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## **A new pipid from the Cretaceous of Africa (In Becetèn, Niger) and early evolution of the Pipidae**

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## Abstract

Pipimorpha and its crown-group Pipidae possess one of the most extensive fossil records among anurans, known since the Early Cretaceous in both Laurasia and Gondwana. Pipimorph diversification may have been driven by the breakup of West Gondwana during the Cretaceous. Numerous fossils from South America have been unearthed in the last decade, documenting this event. Unfortunately, Cretaceous pipimorphs from Africa have been limited to a few well-preserved taxa from sub-Saharan Africa and the Arabian Peninsula, which hinders our comprehension of pipimorph diversification during this key period. The site of In Becetèn, in Southeast Niger, is one of the few mid-Late Cretaceous (Coniacian-Santonian) sites from which a pipid, *Pachycentrata taqueti*, is known. Here, we describe a second pipid from the same locality. This taxon is known by a relatively complete braincase. Phylogenetic analyses confirm its position as a pipid, with pipinomorph affinities. This makes In Becetèn the oldest site with at least two pipids. Phylogenetic results are congruent with recent pipimorph relationships, with the presence of an endemic extinct clade in South America, Shelaniinae. The phylogenetic results also allow us to review the proposed definition for Pipimorpha and its subclades and propose new systematic definition for them. Temporal calibration of the phylogenetic tree based on the fossil record implies that Pipidae underwent two vicariance events during the Early/Late Cretaceous, during the breakup of western Gondwana. Between these two events, pipids diverged in Africa, giving rise to major extant clades. This study highlights the importance of Africa for early pipid diversification during the Cretaceous and of the opening of the Southern Atlantic Ocean for anuran dispersion and diversification.

Keywords: Anura, Pipidae, Cretaceous, Africa, Phylogeny, Paleobiogeography.

## Introduction

The Pipimorpha, which includes extant aquatic pipids, possess one of the most extensive fossil records (at least 26 extinct genera known) of any anuran clade, with numerous remains attributed to the clade since the Early Cretaceous (Marjanović and Laurin, 2014; Báez et al., 2021). In particular, they possess an extensive Cretaceous fossil record from both Gondwana and Laurasia (Gardner and Rage, 2016; Báez et al., 2021). This period is key for the evolutionary history of pipimorphs as the clade diversified rapidly (Frazão et al., 2015; Feng et al., 2017), possibly driven by the breakup of the West Gondwanian subcontinent, made of South America and Africa (Powell et al., 1980; Gaina et al., 2013; Will and Frimmel, 2018). During the last decade, several well-preserved pipimorphs have been described from South America (Leal and Brito, 2006; Báez et al., 2009, 2021; Carvalho et al., 2019), documenting the early diversification and evolution of this clade in particular during the Early/Late Cretaceous transition, around the time when Africa and South America became separated (Báez et al., 2021).

Few pipimorphs are known from the Cretaceous of Africa, and these are mostly restricted to the Early Cretaceous of the Arabian Peninsula (three pipimorphs known; *Nevobatrachus* Mahony, 2019; *Shomronella* Estes et al., 1978; *Thoraciliacus* Nevo, 1968; Gardner and Rage, 2016) and the Late Cretaceous of South Africa (two pipimorphs known; *Vulcanobatrachus* Trueb et al., 2005; *Eoxenopoides* Haughton et al., 1931). In addition, only two pipid taxa are known, *Oumtkoutia anae* Rage and Dutheil, 2008 from Morocco and *Pachycentrata* (replacement name for *Pachybatrachus*; Báez and Rage, 2004) *taqueti* Báez and Rage, 1998 from Niger. Both are from lower Late Cretaceous outcrops.

During the late 1990s, a strange pipid, *Pachycentrata taqueti* (*Pachybatrachus taqueti* in Báez and Rage, 1998), was described from the Coniacian-Santonian beds of In Becetèn (Niger; Báez and Rage, 1998, 2004). In addition to this taxon, a braincase, attributed to an indeterminate xenopodinomorph (Báez and Púgener, 2003), a clade composed of Xenopodinae (*Xenopus* + *Silurana*) and all taxa closer to the latter than to all other extant pipids, was described (Báez and Rage, 1998: fig. 3H-K). Only *P. taqueti* has been included in phylogenetic analyses (Trueb et al., 2005; Báez et al., 2007; Gómez, 2016; Carvalho et al., 2019; Aranciaga Rolando et al., 2019). As part of an ongoing study of the anuran diversity of In Becetèn, we here take the opportunity to redescribe this braincase, and include it in a phylogenetic analysis of the pipimorphs to test whether it can be attributed to the Xenopodinomorpha as originally proposed. In addition, the phylogenetic analysis also suggests several scenarios about pipimorph dispersals between South America and Africa. This constrains the timing of the separation of these two continents by the South Atlantic Ocean, as we show below.

## Geological context

All specimens came from the site of In Becetèn (also known as In Becetem, In Beceten, In'Betetén, In Béceten, Ibesseten and erroneously Ibeceten; pers. com. D. Dutheil, Dec. 2021). They were collected during three expeditions in 1970, 1972 and 1973, organised by the Muséum national d'Histoire naturelle de Paris (France), led by P. Taquet and D. Russell (Broin et al., 1974). Anuran specimens were recovered from thin black/grey shale beds (de Broin et al., 1974; Moody and Sutcliffe, 1991; Meunier and Larsson, 2018) either during screen-washing operations or were exposed on the ground surface (de Broin et al., 1974). The site of In Becetèn is located 80 km east north-east of the town of Tahoua, in the

southwestern region of the Republic of Niger (Fig. 1; Báez and Rage, 1998: fig. 1). This site has been known since the 1970s, for its diverse vertebrate fauna (de Broin et al., 1974), because with the exception of mammals, all large continental vertebrate clades (Dinosauria, Pseudosuchia, Teleostei, Squamata, Lissamphibia) have been identified (Broin et al., 1974; Patterson, 1993; Gayet and Meunier, 1996; Báez and Rage, 1998; Lapparent, 2000; Gardner and Rage, 2016; Lapparent de Broin et al., 2020).

[Insert Figure 1 here]

The site of In Becetèn is located within the Iullemeden (or Iullmeden) basin. This Basin represents a vast sedimentary basin of Northern Africa, characterised by an alternation of marine and continental deposits established during the Cretaceous and the Paleogene (Greigert, 1966; Greigert and Pognet, 1967; Broin et al., 1974; Moody and Sutcliffe, 1991). Within this basin, fossiliferous layers, including those of In Becetèn, are part of the Ibeceten Formation (Moody and Sutcliffe, 1991). This formation is composed of an alternation of shales and sandstones (Moody and Sutcliffe, 1991).

A precise age for the Ibeceten Formation is currently difficult to propose, as it is the case for most continental Formations from the Late Cretaceous of Africa, with most of them referred to the Senonian (part of the Late Cretaceous, from the Coniacian to Maastrichtian; Moody and Sutcliff, 1991). The Ibeceten Formation has been incorporated into the Damergou Series, which spans from Late Cretaceous to Eocene (Moody and Sutcliffe, 1991).

The Damergou series unconformably overlies Cenomanian deposits. The Talrass Formation, at the base of the Damergou series, is overlaid by the 'White Limestone' Formation composed of marine limestone, dated and correlated to the Late Turonian transgression (Moody and Sutcliffe, 1991). The Ibeceten Formation overlays this 'White Limestone' Formation and represents nonmarine and marine deposits. The base of the

Ibeceten formation is composed of nonmarine beds, where anuran specimens were collected (Broin et al., 1974; Moody and Sutcliffe, 1991), and upper marine beds dated from the Santonian/Campanian marine transgression (Moody and Sutcliffe, 1991). The unit overlaying the Ibeceten Formation is composed of marine beds dated to the Campanian-Maastrichtian (Greigart and Pougnet, 1967; Moody and Sutcliffe, 1991). The Ibeceten Formation is thus dated to the Coniacian or Santonian (Early Senonian; Broin et al., 1974). However, correlations of the Iullemeden Basin with other African Cretaceous basins suggest that the Ibeceten Formation dates from the Santonian (Mateer et al., 1992). Nevertheless, in the absence of recent stratigraphical work on the In Becetèn site, we follow previous paleontological studies and considered the site to be Coniacian or Santonian.

The nonmarine Ibeceten beds are considered to represent fluvial-lacustrine deposits, based on fossil evidence (Greigart, 1966; Moody and Sutcliffe, 1991). However, paleogeographical studies of the region have shown that several transgression/regression events took place in the Iullemeden Basin (Moody and Sutcliffe, 1991) during the Late Cretaceous. Stratigraphical evidence from neighboring sites (based on fossil evidence; Moody and Sutcliffe, 1991) indicates that paleoshoreline was near the site (Moody and Sutcliffe, 1991). Marine influence within the fossiliferous beds thus cannot be excluded.

## **Materials and methods**

### **Institutional abbreviations**

**MNHN:** Muséum national d'Histoire naturelle, Paris, France. All specimens are stored within the Paleontological collection of the MNHN of Paris (France) in the Amphibians and Reptiles

section, under the collection number MNHN.F.IBC XXXX (indicating they are part of the fossil collection from In Bécetèn).

### **Micro-CT scan**

MNHN.F.IBC 1602 was micro-CT scanned at the AST-RX (Accès Scientifique à la Tomographie à Rayons X) at the UMS 2700, MNHN (Paris France). A nanofocus beam of 180 kV of the CT scanner was used with the following parameters: voltage, 125 kV; current, 245  $\mu$ A; voxel size, 7.847  $\mu$ m; slice resolution, 1666 x 1676 pixels. A total of 2312 virtual slices were reconstructed. These slices were imported into the 3D reconstruction software Mimics 21.0 (Materialise, Leuven, Belgium). Before importation, slices were cropped to remove empty space. To decrease data size, slices were converted from 16 to 8 bits. The dataset thus includes 1868 slices, with an image resolution of 1300 x 1222 pixels and a voxel size of 15.69  $\mu$ m for the volume file (see Appendix S1 in Supplemental Data 1). The 3D model was produced by segmentation of each bone using the ‘thresholding’ function (using the contrast on grayscale images). We used the same voxel resolution of 15.69  $\mu$ m, with a smoothing factor of 3 for one iteration, to homogenize the model resulting from manual segmentation. Data produced by segmentation were exported in the software 3matic 9.0 as a separate file (see Appendix S2, S3 in Supplemental Data 1).

