# The archaic ilial morphology of an enigmatic pipid frog from the upper Pleistocene of the South American pampas

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# THE ARCHAIC ILIAL MORPHOLOGY OF AN ENIGMATIC PIPID FROG FROM THE UPPER PLEISTOCENE OF THE SOUTH AMERICAN PAMPAS

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ABSTRACT—Pipids are odd-looking frogs with a derived morphology that has been considered to be the result of a successful adaptation to a fully aquatic lifestyle. This monophyletic group comprises 33 extant species arranged in three clades mainly distributed in tropical regions of northern South America (*Pipa*) and sub-Saharan Africa (Xenopodinae and Hymenochirini). Their fossil record, however, documents greater diversity and wider distribution in South America in the Cretaceous and Paleogene. Recently, isolated postcranial bones bearing distinctive pipid features have been collected from Pleistocene beds in Argentina, nearly 2000 km farther south than their present distribution on the continent. Here, we describe a well-preserved pipid ilium possessing features unknown in the living taxa. The fossil is from a new Lujanian (late Pleistocene) locality of the Pampean Region, thereby confirming the intriguing presence of this group in southern South America. We provide a detailed anatomical evaluation of the adult iliac morphology of pipimorphs and use these data, along with molecular data, in a parsimony analysis of living and extinct pipoid taxa to estimate the relationships of the new material. This analysis places the fossil as a stem xenopodine in an unresolved polytomy together with "*Xenopus*" *romeri* from the upper Paleocene–lower Eocene of Brazil and two taxa from the Eocene of Patagonia. These Pleistocene pipid records in the Pampean region and subsequent disappearance may reflect latitudinal shifts owing to the rapid climate changes related to the glacial/interglacial cycles.

## INTRODUCTION

Pipids are odd-looking frogs with a derived morphology that has long been considered to be the result of a successful adaptation to a fully aquatic lifestyle. Recent molecular studies have corroborated the monophyly of Pipidae (Frost et al., 2006; Pyron and Wiens, 2011), comprising 33 extant species that are grouped into three clades mainly distributed in tropical to subtropical areas of northern South America (*Pipa*) and sub-Saharan Africa (Xenopodinae and Hymenochirini). However, there has been some disagreement regarding the relationships among these three lineages, probably as a result of the different sources of data, as well as the different methodological approaches implemented in the phylogenetic analyses. Parsimony analyses of morphological data sets have resulted in the sister-group relationship of *Pipa* and Hymenochirini (Cannatella and Trueb, 1988a, 1988b; Báez and Púgener, 2003; Báez et al., 2007), a relationship also recovered by the analysis of DNA sequences of mitochondrial and one nuclear genes (Evans et al., 2004; Evans, 2008). Conversely, the closer relationship of the African lineages with respect to *Pipa* was obtained when a molecular data set with two nuclear additional genes was analyzed using maximum likelihood and Bayesian methods of phylogenetic reconstruction (Roelants et al., 2007). This latter result had been suggested by Sokol (1977) based on morphological data, and also was recovered by the maximum likelihood analyses of new nuclear and mitochondrial data sets (Irisarri et al., 2011; Pyron and Wiens, 2011).

With regard to the fossil record, the pipoid lineage represented today by crown-group Pipidae (i.e., pipimorphs sensu Ford and Cannatella, 1993) dates to the Berriasian–Hauterivian of northern Israel (Estes et al., 1978), then part of the African Plate; however, the record of pipoids in the Upper Jurassic of North America (Henrici, 1998) suggests that the earliest part of their history might be as yet largely unknown. Indeed, the available paleontological evidence indicates that pipimorphs had a wider distribution in the Cretaceous and Paleogene compared to their present range (Báez, 1996, 2000; Báez and Púgener, 2003; Rage and Dutheil, 2008). In South America, the oldest known records of this lineage occur in the mid-Cretaceous beds of southern Argentina (Báez et al., 2000), and possibly also northeastern Brazil (Báez et al., 2009), whereas several Late Cretaceous and Paleogene units have yielded remains ascribed to this group (Báez, 2000; Bedani and Haddad, 2002). Here, we report on a new Pleistocene record of pipids in the pampas of Argentina, which confirms the relatively recent presence of this group of frogs further south than their present distribution (Báez et al., 2008). The material consists of a single ilium with a distally broken shaft, but the distinctive morphology of this element, which traditionally has been used in the identification of anurans based on isolated bones, allows a confident taxonomic placement at the familial level.

We provide a detailed anatomical evaluation of the adult iliac morphology of pipimorphs and use this evidence in a parsimony analysis of living and extinct pipoid taxa; molecular data also are included in this analysis to estimate the relationships of the taxon from the new upper Pleistocene locality. We discuss the evidence from iliac characters and assess the importance of the recent, unexpected records of pipids in southern South America
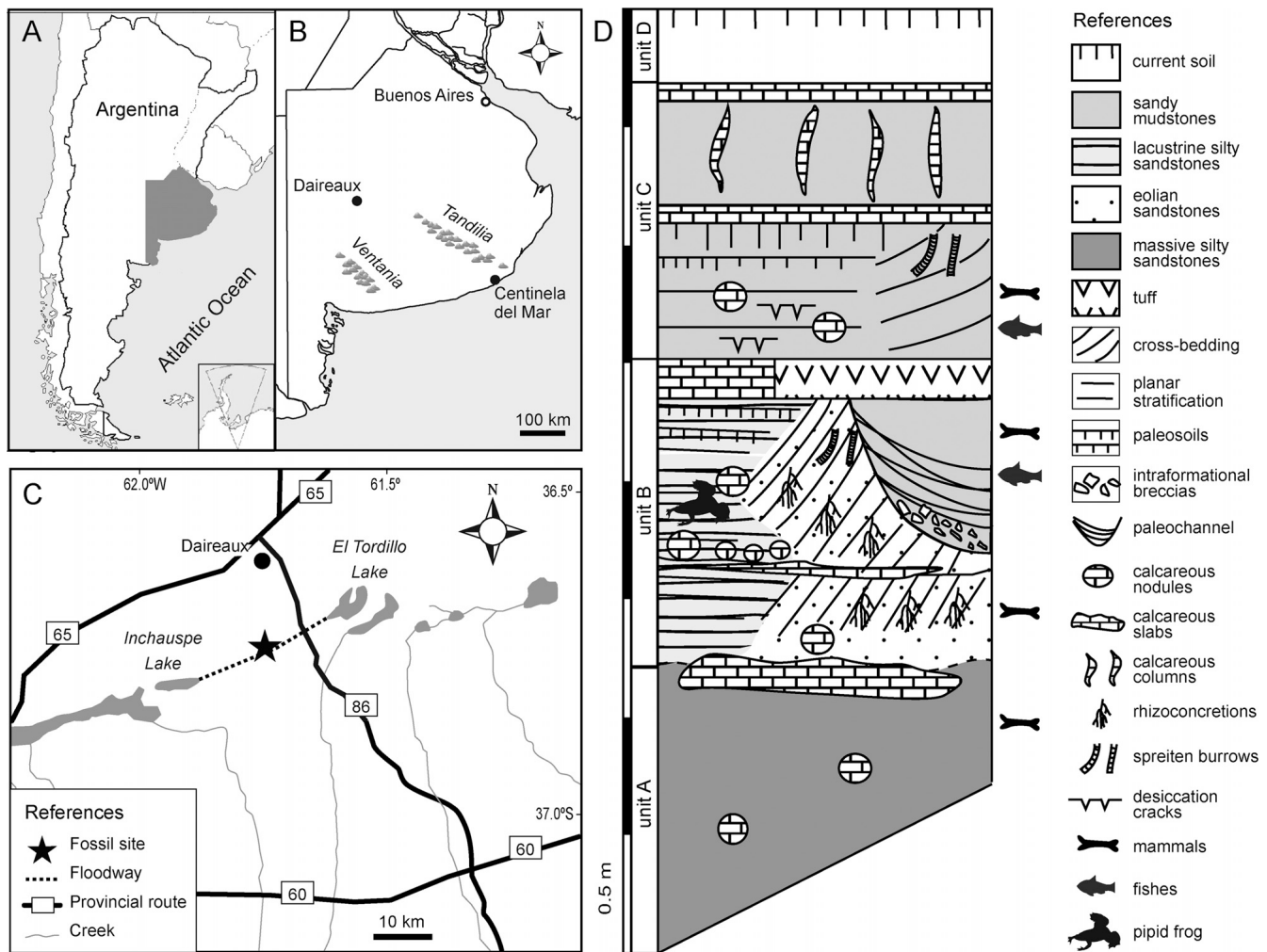
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FIGURE 1. **A**, map of Argentina, highlighting Buenos Aires Province in dark grey; **B**, map of Buenos Aires Province showing the location of Daireaux and Centinela del Mar localities; **C**, map of the study area showing the fossil site from which the pipid material was recovered; **D**, composite stratigraphic column of Daireaux outcrops showing fossiliferous levels.

