geodiversitas

2026 • 48 • 4

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art. 48 (4) — Published on 12 March 2026
www.geodiversitas.com

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Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

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ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Anurans of In Becetèn (Republic of Niger): the most diverse site for amphibians in Mesozoic Africa

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Submitted on 7 February 2025 | accepted on 10 April 2025 | published on 12 March 2026

urn:lsid:zoobank.org:pub:35876AF3-E61D-4B48-BBDA-68CB721241B7

Lemierre A., Folie A., Bailon S. & Laurin M. 2026. — Anurans of In Becetèn (Republic of Niger): the most diverse site for amphibians in Mesozoic Africa. *Geodiversitas* 48 (4): 51-67. https://doi.org/10.5252/geodiversitas2026v48a4. http://geodiversitas.com/48/4

ABSTRACT

In Becetèn (Niger) represents one of the most diverse continental vertebrate faunas from the Late Cretaceous of Africa. Recently, anurans, in particular aquatic pipimorphs, have generated renewed interest, with the identification of four distinct pipimorph taxa. Here we describe the remaining anuran specimens from In Becetèn, which represent at least three new anuran taxa that cannot be assigned to pipimorphs (Anura indet, Neobatrachia and a ranoid). Among them, one taxon, documented by ornamented cranial material, is a large Neobatrachia incertae sedis, as suggested by our phylogenetic analyses. This marks only the third Mesozoic occurrence of neobatrachians in Africa. In addition, an isolated humerus is referred as a new unnamed ranoid and is not only the oldest known occurrence of the clade, but also the first known Mesozoic specimen of this cosmopolitan family from Africa. With at least seven anuran taxa identified, In Becetèn is the most diverse locality of Africa, and one of the most diverse localities across the Late Cretaceous (Coniacian or Santonian).

KEY WORDS
Anura,
Africa,
Cretaceous,
Neobatrachia,
phylogeny.

RÉSUMÉ

Anoures d'In Becetèn (République du Niger) : le site le plus diversifié en amphibiens du Mésozoïque africain.
Le site d'In Becetèn (Niger) a livré une des faunes de vertébrés continentaux les plus diversifiés du Crétacé supérieur d'Afrique. Récemment, les anoures, en particulier les pipimorphes aquatiques, ont été le sujet de plusieurs études, avec l'identification de quatre taxons distincts. Nous décrivons ici les autres spécimens d'anoures d'In Becetèn, qui permettent d'identifier au moins trois nouveaux taxons qui ne peuvent pas être attribués aux pipimorphes (Anura indet., Neobatrachia indet. et un ranoïde). Parmi ces taxons, l'un, identifié par plusieurs éléments crâniaux ornementés, est un gros néobatracien de position phylogénétique indéterminée (d'après nos analyses phylogénétiques). Cela marque la troisième occurrence mésozoïque des néobatraciens en Afrique. Un humérus isolé est aussi attribué aux Neobatrachia, plus précisément aux Ranoidea. Cet humérus est non seulement la plus ancienne occurrence du clade, mais également la première occurrence mésozoïque de ce vaste clade cosmopolite en Afrique. Avec au moins sept taxons d'anoures identifiés, In Becetèn est la localité la plus riche en amphibiens d'Afrique au Mésozoïque, et une des plus diversifiées durant le Crétacé supérieur au niveau mondial (Coniacien ou Santonien).

MOTS CLÉS
Anoure,
Afrique,
Crétacé,
Neobatrachia,
phylogénie.

INTRODUCTION

In Becetèn is a rich vertebrate locality from the Late Cretaceous of Niger (Broin *et al.* 1974). In the original description of the fauna, actinopterygians, dipnoans, crocodiles, dinosaurs, chelonians, squamates and lissamphibians were identified (Broin *et al.* 1974). However, no material was illustrated at that time. Several studies followed, but the fauna remained incompletely studied (Gayet & Meunier, 1996; Gayet *et al.* 1997; Báez & Rage 1998). The anurans of In Becetèn have received more attention in the recent years, with three new pipimorphs (including a new pipid) identified (Lemierre *et al.* 2023, 2025). In total, four pipimorphs are now known in In Becetèn, a unique diversity among Mesozoic and Paleogene localities (Gardner & Rage 2016; Barcelos & dos Santos 2022). However, little information exists on non-pipid anurans from In Becetèn. Several postcranial elements were assigned to an unknown Ranidae in the original study (Broin *et al.* 1974), with one illustrated and reassigned to Ranoidea a decade later (Rage 1984: fig. 1A). In addition, a second non-pipimorph anuran, with ornamented cranial bones was mentioned (Gardner & Rage 2016: 180) but not studied. Here, we describe all anuran specimens from In Becetèn not assigned to Pipimorpha. Among them, we describe and illustrate the ornamented anuran previously mentioned, and include this taxon in a phylogenetic analysis, to test its affinities. We then discuss and compare the diversity of anurans in In Becetèn to other Mesozoic localities.

GEOLOGICAL SETTING

All specimens are from the site of In Becetèn, Niger (also known as Ibessetene, In Becetem, In Beceten, In'Betetén, In Béceten and erroneously Ibeceten; 15°14'2"N, 5°48'31"E). They were collected during three expeditions organised in 1970, 1972 and 1973 by the Muséum national d'Histoire naturelle, and led by P. Taquet and D. Russell (Broin *et al.* 1974). The site of In Becetèn is located 80 km east of the town of Tahoua, in the South-eastern region of the Republic of Niger (Lemierre *et al.* 2023: fig. 1 for detailed information). The site is considered Coniacian or Santonian (Late Cretaceous, 91.1 to 83.4 Ma; Moody & Sutcliffe 1991).

MATERIAL AND METHODS

INSTITUTIONAL ABBREVIATIONS

MNHN	Muséum national d'Histoire naturelle, Paris;
UCRC	University of Chicago research collection, Chicago.

COLLECTION ACRONYM

MNHN.F	Paleontological collection of the MNHN;
IBC	specimens from In Becetèn in the MNHN.F collection;
PV	specimens stored within the vertebrate paleontology section of the UCRC.

TERMINOLOGY

The anatomical terminology used herein is based on Roček (1981) and Biton *et al.* (2016) for cranial features, Bolkay (1919) and Sanchíz (1998) for postcranial anatomy, and Gómez & Turazzini (2016) for iliac features.

PHYLOGENETIC ANALYSIS

Our data matrix includes 88 taxa and 143 morphological characters and is derived from that of Lemierre & Blackburn (2022; see Appendix S1-S4). We added our new unnamed neobatrachian to test its neobatrachian affinities. This taxon was scored using personal observations based on direct examination of the specimens under a binocular lens (magnification × 6 12, 25 and 50). The analysis was performed using TNT v.1.5 (Goloboff & Catalano 2016) under equal weights. All analyses were conducted with cline characters ordered (characters 3, 9, 10, 14, 26, 34, 51, 52, 68, 93, 112, 121, 124, 125 and 126) in the analysis (Rineau *et al.*

2015, 2018). The analysis 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* Stejneger, 1899 (Ascaphidae), and when more than one most parsimonious tree was found, a strict consensus was obtained. Node support was evaluated using Bremer support and standard nonparametric bootstrapping (Felsenstein 1985; Bremer 1988), with searches of 1000 replicates and collapsing groups below 5% frequency. Because the phylogeny resulting from the above analysis is strongly at odds with relationships inferred from analyses with molecular genetic data, we performed an additional analysis using a constraint tree reflecting a consensus of recent molecular phylogenetic analyses (Feng *et al.* 2017; Streicher *et al.* 2018; Hime *et al.* 2021; Portik *et al.* 2023). We focused on the backbone of the tree and large-scale patterns of relationships within Hyloidea Rafinesque, 1815 and Ranoidea Rafinesque, 1815. We used the same constraints as in Lemierre & Blackburn (2022): 1) Pelobatoidea Bonaparte, 1850, Alytoidea Dubois, Ohler & Pyron, 2021, Neobatrachia Reig, 1958 as monophyletic; 2) *Heleophryne* Sclater, 1898 as the sister-taxon to all neobatrachians; 3) Hyloidea and Ranoidea as monophyletic; 4) within Hyloidea, we constrained Calyptocephalellidae, Neoaustrarana, *Telmatobius* Wiegmann, 1834 and a clade representing all other hyloids; and 5) within Ranoidea, we constrained Afrobatrachia, Natatanura and Microhylidae. In addition, we constrained Pyxicephaloidea Bonaparte, 1850 (Lemierre & Laurin 2021) as monophyletic within Natatanura. We did not constrain the placement of any extinct taxa, and we also left relationships within constraint clades (e.g., Pelobatoidea, Natatanura) as polytomies so that relationships within them could be inferred by our morphological data.

