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► **To cite this version:**

Alfred Lemierre, Michel Laurin. Conversion of the names Pyxicephaloidea, Pyxicephalidae and Pyxicephalinae (Anura, Ranoidea) into phylogenetic nomenclature. *Bionomina: International Journal of Biological Nomenclature & Terminology*, 2021, 25 (3), pp.81-92. 10.11646/bionomina.25.1.7. hal-03512450

HAL Id: hal-03512450

<https://hal.science/hal-03512450>

Submitted on 12 Oct 2022

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Running title: PYXICEPHALOIDEA, PYXICEPHALIDAE AND PYXICEPHALINAE

Article

Conversion of the names *Pyxicephaloidea*, *Pyxicephalidae* and *Pyxicephalinae* (Anura, Ranoidea) into phylogenetic nomenclature

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Abstract

The recent publications of the sixth edition of the *PhyloCode* and of the monograph *Phylonyms* now allow the publication of nomenclatural acts that will establish priority under that code. This includes defining existing and newly proposed taxon names in conformity with the *PhyloCode*. Among amphibian taxa, very few names have been converted so far, and we take the opportunity of our recent phylogenetic analysis of neobatrachians focusing on an extinct genus of *PYXICEPHALIDAE*, *Thaumastosaurus*, from the Eocene of Western Europe, to convert the names *Pyxicephaloidea*, *Pyxicephalidae* and *Pyxicephalinae* into phylogenetic nomenclature, following the *PhyloCode* rules.

Keywords: Phylogenetic nomenclature, *PhyloCode*, amphibians, *Pyxicephalidae*

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* (Anonymous 1999, 2012) are presented according to the following standard formats: *italic lower-case letters* for nomina of species and genera (e.g. *Pyxicephalus*, *Pyxicephalus adspersus*); *ITALIC SMALL UPPER CASES* for nomina of families, subfamilies, tribes and related ranks (e.g., *PYXICEPHALIDAE*); **BOLD SMALL UPPER CASES** for nomina of orders, classes, phyla and taxa at other higher ranks (e.g., **AMPHIBIA**).

[B] Nomina managed under the *PhyloCode* are presented in **bold italic lower-case letters** (e.g., ***Pyxicephalidae***).

Other conventions

~ : but not

∇ : clade

RegNum registration number : Registration number of the name definition on the RegNum website.

1. Introduction

Since its first edition in 2000 (Cantino & Queiroz 2020), the *PhyloCode* has evolved to propose an alternative to the rank-based nomenclature system traditionally used, by proposing a system based on phylogenetic principles. Its objective is not to replace existing names, but rather to provide another system for governing the application of said names. With the publication of the sixth edition of the *PhyloCode* (Cantino & Queiroz 2020) and of the monograph *Phylonyms* (Queiroz & Cantino 2020), it is now possible to publish nomenclatural acts (definitions of new or converted names that will establish priority under that code) that will have official standing under the *PhyloCode*. The first set of nomenclatural acts established under the *PhyloCode* was published in the monograph *Phylonyms* (Queiroz *et al.* 2020). Now, nomenclatural acts valid under the *PhyloCode* can be published in regular journals. Among amphibian taxa, much remains to be done because only *Amphibia* (Laurin *et al.* 2020a), *Lissamphibia* (Laurin *et al.* 2020b), *Caudata* (D. B. Wake 2020) and *Gymnophiona* (M. H. Wake 2020) have been converted so far. Building on our recent phylogenetic analysis of the “RANOIDEA” Ford and Cannatella, 2004 (~SCOPTANURA in Dubois *et al.*, 2021), we take the opportunity to convert three taxon names on which our recent work focuses (Lemierre *et al.* 2021). We follow the nomenclature proposed by Dubois *et al.* (2021) in their recent work regarding the names that we convert.