to unravel the history of the group in this continent. However, further progress in our understanding of their evolution in the Pleistocene likely awaits the discovery of additional, more complete materials.

**Institutional Abbreviations—CPBA-V**, Palaeontología, Vertebrados, Departamento de Ciencias Geológicas, Universidad de Buenos Aires, Buenos Aires, Argentina; **DGM**, Direção de Geologia e Mineria, Rio de Janeiro, Brazil; **FCEN**, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; **KU**, Natural History Museum, University of Kansas, Lawrence, Kansas, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MLP**, Museo de La Plata, La Plata, Argentina; **MMP**, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia,' Mar del Plata, Argentina; **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.

## GEOLOGIC SETTING

The system of interconnected lakes known as 'Lagunas Encadenadas' in western Buenos Aires Province, Argentina, is situated in an endorheic basin that extends across a east-northeast structural lineament (Vallimanca lineament of Kostadinoff, 2007), north of the valley between the Ventania and Tandilia mountain ranges (Fig. 1). 'Pampean' sediments traditionally regarded as late Cenozoic in age are exposed in cutbanks along the margins of a floodway between two of the lakes, Inchauspe and El Tordillo, in the eastern part of the system. Sandy sediments dominate the stratigraphic sequence, which is thought to represent a fluvio-lacustrine system that formed within sand-dune fields (Isla et al., 2010). Lacustrine green, yellowish, or whitish silty sandstones that pass laterally to cross-bedded sandstones (Unit B; Fig. 1D) have yielded abundant vertebrate remains, including fishes, testudines, toxodonts, xenarthrans, rodents, and the anuran material described herein. Especially significant from a biostratigraphic viewpoint are the mammalian taxa; the presence of the gigantic glyptodont *Doedicurus clavicaudatus*, together with other elements of the megafauna, clearly indicate that these beds are referable to the *Equus* (*Amerhippus*) *neogaeus* Biozone (Isla et al., 2010) that is the basis for the recognition of the local

Lujanian Stage/Age sensu Cione and Tonni (1999, 2005). The Lujanian Stage is usually considered to represent the late Pleistocene (i.e., 130 ka to 7 ka) according to the radiometric dating of fossil bearing beds (Cione et al., 2009). It spans a temporal interval characterized by highly fluctuating climatic-environmental conditions. In the Pampean Region, available evidence suggests a trend towards climatic deterioration from the relatively warmer and wetter earlier Lujanian times (Tonni, 2009). The stratigraphic sequences recorded at Daireaux provide evidence of increasing eolian deposition processes and high mobility of the sand dunes; this might have affected the extent and distribution of the water bodies. This evidence is compatible with a transition to colder and drier prevailing conditions (Iriondo, 1999), as those inferred for the interval that immediately preceded the glacial period culminating about 18 ka (Last Glacial Maximum, LGM). However, the lack of absolute dates prevents us from unambiguously determining if the vertebrate-bearing beds at Daireaux correspond to Lujanian deposits of the interval preceding (Lujanense Verde Inferior, OIS3) or succeeding (Lujanense Verde Superior, OIS2) the LGM (Toledo, 2011).

## MATERIALS AND METHODS

Pipids have been considered stereotyped in their configuration of the pelvic girdle relative to other anurans because of its peculiar morphology, characterized by the broad 'U'-shape in dorsal aspect, the presence of a well-developed dorsolateral crest on the ilium, the markedly longer than high, dumbbell-shaped acetabulum, and the transverse, rather than lateral, preacetabular zone (Trueb, 1996). However, the considerable variation of this structure within Pipidae has not been addressed in detail; consequently, we performed a comparative anatomical analysis of the ilium in a relatively wide sample of extant pipids, which are listed in Appendix 1. We also extended our observations to several extinct pipimorphs for which the main features of the ilium can be confidently scored either from actual remains or peels. In this regard, we considered several South American fossil taxa, such as the mid-Cretaceous *Avitabatrachus uliana* from Patagonia (Báez et al., 2000), the Campanian *Saltenia ibanezi* from northwestern Argentina (Báez, 1981), the Eocene *Shelania pascuali* and *S. laurenti* from northwestern Patagonia (Báez and Trueb, 1997; Báez and Púgener, 1998), and the late Paleocene–early Eocene "*Xenopus*" *romeri* from Brazil (Estes, 1975). We also examined casts of *Eoxenopoides reuningi* from the Paleogene of the Republic of South Africa (Estes, 1977) and considered iliac features of a few extinct pipid taxa from Africa available in the literature, namely the Cenomanian *Oumtkoutia anae* (Rage and Dutheil, 2008) and Miocene isolated xenopodine ilia from Morocco (Vernaud-Grazzini, 1966).

Drawings of the examined materials were obtained with the aid of a Nikon SMZ 1000 stereomicroscope with a camera lucida attachment and photographs were taken with a Nikon Coolpix 990 digital camera. Iliac terminology (Fig. 2) mainly follows that of Chantell (1964) and Tyler (1976), with additional terms currently used (e.g., interiliac scar). We have followed Gardner et al. (2010) in applying operational terminology to ilia, using the term 'proximal' to indicate 'toward the acetabulum' and the term 'distal' to indicate 'toward the tip of the shaft that articulates with the sacrum.' Measurements were taken from digital photographs or drawings of the specimens using TPSDig Ver. 2.05 software (Rohlf, 2006). The anatomical orientation of elements and the definition of the measurements are shown in Figure 2A–C. To estimate the total length of the iliac shaft of the fossil specimen, we have conducted a quantitative analysis based on the proportions of the ilium (lengths of the iliac body [IBL] and iliac shaft [ISL] in different extant and extinct pipid taxa listed in Table 1; these measurements (Fig. 2B) were log-transformed and a
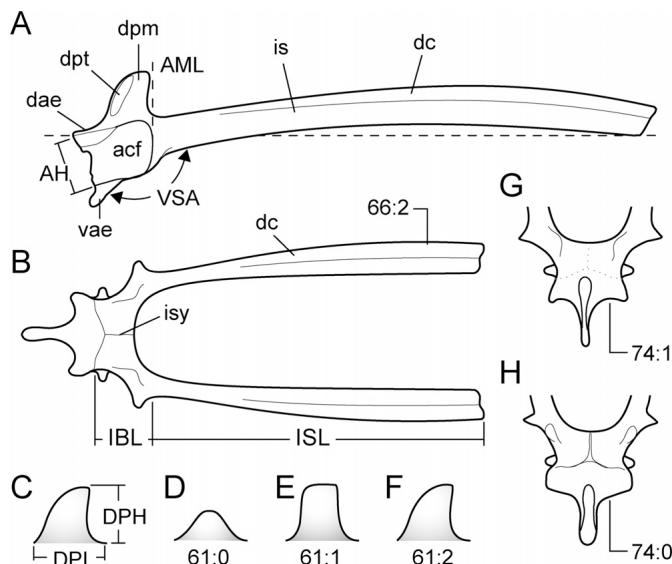