The anatomical terminology used herein is based on Roček (1980) and Biton et al. (2016) for cranial features, and Sanchíz (1998) for postcranial ones. Anatomical terminology for cranial nerves follows Gaupp (1896).

### **Phylogenetic analyses**

Our data matrix (Appendix S4 in Supplemental Data 1) includes 43 taxa and 176 osteological characters and is derived from that of Aranciaga Rolando et al. (2019; see Appendix S5 in



Supplemental Data 1 for the list of characters). We added five extinct pipimorph taxa; (1) *Aygroa anoualensis* Jones et al., 2003, (2) *Cratopipa novaolindensis* Carvalho et al., 2019; (3) *Xenopus arabiensis* Henrici and Báez, 2001; (4) '*Xenopus*' *stromeri* Ahl, 1926 and (5) *Inbecetanura ragei* gen. nov. et sp. nov. (see Appendix S6 in Supplemental Data 1). Except for *Inbecetanura* gen. nov., newly added taxa were scored from both personal observation and literature (Henrici and Báez, 2001; Jones et al., 2003; Carvalho et al., 2019; Lasseron et al., 2019; Báez et al., 2021). Several other taxa were rescored (see Appendix S7 in Supplemental Data 1) from both personal observations on specimens and on a 3D model (holotype of *Oumtkoutia anae*), and from literature (Estes, 1975; Trueb, 1999; Rage, 2008).

All analyses were performed using TNT v.1.5 (Goloboff and Catalano, 2016) under equal weights. All analyses were conducted with clinal characters ordered (characters 18, 32, 33, 36, 38, 39, 59, 74, 82, 97, 98, 108, 120, 141, 145, 149, 173) in the analyses with or without topological constraint (Rineau et al., 2015; 2018). All analyses consisted of heuristic searches with 1000 random addition sequences of taxa, followed by tree bisection-reconnection (TBR) branch swapping, holding 10 trees per repetitions. The final trees were rooted on *Ascaphus truei* (Ascaphidae), and when more than one most parsimonious tree was found, a strict consensus was obtained. Constrained analysis was performed using the topology of Jetz and Pyron (2018) for extant taxa (Fig. S1). Node support was quantified using Bremer support and standard bootstrap, with traditional searches of 1000 replicates, collapsing groups below 5% frequency.

### **Nomenclatural typographic conventions**

Throughout this paper, we use the following conventions for the writing of different kinds of nomina (scientific names):

[A] Nomina managed under the current International Code of Zoological Nomenclature (Reference) are presented according to the following standard formats: italic lowercase letters for nomina of species and genera (e.g. *Inbecetenanura*, *Inbecetenanura ragei*)

[B] Nomina managed additionally under the PhyloCode (following Recommendations 6.1A) are presented in bold italic lower-case letters (e.g., ***Pipidae***).

~ : but not.

∇ : clade.

RegNum registration number: registration number of the name definition on the RegNum website <https://www.phyloregnum.org>

### **Systematic palaeontology**

**Anura** Duméril, 1805

**Pipoidea** Fitzinger, 1843

**Pipimorpha** Ford and Cannatella, 1993

**Gondwanamorpha**, nomen novum

**Pipidae** Gray, 1825

?**Pipinomorpha** Báez and Púgener, 2003

Genus *Inbecetenanura* gen. nov.

**Type species.** *Inbecetenanura ragei* sp. nov.

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

**Derivation of the name.** The name *Inbecetenanura* (female) is a combination of In Becetèn, the type locality, and “anura”, latin word for the crown clade of frogs and toads.

*Inbecetenanura ragei* gen. nov. and sp. nov.

Unidentified genus and species: Báez and Rage, 1998 p. 680-684, text-figs 3H-K, pl. 1 : figs 8-11.

**Holotype.** One braincase with otic capsules (MNHN.F.IBC 1602).

**Derivation of the name.** Named after the late Dr. Jean-Claude Rage, palaeontologist from the MNHN, to honour his work on amphibians from Africa, including from In Becetèn.

**Stratigraphic range.** Coniacian or Santonian (91.1 to 83.4 Ma).

**Diagnosis.** Pipid frog that differs from all Xenopodinae in (1) having the parasphenoid posteromedial extent ending well anterior to the ventral margin of the foramen magnum (ending near the ventral margin of the foramen magnum in Xenopodinae); (2) having olfactory foramina completely bound in bone (bound in cartilage in Xenopodinae) and (3) having its orbitonasal foramina completely bound in bone (incompletely bound in bone in Xenopodinae, except in *Xenopus laevis*).

Differs from all other pipinormorphs in (1) having the floor of the braincase rounded in the orbital region (distinctly angled in all other pipinormorphs) and (2) in having the anterior margin of the *fenestra frontoparietalis* of the sphenethmoid completely delimited by bone (not delimited in bone in all other pipinormorphs, except *Eoxenopoides*).

Differs also from *Pachycentrata taqueti* in (1) lacking a vermicular ornamentation on the cranial bones (present in *Pachycentrata*); (2) lacking a posterior bony expansion of the prooticoccipital, located posterolaterally to the occipital condyles (present in *Pachycentrata*) and (3) having ovoid occipital condyles (crescentic in *Pachycentrata*).

Differs from *Oumtkoutia anae* in (1) having wider and larger optic and oculomotor foramina (small circular foramina in *Oumtkoutia*; Rage and Dutheil, 2008: fig. 6); (2) having lateral expansion of the parasphenoid at midlength (absent in *Oumtkoutia*); (3) having ovoid occipital condyles (crescentic in *Oumtkoutia*) and (4) having a wider orbitonasal foramen (small and circular in *Oumtkoutia*; Rage and Dutheil, 2008: fig. 4).

Differs from *Eoxenopoides* in (1) having a slight orbital constriction (absent in *Eoxenopoides*); (2) having a posterior end of the frontoparietal convex posteriorly (convex posteriorly and forming a small posterior process in *Eoxenopoides*); (3) extensive fusion of the bones of the braincase (frontoparietal, sphenethmoid, parasphenoid, exoccipitals) with sutures barely visible; (4) having lateral expansion of the parasphenoid present midlength (absent in *Eoxenopoides*) and (5) in having the parasphenoid ending posteriorly well anterior to the foramen magnum (almost at the level of the foramen magnum in *Eoxenopoides*).

Differs also from *Hymenochirus* and *Pseudhymenochirus* in (1) having a rounded braincase in lateral view (wedge-shaped in *Hymenochirus* and *Pseudhymenochirus*), (2) having frontoparietal lacking anterolateral processes and (3) lacking a medial ramus of the pterygoid fused to the otic region of the braincase. Differs additionally from *Pseudhymenochirus* in having frontoparietal and nasals not fused to each other (fused in *Pseudhymenochirus*).

Differs from *Pipa* in (1) having a rounded braincase in lateral view (wedge-shaped in *Pipa*); (2) lacking anterolateral processes of the frontoparietal; (3) having the floor of the braincase in the orbital region rounded (distinctly angled in *Pipa*); (4) having occipital condyles ovoid

(flat and circular in *Pipa*); (5) occipital condyles narrowly separated (well separated in *Pipa*) and (6) having the anterior margin of the frontoparietal rounded (acuminated in *Pipa*).

## Results

### Description of *Inbecetenanura ragei* sp. nov

The holotype is an incomplete braincase, with the following bones preserved: frontoparietals, sphenethmoid, parasphenoid, prootic and exoccipitals. The last two bones are fully fused together, forming a prooticooccipital complex. This braincase exhibits an intense hyperossification, with a fusion of all bones, leaving the sutures barely visible (Fig. 2). The braincase is fully enclosed in bone, with the lateral walls fully ossified (Fig. 2). In lateral view, the braincase is rounded.

[Insert Figure 2 here]

**Frontoparietals.** The frontoparietals are fully fused, without any trace of medial suture and forming an azygous bone. Hence, they will be referred to as a single bone in the description. The fusion to the neighboring bones made its segmentation difficult. However, its margins are still distinguishable (Fig. 2C). The anterior region of the frontoparietal is smaller than the posterior region, indicating a slight orbital constriction.

[Insert Figure 3 here]

The frontoparietal is lacking anterodorsal, rostral and posterolateral processes (Fig. 2A, 3A). In dorsal view, faint parasagittal crests are present on each side, delimiting a flat and smooth frontoparietal table (Fig. 2C, 3A). On the frontoparietal table, several shallow pits are visible.

They likely represent damage caused by taphonomy or diagenesis. Other artefacts, such as striations extending anteroposteriorly, are visible on the frontoparietal table (Fig. 2E).

The anterior margin of the frontoparietal is convex. The bone covers most of the sphenethmoid, leaving only a small region visible in dorsal view (= *septum nasi* in Fig. 2A). In the anterior region of the frontoparietal, the pineal foramen is present in medial position (Fig. 2A, C, 3A, B). On the dorsal surface of the frontoparietal, a shallow groove extends from the pineal foramen up to the anterior margin of the bone. Posteriorly, the frontoparietal is extensive and covers most of the medial region of the prooticoccipital. The posterior margin of the bone is convex.

In ventral view, the anterior region of the bone is smooth. It is delimited posteriorly by the *fenestra frontoparietalis* (Fig. 3B). The anterior margin of the fenestra is convex. Midlength of the *fenestra frontoparietalis*, the *facies cerebralis anterior* (Jarošová and Roček, 1982) are a paired anteroposteriorly elongate ovoid imprints. Posteriorly, the *facies cerebralis posterior* is large and transversely elongate (Fig. 3B). This configuration of *incrassation frontoparietalis* occurs in several extant and extinct pipids, like *Xenopus laevis* (Špinar, 1976) and *Shelania pascuali* (Báez and Púgener, 1998). This suggests that a *taenia tecti transversalis* was present as a cartilaginous element (Špinar, 1976; Jarošová and Roček, 1982).

**Sphenethmoid.** The sphenethmoid is a rhomboid bone. It is fused ventrally to the parasphenoid, dorsally to the frontoparietal and posterolaterally to the prooticoccipital.

In dorsal view, the anterior region of the bone is covered by the frontoparietal except for the *septum nasi*. The latter is thick and strongly ossified (Fig. 2A, C). The exposed *septum nasi* was likely covered by the nasals, and there is no indication if the nasals were paired or fused

(unlike in *Oumtkoutia anae*; Rage and Dutheil, 2008). The anterior margin of the *fenestra frontoparietalis* is deeply concave anteriorly (Fig. 4A). The *solum nasi* is thick (Fig. 4).