2. Phylogenetic nomenclature

2.1. *Pyxicephaloidea* Bonaparte, 1850 [Lemierre & Laurin], converted clade name (RegNum registration number: 558)

2.1.1. Definition

The largest clade containing *Pyxicephalus adspersus* Tschudi, 1838, *Aubria subsigillata* Duméril, 1856, *Cacosternum boettgeri* Boulenger, 1882 and *Tomopterna natalensis* Smith, 1849, but not *Petropedetes palmipes* Boulenger, 1905 (*PETROPEDETOIDAE*), *Micrixalus fuscus* Boulenger, 1882 (*MICRIXALOIDAE*), *Ericabatrachus baleensis* Largen, 1991 (*ERICABATRACHOIDAE*), *Pelophylax ridibundus* Pallas, 1771 (*RANOIDAE*) and *Conraua goliath* Boulenger, 1906 (*CONRAUOIDAE*). Abbreviated definition: max total ∇ (*Pyxicephalus adspersus* Tschudi, 1838, *Aubria subsigillata* Duméril 1856, *Cacosternum boettgeri* Boulenger 1882 ~*Petropedetes palmipes* Boulenger, 1905, *Micrixalus fuscus*, Boulenger, 1882, *Ericabatrachus baleensis* Largen, 1991, *Pelophylax ridibundus* Pallas, 1771 and *Conraua goliath* Boulenger, 1906).

2.1.2. Etymology

Named after the eponymous genus *Pyxicephalus* Tschudi, 1838. Derived from the ancient Greek *pyxis* (‘round’ box) and *kephalē* (head). These two roots refer to the bulky head of *Pyxicephalus adspersus* Tschudi 1838.

2.1.3. Reference phylogeny

The primary reference phylogeny is Jetz & Pyron (2018: fig. S1; see also Dubois *et al.* 2021: appendix A2. tree 1) for the relationship between and within the two extant clades of *PYXICEPHALOIDAE*, *PYXICEPHALIDAE* and *CACOSTERNIDAE*, and for the position of *PYXICEPHALOIDEA* among *RANOIDEA*. Other phylogenies focused on *NATATANURA* (~*PANANURA* in Dubois *et al.* 2021) include Yuan *et al.* (2019, fig. 2) and those by Bittencourt-Silva *et al.* (2016, fig. 4), Cai *et al.* (2019, fig. 4), more focused on *PYXICEPHALOIDAE* and one more focused on *CACOSTERNIDAE* by Van der Meijden *et al.* (2011, fig.1–2).

2.1.4. Composition

Pyxicephaloidea encompasses two clades: [1] the *PYXICEPHALIDAE* Bonaparte, 1850, comprising *Pyxicephalus* Tschudi, 1838, *Aubria* Boulenger, 1917 and *Thaumastosaurus* De Stefano, 1903, and [2] the *CACOSTERNIDAE* Noble, 1931, comprising *Amietia* Dubois, 1987, *Anhydrophryne* Hewitt, 1919, *Arthroleptella* Hewitt, 1926, *Cacosternum* Boulenger, 1887, *Microbatrachella* Hewitt, 1926, *Natalobatrachus* Hewitt & Methuen, 1912, *Nothophryne* Poynton, 1963, *Poyntonina* Channing & Boycott, 1989, *Strongylopus* Tschudi, 1838 and *Tomopterna* Duméril & Bibron, 1841.