FIGURE 2. General osteological terminology and iliac measurements used in this study. **A**, right ilium of *Xenopus laevis* in acetabular view; **B**, pelvis of *Xenopus laevis* in dorsal view; **C**, dorsal prominence of *Xenopus laevis* in acetabular view; **D**, 'bell-shaped' dorsal prominence; **E**, rectangular dorsal prominence; **F**, asymmetrical dorsal prominence. Posterior portion of pelvis in dorsal view of **G**, *Xenopus muelleri*; **H**, *Pipa carvalhoi*. Numbers before the colon indicate the character and numbers after the colon indicate the character state. **Abbreviations**: **acf**, acetabular fossa; **AH**, acetabular height; **AML**, anterior level of acetabular margin; **dae**, dorsal acetabular expansion; **dc**, dorsal crest; **DPH**, dorsal prominence height; **DPL**, dorsal prominence length; **dpm**, dorsal prominence; **dpt**, dorsal protuberance; **IBL**, iliac body length; **is**, iliac shaft; **ISL**, iliac shaft length; **isy**, interiliac symphysis; **vae**, ventral acetabular expansion; **VSA**, angle between the ventral acetabular expansion margin and the iliac shaft. Not to scale.

regression analysis was performed (Table 1). The estimated total length was used to calculate the percentage represented by the preserved portion.

In order to investigate the phylogenetic placement of the taxon represented by the ilium from Daireaux, we performed a phylogenetic analysis. Sixteen characters (characters 58–71, 73, 74; Appendix 2) concerning the morphology of the ilium were scored for the included taxa and incorporated into a modified version of Báez et al.'s (2007) data matrix. Three of these characters (58, 62, 63) have been used previously by Bever (2005; his characters 3, 5, and 8); parenthetically, it should be noted that the term dorsal protuberance has been erroneously applied to the base of the prominence by this author owing to a misinterpretation of Sanchíz's (1998) definition. In turn, the morphological matrix (Appendix 3) was supplemented with DNA sequence data from three mitochondrial (12s, tRNAVal, 16s) and two nuclear (28s, RAG-1) genes obtained from GenBank (see Supplementary Data 1; available online at www.tandfonline.com/UJVP). For nuclear and mitochondrial genes, multiple sequence alignments were achieved using MUSCLE Ver. 3.8 (Edgar, 2004) with default parameters.

The combined data matrix with 5580 characters and 22 taxa (Supplementary Data 1) was analyzed under maximum parsimony as the optimality criterion using TNT Ver. 1.1 (Goloboff et al., 2008). In the analysis, 500 rounds of random addition sequences were followed by the tree bisection and reconnection branch swapping algorithm keeping up to 10 trees on each round, under equal weights. Node support was estimated in TNT using Bremer-support indices (indicated above each node) and by

TABLE 1. Length measurements (in mm) and linear regression equation* of selected iliac dimensions (IBL; ISL).

| Taxon | IBL | ISL |
|---|---|---|
| †*Daireaux pipid*, MMP M-5121 | 4.20 | 16.90 (preserved portion) |
| †*Eoxenopoides reuningi*, SAM K-4956 | 1.81 | 10.23 |
| †*Llankibatrachus truebae*, BAR 2469–10 | 2.12 | 13.00 |
| *Pipa carvalhoi*, MACN 42606 | 3.31 | 21.13 |
| *Pipa carvalhoi*, MACN 42607 | 3.60 | 24.61 |
| *Pipa parva*, MACN 42614 | 2.00 | 12.09 |
| *Pipa parva*, MACN 42615 | 3.02 | 19.15 |
| *Pipa pipa*, MACN 42612 | 5.76 | 35.45 |
| *Pipa pipa*, MACN 42613 | 8.26 | 53.91 |
| *Shelania pascuali*, CPBA-V-12219 | 6.37 | 31.17 |
| *Silurana tropicalis*, MACN 42633 | 2.81 | 20.35 |
| †*Vulcanobatrachus mandelai* (Trueb et al., 2005) | 1.82 | 12.25 |
| *Xenopus boumbaensis*, KU 206928 | 1.96 | 12.22 |
| *Xenopus fraseri*, MACN 42629 | 2.00 | 13.50 |
| *Xenopus gilli*, MACN 42630 | 1.76 | 10.93 |
| *Xenopus gilli*, KU 206865 | 2.41 | 19.51 |
| *Xenopus laevis*, FCEN uncatalogued | 4.64 | 31.62 |
| *Xenopus laevis*, FCEN 1435 | 4.52 | 32.43 |
| *Xenopus largeni*, KU 206863 | 2.13 | 15.98 |
| *Xenopus muelleri*, MACN 42631 | 3.30 | 28.25 |
| *Xenopus pygmaeus*, KU 206872 | 1.63 | 8.13 |
| *Xenopus vestitus*, KU 206873 | 2.13 | 15.26 |
| *Xenopus wittei*, MACN 42624 | 2.07 | 15.60 |
| *Xenopus wittei*, KU195673 | 2.02 | 14.59 |

*Linear equation regression on log-transformed iliac dimensions: $y = ax + b$; $y = \log (ISL)$; $x = \log (IBL)$; $a = 1.0283$; $b = 0.8073$; $r$ (correlation coefficient) $= 0.95896$. The estimated complete ISL of the MMP M-5121 is 28.06 mm, though nearly 60% of the iliac shaft is preserved. **Abbreviations**: **IBL**, iliac body length; **ISL**, iliac shaft length.

symmetric resampling (500 replicates), expressed as frequency differences (GC; indicated under the nodes).

SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813
XENOANURA Savage, 1973 ( = Pipoidea Ford and Cannatella, 1993)
PIPIDAE Gray, 1825
Gen. et sp. indet.
(Fig. 3)

**Referred Material**—MMP M-5121, a nearly complete right ilium.

**Horizon and Locality**—The material was collected in a yellowish-green silty sandstone (Fig. 1D) that outcrops on the margin of the floodway that joins the small lakes El Tordillo and Inchauspe, about 5 km west of junction of the floodway with provincial Route 86, south of the town of Daireaux, Buenos Aires Province, Argentina (Fig. 1A–C). The pipid collecting site (36°44′33.34″S 61°45′5.20″W) is located between the La Larga and Puente Lauman sites, where geological sections have been studied (Isla et al., 2010); because the outcrops are nearly continuous along the floodway, the fossil locality is comprehensively called Daireaux. These beds contain remains of fossil mammalian taxa representative of Lujanian age (late Pleistocene; 0.13 to 0.01 Ma). Absolute dating of the mammal bearing bed has not yet been obtained.

**Description**—The material consists of an almost complete right ilium with most of the shaft (60%) preserved; the element is well ossified and presumably belongs to an adult individual. The proximal portion of the shaft has a rounded cross-section, only slightly mediolaterally compressed. Distally, the shaft is dorsoventrally flattened; as a result of this flattening the distal one-half of the preserved portion of the shaft has an oval cross-section and a subtle lateral edge, whereas the medial margin is rounded throughout the preserved shaft. A dorsal crest is lacking along the available portion of the shaft. A thin oblique ridge extends diagonally, posterodorsally-anteroventrally, on the lateral side of the shaft; this ridge originates near the anterior margin of the acetabular fossa and extends for nearly one-third of the preserved shaft. Another oblique ridge is clearly visible along the proximal portion of the medial side of the shaft, extending onto the body of the bone. A conspicuous wide-based dorsal prominence extends from the area of articulation with the ischium to a point slightly anterior of the acetabular fossa. The dorsal prominence has low-angled anterior and posterior slopes and a sharp dorsal edge. It bears a feeble elongated dorsal protuberance on the posterior slope near the apex of the prominence. In acetabular view, the region dorsal to the acetabular fossa and adjacent to the dorsal prominence along the ischiadic margin is as high as the acetabular fossa. The acetabular fossa is shallow with an extruded ventral margin and an even dorsal one; the posteriorly converging directions of both dorsal and ventral margins confer a horseshoe-shaped outline to the fossa. The ventral acetabular expansion is only slightly exposed in acetabular view. Medially, there is a prominent expansion that formed an extensive symphysis with the contralateral ilium. The available evidence indicates that the ilium was not fused to the ischium.

