacks features observed in *Patagopipa* and other Shelaniinae, namely: the frontoparietal, which is three times longer than wide, lacking interorbital constrictions (170-1), and the transversely expanded presacral vertebral (172-1). Furthermore, *Llankibatrachus* shares derived features with crown pipids that are absent in *Patagopipa* (it is possible that some of these traits could be the result of the ontogenetic stage of the specimen), as for example, fused scapula and coracoid and notably expanded sacral diapophyses (see section 2). In addition, *Llankibatrachus* differs from *Patagopipa* by the presence of well-developed parasagittal crests on the frontoparietal bone, by the presence of a supraorbital flange, the frontoparietal with acute anterior margin, by posteriorly directed presacral ribs II-IV, and by the straight distal margin of sacral diapophyses, among other minor anatomical details.

From the Eocene–Oligocene of Brazil, Bedani and Haddad (2002) described the genus and species *Paleopipa aiuruoca*. In spite of this, the taxon was described only in a preliminary way, and these illustrations are not enough informative; the shape of the frontoparietal bone, the inflate and posteriorly extended otic capsules, the ilium with the distal end of shaft dorsoventrally flat, and

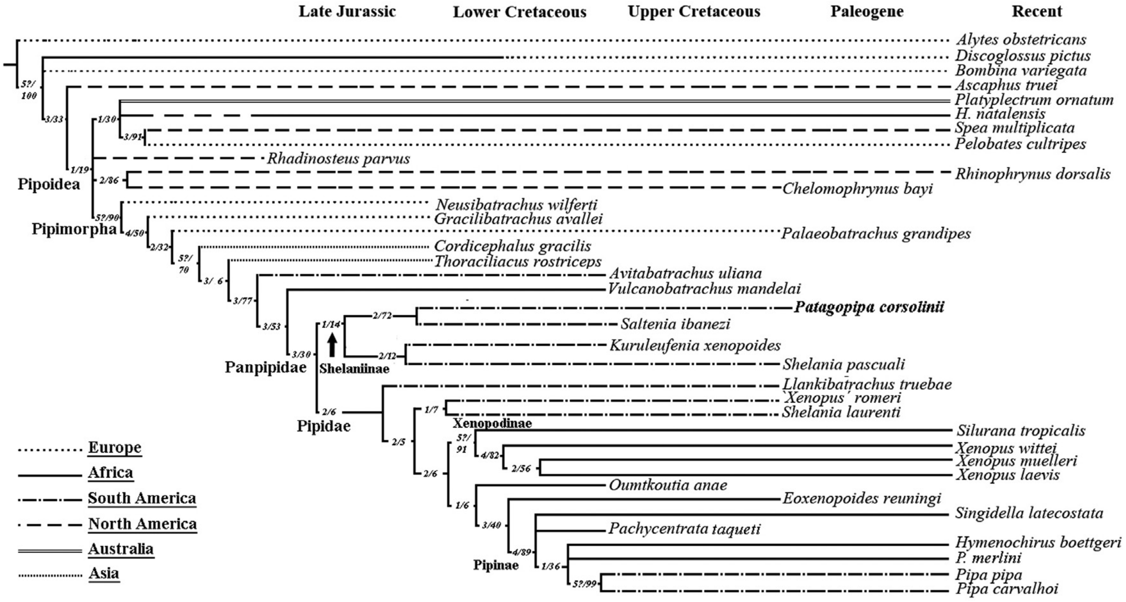

Fig. 4. Strict consensus cladogram showing the phylogenetic position of *Patagopipa corsolini*. The node support is indicated in the nodes; the Bremer support is on the left and the bootstrap absolute frequencies on the right.

Fig. 4. Cladogramme de strict consensus montrant la position phylogénétique de *Patagopipa corsolini*. À noter que le support est indiqué dans les nœuds : à gauche, support Brenner ; à droite, fréquences absolues *bootstrap*.

second ribs strongly anterolaterally oriented indicate that this taxon may be included within Shelaniinae. *Paleopipa* differs from *Patagopipa* by having frontoparietals with mid-length transverse constriction, strongly expanded sacral diapophyses, and gracile and elongate humerus (Bedani and Haddad, 2002).