[Insert Figure 4 here]

The *septum nasi* is ossified and elongate anteroposteriorly (Fig. 4B). Its anterior margin is broken but it suggests that the *septum* was fully ossified. This *septum* separates the two nasal cavities medially. Each nasal cavity is large and opens anterolaterally (Fig. 4B). In each nasal cavity, the paired orbitonasal foramina are preserved. Both foramina open externally as anteroposteriorly elongated foramina on the lateral side of the sphenethmoid (Fig. 2G, 4B). At the bottom of each nasal cavity, the nasal foramen is small and circular (Fig. 4B). On the surface of the internal walls of the nasal cavities, shallow anteroposteriorly oriented striations are visible (Fig. 2E). They likely resulted from diagenetic damages.

The sphenethmoid ossification has invaded the orbital cartilage, fusing posteriorly with the prooticoccipital around the level of posterior margin of the fused optic and oculomotor foramina (Fig. 2B, D). Posterior to the orbitonasal foramen, several anteroposteriorly oriented shallow striations are present on each lateral wall of the sphenethmoid. They likely represent diagenetic damages. Posteriorly, a large opening, the fused optic and oculomotor foramina, is present. This opening is elongate anteroposteriorly and constricted at midlength, allowing for partial distinction of the two foramina (Fig. 2G). The optic foramen (anterior region of the opening) seems elongated anteroposteriorly (Fig. 2G), while the oculomotor foramen (posterior region of the opening) is elongated dorsoventrally (Fig. 2G). Slightly below the level of the oculomotor foramen, a small canal and an internal carotid foramen are located on the lateral surface of the braincase (Fig. 2G) medial to the pseudobasal process (ossified portion of the palatoquadrate; Pyles, 1988; Trueb et al., 2000). The internal carotid foramen opens anteriorly (Fig. 2G). Ventral to this foramen, a small circular foramen (putative palatine

foramen) is present (Fig. 2D). Dorsal to the fused optic and oculomotor foramina, a small circular trochlear foramen is also present.

In ventral view, the cultriform process of the parasphenoid covers most of the ventral surface of the sphenethmoid (Fig. 2D, 3C).

**Prooticooccipital complex.** The prooticooccipital is strongly ossified, without a trace of sutures between the different bones, forming one complex fused anteriorly to the sphenethmoid, dorsally to the frontoparietal, and ventrally to the parasphenoid (Fig. 2A- D). In dorsal view, the crista parotica is fully ossified, with an anterolateral expansion (Fig. 2A, C). Except for the epiotic eminence present medially on each side, there are no crests. Medially, both exoccipitals are fused dorsally, forming a thin bridge that roofs the posteriormost portion of the braincase, posterior to the frontoparietal. In anterior and lateral views, the prootic foramen is elongate lateromedially (Fig. 2E, G). This foramen is separated from the fused optic and oculomotor foramina by the prepalatine connection (ossified *pila metopica* and *antopica*; Paterson, 1946). Ventrolateral to the fused optic and oculomotor foramina (and anteroventral to the prootic foramen), an anteroposteriorly elongated process is present (Fig. 2E, G). Its position is similar to the pseudobasal process (see De Beer, 1926; Pyles, 1988, see also “basal process” in Kotthaus, 1933; Reiss, 1997) identified in anurans. Hence, we interpret this structure as a pseudobasal process (identified as “pseudobasal articulation” in Báez and Rage, 1998). In ventral view, a shallow depression is visible between the posterior margin of the pseudobasal process and the anterior margin of the otic capsules (Fig. 2D). This depression seems to extend medially into a small canal (Fig. 2D). These canals are interpreted as remnants of the eustachian canals (Fig. 2D). There are no marks of fusion between the medial ramus of the pterygoid and the ventral surface of the braincase. Thus, the medial ramus of the pterygoid was not fused to the otic capsule (contrary



to the condition observed in *Hymenochirini*; Cannatella and Trueb, 1988). The otic capsules are crushed and broken, so almost no information can be recovered.

In posterior view, the foramen magnum is lateromedially wide (Fig. 1F, H). This might suggest the posterior region of the braincase was crushed dorsoventrally. The preserved right occipital condyle is dorsolaterally-ventromedially elongated. Judging by the putative position of the occipital condyles, they were narrowly spaced, but not connected posteromedially. Thus, the occipital articulation corresponds to the Type II of Lynch, 1971 (occipital cotyles narrowly spaced, two distinct articular facets).

Laterally, and partially hidden in posterior view, a large condyloid fossa is preserved. A large broken jugular foramen is preserved too (Fig. 2H). Ventrolateral to this foramen (within the condyloid fossa), a small dorsoventrally elongated foramen is visible on the right side. It opens intracranially within the otic capsules (Fig. 2G). Thus, it is interpreted as the inferior perilymphatic foramen. The foramen for the *arteria occipitalis* is small and located on each side of the posterior margin of epiotic eminence (Fig. 2H). It opens into a canal, extending anteromedially and exiting intracranially into the braincase.

**Parasphenoid.** This unpaired bone is fused to the surrounding elements and has been slightly crushed; its limits are hard to differentiate (Fig. 2B, D). The parasphenoid is a lanceolate bone that lacks subotic alae.

The cultriform process extends anteriorly to the level of the nasal cavities, but it does not seem complete (Fig. 2D, 3C). It narrows anteriorly. There is no indication that an azygous vomer was fused to the bone (contra Báez and Rage, 1998). Posterior to the level of the orbitonasal foramen, the margin of the parasphenoid is difficult to discern, but the cultriform process seems to widen gradually up to the level of the optic foramen. The bone widens abruptly at the anterior margin of the optic foramen, forming a large lateral expansion,

occupying most of the ventral width of the braincase (Fig. 2B, D; 3C). The cultriform process then narrows posterior to the anterior margin of the prootic foramen. The posterior margin of the parasphenoid is convex and slightly tapered (Fig. 2D; 3C). This margin is located well anterior to the foramen magnum, at the mid-level of the otic capsules.

[Insert Figure 5 here]

**Endocast of the braincase.** The preservation of the braincase allowed for the segmentation of most of its endocast, except the region of the otic capsules. The pathway for the olfactory nerve (CN I) is very short anteroposteriorly (Fig. 5A), and a barely discernible bulge ventral to the base of the CN I might be olfactory bulbs. The orbitonasal duct is short anteroposteriorly and flattened dorsoventrally. Both hemispheres of the telencephalon diverge (from each other) and protrude posteriorly (Fig. 5A, C). They are elongate anterolaterally, and their impressions on both endocast and frontoparietal are faint (Fig. 3B, 5A). Lateral to the telencephalon, both optic and oculomotor nerves pathways (CN II and CN III) are present (Fig. 5A, C). Posterior to the telencephalon no cranial nerves are discernible at the level of the prootic foramen (Fig. 5A, B). The optic lobe is an ovoid bulge elongate transversally. Anterior to the optic lobe, the hypothalamus is protruding as two small ovoid bulges on the ventral surface of the endocast (Fig. 5B, C). A partial pathway for the occipital nerves (cranial nerves IX and X) is preserved on the right side (Fig. 5B). These nerves exit the skull via the condyloid fossa.

## Discussion

The braincase of *Inbecetenanura* (MNHN.F. IBC1602) can be referred to pipids in (1) having orbitonasal foramina fully enclosed in bone; (2) having a lanceolate parasphenoid lacking subotic alae; (3) having optic foramina fully enclosed in bone; (4) having an azygous

frontoparietal (also present in numerous anuran clades) and (5) having fused parasphenoid and braincase. This braincase can be differentiated from *Pachycentrata* in (1) lacking pachyosteosclerosis, (2) lacking vermicular ornamentation on its dorsal surface; (3) lacking anterolateral process on the frontoparietal; (4) having ovoid occipital condyles (crescent shaped in *Pachycentrata*); (5) having a rounded braincase in lateral view (wedge-shaped in *Pachycentrata*). It can also be differentiated from *Eoxenopoides* in (1) having a heavily ossified skull with large fusion of frontoparietal, braincase and parasphenoid (all bones are sutured together and not fused in *Eoxenopoides*); (2) having a rounded posterior margin of the frontoparietal (pointed in *Eoxenopoides*); (3) having parasagittal crests; (4) having an ossified anterior region of the prooticoccipitals and (5) having a posterior end of the parasphenoid well anterior to the ventral margin of the foramen magnum. *Inbecetenanura* also differs from *Oumtkoutia* in (1) having parasagittal crest on its frontoparietal; (2) having a large pseudobasal process; (3) having ovoid occipital condyles and (4) not having the frontoparietal narrowing anteriorly.

As mentioned in its original description ('Unidentified genus and species' in Báez and Rage, 1998: [680-684]), *Inbecetenanura* resembles '*Xenopus*' *romeri* Estes, 1975 in having (1) highly ossified ethmoidal region; (2) anteriorly extended ossified septum nasi; (3) large pseudobasal process anterior to the eustachian canal; (4) cultriform process of the parasphenoid extending anterior to the nasal cavities level; (5) pineal foramen anterior on the frontoparietal and (6) crista parotica lacking dorsal crest. However, *Inbecetenanura* differs from '*Xenopus*' *romeri* in (1) lacking anterolateral process on the frontoparietal and in having (2) ovoid occipital condyles; (3) a posterior margin of the parasphenoid well anterior to the ventral margin of the foramen magnum and (4) a broader anterior region of the cultriform process.

*?Inbecetenanura*

**Cranial bones.** Three incomplete sphenethmoids are tentatively referred to *Inbecetenanura*: MNHN.F.IBC 1969a, b, 2061.

[Insert Figure 6 here]

They bear a bony *septum nasi* that seems to project anteriorly (Fig. 6A, C). Their orbitonasal foramina are fully enclosed in bone (Fig. 6). These foramina are small and anteroposteriorly elongated. On the dorsal surface of the sphenethmoids, the anterior margin of the *fenestra frontoparietalis* is deeply concave anteriorly (Fig. 6A). In ventral view, the parasphenoid imprint shows that the cultriform process of the parasphenoid narrows anteriorly and is extended anteriorly, past the orbitonasal foramina (Fig. 6B). The nasal cavities are large and elongate laterally (Fig. 6D). A small circular foramen is presents anterior to the orbitonasal foramen (Fig. 6C). It opens within the nasal cavity, but its function is unknown.