COMPARISONS AND PHYLOGENETIC POSITION

The ilium from Daireaux conforms to those of other pipids in having an elongate acetabulum, well-developed dorsal prominence, reduced pre-, ventral, and dorsal acetabular expansions, and a broad contact between the medially expanded acetabular regions of left and right ilia, both dorsally and ventrally. It resembles the ilia of pipids recovered recently from late middle Pleistocene beds at Centinela del Mar, on the coastal cliffs of the province of Buenos Aires (Fig. 1; Báez et al., 2008), from which it differs slightly in the shape of the acetabulum. The latter were found in association with a few incomplete sacrourostylar complexes in which the sacrum is totally fused to the urostyle, as in most known pipimorphs, and bears an anterior condyle for the articulation with the last presacral centrum. The available information is still insufficient to ascertain whether the materials from these two Pleistocene localities represent the same species.

Three main morphological aspects can be addressed in the comparisons of the Daireaux specimen with the ilia of other pipimorph taxa, as follows: (1) presence and degree of development, longitudinal extent, and orientation of the dorsal crest; (2) shape of the dorsal prominence; and (3) degree of exposure of the dorsal acetabular expansion in acetabular aspect. With regard to the former, the presence of a dorsal crest on the iliac shaft has been considered a feature that characterizes extant pipid taxa (Trueb, 1996; Gardner et al., 2010); however, there is variation within Pipidae. In *Silurana tropicalis*, the iliac shaft bears a low, almost ridge-like, crest that is dorsally oriented and restricted to the anterior two-thirds of the shaft (Fig. 4F). The iliac crest is better developed in the species of *Xenopus* examined; this crest may extend along the distal half (*X. wittei*, *X. gilli*, *X. muelleri*) or the anterior three-quarters of the shaft (*X. laevis*; Fig. 2A, B). The dorsal crest is evident even in a young post-metamorphic *Xenopus fraseri* examined. In the species of *Pipa*, the crest is mainly laterally directed and its width increases anteriorly (Fig. 4E); it extends nearly along the entire shaft as in *Hymenochirus boettgeri* (Fig. 4G), but in the latter species it is dorsolaterally oriented. In contrast with the condition in extant pipids, a dorsal crest is lacking along the proximal two-thirds of the shaft of the ilium from Daireaux. This feature is shared with *Avitabatrachus* and "*Xenopus*" *romeri*. In the former, for which the entire shaft is known (Fig. 4H), a crest is absent, as seems to be the case in
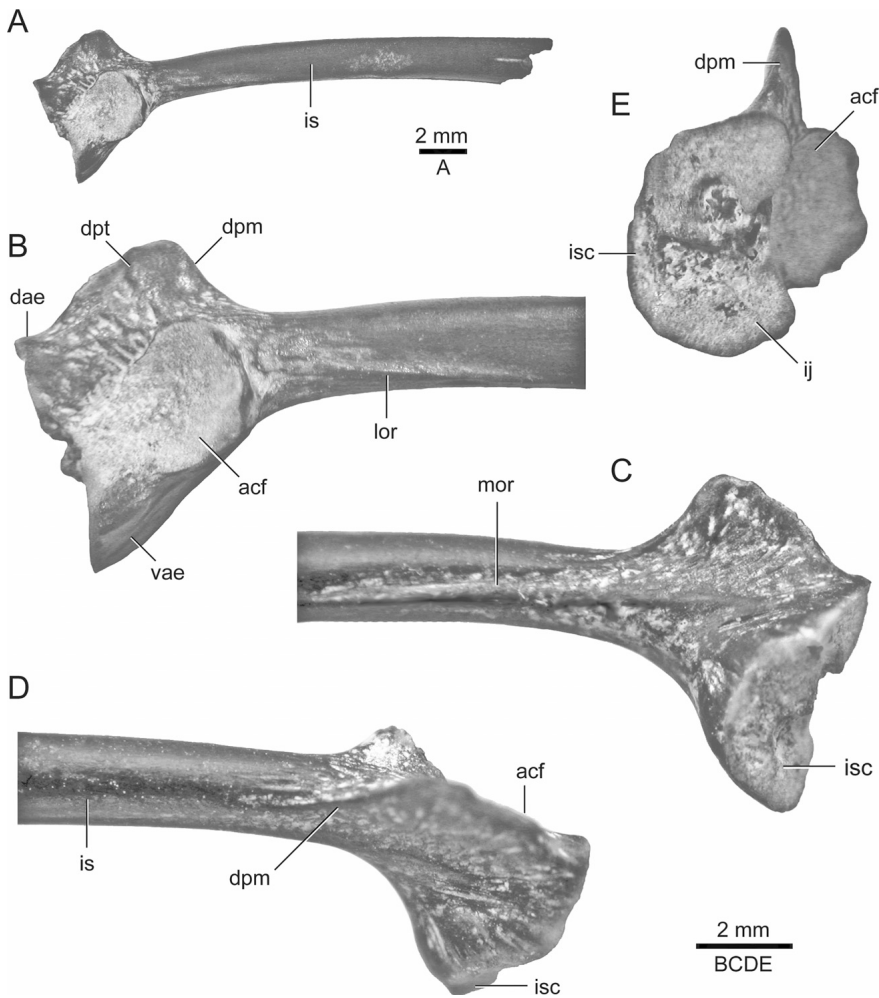
FIGURE 3. Pipid from Daireaux, MMP M-5121, incomplete right ilium. **A**, general aspect in acetabular view. Detail of proximal portion in **B**, acetabular; **C**, medial; **D**, dorsal; and **E**, posterior views. **Abbreviations**: **lor**, lateral oblique ridge; **mor**, medial oblique ridge; **ij**, ischiadic junction; **isc**, interiliac scar; other abbreviations as in Figure 2.

*Eoxenopoides*, *Saltenia*, and *Shelania pascuali*, in which the distal half of the iliac shaft is dorsoventrally depressed, bearing a shallow longitudinal groove (Fig. 4J).

A dorsal prominence that is longer than high and with its apex located well posterior to the level of the anterior margin of the acetabular fossa occurs in the pipid from Daireaux, as well as in the other extinct taxa examined, including the pipid from Centinela del Mar (Báez et al., 2008:fig. 2), and the species of *Pipa* (Fig. 4A) and *Pseudhymenochirus*. Disarticulated pipid ilia from the Upper Cretaceous of Niger (Báez and Rage, 1998) and *Oumtkoutia anae*, of uncertain taxonomic position (Rage and Dutheil, 2008), also have wide-based, low dorsal prominences. In contrast, in xenopodines and *Hymenochirus*, the dorsal prominence is nearly as high, or higher, as it is long, and its apex is at the level of the anterior margin of the acetabular fossa (Fig. 4B–D). However, the dorsal prominence is conspicuously long in the new material, lacking the bulky dorsal protuberance that occurs in most species of *Pipa* and *Hymenochirus* (Fig. 4A, D).