SYSTEMATIC PALAEONTOLOGY

Order ANURA Duméril, 1805
Suborder NEOBATRACHIA Reig, 1958
Superfamily Ranoidea Gray, 1825

Ranoidea gen. et sp. indet.
(Fig. 1)

Referred material. — One incomplete right humerus (MNHN.F.IBC1603; Fig. 1).

Description

This humerus was regarded as a possible Ranidae in the first publication of the In Becetèn fauna (Broin *et al.* 1974). MNHN.F.IBC1603 was later illustrated and shortly described in 1984 (Rage 1984: fig. 1A) and considered to be a "Ranoid". The specimen is the distal half of a right humerus (Fig. 1). Most of the distal head is preserved (Fig. 1). The diaphysis is straight and not curved ventrally (Fig. 1A-F). The crista ventralis is well developed (Fig. 1D, F). Most of the preserved region of the crista ventralis is divided into two ridges, with an elongate groove between the two; only the distalmost portion forms a single crest (i.e., no crista paraventralis; Fig. 1A, D). The crista medialis is thin (Fig. 1B, C, D, F). The fossa cubitalis ventralis is triangular and distally broader than its proximo-distal diameter (width greater than height; Fig. 1A, D). The fossa is shallow (although it seems deeper in Fig. 1A) but well delimited by a thin, distinct ridge (Fig. 1A, D). The eminentia capitata is well developed and not shifted laterally from the diaphysis axis (Fig. 1A, D). The epicondylus ulnaris is well prominent, reaching distally the level of the eminentia capitata (Fig. 1A, B, D, E), while the epicondylus radialis appears to be confluent with the eminentia (Fig. 1A, B, D, E). The olecranon scar extends proximally, with a pointed and tapered proximal margin (Fig. 1B, E).

Discussion

This humerus is similar to the neobatrachian morphology in having: 1) a well-developed eminentia capitata; and 2) asymmetrical epicondyles (Prasad & Rage 2004; Rage *et al.* 2021). Furthermore, the crista ventralis is divided into two ridges in numerous neobatrachians (this may denote muscular insertion; Otero *et al.* 2014). Moreover, the presence of: 1) a straight diaphysis; 2) a shallow fossa cubitalis ventralis; 3) an eminentia capitata not shifted laterally; and 4) an epicondylus ulnaris more developed than the epicondylus radialis, is similar to ranoid morphology (Rage *et al.* 2013; Lapparent de Broin *et al.* 2020). In addition, a well-delimited fossa cubitalis ventralis, although rare (Rage 1984), is observed in several ranoid taxa from the Eocene of the Quercy Phosphorites (Rage 2016) and among extant ranoids (Worthy 2001). MNHN.F.IBC1603 is therefore similar to ranoids and can be attributed to the Ranoidea. The presence of a distinct crista medialis is often linked to sexual and/or ontogenetic dimorphism (Duellman & Trueb 1994). This suggests that this humerus might belong to a male ranoid. A humerus from the Cenomanian of the Kem Kem (Morocco) with ranoid affinities has also been recently described (UCRC-PV104; see Lemierre & Blackburn 2022: fig. 6A-C). Both humeri share: 1) a straight diaphysis; 2) a well-developed eminentia capitata; 3) asymmetrically developed epicondyles; 4) an eminentia capitata not shifted from the diaphysis axis; and 5) a shallow fossa cubitalis ventralis. However, MNHN.F.IBC1603 differs from UCRC-PV104 in: 1) having a more developed crista ventralis divided into two ridges; 2) a well-delimited fossa cubitalis; 3) a more protruding epicondylus ulnaris; 4) an olecranon scar more extended proximally; and 5) in having a discrete crista medialis. Thus, we think that these humeri likely represent different taxa. Furthermore, MNHN.F.IBC1603 possesses more ranoid characters than UCRC-PV104. In conclusion, MNHN.F.IBC1603 is attributed to a new unidentified male ranoid, and thus represent the oldest occurrence of Ranoidea.

Neobatrachia gen. et sp. indet.
(Fig. 2B-O)

Referred material. — 22 fragmentary maxillae (MNHN.F.IBC1983, IBC1984 and IBC1985) and eight fragments of exocranium (MNHN.F.IBC1986) that include incomplete frontoparietal, nasals and squamosals.

Fig. 1. — Indeterminate Ranoidea of In Becetèn: **A**-**C**, MNHN.F.IBC1603, distal half of right humerus in ventral (**A**), dorsal (**B**) and medial (**C**) views; **D**-**F**, interpretative drawing of the same specimen in ventral (**D**), dorsal (**E**) and medial (**F**) views. Abbreviations: **cm**, crista medialis; **cv**, crista ventralis; **ec**, eminentia capitata; **er**, epicondylus radialis; **eu**, epicondylus ulnaris; **dia**, diaphysis; **fc**, fossa cubitalis ventralis; **ols**, olecranon scar. Scale bar: 2 mm. Photos and drawings: Alfred Lemierre.

DESCRIPTION

Maxilla

The maxilla is thick and heavily ossified (Fig. 2). Most fragments are ornamented by small closely spaced tubercles forming a honeycomb pattern (Fig. 2B, C). The ornamentation covers most of the preserved labial surface of maxillae, except for a narrow strip along the ventral margin of the bone (Fig. 2B). The pars facialis is incomplete but seems high on most of its length (Fig. 2B). The lamina horizontalis is prominent, rounded (in cross-section; Fig. 2D) and slightly project lingually (Fig. 2D, F). Although no teeth are preserved, the pars dentalis shows that the maxilla was toothed (12 teeth positions preserved on the largest maxilla fragment; Fig. 2E-G). The pars dentalis is dorsoventrally shallow and extends posteriorly beyond the pterygoid process (Fig. 2F). The pterygoid process is well developed and projects lingually (Fig. 2F). Posterior to this process, the maxilla narrows dorsally (Fig. 2E). Unfortunately, the posterior end of the maxilla has not been preserved. Anterior to the pterygoid process, the lamina horizontalis dorsally bears a shallow groove for the palatoquadrate (Fig. 2C). The pars facialis is high near the anterior margin of the maxilla, and likely indicates the presence of an anterodorsal process (Fig. A, G) as in *Calyptocephalella* Strand, 1928 or *Ceratophrys* Wied-Neuwied, 1824. The anterior tip of the maxilla shows a deep fossa for the articulation with the premaxilla (Fig. 2G).

Nasal

Two fragments (both included under MNHN.F.IBC1986) are slender, flat pieces of bone. The dorsal surface is covered by the same ornamentation as in the maxillae (Fig. 2H).

Frontoparietal

The dorsal surface bears ornamentation similar to the one recovered in maxillae and nasal fragments (Fig. 2I). The pars contacta is curved externally (Fig. 2J, K). The pars contacta delimits a dorsal flange. This flange is interpreted as the tectum supraorbitale (Fig. 3I, J).

Squamosal

Several fragments of ornamented bone are interpreted as fragments of the squamosal. The best-preserved bone (MNHN.F.IBC1986c; Fig. 2L-M) represents the posterior process which bears a rounded posterior margin (Fig. 2L). It is missing its medial margin, which suggests that it might have extended further and that a ramus paroticus was present (Fig. 2M). The base of a posterolateralis process and of the lamella alaris are preserved (Fig. 2L, M). Other specimens preserve part of the lamella alaris (Fig. 2N, O). The external surface is ornamented and thickened internally, forming a triangular surface (Fig. 2O). This fragment likely represents the lamella alaris of the ramus zygomaticus. Unfortunately, there is no indication whether and how the squamosal articulates with the maxilla.