**Discussion and attribution.** Enclosure of the orbitonasal foramen in bone is characteristic of pipids. The shape and size of this foramen is consistent with the one of *Inbecetenanura* (holotype specimen, MNHN.F.IBC 1650), with the exception of the presence of a second foramen opening laterally within the nasal cavity. In addition, the parasphenoid imprint matches the shape of the parasphenoid recovered in *Inbecetenanura* (Fig. 2D). The sphenethmoids are distinct from the sphenethmoid of *P. taqueti* in lacking ventral ornamentation. These elements could be referred to *Inbecetenanura*, but their poorly preserved stage and the fact that they are disarticulated (see below) render the attribution questionable.

The presence of isolated sphenethmoids is puzzling. In *Inbecetenanura ragei* and *P. taqueti* the sphenethmoid is fused to the rest of the braincase. Disarticulated sphenethmoids could pertain to immature specimens, but they are at least as large as the one of the holotype of

*Inbecetenanura*. This could indicate either that the holotype of *Inbecetenanura*, MNHN.F.IBC 1602, belongs to a small individual or a young adult, or that these sphenethmoids belong to a third pipimorph taxon from In Becetèn.

### **Pipimorpha indet.**

#### **Vertebral column**

**Presacral vertebrae.** An almost complete presacral vertebra (MNHN.F.IBC 1650; briefly described in Báez and Rage, 1998) is attributed to *Pipimorpha indet.* (Fig. 7A–E). Four presacral centra (MNHN.F.IBC 1997a–d) are also tentatively attributed to *Pipimorpha indet.*

MNHN.F.IBC 1650 is opisthocoelous and bears a well individualized but low neural spine (Fig. 7A–E). The anterior condyle is dorsoventrally compressed and protrudes anteriorly. A small shallow depression is present on each side of this anterior projection. The vertebral canal is large and oval. Similar to the condyle, the cotyle is also dorsoventrally compressed (Fig. 7B). Lateral to the vertebral canal, a large spinal foramen opens posterolaterally on each side of the neural walls (Fig. 7B, E).

[Insert Figure 7 here]

In dorsal view, the prezygapophysis is rectangular and bears a flat dorsally oriented articular surface (Fig. 7C). The anterior region of MNHN.F.IBC 1650 is smooth, except for a thin neural ridge. The anterior margin of the dorsal surface bears a medial notch. The postzygapophyses are not preserved, but they were located close to the medial region of the vertebral canal.

Posteriorly, the dorsal surface of the neural arch is covered by irregular ridges on both sides of the neural spine. The neural spine is very low and reduced to a thin ridge that projects posteriorly. Its posterior end is not preserved (Fig. 7C). The presence of the notch on the anterior margin indicates that neural spines overlapped, and vertebrae were imbricated. There are no anteroposterior grooves nor additional bone deposits (representing pachyostosis as in *Pachycentrata taqueti*; Báez and Rage, 1998: fig. 3A, D) on the ventral surface (Fig. 7D). The transverse processes are broken at their base (Fig. 7A–E). The base of the processes is dorsoventrally flattened.

Four centra (MNHN.F.IBC 1997a–d) bearing a dorsoventrally compressed anterior condyle and a wide posterior cotyle are also attributed to the same taxon as MNHN.F.IBC 1650 (Fig. 7F–G). Shallow depressions are present on each side of the anterior condyle (Fig. 7F–G). In dorsal view, the neural walls do not extend on the whole length of the centrum, leaving a posterior opening. Medially, this opening extends into a shallow medial groove that extends anteriorly towards the anterior condyle. The groove can be interpreted as the canal for the spinal nerve. Broken bases of bony walls within the centra indicates that a spinal foramen was present. The centra thus share sufficient similarities with MNHN.F.IBC 1650 to be referred to the same taxon.

**Sacrococcyges.** Three incomplete sacrococcyges (fused sacral vertebra and urostyle), MNHN.IBC 1972, 1973a, b are tentatively attributed to *?Inbecetenanura* (Fig. 7H–K).

The anterior condyle is compressed dorsoventrally and protrudes anteriorly. The vertebral canal is subrectangular and wide (Fig. 7J). There is no sign of bone accretion on the anterior surface of the bone. On the best-preserved specimen, the posterior region of the left prezygapophysis (MNHN.F.IBC 1972; Fig. 7I) is preserved and shows that the articular surface is flat and subrectangular. The neural crest (fusion of the neural spine of the sacral vertebra and the dorsal crest of the urostyle) is low. It is present on the whole length of the

sacrococcygeal fragments (Fig. 7I, 7K). Anteriorly, a deep sagittal notch opens on the neural arch (Fig. 7I). This indicates that the sacrococcyx was overlapping with the preceding presacral vertebra. The sacral diapophyses are broken at their bases. Nevertheless, they were obviously large and anteroposteriorly expanded. A thin oblique medial ridge is present on each side of the neural crest. It extends posterolaterally following the posterior margin of the sacral diapophyses (Fig. 7I). Shallow longitudinal grooves are present on the ventral surface in MNHN.F.IBC1973 and may correspond to more a mature individual (as in *Pachycentrata*, Báez and Rage, 1998).

In lateral view, a single large spinal foramen is present (Fig. 7J, K). This suggests that only the sacral vertebra and urostyle are incorporated into the sacrococcyges. The two remaining sacrococcyges (MNHN.F.IBC 1973a, b) are very incomplete, preserving the anteriormost portion of the element. However, they are similar to MNHN.F.IBC 1972 in bearing (1) a low neural crest; (2) a thin oblique medial ridge on each side of the neural crest. They are all attributed to the same taxon.

### **Discussion and attribution**

The posterior cotyle of MNHN.F.IBC 1650 (a presacral vertebra; Fig. 7B) matches relatively well in shape and size to the anterior condyle of MNHN.F.IBC 1972 and 1973 (sacrococcyges, Fig. 7H). In addition, the prezygapophyses of the presacral vertebra (Fig. 7C) and the ones preserved on the sacrococcyx (Fig. 7I) all have flat and subrectangular articular facets. The inferred position of the postzygapophyses in MNHN.F.IBC 1650 (Fig. 7C) correspond to the position of the prezygapophyses in MNHN.F.IBC 1972 (Fig. 7I). For these reasons, we here interpret and decide to attribute the presacral vertebra and the two sacrococcyx to the same taxon, an indeterminate pipimorph. The presence of opisthocoelous

vertebrae and a sacrococcyx is characteristic of pipids (Gómez, 2016). The presence of a large spinal foramen on presacral vertebrae is uncommon in mature anurans. Its presence is usually a marker of immaturity (Duelleman and Trueb, 1994) except in several extinct pelobatids (Sanchiz and Mlynarski, 1979; Augé et al., 1997; Rage and Augé, 2015). In pipids, this is known in Xenopodinae, but only on the atlantal complex (Cannatella and Trueb, 1998). The presence of irregular ridges on the dorsal surface of the presacral vertebrae is also known in *Xenopus stromeri* (Rage, 2008). This combination of vertebral characters appears to be unique within Anura (at least within Pipoidea). Another feature that deserves attention is the presence of shallow depressions lateral to the condyle (Fig. 7A-C). These depressions resemble accessory articulation identified in extant Hymenocherini, *Pipa* and the extinct *Avitabatrachus* (Baez et al., 2022: fig. 4). The presence of “accessory articulation” would suggest MNHN.F.IBC 1650 and the four isolated centra belonged to a skeletally mature specimen (Báez et al., 2022).

Presacral vertebra MNHN.F.IBC 1650 and sacrococcyges MNHN.F.IBC 1972, 1973a, b are lacking the vermicular ornamentation and pachyostosis present in *Pachycentrata taqueti*. The sacrococcyges also bear a single pair of spinal foramina (two pairs of spinal foramina in *P. taqueti*). The vertebrae and sacrococcyges described here cannot therefore be attributed to *P. taqueti*. Association between the postcranial bones and the braincase of *Inbecetenanura* is not directly possible because they have not been found in association. However, it would be unlikely that two distinct pipid taxa, one known by cranial elements, the second by postcranial elements, are present in In Becetèn (in addition to *Pachycentrata*). Unfortunately, it is not possible, with the current materials, to assign any vertebral element to *Inbecetenanura*. Therefore, we refer these vertebral elements to Pipimorpha indet. They could belong to *Inbecetenanura*, or represent a third unknown pipimorph in In Becetèn.



To sum up, we attribute the presacral vertebra MNHN.F.IBC 1650, the four presacral centra MNHN.F.IBC 1997a–to 1997d and three sacrococcyges MNHN.F.IBC 1972, and 1973a and 1973b to Pipimorpha indet., as well as three sphenethmoids (MNHN.F.IBC 1969a, b 2061) to *?Inbecetenanura*.

### **Nomenclatural note**

Báez and Púgener (2003: 454) erected the taxa Pipinomorpha and Xenopodinomorpha and provided the following phylogenetic definition for the former: “Pipinomorpha includes Pipinae and fossil taxa, as *Eoxenopoides* according to this analysis, more closely related to this crown group than to Xenopodinae”. Báez and Púgener (2003) did not define explicitly Xenopodinomorpha or Pipinae, but they provided additional information to infer their intent (Báez and Púgener, 2003: 454): “Pipidae comprises two clades for which we propose the stem-based names Pipinomorpha and Xenopodinomorpha”. Thus, it is clear that Pipidae was conceptualized as a crown-group, while Pipinomorpha and Xenopodinomorpha must be total groups to preserve the arrangement Pipidae = Pipinomorpha + Xenopodinomorpha. Their topology was based on a morphological analysis that incorporated many extinct taxa; it is thus comparable to our unconstrained analysis, notably in placing Hymenochirini closer to *Pipa* than to *Xenopus*. Thus, Báez and Púgener (2003: fig. 13) included Hymenochirini in Pipinae. Under our constrained analysis, as in molecular phylogenies of pipids (Frost et al., 2006; Cannatella, 2015), the taxon Hymenochirini is closer to *Xenopus* than to *Pipa*.