Also, the ilium from Daireaux, as the other fossil ilia examined, differs from those of living pipids in having a wider dorsal acetabular expansion exposed in acetabular aspect, a feature perhaps associated with a less extensive interiliac symphysis in the dorsal portion of the medial region of the acetabulum. Additionally, the well-developed oblique ridge anterior to the acetabulum also occurs in *Pipa*, *Avitabatrachus*, and "*X.*" *romeri* (Fig. 4) and it has also been noted in disarticulated Cretaceous ilia from Niger (Báez and Rage, 1998). This feature seems to be present in the isolated ilia from the Miocene of Morocco assigned to Xenopodinae (Vergnaud-Grazzini, 1966).

Our parsimony analysis of extant and extinct pipids based on morphological and molecular data recovered the sister-group relationship of *Pipa* and Hymenochirini, as well as that of *Silurana* and *Xenopus* (Fig. 5). In this context, the Daireaux pipid unambiguously resulted as a member of the stem of Xenopodinae together with Paleogene taxa in an unresolved polytomy, because it is shown in the strict consensus of five most parsimonious trees (tree length [TL] = 4099; consistency index [CI] = 0.537; retention index [RI] = 0.402; Fig. 5). Despite the limitations imposed by the paucity of the information on the iliac morphology among fossil taxa, it is clear that the ilium from Daireaux belongs to a pipimorph taxon based on the presence of presumably derived states of the iliac characters that optimize at the base of this clade. These are (1) presence of a distinct oblique ridge on the lateral surface of the base of the iliac shaft (character [c] 69, $0 \rightarrow 1$), which reverts in crown xenopodines; (2) narrow exposure of the dorsal acetabular expansion (c 72, $0 \rightarrow 1$); and (3) oval distal cross-section the iliac shaft (c 59, $0 \rightarrow 1$). We were unable to find unique derived iliac characters for Pipidae, as well as for the two main lineages within this clade recovered in the analysis (Fig. 5); however, this combined analysis has revealed that the configuration of the ilium from Daireaux lacks all the features that optimize at the respective bases of extant clades, with the exception of the expanded interiliac symphysis (c 70:2), which might have developed convergently in pipines and in the
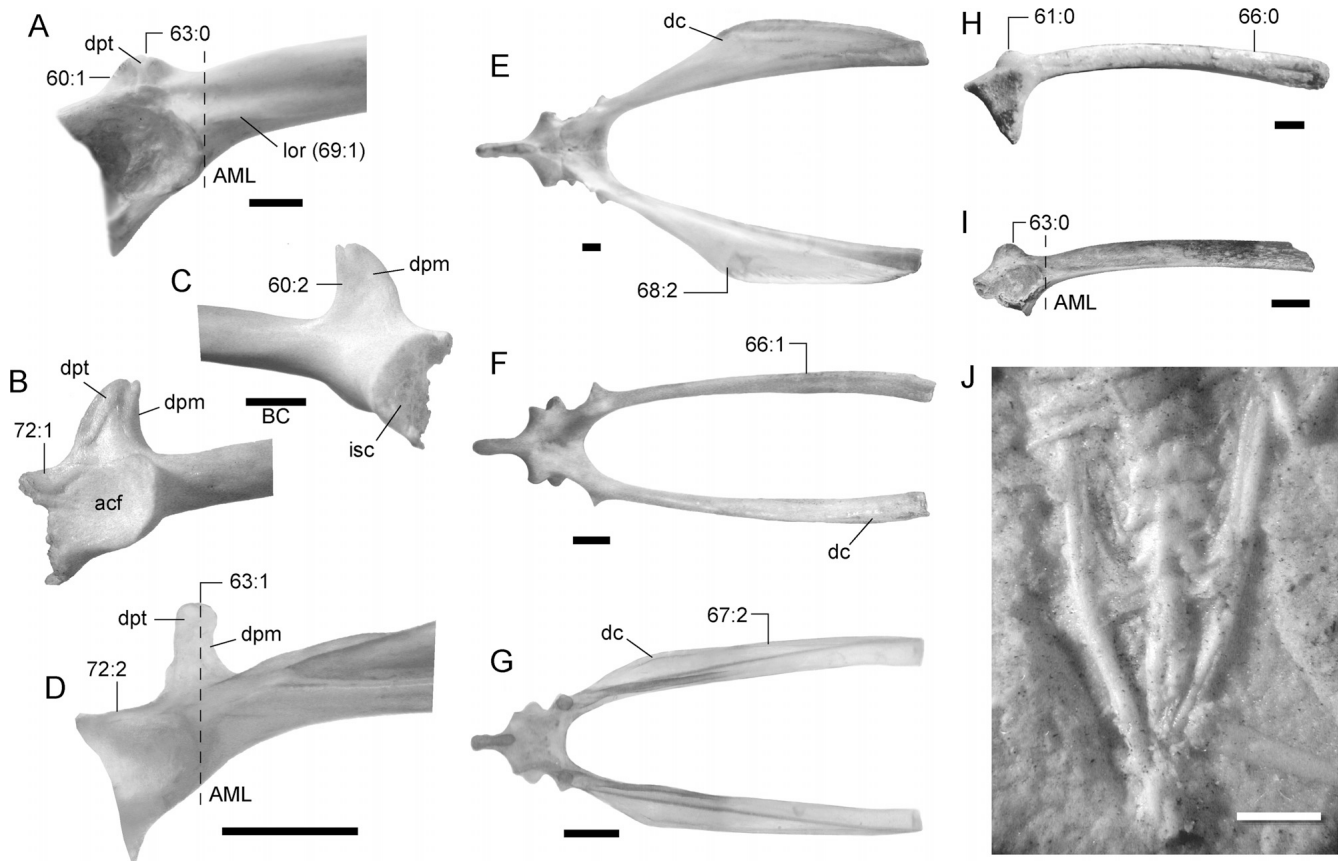
FIGURE 4. Iliac morphology of selected extant and extinct pipids. Proximal portions of right ilia of **A**, *Pipa pipa*, MACN 42612, in acetabular view; **B–C**, *Xenopus laevis*, FCEN uncatalogued, in (**B**) acetabular and (**C**) medial views; **D**, *Hymenochirus boettgeri*, MACN 42621, in acetabular view; pelvis in dorsal view of **E**, *Pipa pipa*, MACN 42612, **F**, *Silurana tropicalis*, MACN 42633, and **G**, *Hymenochirus boettgeri*, MACN 42621; ilia in acetabular view of **H**, *Avitabatrachus uliana*, MUCPv 123, and **I**, "*Xenopus*" *romeri*, DGM 578; **J**, pelvis in dorsal view of *Eoxenopoides reuningi*, SAM K-4956. Numbers before the colon indicate the character and numbers after the colon indicate the character state. **Abbreviations**: as in Figures 2 and 3. Scale bars equal 2 mm.

clade that includes *Shelania pascuali*, *Xenopus*, and *Silurana*. The nearly circular proximal cross-section of the iliac shaft is a reversal (c 58, 1 → 0) that is shared with crown xenopodines but also with several South American Paleogene taxa in an unresolved polytomy. In summary, the ilium from Daireaux has a combination of characters unknown in extant pipids; most of these characters are plesiomorphic for pipids in general, such as the low (c 60:1) and bell-shaped dorsal prominence (c 61:0), and apex of dorsal prominence posterior with respect to the acetabular fossa (c 63:0). It is also noteworthy that some of these characters also occur in described (Baez, 1987) and undescribed disarticulated ilia from the Upper Cretaceous of Patagonia.