Discussion

Ornamentation on dermal bones in anurans occurs in various anuran clades (Paluh *et al.* 2020). However, combination of osteological characters can be here used to exclude certain major clades. *Latonia* Meyer, 1843 (Alytidae Fitzinger, 1843) is the only known alytid exhibiting dermal ornamentation (Roček 1994). However, its current stratigraphic range is limited only to Oligocene and Neogene of Europe and Northern Africa (Gardner & Rage 2016; Syromyatnikova *et al.* 2019). In addition, our ornamented taxon can be differentiated from *Latonia* in having a rounded medial margin of the lamina horizontalis (pointed in *Latonia*). Pelobatids are known to exhibit dermal ornamentation (Roček 2013) that resembles the ornamentation of the In Becetèn specimens (tubercles closely spaced together). However, our specimens differ from all pelobatids in lacking an elongate palatine process of the maxilla (Roček 2013). Furthermore, no pelobatids are known within the fossil record of Gondwana (a "Pelobatidae" was mentioned in the Upper Cretaceous of Madagascar, but the attribution is considered erroneous; Asher & Krause 1998; Gardner & Rage 2016) (Gardner & Rage 2016). The In Becetèn ornamented specimens can also be differentiated from Pipimorpha in: 1) having a well-developed squamosal (small and reduced squamosal in Pipimorpha); and 2) a rather thick maxilla (slender maxillae in Pipimorpha). Two anurans of indeterminate phylogenetic position from North America possess similar ornamentation: *Scotiophryne* Estes, 1969 and *Theatonius* Fox, 1976. *Scotiophryne* is known from the Late Cretaceous and might also occur in Early Cretaceous and Paleocene (Roček 2013; Gardner & DeMar 2013). *Scotiophryne* differs from our taxon in having a narrow horizontal lamina (Gardner 2008). *Theatonius* is known from Late Cretaceous deposits (Gardner & DeMar 2013). *Theatonius* differs from our taxon in lacking teeth on its maxillae. Thus, our taxon can be excluded from Leiopelmatoidea, Alytoidea, Pipimorpha, and Pelobatoidea. The only major clade left is the Neobatrachia. This includes several extinct and extant hyperossified taxa.

Two neobatrachians are known in the Mesozoic of Africa, *Beelzebufo ampinga* Evans, Jones and Krause, 2008 from the Maastrichtian of Madagascar and *Cretadhefdaa taouzensis* Lemierre & Blackburn, 2022 from the Cenomanian of Morocco. *Beelzebufo ampinga*, *Cretadhefdaa taouzensis* and our specimens share: 1) ornamentation extending on most of the lateral surface of the maxilla (Fig. 2B); and 2) the presence of a tectum supraorbitale (Fig. 2I-J). The latter is also shared with *Cretadhefdaa* Lemierre & Blackburn, 2022. However, *Beelzebufo* does not possess a distinct processus frontalis (present in our taxon; Fig. 2F) and all known *Beelzebufo* specimens are far larger than our specimens. Our specimens can be differentiated from *Cretadhefdaa* in: 1) having an ornamentation made of small tubercles resembling a honeycomb pattern (deep pits and ridges in *Cretadhefdaa*); and 2) lacking ornamentation on the lateral surface of the pars dentalis (present in *Cretadhefdaa;* Lemierre & Blackburn 2022: fig. 3E-G).

Another Mesozoic hyperossified neobatrachian is *Hungarobatrachus szukacsi* Szentesi & Venczel, 2010 from the Santonian of Hungary. Our specimens are similar to *Hungarobatrachus* in having: 1) ornamentation extending on most of the lateral surface of the maxilla (Fig. 2B); 2) a well-developed pterygoid process of the maxilla (Fig. 2C, F); and 3) a tectum supraorbitale (Fig. 2I-J). However, our specimens differ from *H. szukacsi* in: 1) having a well-developed lamina horizontalis (moderately developed in *H. szukacsi*); and 2) in having the maxillary tooth row extending posteriorly beyond the pterygoid process.

One last hyperossified neobatrachian from the Mesozoic is *Baurubatrachus* Báez & Perí, 1989 from the Maastrichtian of Brazil. *Baurubatrachus* and our specimens differ in the ornamentation on their cranial remains (pits and ridges in *Baurubatrachus*; Báez & Gómez 2018). However, both are similar in having: 1) the medial margin of the lamina horizontalis rounded (in cross-section, Fig. 2D); and 2) a crista dentalis ending slightly beyond the pterygoid process (Fig. 2F).

In Africa, the next oldest hyperossified neobatrachian is the ranoid *Rocekophryne ornata* Rage *et al.*, 2021 from the Early Eocene of Algeria. Our specimens can be differentiated from *Rocekophryne* in having: 1) a different ornamentation (deep pits and ridges in *Rocekophryne*; Rage *et al.* 2021); 2) ornamentation extending ventrally to cover the entire lateral surface of the pars dentalis; and 3) in having

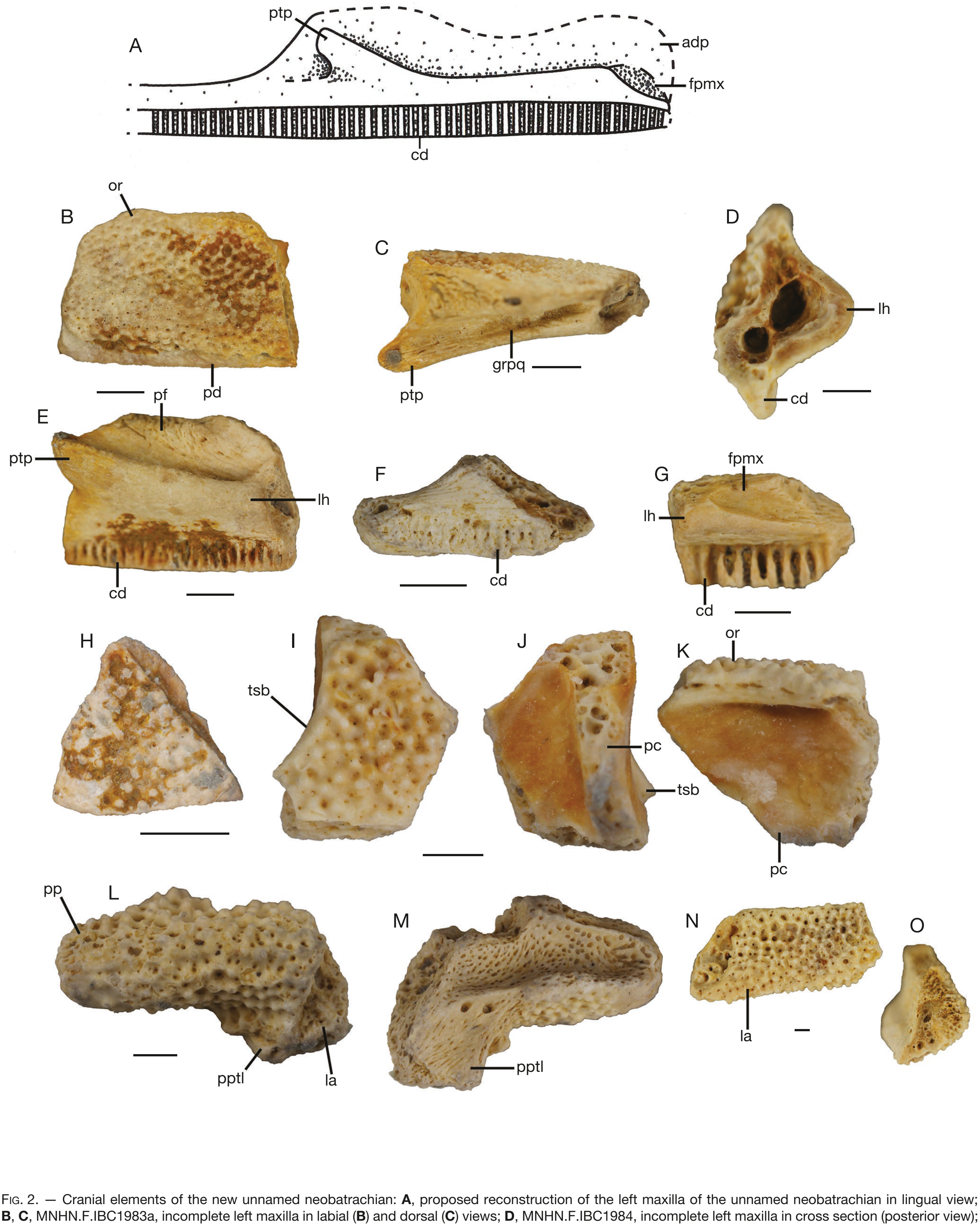

FIG. 2. — Cranial elements of the new unnamed neobatrachian: **A**, proposed reconstruction of the left maxilla of the unnamed neobatrachian in lingual view; **B**, **C**, MNHN.F.IBC1983a, incomplete left maxilla in labial (**B**) and dorsal (**C**) views; **D**, MNHN.F.IBC1984, incomplete left maxilla in cross section (posterior view); **E**, MNHN.F.IBC1983a, left maxilla in lingual view; **F**, MNHN.F.IBC1985a incomplete posterior left maxilla in lingual view; **G**, MNHN.F.IBC1985b, incomplete anterior left maxilla in lingual view; **H**, MNHN.F.IBC1986a, putative incomplete nasal in dorsal view; **I**-**K**, MNHN.F.IBC1986b, incomplete frontoparietal in dorsal (**I**), ventral (**J**) and lateral (**K**) views; **L**, **M**, MNHN.F.IBC1986c, posterior region of a right squamosal in lateral (**L**) and medial (**M**) views; **N**, **O**, likely anterior incomplete region of a squamosal in labial (**N**) and anterior or posterior (**O**) views MNHN.F.IBC1986d. Abbreviations: **adp**, antero dorsal process; **cd**, crista dentalis; **fpmx**, fossa for the insertion of the premaxilla; **grpq**, groove for the palatoquadrate bar; **la**, lamella alaris; **lh**, lamina horizontalis; **or**, ornamentation; **pc**, pars contacta; **pd**, pars dentalis; **pf**, pars facialis; **pp**, processus posterior; **ptp**, pterygoid process; **pptl**, processus posterolateralis; **tsb**, tectum supraorbitale. Scale bars: B-H, 2 mm; I-M, 1 mm. Photos and drawing: Alfred Lemierre.