In order to apply the names Xenopodinomorpha and Pipinomorpha in the context of our constrained analysis (and of recent molecular phylogenies), it is necessary to reformulate slightly the phylogenetic definitions. In conformity with the recommendations of Taylor

(2007), we attempt to capture as best as we can the intent of Báez and Púgener (2003: 454) while keeping in mind the requirements of the PhyloCode (Cantino and de Queiroz, 2020). We also consider the updated phylogenetic context provided by many molecular phylogenies published since 2003, which show that the position of Hymenochirini differs between trees based on morphological data, which place Hymenochirini close to *Pipa*, and trees based on molecular data, which place Hymenochirini close to *Xenopus* (Frost et al., 2006; Pyron and Wiens, 2011; Cannatella, 2015; Jetz and Pyron, 2018). Given that the names Xenopodinomorpha and Pipinomorpha derive from *Xenopus* and *Pipa* respectively, their phylogenetic definition should be based on the type-species of these two nominal genera, in conformity with Article 11.10 of the PhyloCode (Cantino and de Queiroz, 2020). We therefore suggest the following phylogenetic definition of Pipidae, Xenopodinomorpha and Pipinomorpha:

***Pipidae*** Gray, 1825, converted clade name

RegNum registration number : 809

**Definition.** *Pipidae* is the smallest clade that includes *Xenopus laevis* Daudin 1802 and *Pipa pipa* Linnaeus 1758. Abbreviated definition: min crown  $\nabla$  (*Xenopus laevis* Wagler, 1827 and *Pipa pipa* Linnaeus, 1758).

**Etymology.** Named after the eponymous genus *Pipa*.

**Reference phylogeny.** The primary reference phylogeny is the equal weight unconstrained analysis from this study (Fig. 8). Other reference phylogenies include the equal weight constrained (using a molecular based topology; see Materials and Methods) analysis from this study (Fig. 9), Báez et al (2007: fig. 6), Gómez (2016: fig. 5), Aranciaga Rolando et al (2019: fig. 4) and Cannatella (2015: fig. 3).

**Composition.** Under morphological analyses (Fig. 8), which were published in most paleontological studies of Pipidae, it includes the extant *Xenopus* Wagler, 1827, *Silurana* Gray, 1864, *Pipa* Linnaeus, 1758, *Hymenochirus* Boulanger, 1896, *Pseudhymenochirus* Chabanaud, 1960 and the extinct '*Xenopus*' *stromeri* Ahl, 1926, *Eoxenopoides* Haughton, 1931, *Singidella* Báez and Harrison, 2005, *Oumtkoutia* Rage and Dutheil, 2008, *Pachycentrata* Báez and Rage, 2004 and *Inbecetenanura* nov. gen. Under molecular-based or constrained (using a molecular based topology) analyses (Fig. 9), this clade could encompass all above taxa except *Eoxenopoides*.

*Diagnostic apomorphies.* See Supplementary Data S8.

***Xenopodinomorpha*** Báez and Púgener, 2003, converted clade name

RegNum registration number :810

**Definition.** *Xenopodinomorpha* is the largest clade that includes *Xenopus laevis* Daudin 1802 but not *Pipa pipa* Linnaeus 1758. Abbreviated definition : max total  $\nabla$  (*Xenopus laevis* Daudin, 1802 and  $\sim$  *Pipa pipa* Linnaeus, 1758).

**Etymology.** Combination of the eponymous genus *Xenopus* and “morpha” (derived from the ancient Greek “morphḗ”, shape. It refers to the close phylogenetic relationships between extinct taxa and *Xenopus*, all assigned to this clade.

**Reference phylogeny.** The primary reference phylogeny is the equal weight unconstrained analysis from this study, where it is redundant with Xenopodinae (Fig. 8). Other reference phylogenies include the equal weight constrained analysis from this study (Fig. 9), Báez et al (2007: fig. 6), Gómez (2016: fig. 5), Aranciaga Rolando et al (2019: fig. 4) and Cannatella (2015: fig. 3).

**Compositions.** Under unconstrained morphological analyses, which were published in most paleontological studies of this taxon, the clade includes *Xenopus* Wagler, 1827 and *Silurana* Gray, 1864. Under molecular-based or constrained analyses (Fig. 9), this clade could encompass the extant *Xenopus*, *Silurana*, *Hymenochirus*, *Pseudhymenochirus* and the extinct *Pachycentrata*, *Singidella* and *Oumtkoutia*.

**Diagnostic apomorphies.** See Supplementary Data S8.

***Pipinomorpha*** Báez and Púgener, 2003, converted clade name

RegNum registration number :811

**Definition.** *Pipinomorpha* is the largest clade that includes *Pipa pipa* Linnaeus 1758 but not *Xenopus laevis* Daudin 1802. Abbreviated definition: max total  $\nabla$  (*Pipa pipa* Linnaeus, 1758 and  $\sim$  *Xenopus laevis* Daudin, 1802).

**Etymology.** Named after the eponymous genus *Pipa*. and “morpha” (derived from the ancient Greek “morphé”, shape. It refers to the close phylogenetic relationships between extinct taxa and *Pipa*, all assigned to this clade.

**Reference phylogeny.** The primary reference phylogeny is the equal weight unconstrained analysis from this study (Fig. 8). Other reference phylogenies include the equal weight constrained analysis from this study (Fig. 9), Báez et al (2007: fig. 6), Gómez (2016: fig. 5) and Aranciaga Rolando et al (2019: fig. 4).

**Compositions.** Following morphological based unconstrained analyses (Fig. 8), this clade could include the extant *Pipa*, *Hymenochirus* and *Pseudhymenochirus* and the extinct *Eoxenopoides*, *Inbecetenanura*, *Pachycentrata*, *Singidella*, *Oumtkoutia* and ‘*Xenopus*’

*stromeri*. According to phylogenies based on molecular data or phylogenies based on morphological data but constrained by the molecular topology, this clade includes only *Pipa*.

**Diagnostic apomorphies.** See Supplementary Data S8.

This set of three definitions forms a node-stem triplet (as defined by Sereno, 1998) that preserves the intended nomenclature of Báez and Púgener (2003: 454), namely that ***Pipidae*** includes (only) two sister-clades, ***Xenopodinomorpha*** and ***Pipinomorpha***.

A recent study by Aranciaga Rolando et al. (2019) retrieved several pipimorphs as a clade, placed as the sister-group of Pipidae. To accommodate these relationships, they erected the names Shelaniinae (for the new clade) and Panpipidae (as Shelaniinae + Pipidae and others taxa). They provided the following definitions : Panpipidae as “ the 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 *Palaeobatrachus grandipes*” (Aranciaga Rolando et al., 2019: 727) and Shelaniinae as “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*” (Aranciaga Rolando et al., 2019: 729). Their topology (Aranciaga-Rolando et al., 2019: fig. 4) was based on a morphological analysis that incorporated many extinct taxa; it is thus comparable to our unconstrained analysis, notably in placing Hymenochirini closer to *Pipa* than to *Xenopus* and recovering several extinct pipids as pipinomorphs. However, both definitions include the taxon ‘*Shelania laurenti*’ as an internal specifier. This taxon is not the type-species of *Shelania* Casamiquela, 1960; rather, the type-species is *Shelania pascuali* Casamiquela, 1960. Thus, neither definition follows Article 11.10 of the PhyloCode (Cantino and de Queiroz, 2020).

In addition, the use of the prefix ‘Pan’, according to Articles 10.3 and 10.5 of the PhyloCode, should be reserved for total clades, which are delimited by extant clades. Thus, the name Pan-

pipidae should refer to **the** total-group of Pipidae rather than the crown-group Pipidae and part of its stem-group (as proposed by Aranciaga Rolando et al., 2019). This means that Pan-pipidae would correspond to the definition proposed by Ford and Cannatella (1993: 104) for Pipimorpha : “We define the new stem-based name Pipimorpha to be those taxa that are more closely related to living Pipidae than to living *Rhinophrynus*”. Articles 10.1 and 10.2 of the PhyloCode indicate that clades names can either be converted (from a pre-existing name) or established. Regarding total clades, if a name needs to be established, the prefix “Pan-“ needs to be used (Article 10.3), as within Pan-Pipidae. However, Article 10.6 states that “If there is a pre-existing name that has been applied to a particular total clade, that name may be converted or a panclade name may be established instead” (the choice is left to the discretion of the authors; following Recommendation 10.1). As Pipimorpha was clearly established as a total (stem-based) clade by its authors, we chose to convert Pipimorpha as the total clade of Pipidae. Similarly, we prefer to define the names *Xenopodinomorpha* and *Pipinomorpha* (which were clearly conceptualized as total clades by their authors) in conformity with the PhyloCode than to erect panclade names for these total clades. We note that these names have been used several times since these taxa were erected (Pipimorpha, *Xenopodinomorpha* and *Pipinomorpha* respectively yield 77, 15, and 11 references in Google Scholar, as of March 29, 2022), which is one of the justifications for our choice. Thus, we propose an emended definition of Shelaniinae and Pipimorpha. In addition, we also propose a replacement name for Pan-Pipidae.

**Commenté [ML1]:** Reformulated because a name, by itself, does not define anything. It only refers to something through its definition.

*Pipimorpha* Ford and Cannatella, 1993, converted clade name

RegNum registration number :812

**Definition.** The total clade composed of the crown clade *Pipidae*, and all extinct organisms or species that share a more recent common ancestor with *Pipidae* than with any extant taxa that are not members of *Pipidae*. Abbreviated definition: total  $\nabla$  of *Pipidae*.

**Etymology.** Combination of the clade name “Pipidae” and “morpha”, derived from the Greek “morphē” meaning shape, appearance.

**Reference phylogeny.** The primary reference phylogeny is the equal weight unconstrained analysis from this study (Fig. 8). Other reference phylogenies include the equal weight constrained analysis from this study (Fig. 9), Báez et al (2007: fig. 6), Gómez (2016: fig. 5), Aranciaga Rolando et al (2019: fig. 4) and Cannatella (2015: fig. 3).