In sum, *Patagopipa* is a pipid frog well-nested among Shelaniinae, being the sister group of the Late Cretaceous *Saltenia*. In the phylogenetic analysis, both taxa, share: long metacarpals compared with radio-ulna length (135-1); otic capsules posteriorly expanded surpassing the posterior margin of the occipital condyles (168-1); frontoparietal rounded in shape (169-1); and vertebrae two or three times wider than long (rectangular-shaped when viewed dorsally) (172-1). Furthermore, *Saltenia* and *Patagopipa* share some features that deserve a more detailed study: absence of parasagittal crests and sacral diapophyses poorly developed and slightly more posteriorly than anteriorly expanded. Its unique combination of characters indicates that *Patagopipa corsolini* is a valid genus and species of pipimorph toad.

3.2. Paleobiogeographical implications

The present phylogeny agrees in some respects with previous phylogenetic hypotheses (Báez and Trueb, 1997; Báez and Púgener, 1998; Gómez, 2016; Trueb, 1999; Trueb and Báez, 2006). All these analyses evidence a complex biogeographic scenario of pipimorph evolution. In fact, stem pipoids include both South American and African taxa. Panpipids include the South American Shelaniinae and *Llankibatrachus*, whereas crown Pipidae encompass both African and South American lineages. This complex pattern makes the biogeographic history of pipoids very difficult to interpret.

Most authors agreed in that South America and Africa were completely separated by the opening of the Atlantic Ocean by Turonian times (80 Mya). This resulted in the “splendid isolation” of South American floras and faunas, which remained isolated from other landmasses until Late Neogene times (see Pascual and Ortiz Jaureguizar, 2007). In spite of this, some authors proposed that faunistic interchanges between Africa and South America occurred through island chains or subaerial terrestrial bridges (see Ezcurra and Agnolín, 2012; Oliveira et al., 2010).

Trueb et al. (2005) and Rage et al. (2013) proposed that pipoids were widespread along Western Gondwana by Cretaceous times, before the severing of both landmasses. Later, by Turonian times, both landmasses separate each other and pipoids evolved separately on both continents. The present analysis argues against such proposal. The interleaved occurrence of African and South American taxa may imply that, during Turonian times, a large number of pipoids (including living pipids) were present and diversified during Early Cretaceous times before the severing of both continents, which is unlikely and inconsistent with molecular and paleontological data. Thus, based on the present analysis and previous phylogenetic hypotheses, it is more likely that the occurrence of several pipoid clades on both sides of the Atlantic Ocean may be the result of a transoceanic dispersal. In this context, two main hypotheses have been proposed by previous authors.

Estes (1975) explored the hypothesis that panpipids may have crossed from Africa to South America in post-Aptian times by means of floating islands of vegetation, a hypothesis proposed by Hoffstetter (1974) for explaining monkey and caviomorph arrival to South America during Eocene times.

However, the present phylogeny contradicts Estes' (1975) hypothesis. In fact, the presence of several interleaved South American and African panpipid clades contrasts with a single westward-directed floating island model. On the contrary, the present phylogenetic hypothesis sustains several bidirectional dispersals between both landmasses.

In this sense, the presence of several panpipid groups in both Africa and South America was interpreted by Cannatella (2015) as being the result of several eastward and westward dispersals of panpipids during the Paleogene, suggesting that vicariance does not seem a feasible explanation for panpipid distribution and phylogeny. In this way, Cannatella (2015) suggested that panpipids may have dispersed from South America to Africa and vice-versa during the Earliest Tertiary through an island chain connecting both continents.

This is in agreement with Bonaparte (1984), who proposed that important faunistic similarities between Tertiary faunas of South America and Europe might be explained by dispersion from Africa to South America and vice-versa using the Walvis Ridge–Rio Grande Rise terrestrial passage or island chain. This agrees with minimal divergence times between several South American and African extant plant and animal groups that are calibrated well after the purported latest separation between both landmasses, suggesting dispersal events between Africa and South America after their separation (see details in Ezcurra and Agnolín, 2012); see also Oliveira et al., 2010) built upon this evidence a new paleobiogeographical model to explain these unexpected patterns in several clades, mainly reptiles, indicating that Africa, South America, and Europe retained deep biogeographical ties up to Paleogene times. In this sense, recent authors sustained a late faunistic connection between Africa and South America based on herpetofaunal evidence (e.g., Agnolín, 2012; Hofmeyr et al., 2016; Pereira and Schrago, 2017; Vidal et al., 2008). The multiple panpipid interchanges (at least three different bidirectional interchanges based on present phylogeny) between South America and African in post-Cretaceous times are in agreement with Ezcurra and Agnolín's (2012) model suggesting a late Africa–South America terrestrial biotic interchange up to the Earliest Tertiary times.

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