an anterodorsal process (Fig. 2A). However, our specimens and *Rocekophryne* are similar in having a rounded lamina horizontalis (Fig. 2H). Another extinct hyperossified ranoid is *Thaumastosaurus* De Stefano, 1903, of which at least three to five taxa are known (Lemierre *et al.* 2021; Georgalis *et al.* 2023). Our specimens differ from *Thaumastosaurus* in: 1) having an ornamentation made of small tubercles and pits (deep pits and ridges in *Thaumastosaurus*; Fig. 2B); and 2) having a well-developed pterygoid process (Fig. 2D, F).

Thus, the In Becetèn ornamented anuran can be mainly differentiated from all extinct hyperossified anurans with the following characters: 1) a dermal ornamentation made of small closely spaced tubercles forming a honeycomb pattern (shared with *Theatonius* and *Scotiophryne*); and 2) a well-developed pterygoid process (shared with *Hungarobatrachus*).

Known extant hyperossified and ornamented neobatrachians mainly occur among hyloids, except for three genera, *Aubria* Boulenger, 1917, *Cornufer* Tschudi, 1838 and *Pyxicephalus* Tschudi, 1838. *Aubria* and *Pyxicephalus* (in the African endemic family Pyxicephalidae) both possess the same characteristics on their maxillae as *Thaumastosaurus* De Stefano, 1903, except for having a more developed pterygoid process (Sheil 1999). Thus, our specimens can be differentiated from all Pyxicephalidae (*Thaumastosaurus*, *Aubria* and *Pyxicephalus*). *Cornufer* is a hyperossified ranoid (family Ceratobatrachidae) from Indonesia. Its maxilla bears no anterodorsal process, and its anterior region is low and mostly devoid of ornamentation. Furthermore, the lamina horizontalis projects lingually into a thin blade in *Cornufer*. Thus, our specimens likely differ from all known hyperossified ranoids.

All remaining ornamented taxa are found within the Hyloidea, mainly among Ceratophryidae Tschudi, 1838 and Calyptocephalellidae Reig, 1960. Our taxon resembles the Ceratophryidae in (likely) having an anterodorsal process on its maxilla. Our taxon differs from all ceratophryids in having a lamina horizontalis slightly protruding from the lingual surface of the maxilla (flattened in Ceratophryidae).

Calyptocephalellidae and its type genus, *Calyptocephalella*, are known throughout the South American fossil record since the Late Cretaceous (Agnolin 2012; Muzzopappa 2019; Muzzopappa *et al.* 2020). Incomplete specimens attributed to this clade have all been referred to *Calyptocephalella*, an attribution considered equivocal (Nicoli *et al.* 2017). Hence, we will consider all materials referred to *Calyptocephalella* as Calyptocephalellidae in this comparison. Our specimens resemble calyptocephalellids in having: 1) ornamentation covering the lateral surface of the maxilla, except for a thin strip of bone ventrally along the margin of the crista dentalis (Fig. 2B); and 2) in having an anterodorsal process (Fig. 2A). However, our specimens differ from calyptocephalellids in lacking a distinct lamina horizontalis on most of the length of the maxilla (in calyptocephalellids, the lamina horizontalis is flattened lateromedially only at the level of the orbit; Muzzopappa & Báez 2009: fig. 3.2).

To summarize, we can exclude our specimens from all non-neobatrachian anuran clades, but we did not recover known synapomorphies to firmly attribute these fossils to Neobatrachia. However, they seem to share several characters on the maxilla with neobatrachian clades, like the presence of an anterodorsal process. Thus, these ornamented specimens represent a new neobatrachian taxon, here informally called "Neobatrachia gen. et sp. indet.". We refrain from erecting a formal taxon in the absence of better-preserved materials. To assess its affinities, we included this unnamed neobatrachian in a morphological dataset composed of extant and extinct anurans with emphasis on neobatrachians.

Anura gen. et sp. indet.

Referred material. — Nine fragments of maxillae (MNHN.F.IBC1989a, IBC1989b, IBC1991a-IBC1991f, IBC2063).

Description

Maxillae

Three maxilla morphotypes distinct from the unnamed neobatrachian can be identified within In Becetèn: maxillary morphotypes A, B and C.

The two fragments attributed to the maxillary morphotype A (MNHN.F.IBC1989a, IBC1989b) bear ornamentation made of pits and ridges on their labial surface (Fig. 3A, B). This ornamentation covers the whole pars facialis, and most of the pars dentalis, leaving only a thin strip of smooth bone along the margin of the crista dentalis (Fig. 3B). The crista dentalis is shallow. One fragment (MNHN.F.IBC1989a) bears a distinct, rounded lamina horizontalis lingually (Fig. 3C). On the second fragment (MNHN.F.IBC1989b), there is no lamina horizontalis (Fig. 3D). Morphotype A can be differentiated from the above unnamed neobatrachian in being ornamented by pits and ridges (instead of small tubercles).

Four fragments are assigned to the maxillary morphotype B (MNHN.F.IBC1991a, IBC1991b, IBC1991c, IBC1991d). Three of them lack ornamentation on their labial surface (Fig. 3E, F). The only exception is the largest fragment (MNHN.F.IBC1991a), where a faint patch of rugose ornamentation is present near the base of the frontal process (Fig. 3E). All fragments bear a crista dentalis, with poorly-preserved teeth (Fig. 3C, D, G, I). In lingual view, the rounded, prominent lamina horizontalis is distinct on all fragments (Fig. 3G). The recessus vaginiformis is shallow, but well delimited ventrally and anterodorsally by two crests (Fig. 3G). The anterodorsal crest (processus palatinus) extends dorsally onto the lingual surface of the frontal process. This morphotype can be differentiated from the maxillary morphotype A and the unnamed neobatrachian in: 1) lacking ornamentation on its labial surface; and 2) by a thin lamina horizontalis that protrudes lingually.

Two fragments are assigned to the maxillary morphotype C (MNHN.F.IBC1991e, IBC2063). Their labial surface is covered in small pits and ornamentation imparting rugo-