## PAMPEAN PLEISTOCENE RECORDS

The material described herein confirms that pipids had a more southern distribution in the Pleistocene than they do today (Baez et al., 2008). Although these recent Pleistocene finds provide valuable data to our information on this group, they pose more questions than answers on its evolution and biogeography. The material from Daireaux, and also the recently described material from Centinela del Mar, represent taxa that retained surprisingly archaic ilial traits. These traits are not present in the living South American pipids that we examined, but they were widespread among extinct forms that inhabited Patagonia in the latest Creta-ceous (Báez, 1987) and Paleogene (Báez and Trueb, 1997; Báez and Púgener, 1998, 2003). These latter records constitute the southernmost known occurrences of pipids in South America, documenting their presence at a time when South America and Africa were already separated by an oceanic gap (Nürnberg and Müller, 1991; Eagles, 2007) and the climatic conditions in middle latitudes were milder than those of today (Iglesias et al., 2007; Wilf et al., 2009). Although the post-Eocene cooling and drying in Patagonia, with the gradual disappearance of aquatic biotopes (Ortiz Jaureguizar and Cladera, 2006; Barreda and Palazzesi, 2007), might be connected to their demise in these southern regions, the scanty fossil record of pipids north of this area does not furnish enough direct evidence of their subsequent Cenozoic biogeographic history and pattern of diversification in the continent. Nevertheless, we can speculate that the drying trend and expansion of xeric environments in central and western Argentina in the late Miocene and Pliocene (Verzi and Quintana, 2005; Ortiz Jaureguizar and Cladera, 2006) might have resulted in a northward shifting of the southern border of the range of the aquatic pipids at that time.

Our analysis finds the Daireaux pipid to be related to xenopodines, suggesting that it belongs to a lineage that persisted in South America well after their divergence from crown-group representatives that today populate Africa. This putative relationship points to a Mesozoic radiation of xenopodines prior to the final breakup of western Gondwana (ca. 100 Ma; Eagles,
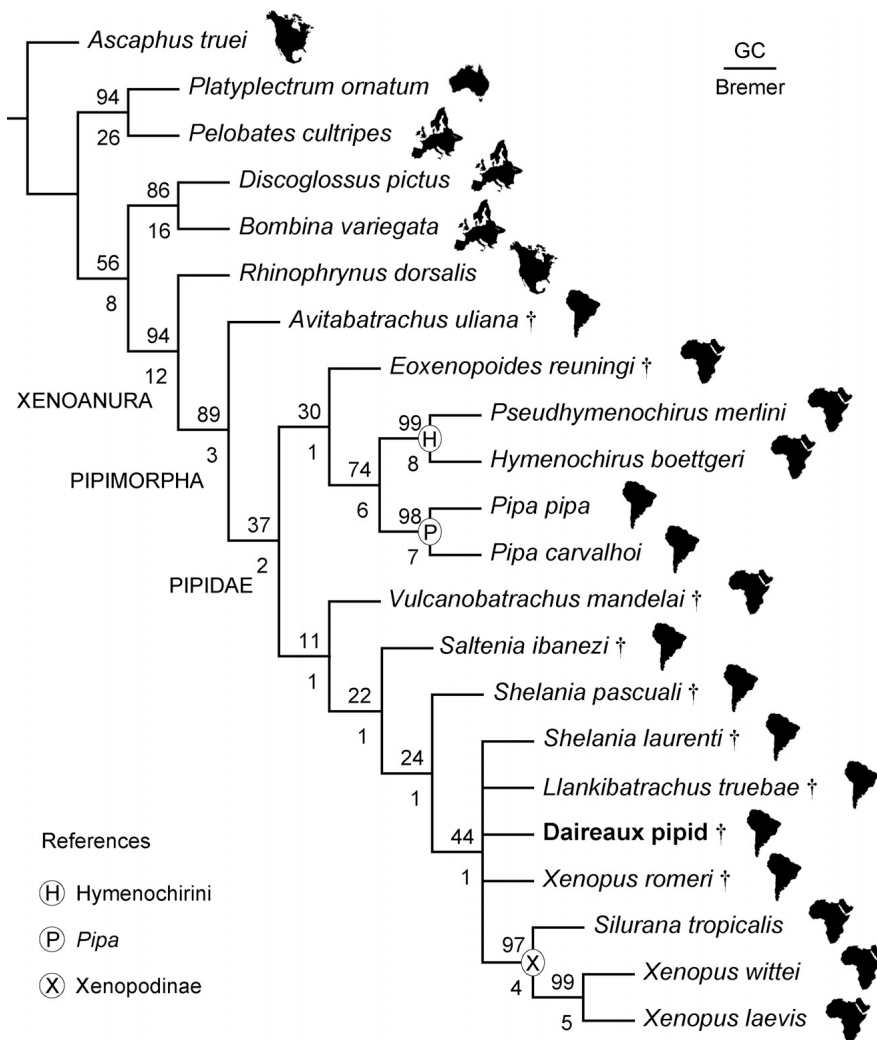
FIGURE 5. Strict consensus of pipoid interrelationships from five most parsimonious trees of 4099 steps showing the phylogenetic position of the pipid from Daireaux recovered in the combined analysis. Continent of distribution or provenance is indicated by black silhouettes: Africa; Australia; Europe; North America; South America. **Abbreviation**: **GC**, group support values calculated by symmetric resampling and expressed as frequency differences.

2007; Torsvik et al., 2009), in agreement with estimated molecular divergence times among the three pipid lineages around 130–100 Ma (Roelants et al., 2007; Blackburn et al., 2010). Although this hypothesis on the phylogenetic position of the Daireaux pipid will have to be tested by the future discovery of other skeletal remains, the recovered ilium documents the persistence into the late Pleistocene of a taxon possessing plesiomorphic features, at the same time revealing the occurrence of an extinction event.

During the Pleistocene, short, warmer, and wetter periods repeatedly punctuated the otherwise dry and cold conditions (Iriondo, 1999). Latitudinal shifts in the distribution of many vertebrate taxa in response to these rapid climate changes have been recorded in the Pampean region and northern Uruguay (Vucetich and Verzi, 2002; Ubilla et al., 2004; Verzi et al., 2004; Vucetich et al., 2005). Although no Neogene pipid records in South America are known, it is possible that these now-extinct pipids may have survived into the Neogene in the north of the continent under more favorable climatic conditions, but their survival in restricted areas at mid-latitudes cannot be ruled out. The development of wetlands with extensive water bodies during one or more warm-humid pulses in the Pleistocene glacial/interglacial cycles may have facilitated their southern migration but the available evidence does not shed light on this issue nor on the causes of the subsequent disappearance of representatives of the family south of the Tropics.

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APPENDIX 1. Specimens examined for the osteological comparisons and phylogenetic analysis. **Abbreviations**: **CS**, cleared and stained; **DL**, data taken from the literature; **DS**, dry skeleton; **UN**, uncatalogued.

*Ascaphus truei*, DL (Gardner et al., 2010)
*Bombina variegata*, FCEN 401 (DS)
*Discoglossus pictus*, FCEN UN (DS)
†*Eoxenopoides reuningi*, SAM-K 4597, 4599, 4600, 4603, 4604, 4610, 4615, 4619, 4620, 9938, 9940, 9945, 9956. Latex molds.
*Hymenochirus boettgeri*, MACN 42621 (CS)
*Pelobates cultripes*, MACN 42618 (CS), 42619 (CS)

*Pipa carvalhoi*, MACN 42606 (DS), 42607 (DS), 42608 (DS), 42609 (CS), 42610 (CS)
*Pipa parva*, MACN 42614 (DS), 42615 (DS)
*Pipa pipa*, MACN 42612 (DS), 42613 (DS)
*Pipa snethlageae*, MACN 42611 (DS)
*Platyplectrum ornatum*, MACN 42620 (DS)
*Rhinophrynus dorsalis*, MACN 42616 (CS), 42617 (DS)
†*Saltenia ibanezi*, CPBA-V- 9743, MLP 62-XII-66. Latex molds.
†*Shelania pascuali*, PVL 3393, 3396; BAR 3330–44, 3722–44; CPBA-V-12219, 12231, 12224; MPEF-PV 1150, 1562. Latex molds.
*Silurana tropicalis*, MACN 42625 (CS), 42633 (DS)
*Xenopus boumbaensis*, KU 206928 (DS)
*Xenopus fraseri*, MACN 42627 (CS), 42628 (CS), 42629 (DS)
*Xenopus gilli*, MACN 42630 (DS), KU 206865 (DS)
*Xenopus laevis*, FCEN 1435 (DS), UN (DS)
*Xenopus largeni*, MACN 42622 (CS), 42634 (DS), 42635 (DS), KU 206863 (DS)
*Xenopus muelleri*, MACN 42631 (DS)
*Xenopus pygmaeus*, KU 206872 (DS)
*Xenopus vestitus*, KU 206873 (DS)
*Xenopus wittei*, MACN 42623 (CS), 42624 (DS), KU195673 (DS)
*Xenopus* sp., MACN 42626 (CS), 42632 (DS)
†*"Xenopus" romeri*, DGM 572

APPENDIX 2. Description of characters used in phylogenetic analysis. Character list modified from Báez et al. (2007). All multistate characters were treated as unordered.