**Composition.** *Pipimorpha* includes the extant *Xenopus*, *Pipa*, *Hymenochirus*, *Pseudhymenochirus* and *Silurana*. It also (currently) includes the extinct *Aygroua* Jones et al., 2003, *Nevobatrachus* Mahony, 2019, *Thoraciliacus* Nevo, 1968, *Cratopipa* Carvalho et al., 2019, *Avitabatrachus* Báez et al., 2000, *Vulcanobatrachus* Trueb et al., 2005, *Neusibatrachus* Seiffert, 1972, *Gracilibatrachus* Báez, 2013, *Pachycentrata*, *Inbecetenanura*, *Singidella*, *'Xenopus' romeri* Estes, 1975, *'Xenopus' stromeri*, *Shelania* Casamiquela, 1960, *'Shelania' laurenti* Báez and Púgener, 1998, *'Xenopus' hasaunus* Špínar, 1978, *Shomronella jordanica* Estes et al., 1978, *Oumtkoutia*, *Eoxenopoides*, *Llankibatrachus* Báez and Púgener, 2003, *Kuruleufenia* Gómez, 2016, *Patagopipa* Aranciaga Rolando et al., 2019, *Saltenia* Reig, 1959, and Palaeobatrachidae Cope, 1865.

**Diagnostic apomorphies.** See Supplementary Data S8.

*Gondwanamorpha* nomen novum

RegNum registration number :813

**Definition.** The smallest clade that includes *Shelania pascuali*, *Pipa pipa*, *Hymenochirus boettgeri*, *Xenopus laevis* and *Silurana tropicalis*. Abbreviated definition: min total  $\nabla$  (*Shelania pascuali* Casamiquela, 1960, *Xenopus laevis* Daudin, 1802, *Hymenochirus boettgeri* Tornier, 1896, *Pipa pipa* Linnaeus, 1758 and *Silurana tropicalis* Gray, 1864).

**Etymology.** Combination of the name ‘Gondwana’ and “morpha”, derived from the Greek “morphḗ” meaning shape, appearance.

**Reference phylogeny.** The primary reference phylogeny is the equal weight unconstrained analysis from this study (Fig. 8). Other reference phylogenies include Báez et al (2007: fig. 6), Gómez (2016: fig. 5) and Aranciaga Rolando et al (2019: fig. 4).

**Composition.** Following morphology-based analyses (Fig. 8), this clade includes Shelaniinae (see definition below), ‘*Shelania*’ *laurenti*, *Llankibatrachus trubei*, ‘*Xenopus*’ *romeri* and Pipidae. Under constrained (using the molecular topology) analyses (Fig. 9), Gondwanamorpha would also include *Vulcanobatrachus*.

**Diagnostic apomorphies.** See Supplementary Data S8.

*Shelaniinae* Aranciaga Rolando, Agnolín and Corsolini et al., 2019, converted clade name

RegNum registration number :814

**Definition.** The largest clade that includes *Shelania pascuali* but not *Pipa pipa*, *Hymenochirus boettgeri*, *Silurana tropicalis*, and *Xenopus laevis*. Abbreviated definition: max total  $\nabla$  (*Shelania pascuali* Casamiquela, 1960 and ~ *Xenopus laevis* Daudin, 1802, *Hymenochirus boettgeri* Tornier, 1896, *Pipa pipa* Linnaeus, 1758 and *Silurana tropicalis* Gray, 1864).

**Etymology.** Named after the eponymous genus *Shelania*.



**Reference phylogeny.** The primary reference phylogeny is the equal weight unconstrained analysis from this study (Fig. 8). Other reference phylogenies include Báez et al (2007: fig. 6), Gómez (2016: fig. 5) and Aranciaga Rolando et al (2019: fig. 4).

**Composition.** Under the unconstrained analysis (Figs. 8, 10), this taxon includes the extinct *Shelania pascuali* Casamiquela, 1960, *Saltenia*, and *Kuruleufenia*. *Shelaniinae* has been recovered with this composition in both morphological unconstrained analyses (Fig. 8; Aranciaga Rolando et al., 2019; Carvalho et al., 2020) and constrained morphological analyses (based on the topology of Jetz and Pyron, 2018).

**Diagnostic apomorphies.** See Supplementary Data S8.

## Phylogenetic analyses

Phylogenetic relationships of extant and extinct xenoanurans have been controversial for the past decade, with several recently described extinct taxa (Báez et al., 2007; Rage and Dutheil, 2008; Gómez, 2016; Carvalho et al., 2019; Aranciaga Rolando et al., 2019; Báez et al., 2021) variably placed either close to Xenopodinae (*Xenopus* + *Silurana*) or Pipinae (*Pipa* + Hymenochirini). To accommodate these extinct taxa, several clade names have been proposed, following the work of Báez and Púgener (2003). *Xenopodinomorpha* and *Pipinomorpha* were erected to accommodate extinct taxa closer to Xenopodinae or Pipinae respectively (Báez and Púgener, 2003; also see the nomenclatural note above).

**Equal weight analysis.** A phylogenetic analysis under equal weight and ordered yielded four MPTs with a score of 657 steps. The strict consensus (CI = 0, 359; RI = 0, 691; Fig. 8) recovered a *Pipimorpha* clade placed within a tetrachotomy with the extinct *Rhinophrynus parvus*, a clade composed of *Rhinophrynus dorsalis* + *Chelomorphyneus bayi*, and a clade

**Commenté [ML2]:** Addition necessary because given its definition, it always exists, even if under some conceivable topologies, it might include only the internal specifier, among known taxa.

made of ((*Spea* + *Pelobates*) + (*Hadromophryne* + *Platyplectrum*)). **Pipimorpha** is poorly supported by three synapomorphies: (1) the distal region of the ilial shaft circular and not compressed mediolaterally in cross-section (character 137, 0→1); (2) the presence of a low ridge on the dorsal surface of the ilium (character 145: 0→1); and (3) an interiliac scar ample but restricted to the ventral part of the ilia (character 149, 0→1).

[Insert Figure 8 here]

Interestingly, the extinct African *Aygroua anoualensis* Jones et al., 2003 is recovered as the sister-taxon to all other pipimorphs, supported by three synapomorphies, all on the ilium. The pipimorph *Cratopipa novaolindensis* Carvalho et al., 2019 appears to form a clade with the Cretaceous *Thoraciliacus rostriceps*, but this is poorly supported by two synapomorphies: (1), the presence of transverse process on the urostyle (character 105, 1→0) and (2), fusion of the ilium and ischium (character 152, 0→1). This clade is a sister-clade to all other gondwanan pipimorphs.

**Gondwanamorpha** is recovered, poorly supported by seven synapomorphies (see Appendix S9 in Supplemental Data 1). **Shelaniinae** is poorly supported by six synapomorphies (see Appendix S8; identical to the ones recovered in Aranciaga Rolando et al., 2019). Within **Gondwanamorpha**, we also find ‘*Shelania*’ *laurenti* Casamiquela, 1961 and ‘*Xenopus*’ *romeri* Estes, 1975 within a trichotomy with **Pipidae**. **Pipidae** is supported by five synapomorphies (see Appendix S9 in Supplemental Data 1). Within **Pipidae**, Xenopodinae is redundant with **Xenopodinomorpha**. Xenopodinae is recovered as the sister-clade of **Pipinomorpha**, containing the extant *Pipa*, *Hymenochirus* and *Pseudohymenochirus* and several extinct taxa.

Xenopodinae is here composed of *Silurana* and a clade that includes the extant *Xenopus* species and the extinct *Xenopus arabiensis*. Xenopodinae is strongly supported by

eighteen synapomorphies, many of them recovered within other phylogenetic analyses (Báez and Púgener, 2003; Gómez, 2016) and used as diagnostic apomorphies for this clade (Frost et al., 2006). *Pipinomorpha* is poorly supported by one synapomorphy, the loss of a distinct pterygoid knob on the basal process of the otic capsule (character 59: 2→0).

*Inbecetenanura* is placed within *Pipinomorpha* (Fig. 8) as the sister-group of all other pipinomorphs, differentiated by two synapomorphies, (1) the presence of a supraorbital flange on the frontoparietal (7: 0→1) and (2) the absence of an epiotic eminence on the medial margin of the prootic (171: 1→0). *Pachycentrata taqueti* is recovered as a sister-taxon to the Eocene *S. latecostata*, moderately supported by two synapomorphies: (1) the presence of an occipital artery housed in a closed canal (10, 0→1) and (2) the anterior extension of the cultriform process of the parasphenoid ending at antorbital level (18, 3→1). Extant pipines are recovered as a clade strongly supported by seven synapomorphies (see Appendix S8).

**Constrained analysis.** Three main extant pipid clades are recognized in the literature (Frost et al., 2006; Jetz and Pyron, 2018), Xenopodinae (*Xenopus* + *Silurana*), Hymenochirini (*Hymenochirus* + *Pseudohymenochirus*) and Pipinae (*Pipa*). The first major phylogenetic analyses (based on osteological characters; Cannatella and Trueb, 1988; Ford and Cannatella, 1993) recovered the Xenopodinae as a sister-clade to all other *Pipidae* and placed Hymenochirini as a clade of Pipinae. Addition of several extinct pipimorphs and pipids did not raise doubts about these relationships (Báez and Trueb, 1997; Báez and Púgener, 1998; Trueb, 1999; Báez and Púgener, 2003; Trueb et al., 2005; Gómez, 2016). However, the rise of molecular phylogenetic analyses proposed completely different relationships for extant Pipidae (Frost et al., 2006; Pyron and Wiens, 2011; Cannatella, 2015; Jetz and Pyron, 2018), with Pipinae composed of only *Pipa*, as a sister-clade to Dactylethrinae (Xenopodines + Hymenochirini). This conflict between morphological and molecular phylogenetic analyses is

still unresolved (Bewick et al., 2012; Cannatella, 2015) and the relationships and position of the various extinct *Pipidae* might differ between both topologies.

To address this conflict, we performed phylogenetic analyses constrained on a topology taken from Jetz and Pyron (2018), to see if the placement of In Bécetèn taxa is impacted.

**Constrained equal weight analysis.** We recovered 32 MPTs with a score of 682 steps. The strict consensus (CI = 0, 338; RI = 0, 663; Fig. 9) recovered Xenoanura, *Pipimorpha* and *Pipidae*. Pipoidea is composed of an unresolved trichotomy with *Pipimorpha*, Rhinophrynidae and *Rhadinostenus parvus* (Fig. 9). Pipoidea is supported by four synapomorphies: (1), frontoparietals completely fused (character 4, 0→1); (2), absence of subotic alae of the parasphenoid (character 17, 0→1); (3) cultriform process of the parasphenoid extending up to the vomers anteriorly (character 19, 0→2); (4) sphenethmoid not exposed dorsally (between the roofing dermal bones; character 48, 1→0). *Pipimorpha* is supported by the same synapomorphies from the unconstrained analysis. *Aygroua anoualensis* is a sister-taxon to all pipimorphs.