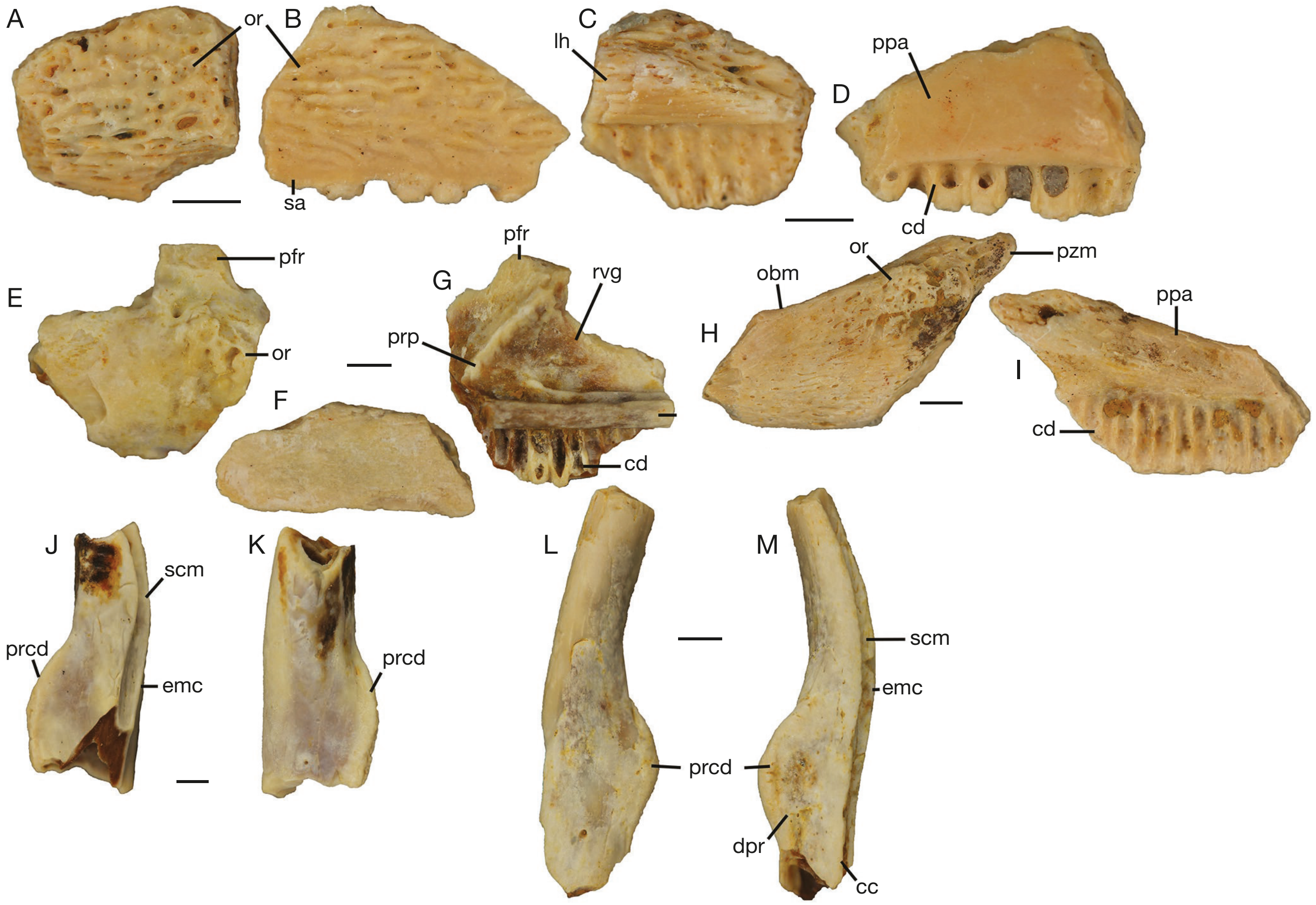

Fig. 3. — Cranial elements of indeterminate anurans: **A**-**D**, right maxilla morphotype A MNHN.F.IBC1989a and 1989b respectively in labial (**A**, **B**) and lingual (**C**, **D**) views; **E**-**G**, right maxilla morphotype B in labial (**E**, **F**) views (MNHN.F.IBC1991a, b) and lingual (**G**) view (MNHN.F.IBC1991a); **H**, **I**, left maxilla morphotype C (MNHN.F.IBC2063) in labial (**H**) and lingual (**I**) views; **J**, **K**, right angulosplenial morphotype A (MNHN.F.IBC1988) in dorsal (**J**) and ventral (**K**) views; **L**, **M**, right angulosplenial morphotype B in dorsal (**L**) and ventral (**M**) views. Abbreviations: **cc**, coronoid crest; **cd**, crista dentalis; **dpr**, depression; **emc**, extern mandibular crest; **lh**, lamina horizontalis; **obm**, orbital margin; **or**, ornamentation; **pfr**, frontal process; **ppa**, pars palatina; **prcd**, coronoid process; **prp**, processus palatinus; **pzm**, zygomaticomaxillaris process; **rvg**, recessus vaginiformis; **scm**, sulcus pro cartilagine Meckeli. Scale bars: 1 mm. Photos: Alfred Lemierre.

sity (Fig. 3H). This ornamentation seems to extend onto the whole labial surface. The maxilla is toothed (Fig. 3I). The zygomaticomaxillaris process projects posterodorsally (Fig. 3H, I). The orbital margin strongly decreases in height posterior to the latter process (Fig. 3H). Lingually, the lamina horizontalis is indistinct from the lingual surface of the maxilla (Fig. 3I), and no pterygoid process is present. The presence of a zygomaticomaxillaris process indicates that squamosal and maxilla were articulated in the maxillary morphotype C. This morphotype differs therefore from maxillary morphotypes A and B and the unnamed neobatrachian in being ornamented over the whole labial surface of the maxilla. It is also differentiated from the unnamed neobatrachian in: 1) lacking a pterygoid process; and 2) lacking a distinct lamina horizontalis.

Discussion and attribution

All three maxillary morphotypes are distinct from the unnamed neobatrachian and appear to represent three other distinct taxa. It should be noted that the presence of teeth does not exclude an attribution to the four pipimorph taxa known (Lemierre *et al.* 2023, 2025). Although most pipids lack teeth (Trueb *et al.* 2000), xenopodines and extinct pipimorphs are known to have teeth (Henrici & Báez 2001; Báez & Púgener 2003). However, the ornamentation present in morphotypes A and C differs from that of *Pachycentrata* Báez & Rage, 2004 and the unnamed pipimorph 2 (Báez & Rage 1998; Lemierre *et al.* 2025), while *Inbecetenanura* Lemierre, Bailon, Folie & Laurin, 2023 and the unnamed pipimorph 1 lack ornamentation. Hence, maxillary morphotypes A, B and C can be assigned neither to *Pachycentrata* nor to unnamed pipimorph 2. Furthermore, the presence of small patches of ornamentation in the maxillary morphotype B around the frontal process renders an attribution to *Inbecetenanura* unlikely, as such ornamentation would likely be present on the frontoparietal. Hence, the maxillary morphotype B could be attributed to the unnamed pipimorph 1 or to another non-pipid taxon in In Becetèn. Maxillary morphotypes A and C are assigned to indeterminate non-pipid anurans.

Thus, based on maxilla elements, between three and four non-pipid anuran taxa are present in In Becetèn.

Angulosplenials

Referred material. — Five incomplete angulosplenials (MNHN.F.IBC1987, IBC1988a, IBC1988b, IBC1990, IBC2064).

Description

The angulosplenials are all represented by posterior portions that lack their posteriormost parts. The sulcus pro cartilagine Meckeli is present in the coronoid portion, excluding pipid affinities (Gómez 2016). Two morphotypes can be distinguished, morphotype A (MNHN.F.IBC1987, 1988a, 1988b) and morphotype B (MNHN.F.IBC1990, IBC2064). However, it cannot be excluded that their differences are of ontogenetic nature.

All specimens attributed to angulosplenial morphotype A are large and thick (Fig. 3J). Although only the anterior region of the coronoid process is preserved, it can be inferred that an anteroposteriorly elongate coronoid crest was present (Fig. 3J, K). This crest did not extend as a flange (such as in Pipidae). A shallow depression is present lateral to the coronoid process (Fig. 3J). The sulcus pro cartilagine Meckeli extends on the lateral region of the angulosplenial and narrows posteriorly (Fig. 3J).

Angulosplenial morphotype B differs from morphotype A in: 1) being smaller and medio-laterally thinner; and 2) having a broader and deeper sulcus pro cartilagine Meckeli (Fig. 3L, M). However, as in morphotype A, the sulcus pro cartilagine Meckeli extends on the lateral surface of the bone (Fig. 3K, M) and the coronoid process forms an anteroposteriorly elongated crest (Fig. 3J-M).

Sacral vertebra

Referred material. — One incomplete sacral vertebra (MNHN.F.IBC1992).

Description

MNHN.F.IBC1992 only preserves the centrum and the base of the neural arch (Fig. 4A-D). The vertebra bears an anterior condyle and two posterior condyles. Most of the anterior condyle is eroded, but it seems laterally wide (Fig. 4A). The posterior condyles are circular and well separated from each other (Fig. 4B, D).

Discussion and attribution

This vertebra was attributed to Ranidae in the original study on In Becetèn (Broin *et al.* 1974). The presence of a bicondylar sacro-urostylar articulation and a bicondylar (anterior and posterior condyles) sacral vertebra is known in only Alytoidea and Ranoidea (Duellman & Trueb 1994). Alytoidea are not known in Africa before the Neogene (Gardner & Rage 2016). One taxon from the Late Jurassic/Early Cretaceous of Morocco, aff. *Enneabatrachus* Evans & Milner, 1993, possesses an amphicoelous sacral vertebra with two posterior condyles (Jones *et al.* 2003). However, its affinity, and the referral of non-ilium elements to this taxon, are not certain (Jones *et al.* 2003). In addition, MNHN.F.IBC1992 differs from aff. *Ennabatrachus* in lacking a remnant of notochordal canal separating the posterior condyle. Most characters used for attribution to Ranoidea are found in the neural arch, which is missing. In conclusion, the scant data available are insufficient to refer this element to a specific anuran clade, as it could belong to an unidentified clade (as for the Anoual's specimen; Jones *et al.* 2003) or to an unnamed neobatrachian.