(1) Preorbital region, relative length: (0) one-third, or more, of the skull length; (1) one-quarter, or less, of the skull length.
(2) Nasals, fusion: (0) not fused; (1) fused.
(3) Frontoparietals, relationship with nasals: (0) not overlapping; (1) overlapping.
(4) Frontoparietals, fusion to one another: (0) not fused or partially fused; (1) completely fused.
(5) Frontoparietals, posterolateral extensions: (0) absent; (1) present.
(6) Frontoparietal fenestra, anterior margin: (0) anterior margin formed by sphenethmoidal ossification; (1) anterior margin cartilaginous.
(7) Olfactory foramina, margins: (0) bound completely or partially in bone; (1) bound in cartilage.
(8) Planum antorbitale, ossification: (0) completely cartilaginous or ossified/mineralized less than one-half; (1) ossified/mineralized more than one-half.
(9) Optic foramina, margins: (0) bound in cartilage or cartilage and bone; (1) bound completely in bone.
(10) Floor of the braincase in the orbital region, shape: (0) rounded; (1) distinctly angled.
(11) Eustachian canal: (0) absent; (1) present.
(12) Inferior perilymphatic foramina, presence: (0) present; (1) absent.
(13) Inferior perilymphatic foramina, position: (0) anterior to jugular foramen; (1) posterior to jugular foramen; (2) ventral to jugular foramen.
(14) Superior perilymphatic foramina: (0) present; (1) absent.
(15) Premaxilla, palatine process development: (0) weakly or moderately developed; (1) well developed, long; (2) very long, dagger-like.
(16) Maxilla, relation with premaxilla: (0) not or slightly overlapping premaxilla; (1) overlapping premaxilla with pointed process of the pars facialis that reaches alary process; (2) nearly or completely overlapping premaxilla anteriorly.
(17) Maxilla, antorbital process: (0) absent or weakly developed; (1) present, well developed.

(18) Maxilla, parts in the orbital region: (0) distinct; (1) not distinct.

(19) Maxillary arcade: (0) complete; (1) incomplete.

(20) Septomaxilla, shape: (0) convolute; (1) flat.

(21) Vomers, presence: (0) present; (1) absent.

(22) Vomers, fusion: (0) paired; (1) fused to each other.

(23) Parasphenoid, relationship to braincase: (0) not fused; (1) partially or completely fused.

(24) Parasphenoid, alae: (0) present; (1) absent.

(25) Parasphenoid, anterior extent of cultriform process: (0) not reaching maxillary arcade; (1) reaching maxillary arcade.

(26) Parasphenoid, posteromedial extent: (0) extending near the ventral margin of the foramen magnum; (1) ending well anterior to the ventral margin of the foramen magnum.

(27) Squamosal, shape: (0) 'T'-shaped; (1) conch-shaped.

(28) Squamosal, zygomatic ramus: (0) well developed; (1) reduced or absent.

(29) Prootic, pterygoid knob: (0) absent or poorly developed; (1) well developed.

(30) Pterygoid, anterior ramus: (0) present; (1) absent.

(31) Pterygoid, anterior ramus position: (0) medial to maxilla; (1) dorsal to maxilla.

(32) Pterygoid, medial ramus: (0) present; (1) reduced or absent.

(33) Pterygoid, medial ramus distal margin: (0) lacking indentation; (1) with indentation.

(34) Pterygoid, configuration in otic region: (0) not expanded; (1) expanded to form an otic plate.

(35) Pterygoid, contact between medial ramus and parasphenoid: (0) absent; (1) present.

(36) Pterygoid, fusion to otic capsule: (0) not fused; (1) fused.

(37) Angulosplenial, coronoid process: (0) poorly developed; (1) well developed but short; (2) long, blade-like.

(38) Mentomeckelian bone: (0) present; (1) absent.

(39) Jaw articulation, position: (0) lateral to the otic capsule; (1) at the anterior margin of the otic capsule; (2) posterior to the otic capsule.

(40) Teeth: (0) present; (1) absent.

(41) Posteromedial process of the hyoid apparatus, length: (0) less than one-half of the anteroposterior length of the lower jaw; (1) more than one-half of the anteroposterior length of the lower jaw.

(42) Posteromedial process of the hyoid apparatus, anterior end: (0) wider than posterior end; (1) narrower than posterior end.

(43) Parahyoid bone: (0) present; (1) absent.

(44) Ceratohyal ( = hyale): (0) not ossified; (1) ossified.

(45) Vertebral centra, formation: (0) perichordal; (1) epichordal I, only the most dorsal part of the perichordal tube chondrifies; (2) epichordal II, both dorsal and ventral parts of the perichordal tube chondrify.

(46) Vertebral centra, articulation facets: (0) notochordal; (1) opisthocoelous; (2) procoelous.

(47) Postzygapophyses, articulation facets: (0) flat; (1) with grooves and ridges; (2) curved ventrally.

(48) Posterior presacral vertebrae (except last presacral), posteromedial margin of neural arch: (0) slightly concave to straight or with a minute neural spine; (1) projecting in a well-developed neural spine; (2) deeply notched.

(49) Presacral vertebrae I and II: (0) not fused, weak or no imbrication; (1) not fused, broad imbrication medially only; (2) not fused, broad imbrication involving all the neural laminae; (3) synostotically fused; (4) synchondrotically fused.

(50) Ribs: (0) free ribs present in larvae and adults; (1) free ribs present in larvae and fused to transverse processes in adults; (2) ribs absent in larvae and adults.

(51) Sacrum and urostyle: (0) monocondylar; (1) bicondylar; (2) fused; (3) notochordal.

(52) Clavicle, relationship to scapula: (0) lateral end contacts medial edge of pars acromialis; (1) lateral end overlaps anterior edge of pars acromialis; (2) lateral end is fused to scapula.

(53) Clavicle, medial end: (0) not expanded; (1) expanded.

(54) Scapula, proportions: (0) glenoid area one-third total length of the scapula; (1) glenoid area more than one-third total length of the scapula.

(55) Scapula, medial notch: (0) present; (1) absent.

(56) Cleithrum: (0) not covering the posterior edge of the suprascapular cartilage; (1) covering part of the posterior edge of the suprascapular cartilage.

(57) Coracoid, sternal expansion relative to coracoid length: (0) sternal expansion less than half the length of the coracoid; (1) sternal expansion nearly half the length of the coracoid; (2) sternal expansion nearly the length of the coracoid.

(58) Iliac shaft, shape of the proximal cross-section of the pars cilindriformis: (0) circular or nearly so, iliac shaft not compressed mediolaterally; (1) vertically oval, iliac shaft compressed mediolaterally.

(59) Iliac shaft, shape of the distal cross-section of the pars cilindriformis: (0) circular or nearly so, iliac shaft uncompressed dorsoventrally; (1) horizontally oval, iliac shaft fairly compressed dorsoventrally; (2) flattened, iliac shaft much compressed dorsoventrally.