[Insert Figure 9 here]

*Cratopipa novaolindensis* and *T. rostriceps* form a clade, supported by the same two synapomorphies as in previous analyses (see Appendix S8). *Gondwanamorpha* is recovered as a large unresolved polytomy including *Vulcanobatrachus*, *Llankibatrachus*, ‘*Shelania*’ *laurenti*, ‘*Xenopus*’ *romeri*, *Shelaniinae* and a clade composed of *Eoxenopoides* + Pipidae (Fig. 9). *Gondwanamorpha* is here supported by eight synapomorphies (see S8). Shelaniinae is also recovered and supported by eight synapomorphies (S8). *Pipidae* is recovered as a large unresolved polytomy made of *Inbecetenanura*, ‘*Xenopus*’ *stromeri*, *Oumtkoutia*, *Pipa*, Xenopodinae and a clade made of (*Singidella* + *Pachycentrata* + Hymenocherini). This

polytomy is poorly supported by seven synapomorphies. This unresolved status seems mainly linked to the uncertain position of both *Inbecetenanura* and '*Xenopus*' *stromeri*, as few characters are scored for each (24% and 38% of total character scored respectively). When excluding '*Xenopus*' *stromeri*, *Inbecetenanura* is excluded from **Pipidae** (Fig. S2).

*Pachycentrata* and *Singidella* are recovered as stem-Hymenocherini. When excluding '*Xenopus*' *stromeri*, **Xenopodinomorpha** is recovered, with Xenopodinae, Hymenocherini, *Pachycentrata*, *Singidella* and *Oumtkoutia* (Fig. S2).

## Discussion

### Ontogenetic stage

In the original description of MNHN.F.IBC 1602, the authors suggested that the braincase belonged to an immature individual (Báez and Rage, 1998). This hypothesis was based on (1) a long anterior extension of the otic capsules; (2) a separation of prootic and optic foramina by a bony wall and (3) the presence of weak parasagittal crests on the frontoparietal.

However, a similar extension of the otic capsules in *Inbecetenanura ragei* occurs in several mature individuals of pipid taxa (Trueb et al., 2000). A bony wall between prootic and optic foramina also occurs in mature individuals of several extant and extinct pipids (Estes, 1975; Trueb and Hanken, 1992). Furthermore, parasagittal crests are highly variable in pipids, from absent, as in *Patagopipa* (Aranciaga Rolando et al., 2019) to well-defined, as in *Pipa* (Trueb et al., 2000). As an example, mature specimens of *Shelania pascuali* still bear weak parasagittal crests (Báez and Trueb, 1997). Presence of weak parasagittal crests cannot be taken as a sign of immaturity. In conclusion there is no indication that MNHN.F.IBC 1602 represents an immature individual. Moreover, comparison with immature and mature

individuals of *Pachycentrata taqueti* can be made. The extreme fusion of dermal, palate and endocranial bones of the braincase displayed by *Inbecetenanura* does not occur in braincases of immature *P. taqueti*, but it resembles braincases of mature individuals.

#### **Status and attribution of In Becetèn taxa**

*Pachycentrata taqueti* and *Inbecetenanura ragei* both appear to be pipids. *Inbecetenanura* and *Pachycentrata* are found among pipinomorphs in non-constrained analyses. However, in constrained analyses, *Pachycentrata* is recovered as a stem-Hymenocherini, while *Inbecetenanura* is recovered as a pipid (Fig. 9). Previous mention of the holotype of *Inbecetenanura* considered it a xenopodinomorph (Báez and Rage, 1998; Gardner and Rage, 2016), but they were not based on phylogenetic analyses. *Pachycentrata* has only been recovered as a pipinomorph within previous analyses (Báez and Rage, 1998; Gómez, 2016). Other extinct taxa, like *Oumtkoutia anae* and *Eoxenopoides*, were suggested to be xenopodinomorphs. This conflict seems linked to the position of the Hymenochirini and to the polarization of several characters. As mentioned above, morphological and molecular analyses support conflicting positions of Hymenochirini (Bewick et al., 2012) but molecular-morphological compound analyses yielded results similar to molecular analyses (Bewick et al., 2012; Cannatella, 2015) suggesting a stronger support for the following relationship among pipids: *Pipa* + (Xenopodinae + Hymenocherini). Hence, homologies on key characters for Hymenochirini and *Pipa* (supporting a close relationship in morphological-based analyses) have to be reconsidered and investigated, in particular in the Hymenochirini (Bewick et al., 2012). The only secure attribution for *Inbecetenanura* is to *Pipidae*. We putatively refer *Inbecetenanura* to *Pipinomorpha*, as it is the position recovered in unconstrained analysis.

In conclusion, both *Pachycentrata* and *Inbecetenanura* can be securely assigned to the *Pipidae* family. Both taxa thus represent the second-oldest occurrence of the family, fifteen

million years younger than the oldest occurrence, *Oumtkoutia* (Cenomanian, Rage and Dutheil, 2008). In addition, the pipids of In Becetèn represent the oldest occurrence of two pipid taxa in the same locality.

### **Pipimorph phylogeny**

In their original description, Jones et al. (2003), using ilium character solely, considered the enigmatic *Aygroua anoualensis* (Late Jurassic/ Early Cretaceous) to be closely related to Pipoidea. We recovered *A. anoualensis* as a pipimorph, sister-taxon to all other pipimorphs in every analysis, and thus confirmed its attribution to ***Pipimorpha***. *Aygroua* has been identified in the Ksar Metlili site (Eastern Morocco; Jones et al., 2003; Lasseron et al., 2019) from the Ksar Metlili Formation. This Formation was previously considered to be Lower Cretaceous (Berriasian) age (Haddoumi et al., 2016) but recent faunistic analyses revealed numerous similarities with Middle-Late Jurassic faunae (Lasseron et al., 2019). Although a lower Berriasian age cannot be excluded (Lasseron pers. com), *Aygroua* is slightly older than two pipimorph occurrences, *Neusibatrachus wilferti* (Báez and Sanchiz, 2007) and *Shomronella jordanica* Estes et al., 1978 from the Middle-Upper Berriasian. This makes *A. anoualensis* the oldest pipimorph known and the second oldest pipoid (Fig. 9).

The recently described *Cratopipa novaolindensis* (Carvalho et al., 2019; Báez et al., 2021) appears to be a pipimorph and forms a clade with *Thoraciliacus rostriceps*. Both taxa are Aptian age (*T. rostriceps* is slightly older; Gardner and Rage, 2016; Carvalho et al., 2019) but they are geographically distant from one another. This result is different from the position of *C. novaolindensis* (in ***Shelaniinae***) originally proposed by Carvalho et al. (2019). This difference is likely linked to the rescoring of several key characters (such as the sacro-urostyler articulation) following the redescription of Báez et al (2021).

### ***Gondwanamorph and pipid phylogeny***

*Gondwanamorpha* (~Panpipidae in Aranciaga Rolando et al., 2019) is here recovered in both unconstrained and constrained analyses (Figs. 8, 9). This clade includes *Shelaniinae* as the sister-clade to a clade made of *Llankibatrachus* + trichotomy of *Pipidae* and two gondwanamorphs, '*Shelania laurenti*' and '*Xenopus romeri*' in the unconstrained analysis. This arrangement is similar to the one recovered in Aranciaga Rolando et al (2019: fig. 3). However, when performing under constrained analysis, the cretaceous pipimorph *Vulcanobatrachus* is recovered as a gondwanamorph (Fig. 9). This difference is linked to the position of *Pipa*, placed (following the molecular topology) in the constrained analysis as the sister-taxon to all extant pipids. This position is different from the topology obtained under a morphological unconstrained analysis, where Xenopodinae is recovered as the sister-clade to all other extant pipids, and seems to influence the polarization of several characters, leading to a less resolved topology within Pipidae.

[Insert Figure 10 here]

### **Paleobiogeographical implications**

Pipoid diversification and dispersal through the globe is still unclear. The oldest pipoid, *Rhadinostenus parvus* was recovered from the Late Jurassic of North America (Kimmeridgian, 157-152 ma). The oldest pipimorph seems to be *Aygroa anoualensis* from the Late Jurassic-Early Cretaceous of North Africa (Tithonian-Berriasian, 152-140 ma; Lasseron et al., 2020). These two taxa document the early divergence of two large extant clades (Rhinophrynidae and *Pipimorpha*). Molecular analyses have dated the divergence between these two main pipoid clades to the Middle Jurassic, around 165 Ma (Feng et al., 2017), and this is compatible with the fossil record (Marjanović and Laurin, 2014). However, it should be noted that the taxa used for calibration of the *Pipimorpha* by Feng et al. (2017) were not the oldest representatives of the clade and early pipimorphs were included within a basal polytomy by Marjanović and Laurin (2014). Inclusion of these pipimorphs for node



calibration could push farther back the divergence of Pipoidea. All early occurrences of *Pipimorpha* are centered around the Tethys, in Morocco (Jones et al., 2003), Spain (Báez and Sanchiz, 2007) and Israel (Estes et al., 1978; Gardner and Rage, 2016), which suggests that early diversification of pipimorphs occurred around the Mediterranean region (Fig. 10, 11).

[Insert Figure 11 here]

During the Early/Late Cretaceous transition, pipimorphs occurred across Gondwana (Gardner and Rage, 2016; Báez et al., 2021). Later in the late Cretaceous, pipimorphs are represented by pipids in Africa and shelaniines in South America (Figs. 10, 11).

The rich fossil record of pipimorphs (unconstrained analysis; Fig. 10) or gondwanamorphs (constrained analysis: Fig. 11) spans across Africa and South America. Phylogenetic results show close relationships between South American and African taxa under both topologies (Figs. 10, 11), implying that pipids were able to easily move from one continent to another. Despite the strong aquatic adaptations of extant pipids, this dispersal may not have been as difficult as it might first seem, for two reasons. First, at least some pipids, such as the African pipid *Xenopus laevis*, are known to tolerate moderate salinity (around 20-40% of sea water salinity; Munsey, 1972; Hopkins and Brodie Jr, 2015); second, at least six *Xenopus* species (including *X. laevis*) can move overland (Measey, 2016). The taxonomic distribution of these abilities among other pipids (outside *Xenopus*) is unknown, but they demonstrate that *Xenopus* is adaptable in ways that can facilitate dispersal overland and across brackish water. However, the absence of a more water-proof skin (as in amniotes, like mammals or squamates) in pipids hampers their ability at transatlantic dispersal. Thus, the successive divergences between African and South American gondwanamorphs that occurred until the mid-Cretaceous (according to a literal interpretation of the fossil record) suggest a permanent connection between Africa and South America at that time. This is congruent with current analyses that place the loss of this connection in the mid-Cretaceous, around the Early/Late

**Commenté [ML3]:** This sentence was poorly written and too wordy. For instance, "other terrestrial vertebrates" is wrong because it implies that pipid skin is the most permeable among tetrapods, whereas all lissamphibians have such a skin. The main dichotomy is between lissamphibians and amniotes, so I reformulated accordingly. And I reformulated the end ("hampers") because permeable skin as such is not an absolute problem; many strictly marine organisms (like the amphioxus) have permeable skin.