Urostyles

Referred material. — Two urostyles (MNH.F. IBC1993, IBC1994).

Description

The two urostyles represent two morphotypes, A (MNHN.F.IBC1993) and B (MNHN.F.IBC1994), both attributed to distinct taxa. As they are not coalesced to the sacral vertebra, they are excluded from Pipidae.

Urostylar morphotype A is represented by an incomplete urostyle preserving most of its anterior portion (Fig. 4E-G). It bears two anterior cotyles for sacral articulation. The cotyles are subcircular and closely spaced, separated by a thin dorsoventrally oriented crest (Fig. 4E). Transverse processes are absent (Fig. 4F, G). Most of its neural arch is missing, but it clearly extended into a thin dorsal crest (Fig. 4F). However, neither its height nor posterior extension are known.

Urostylar morphotype B (MNHN.F. IBC1994) also preserves only its anterior portion (Fig. H-J). It bears a single anterior cotyle for sacro-urostylar articulation (Fig. 4H). This cotyle is wide and slightly compressed dorsoventrally. The dorsal crest is low and reduced to a thin ridge around the level of the spinal foramen (Fig. 4I, J).

Discussion and attribution

Urostylar morphotype A differs from morphotype B in: 1) having a bicondylar sacro-urostylar articulation; and 2) having a dorsal crest not reduced to a ridge. These differences are not ontogenetic, so they represent two distinct taxa. Morphotype A can also be differentiated from MNHN.F. IBC1992 (the sacral vertebra) in having closely spaced articular facets (cotyles and condyles) for the sacro-urostylar articulation. Thus, MNHN.F. IBC1992 (sacral vertebra), IBC1993 (urostyle morphotype A) and IBC1994 (urostyle morphotype B) are all attributed to three distinct taxa. Morphotype A cannot be attributed to a specific anuran clade. The presence of monocotylar articulation in Morphotype B is uncommon among anurans. It has been recovered in several unidentified anurans from the Late Cretaceous of North America (Roček *et al.* 2010), in several Bombinatoridae (used as a diagnostic character; Folie *et al.* 2012), Altyidae (Rage & Hossini 2000) and in some Pipimorphs. Within Bombinatoridae Gray, 1825 and Alytidae, urostyles bear a low dorsal ridge, as in morphotype B, but possess transverse processes (unknown in morphotype B). Thus, the scant data available are insufficient to attribute Morphotype B to any anuran clade less inclusive than Neobatrachia. However, it should be noted that monocotylar articulation has been associated with a fairly aquatic lifestyle (Roček *et al.* 2010).

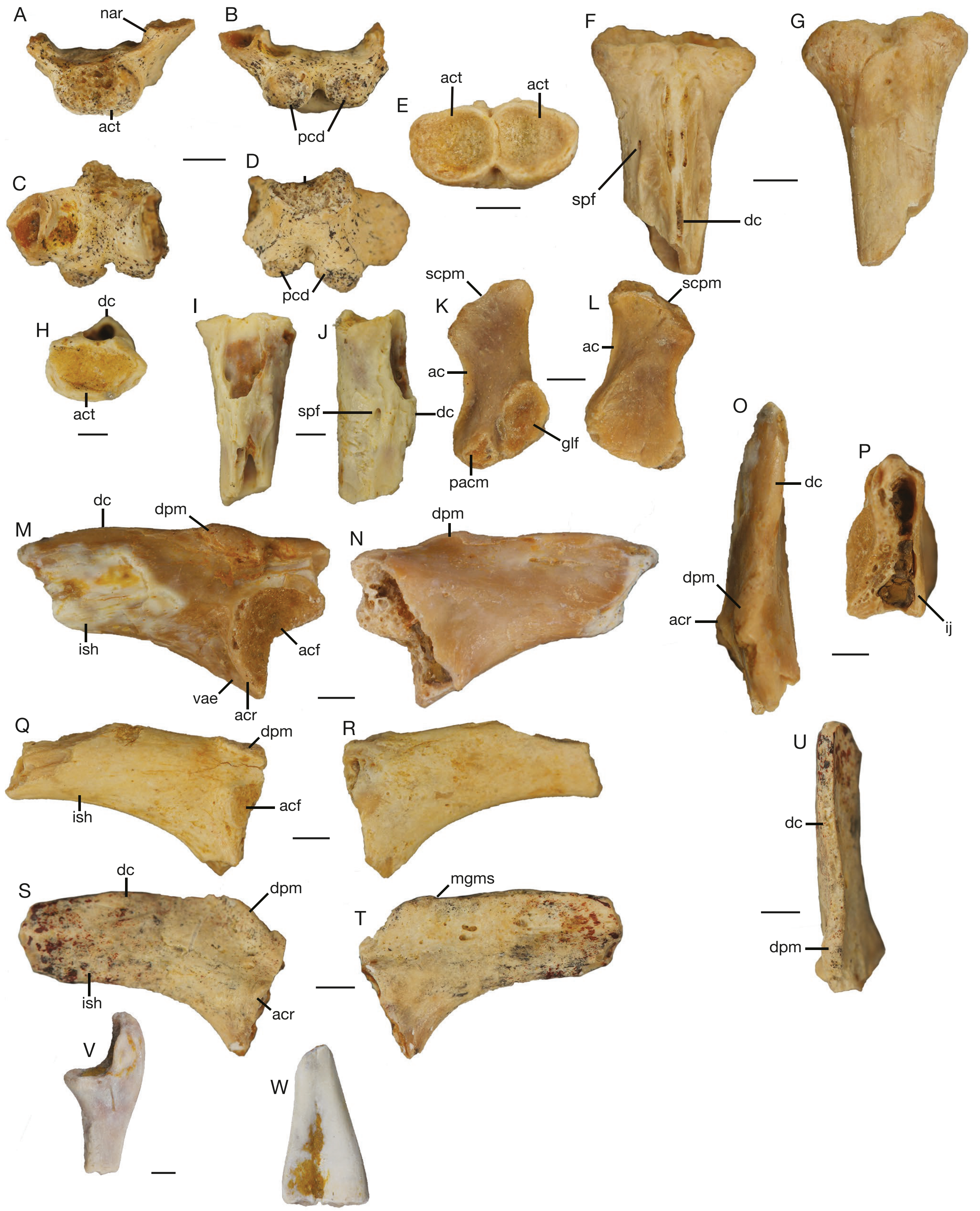

FIG. 4. — Postcranial elements of indeterminate anurans: **A**-**D**, MNHN.F.IBC1992, incomplete sacral vertebra in anterior (**A**), posterior (**B**), dorsal (**C**) and ventral (**D**) views; **E**-**G**, MNHN.F.IBC1993, urostyle morphotype A in anterior (**E**), dorsal (**F**) and ventral (**G**) views; **H**-**J**, MNHN.F.IBC1994, urostyle morphotype B in anterior (**H**), dorsal (**I**) and lateral (**J**) views; **K**, **L**, MNHN.F.IBC1996, incomplete scapula in medial (**K**) and lateral (**L**) views; **M**-**P**, MNHN.F.IBC1600, left ilium morphotype A in lateral (**M**), medial (**N**), dorsal (**O**) and posterior (**P**) views; **Q**, **R**, MNHN.F.IBC1601, left ilium morphotype B in lateral (**Q**) and medial (**R**) views; **S**-**U**, MNHN.F.IBC1995, left ilium morphotype C in lateral (**S**), medial (**T**) and dorsal (**U**) views; **V**, **W**, MNHN.F.IBC1999a and IBC1999b, incomplete radioulnae. Abbreviations: **ac**, anterior crest; **acf**, acetabular fossa; **acr**, acetabular rim; **act**, anterior cotyle; **dc**, dorsal crest; **dpm**; dorsal prominence; **glf**, glenoid fossa; **ij**, ilioischiatic juncture; **ish**, iliac shaft; **mgms**, musculus gluteus magnus scar attachment; **nar**, neural arch remnant; **pacm**, pars acromialis; **pcd**, posterior condyle; **scpm**, suprascapular margin; **spf**, spinal foramen; **vae**, ventral acetabular expansion. Scale bars: 1 mm. Photos: Alfred Lemierre.

Scapula

REFERRED MATERIAL. — One incomplete scapula (MNHN.F.IBC1996).