(60) Dorsal prominence, relative height with respect to that of the acetabular fossa: (0) very low; (1) low to moderately high; (2) very high.

(61) Dorsal prominence, shape in lateral profile: (0) bell-shaped, symmetrical or nearly so with both anterior and posterior margins gently sloping; (1) rectangular, symmetrical or nearly so with both anterior and posterior margins steep; (2) clearly assymetrical with a posterior convex slope and an anterior margin steep and slightly concave.

(62) Dorsal prominence, orientation in dorsal aspect: (0) not inclined, vertically directed; (1) inclined medially; (2) inclined laterally.

(63) Dorsal prominence, relative position of its apex with respect to the anterior margin of acetabular fossa: (0) clearly posterior; (1) approximately same level; (2) clearly anterior.

(64) Dorsal protuberance: (0) inconspicuous; (1) conspicuous.

(65) Dorsal protuberance, shape: (0) elongate, projecting laterally; (1) nearly rounded, projecting laterally; (2) globose, projecting dorsolaterally.

(66) Dorsal crest: (0) absent; (1) present as a low ridge; (2) well developed as a flange (wider than one half of the shaft width).

(67) Dorsal crest, longitudinal extension relative to iliac shaft length: (0) restricted to distal half of the iliac shaft; (1) extends along the anterior three fourths of the iliac shaft; (2) extends lengthwise or nearly so; (3) restricted to the proximal part of the iliac shaft.

(68) Dorsal crest, orientation: (0) directed dorsally; (1) directed dorsolaterally; (2) directed laterally.

(69) Oblique ridge, short ridge anterior to the acetabulum on the lateral surface of the shaft: (0) absent or barely evident; (1) distinct.

(70) Interiliac scar: (0) absent to narrow; (1) ample, but restricted to ventral part of ilia; (2) ample both ventrally and dorsally.

(71) Angle between the margin of the ventral acetabular expansion and the ventral margin of the iliac shaft in acetabular view: (0) acute; (1) nearly straight; (2) obtuse.

(72) Dorsal acetabular expansion, lateral exposure in acetabular view: (0) broad; (1) narrow but distinct; (2) minimal, inconspicuous.

(73) Ilium and ischium, relation: (0) not fused; (1) fused to each other.

(74) Ischium, shape of the posterior wall of the acetabulum in dorsal view: (0) slightly concave; (1) deeply concave.

(75) Pubis: (0) cartilaginous; (1) ossified.

(76) Distal os sesamoides tarsale: (0) absent; (1) present.

APPENDIX 3. Data matrix used in phylogenetic analysis. **?**, missing data or not applicable; **A**, (0, 1); **B**, (1, 2); **C**, (1, 3); **D**, (3, 4); †, extinct taxa.

| | 1 0 | 2 0 | 3 0 | 4 0 | 5 0 |
|---|---|---|---|---|---|
| *Ascaphus truei* | 0000021000 | 01?0000000 | 0000000000 | 0000000000 | 0000000000 |
| †*Avitabatrachus uliana* | 10?10?0100 | 1?????11? | ??01?11000 | ?001001?10 | 00???101DB |
| *Bombina variegata* | 0000000000 | 0000000000 | 0000000000 | 0000001000 | 0100110010 |
| *Discoglossus pictus* | 0000000000 | 0010000000 | 0000000000 | 0000001000 | 0000110110 |
| †*Eoxenopoides reuningi* | 10110?0111 | 1???01011? | 0111101100 | 1001002101 | ?????10031 |
| *Hymenochirus boettgeri* | 1001010111 | 11?0220111 | 1?11011101 | ?001112111 | 0111212241 |
| †*Llankibatrachus truebae* | 10110???10 | 1????11111 | ??11101010 | 1011??2101 | 11?0?10?D1 |
| *Pelobates cultripes* | 0001100000 | 0010000000 | 0000000000 | 0000001000 | 0010020112 |
| *Pipa carvalhoi* | 1011010011 | 11?0110111 | 1?11111100 | 1001102110 | 0110210241 |
| *Pipa pipa* | 1011110011 | 11?0110111 | 1?11A11100 | 1001101121 | ????210241 |
| *Platyplectrum ornatum* | 0000100000 | 0010001000 | 0?00000?00 | 0000001000 | 0110020132 |
| *Pseudhymenochirus merlini* | 10?1010111 | 11?0220111 | 1?11011101 | ?001112111 | 1111212241 |
| *Rhinophrynus dorsalis* | 0011000001 | 0010000000 | 0001000100 | 01??00111 | 0000000122 |
| †*Saltenia ibanezi* | 1011000010 | 1???0?1?1? | 0?11101110 | 10?1002111 | 11?0?100A1 |
| †*Shelania laurenti* | ??11000010 | 1021??111? | 0?11?01?1? | ?????????? | ?????100DB |
| †*Shelania pascuali* | 1A11000010 | 1???011111 | 0111101010 | ?011002101 | 1110?10011 |
| *Silurana tropicalis* | 1011011010 | 10?1010111 | 1?11101010 | 1011002100 | 1110211031 |
| †*Vulcanobatrachus mandelai* | 10?101?0?0 | 1?????1?1? | 1?111?1100 | ????00?111 | 11?0??0?31 |
| *Xenopus laevis* | 1111011010 | 1011010111 | 0111101010 | 1011002100 | 11102110C1 |
| *Xenopus wittei* | 1111011010 | 1011010111 | 0111101010 | 1011002100 | ????211011 |
| †``*Xenopus*'' *romeri* | 1111000010 | 1021?????? | 0111?0??1? | ?????0???? | ????0?100DB |
| †Daireaux pipid MMP M-5121 | ?????????? | ?????????? | ?????????? | ?????????? | ?????????? |

| | 6 0 | 7 0 | |
|---|---|---|---|
| *Ascaphus truei* | 3101101000 | -----0--00 | 110000 |
| †*Avitabatrachus uliana* | 21010?0A11 | 0000-0--1? | 210??? |
| *Bombina variegata* | 0101000011 | 0200-0--01 | 20000? |
| *Discoglossus pictus* | 1101001101 | 3221022000 | 10000? |
| †*Eoxenopoides reuningi* | 2?00??0111 | 00???0--?1 | 2A0010 |
| *Hymenochirus boettgeri* | 22000021?2 | 0011222112 | 221011 |
| †*Llankibatrachus truebae* | 22010100B? | ?????????2 | ???0?0 |
| *Pelobates cultripes* | 2000001000 | -----0--00 | 200000 |
| *Pipa carvalhoi* | 2100102121 | 0001122212 | 220011 |
| *Pipa pipa* | 2101102121 | 0001122212 | 220011 |
| *Platyplectrum ornatum* | 1000000101 | 3221013000 | 10000? |
| *Pseudhymenochirus merlini* | 22000021?1 | 000??221?2 | 221011 |
| *Rhinophrynus dorsalis* | 1100001100 | -----0--0? | 200000 |
| †*Saltenia ibanezi* | 21010?01B1 | ?0???0--?1 | ??00?? |
| †*Shelania laurenti* | 22?1???0?1 | 0000-????2 | 210??? |
| †*Shelania pascuali* | 2101010121 | 0000-0--?2 | 210010 |
| *Silurana tropicalis* | 2211010012 | 2010-10002 | 211010 |
| †*Vulcanobatrachus mandelai* | 2101000??? | ?????????1 | ???00? |
| *Xenopus laevis* | 2211110112 | 2010-21102 | 210110 |
| *Xenopus wittei* | 2211110012 | 1010-20102 | 21111? |
| †``*Xenopus*'' *romeri* | 22?10??0?1 | 0000-0--12 | 2100?? |
| †Daireaux pipid MMP M-5121 | ???????0?1 | 0000-0--12 | 210??? |