Cretaceous transition (Fairhead, 1988; Nürnberg and Müller, 1991; Binks and Fairhead, 1992; McLoughlin, 2001; Will and Frimmel, 2018). After this separation, gondwanamorphs were presumably unable to disperse between both continents, as we see appears to be the case from the mid-Cretaceous onwards (Figs.10, 11; Cannatella, 2015).

This scenario does not require over-water dispersal, contrary to other scenarios proposed recently (Gómez, 2016; Aranciaga Rolando et al., 2019). In addition, it implies that lineages leading to all major extant pipid clades (Pipinae, Hymenochirini and Xenopodinae) likely emerged during the Cretaceous, which implies long ghost lineages for these clades, which are poorly documented in the fossil record (Cannatella, 2015; Gómez, 2016).

## Conclusion

In conclusion, the redescription of an indeterminate pipid from In Becetèn leads to the establishment of a new pipid taxon, *Inbecetenanura ragei* nov. sp. Several postcranial elements from the site are also tentatively attributed to the same taxon. Phylogenetic analyses confirm its placement within *Pipidae*, although some uncertainties remain on its attribution within the clade. We also took the opportunity to convert *Pipimorpha*, *Gondwanamorpha*, *Shelaniinae*, *Pipidae*, *Xenopodinomorpha* and *Pipinomorpha* into the phylogenetic nomenclature as implemented in the *PhyloCode*. In Becetèn is the oldest site where more than one pipid taxon is known. Inclusion of the gondwanian *Aygroua anoualensis* suggests that this taxon is a pipimorph and the sister-taxon to all other pipimorphs. We recover *Shelaniinae*, a recently proposed pipimorph clade, as the closest clade to the *Pipidae* in both the unconstrained and constrained analyses. Phylogenetic results indicate that repeated dispersals of gondwanamorphs between Africa and South America until the mid-Cretaceous at the latest suggests that these continents were still connected, at least through a limited land

bridge, until then. Main pipid clades likely originated during the Cretaceous, with the final opening of Southern and Central Atlantic Ocean. This geological context may have driven a pipid evolutionary radiation around the Early/Late Cretaceous transition. This confirms that the Cretaceous is a key period of the evolutionary history of the *Pipimorpha*.

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## Data availability

The data underlying this article are available in Zenodo, at <http://doi.org/10.5281/zenodo.6624939>.

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## Figure captions

**Figure 1.** Map of the In Becetèn locality. **A**, map of Africa, with Niger highlighted in black; **B**, map of Niger with the Tahoua region highlighted in black square outline; **C**, simplified geological map of the Tahoua and In Becetèn region, modified from Greigert and Pougnet (1965). White star indicates the In Becetèn site. [Full page width]

**Figure 2.** Braincase of *Inbecetenanura ragei* sp. nov. (MNHN.F.IBC 1602, holotype). **A–B**, MNHN.F.IBC 1602 in **A**, dorsal and **B**, ventral views; **C–D**, 3D model of MNHN.F.IBC 1602 in **C**, dorsal and **D**, ventral views; **E–F**, MNHN.F.IBC 1602 in **E**, right lateral and **F**, posterior views; **G–H**, 3D model of MNHN.F.IBC 1602 in **G**, left lateral and **H**, posterior views.

**Abbreviations:** **boc**, broken remnants of otic capsule; **cfo**, condyloid fossa; **cp**, crista parotica; **ee**, epiotic eminence; **auc**, eustachian canal; **fm**, foramen magnum; **fp**, frontoparietal; **icf**, internal carotid foramen; **ipf**, inferior perilymphatic foramen; **jf**, jugular foramen; **ncv**, nasal cavity; **occd**, occipital condyle; **ocmf**, oculomotor foramen; **onf**, orbitonasal foramen; **opf**, optic foramen; **par**, parasphenoid; **pif**, pineal foramen; **plf?**, putative palatine foramen; **ppc**, prepalatine connection; **prf**, prootic foramen; **pro**, prooticoccipital; **psbp**, pseudobasal process; **son**, solum nasi; **sn**, septum nasi; **tn**, tectum nasi; **trf**, trochlear foramen. Dotted lines represent limits of frontoparietal, parasphenoid and Eustachian canals. [Full page width]

**Figure. 3.** Interpretative drawing and reconstruction of the frontoparietal and parasphenoid of *Inbecetenanura ragei* sp. nov. using the 3D reconstruction of the internal surface of the frontoparietal and sphenethmoid of MNHN.F.IBC 1602. Frontoparietal in **A**, dorsal and **B**, ventral views; **C**, parasphenoid in ventral view. **Abbreviations:** **clp**, cultriform process; **dfpf**, dorsal imprint of the fenestra frontoparietalis; **fcad**, facies cerebri anterior; **fcp**, facies cerebri posterior; **fpshp**, frontoparietal-sphenethmoid articulation area; **pif**, pineal foramen; **pm**, posterior margin; **ple**, posterolateral expansion; **psc**, parasagittal crest, **?vimp**, putative vomer imprint of Báez and Rage, 1998. [2/3 page width]

**Figure. 4.** 3D reconstruction of the anterior region of the sphenethmoid of *Inbecetenanura ragei* sp. nov. (MNHN.F.IBC 1602). Model in **A**, dorsal and **B**, anterior views.

**Abbreviations:** **fpf**, fenestra frontoparietalis; **nf**, nasal foramen; **onf**; orbitonasal foramen; **sn**, septum nasi; **son**, solum nasi; **tn**, tectum nasi; **uf**, unknown foramen. [column width]

**Figure. 5.** 3D model of the endocast of the braincase of *Inbecetenanura ragei* sp. nov. (MNHN.F.IBC 1602). Model in **A**, dorsal, **B**, ventral and **C**, left lateral views.

**Abbreviations:** **CN I**, cranial nerve I (olfactory nerves pathways); **CN II**, cranial nerve II (optic nerves pathways); **CN III**, cranial nerve III (oculomotor nerves pathways); **CN IX-X**, cranial nerve IX (pathway for glossopharyngeal nerve) and X (pathway for vagus nerve); **hyp**, hypothalamus; **nal**, orbitonasal duct; **nep**, base of nasal capsule;; **olfb?**, olfactory bulb ?; **oplb**, optic lobe; **tel**, telencephalon. [Full page width]

**Figure. 6.** Sphenethmoid of *Inbecetenanura*. Sphenethmoid (MNHN.F.IBC 1969a) tentatively assigned to *Inbecetenanura* gen. nov. in **A**, dorsal, **B**, ventral, **C**, right lateral and **D**, anterior views. **Abbreviations:** **fpf**, fenestra frontoparietalis; **of**, olfactory foramen; **onf**, orbitonasal foramen; **pri**, parasphenoid imprint; **sn**, septum nasi; **tn**, tectum nasi; **uf**, unknown foramen. Arrow indicates anterior region. [Full page width]

**Figure. 7.** Vertebral elements of *Inbecetenanura*. **A–E**, presacral vertebra (MNHN.F.IBC 1650) in **A**, anterior, **B**, posterior, **C**, dorsal, **D**, ventral and **E**, right lateral views; **F–G**, presacral centrum (MNHN.F.IBC 1997a) in **F** dorsal and **G** ventral views; **H–K**, sacrococcyges (MNHN.F.IBC 1972) in **H**, anterior, **I**, dorsal, **J**, ventral and **K**, left lateral views. **Abbreviations:** **acd**, anterior condyle; **irp**, irregular projection; **mg**, medial groove; **mr**, medial ridge; **nc**, neural crest; **ns**, neural spine; **nw**, neural wall; **pct**, posterior cotyle; **prz**, prezygapophysis; **sa**, sacral diapophysis; **spf**, spinal foramen; **tp**, transverse process. [Full page width]

**Figure. 8.** Strict consensus of 4 MPTs of 649 steps from the unconstrained analysis under equal weights, with multistate characters ordered (CI = 0,359; RI = 0, 692). The † symbol identifies extinct taxa; clade names in bold italic represent names converted in PhyloCode (except *Inbecetenanura ragei*); orange clade represents Pipinomorpha; green clade represents Xenopodinae; numbers above branches designate Bremer support; those below are bootstrap frequencies. [Full page width]

**Figure. 9.** Strict consensus of 47 MPTs of 675 steps from the constrained analysis using a molecular scaffold tree from Jetz and Pyron (2018), performed under EW with multistate characters ordered (CI = 0.339; RI = 0.663). The † symbol identifies extinct taxa; clade names in bold italic represent names converted in PhyloCode (except *Inbecetenanura ragei*); orange clade represents Pipinomorpha; green clade represents Xenopodinae; numbers above branches designate Bremer support; those below are bootstrap frequencies. [Full page width]

**Figure. 10.** Strict consensus of the unconstrained analysis under equal weights mapped onto the stratigraphical chart, with their geographical occurrences. Black bar over branches indicates known fossil record and clade names in bold italic represent names converted in PhyloCode. Position of nodes does not reflect time-calibrated ages. The phylogenetic position of *Palaeobatrachus* is inferred on the position of *Palaeobatrachus grandipes*. [Full page width]

**Figure. 11.** Strict consensus of the constrained analysis under equal weights and excluding '*Xenopus*' *stromeri* mapped onto the stratigraphical chart, with their geographical



occurrences. Black bar over branches indicates known fossil record and clade names in bold italic represent names converted in PhyloCode. Position of nodes does not reflect time-calibrated ages. The phylogenetic position of *Palaeobatrachus* is inferred on the position of *Palaeobatrachus grandipes*. [Full page width]