DESCRIPTION AND REMARKS
The scapula preserves the broken base of its pars acromialis (Fig. 4K, L). The pars glenoidalis is not distinct from the scapular shaft and pars acromialis, forming a large articular facet (Fig. 4K). The suprascapular region is elongated dorsoventrally. The anterior margin bears an extended crest (Fig. 4K, L). No assignment among anurans is possible.

Ilia

REFERRED MATERIAL. — Three incomplete left ilia (MNHN.F.IBC1600, IBC1601, IBC1995).

DESCRIPTION
These three ilia represent three different morphotypes. All three are excluded from Pipimorpha by: 1) having a dorsal crest (iliac morphotypes A and C); 2) presenting a dorsal and ventral acetabular expansion (iliac morphotypes A and B); and 3) lacking an interiliac tubercle (iliac morphotypes A and B).

Iliac morphotype A (MNHN.F.IBC1600; Fig. 4M-P) bears a low dorsal crest (Fig. 4M, N). The iliac shaft is strongly compressed lateromedially. The dorsal prominence is low and forms an elongate oval bulge (Fig. 4M, O) projecting laterally and located anterodorsal to the acetabular rim (Fig. 4M). The ventral acetabular expansion is incomplete but reduced (Fig. 4M). The preacetabular zone is expanded (Fig. 4M). A small depression beneath the ventral acetabular margin could be a preacetabular fossa. The dorsal acetabular expansion is not preserved. No interiliac tubercle seems to be present (Fig. 4P).

Ilia morphotype B (MNHN.F.IBC1601) lacks a dorsal crest (at least on its distal region; Fig. 4Q-R). The dorsal prominence is scarcely distinct from the rest of the bone, forming an ovoid bulge that projects neither medially nor laterally (Fig. 4Q). The acetabular region is too poorly preserved to distinguish any features.

Iliac morphotype C (MNHN.F.IBC1995) is missing most of its acetabular region. The preserved iliac shaft shows a well-developed dorsal crest (Fig. 4S, T). Although its dorsalmost portion is not preserved, the crest is at least the height of the iliac shaft. The dorsal prominence is an anteroposteriorly elongate ovoid bulge (Fig. 4S). The dorsal protuberance projects lateroposteriorly (Fig. 4S, U). Anterior to the dorsal prominence, the notch for the attachment of the musculus gluteus magnus is present (Fig. 4T). The dorsal prominence is located anterior to the acetabular rim.

DISCUSSION AND ATTRIBUTION
Iliac morphotypes A and B are puzzling. The presence of a weakly developed dorsal prominence in morphotype B is reminiscent of several neobatrachians, like *Telmatobius* (Gómez & Turazzini 2016) and Myobatrachidae (Tyler 1976), and the presence of a low dorsal ridge is also known in some neobatrachians (Gómez & Turazzini 2016). However, both ilia are far too incomplete to propose any precise attribution. In addition, these two morphotypes seem to differ from all known ilia from the Cretaceous of North America (Roček *et al.* 2010). Regarding morphotype C, the presence of a high dorsal crest has often been used as a characteristic of ranoids (Rage 1984). However, a high dorsal crest also occurs within Alytoidea, like the Cenozoic *Latonia* (Roček 2013). Thus, we cannot attribute Morphotype C to any clade within Anura.

All three ilia represent three distinct morphotypes, and likely three taxa. However, they are too incomplete to identify them more precisely than Anura, and we cannot determine if they represent any of the other taxa in In Becetèn.

Limb bones

REFERRED MATERIAL. — 25 radioulnae (MNHN.F.IBC1999), five femora (MNHN.F.IBC2034), 22 tibiofibulae (MNHN.F.IBC2035) and three metatarsals (MNHN.F.IBC2002).

DESCRIPTION AND REMARKS
Radioulnae, femora, tibiofibulae and metatarsals, all fragmentary, are assigned to anurans (Fig. 4V, W). However, they do not display peculiar features (such as additional ridges); consequently, no further identification is possible.

PHYLOGENETIC ANALYSES

The parsimony analysis under equal weights, with cline characters ordered and without topological constraints, yielded 10 MPTs that require 1362 steps (CI = 0.163; RI = 0.520). In the strict consensus (Fig. 5), we recovered a monophyletic Neobatrachia. However, within that clade, relationships are poorly resolved (Fig. 5). Neobatrachia is poorly supported by four synapomorphies (Appendix S4). *Heleophryne* is recovered as the sister-taxon to all other neobatrachians, as in molecular analyses (Hime *et al.* 2021). Though hyloids and ranoids form a single large clade (Fig. 5), these are not reciprocally monophyletic and ranoids are found to be diphyletic and nested within hyloids. Diphyletic ranoid (Afrobatrachia + Natatanura as a clade, Microhylidae is recovered with hyloid taxa) is a topology commonly recovered in morphology-based analyses (Báez & Gómez 2018; Lemierre *et al.* 2021) and is likely linked to pectoral girdle characters (absence of ossified omosternum in microhylids). All Mesozoic taxa (except *Arariphrynus* Leal & Brito, 2006) are clustered within a large unresolved polytomy (Fig. 5), which also includes most extant hyperossified and ornamented hyloids, like *Calyptocephalella* and the ceratophryids. This clade is poorly supported (Bermer index of 1 and negligible bootstrap

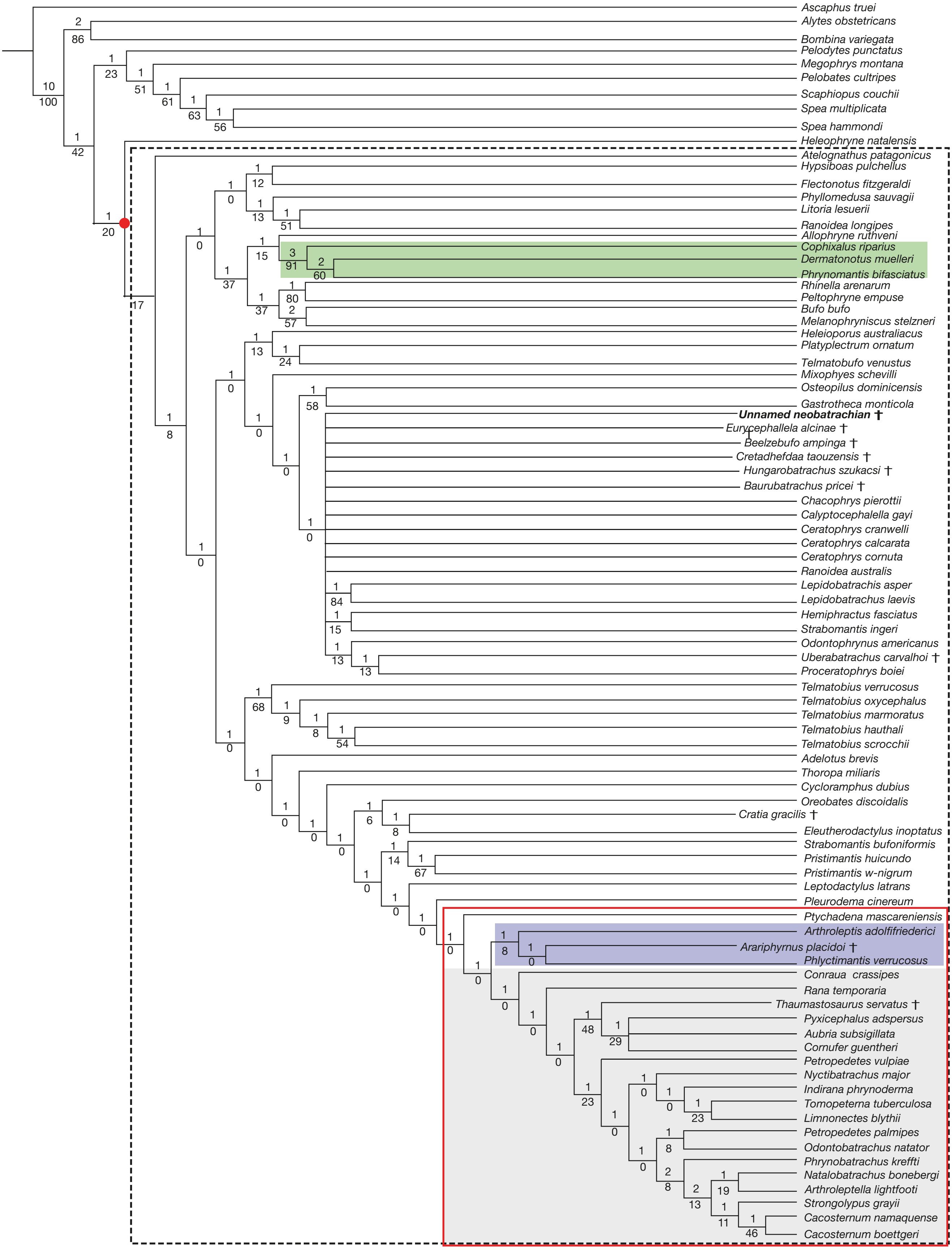

FIG. 5. — Simplified strict consensus (CI = 0.163; RI = 0.520) of the unconstrained phylogenetic analysis performed under equal weight: **red circle**, most recent common ancestor of Neobatrachia; **dotted outline**, Hyloidea + Ranoidea; **red outline**, Natatanura + Afrobatrachia; **green and purple rectangles**, Microhylidae and Afrobatrachia respectively; **grey rectangle**, Natatanura; **numbers above and below branch**, Bremer and bootstrap values respectively.

frequency), despite its 16 synapomorphies (See Appendix S4). The unnamed neobatrachian from In Becetèn is also recovered as a neobatrachian within this polytomy (Fig. 5). *Thaumastosaurus* is recovered as the sister-taxon to all three hyperossified ranoids (*Pyxicephalus*, *Aubria* and *Cornufer*), a position already recovered previously (Lemierre *et al.* 2021: fig. 14A). *Arariphrynus placidoi* is also recovered as a ranoid, within the afrobatrachians (Fig. 5), supported by four synapomorphies. However, it should be noted that *Arariphrynus* does not possess any synapomorphies proposed for Ranoidea or Afrobatrachia, and its position is very unstable in several analyses (Báez & Gómez 2018). This is linked to the poor preservation of its pectoral girdle (see description of *Arariphrynus* in Báez *et al.* 2009). The parsimony analysis under equal weights and using topological constraints yielded 10 MPTs that require 1437 steps (CI = 0.160; RI = 0.522). In the strict consensus, we do recover Ranoidea as monophyletic, but not *Arariphrynus* (Fig. S1). The unnamed neobatrachian from In Becetèn is recovered as the sister-taxon to *Baurubatrachus pricei* Báez & Perí, 1989, from the Late Cretaceous of Brazil, within an unresolved polytomy with *Beelzebufo* Evans, Jones & Krause, 2008, *Calyptocephalella*, *Cretadhefdaa*, and *Hungarobatrachus* (Fig. S1).

DISCUSSION

The neobatrachian(s) of In Becetèn

Phylogenetic analyses including our unnamed ornamented taxon confirm its identification as a neobatrachian. The constrained analysis also points to affinities with hyloids. However, morphology-based parsimony analyses tend to recover ornamented neobatrachians as closely related (Báez & Gómez 2018), even though ornamentation appears to have developed convergently across multiple neobatrachian clades (Paluh *et al.* 2020). As an example, when considering only cranial characters (including ornamentation and hyperossification), ornamented ranoids are recovered as closely related to extant and extinct ornamented hyloids (Báez & Gómez 2018). Furthermore, the fragmentary remains of our unnamed neobatrachian and its few scored characters (13% of all characters) hamper establishment of its affinities. Hence, we attribute our unnamed ornamented taxon to Neobatrachia only.

We also identify one humerus that we attribute to Neobatrachia as well. However, while the unnamed neobatrachian might have a hyloid affinity, the humerus has clear ranoid affinities (if it is indeed a neobatrachian). Hence, we could argue that they represent two distinct neobatrachian taxa. However, a disparity between the affinity of the skull and the postcranial bones is known in ornamented ranoids, as mentioned above. Thus, in the absence of more elements, we consider that at least one unnamed neobatrachian is present in In Becetèn. It is the third known neobatrachian in the Mesozoic of Africa, and the second oldest (Lemierre & Blackburn 2022).

The oldest putative remains attributed to Ranoidea are from the Cenomanian of Sudan (Báez & Werner 1996). However, they have never been described or illustrated, so this attribution needs to be reassessed. A neobatrachian humerus with ranoid affinities has been described from the middle Cenomanian of Morocco (Lemierre & Blackburn 2022: fig. 6A-C), but it lacks several ranoid characters present in MNHN.F.IBC1603. Several ilia from the Late Cretaceous (Maastrichtian) of India have been attributed to Ranoidea (*c.* Ranoides, a taxon erected by Frost *et al.* 2006) or Ranidae (Prasad & Rage 2004) based on their overall morphology. This attribution is poorly supported, as the overall morphology of ilia is convergent within anurans (Roček 2013) and the clade is mainly united by characters of the pectoral girdle (Frost *et al.* 2006; Lemierre *et al.* 2021). The stratigraphically oldest taxon firmly attributed to the Ranoidea is *Thaumastosaurus*, from the Eocene of Western Europe (Laloy *et al.* 2013; Vasilyan 2018; Báez & Gómez 2018; Lemierre *et al.* 2021). Numerous African ranoid clades possess a poor fossil record, mostly restricted to the Neogene (Gardner & Rage 2016). Most of those remains are attributed to extant genera, which renders the comparison or attribution of older remains difficult.

Nevertheless, the Ranoidea is considered to have emerged in Africa during the Early Cretaceous, undergoing a rapid diversification between the Late Cretaceous and the Palaeocene (Bossuyt *et al.* 2006; Frazão *et al.* 2015; Feng *et al.* 2017). The presence of a ranoid in In Becetèn is unsurprising, as molecular timetrees suggest that ranoids already inhabited the continent by the Cretaceous, and paleogeographic reconstructions suggest that Africa was relatively isolated at the time (Rage & Gheerbrant 2020).

Anuran diversity in In Becetèn

Based on both cranial and postcranial remains, at least three to four non-pipimorph anuran taxa are identified within In Becetèn. Among them, at least one is referred to an unnamed neobatrachian. The presence of a neobatrachian shows that the clade was already widespread in the early Late Cretaceous in Western Africa, given the presence of *Cretadhefdaa* in the Cenomanian of Morocco. When including the known pipimorphs, at least 7-8 anuran taxa are known in In Becetèn (Lemierre *et al.* 2023, 2025). This diversity is unique for Mesozoic African sites, with all others known sites yielding three taxa at the most (Gardner & Rage 2016). In addition, In Becetèn is the second richest site (for anurans) in the Mesozoic of Gondwana, surpassed only by the Crato Formation (supposed to be Aptian-Albian in age, Báez *et al.* 2021). Interestingly, at least five taxa from In Becetèn are highly (or totally) adapted to an aquatic lifestyle. Combined with the presence of numerous actinopterygians (Gayet & Meunier, 1996), this suggests that permanent bodies of water were present. Futhermore, the presence of more terrestrial anurans suggests that more ephemeral ponds might also have been present. Thus, the paleoenvironment of In Becetèn was likely composed of both permanent and ephemeral ponds and lakes.

CONCLUSION

Recently, the study of the anuran fauna at In Becetèn documented the presence of seven to eight distinct taxa, making it the richest site of the Mesozoic of Africa, for anurans (Lemierre *et al.* 2023, 2025). Four of these taxa have been previously assigned to Pipimorpha. A new hyperossified taxon, represented mostly by fragments of maxilla, is identified here. Our phylogenetic analysis suggests that this new taxon ("Neobatrachia gen. et sp. indet."; specimens MNHN.F.IBC1983-IBC1986) is a neobatrachian, making it the third Mesozoic occurrence of this clade in Africa. An isolated humerus also likely represents a second neobatrachian, and the oldest, and first Mesozoic occurrence of a ranoid. These neobatrachians, combined with other occurrences in Africa, indicate that the clade was widespread in western Africa in the early Late Cretaceous. Numerous isolated bones indicate that at least two other anurans were present, with one likely adapted to an aquatic lifestyle. The anuran fauna indicates that the paleoenvironment of In Becetèn was likely composed of several lakes and ponds.

Supplementary data

Data supporting this study is available on: https://doi.org/10.7934/P5856.

Acknowledgements

We thank Damien Germain (CR2P, MNHN) for providing access to the specimens. This study was funded by a grant from the Fondation pour la Recherche sur la Biodiversité (FRB) to Alfred Lemierre. We are grateful to Drs David C. Blackburn (University of Florida, United States) and Zbyněk Roček (Institute of Geology of the Czech Academy of Sciences) for their reviews and comments on this manuscript.

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Submitted on 7 February 2025;
accepted on 10 April 2025;
published on 12 March 2026.

APPENDIX 1. — Supplementary material available at https://doi.org/10.7934/P5856.