2.1.5. Diagnostic apomorphies

Unfortunately, no morphological synapomorphies have been identified for this clade (Frost *et al.* 2006), with the different taxa possessing very heterogeneous morphologies. Recent studies have been focused on molecular characters rather than morphological ones (mostly because the former yielded more robust results). However, a recent morphological analysis by Lemierre *et al.* (2021) recovered this clade, supported by a non-unique combination of three synapomorphies: [1] presence of an open groove for pathway of occipital artery on skull (also present in *CERATOBATRACHINAE* for example); [2] pars facialis of maxillae bearing slight ornamentation (also present in *CERATOPHRYIDAE* and *CERATOBATRACHINAE* for example); [3] digits II and III of forelimb of the same length (also present in *PTYCHADENIDAE*, for example). However, these synapomorphies are only for the smallest clade including the sampled taxa from the analyses (see Lemierre *et al.* 2021: Appendix S4 in Supplemental Data 1) and were obtained on a constrained topology taken from the phylogenetic analyses of Jetz & Pyron (2018). In addition, two of these characters are further modified in *Pyxicephalidae* (see below). There is however a high molecular support for this clade (Dubois 2005; Van der Meijden *et al.* 2005; Frost *et al.* 2006), and it is recovered in all recent molecular analyses for anurans or *RANOIDEA* (Pyron & Wiens 2011; Van der Meijden *et al.* 2011; Frazão *et al.* 2015; Feng *et al.* 2017; Jetz & Pyron 2018).

2.1.6. Synonyms

Synonyms are *PHRYNOPSINAE* Noble, 1931 (its type genus was synonymized with *Pyxicephalus*), as mentioned by Loveridge (1936) and Laurent (1946), *CACOSTERNINAE* Noble, 1931 (according to Dubois 1994 and Frost *et al.* 2006), and *TOMOPTERNINI* Dubois, 1987 (according to Frost *et al.* 2006).

2.1.7. Comments

The name *PYXICEPHALIDAE* has been erected early to accommodate the newly described *Pyxicephalus* (Bonaparte 1850). However, this taxon was soon considered a subgenus of *Rana*, a common situation for numerous ranoids taxa (Boulenger 1920*a–b*; Noble 1931), and the name *Pyxicephalus* fell into disuse for more than a century. However, slowly, several subgenera were raised to generic rank (Dubois 1981), as the large genus *Rana* began to be dismantled. For several taxa, including *Aubria* and *Pyxicephalus*, this work linked with the dismantling of *Rana* was still ongoing in the 1980s and 1990s, although Laurent (1953) already recognized *Aubria* as a genus. Thus, Dubois (1981, 1983) dismantled *Rana* into several subfamilies and genera, but conserved *Pyxicephalus* and *Aubria* as subgenera of *Rana*. Poynton & Broadley (1985) split *Rana* further, recognizing *Pyxicephalus* and *Aubria* as genera, but retained them within the Raninae. The two genera were considered close (see *Pyxicephalidae*) and the family *PYXICEPHALIDAE* was used to accommodate this relationship (Dubois 1987).

In addition, several new taxa of African anurans were described (Hewitt & Methuen 1912; Hewitt 1919, 1925, 1926) and considered as distinct genera during the 20th century. To accommodate some of these taxa, Noble (1931) erected *CACOSTERNINAE* as a subfamily of *BREVICIPITIDAE* which included *Cacosternum* and *Anhydrophryne*; he considered them to be close to *ARTHROLEPTINAE*, within the much larger *RANIDAE*. A decade later, Laurent (1941), in his work on African ranids, discarded *CACOSTERNIDAE* and erected the subfamily *PHRYNOBATRACHINAE* (within the *RANIDAE*), in which he placed various African ranids, among which the cacosternins *Anhydrophryne*, *Arthroleptella*, *Cacosternum*, *Natalobatrachus*, *Microbatrachella* and *Nothophryne*. That arrangement was accepted by Dubois (1981, 1982) and Poynton & Broadley (1985). A decade later, Dubois (1992), having elevated the subfamily *PHRYNOBATRACHINAE* to family rank, proposed resurrecting the subfamily *CACOSTERNINAE* within this family.

Affinities of *PYXICEPHALIDAE* and *CACOSTERNINAE* to other *SCOPTANURA* remained unclear, at least until the application of molecular phylogenetics to anurans (Frost *et al.* 2006) and ranoids (Dubois 2005; Scott 2005; Van der Meijden *et al.* 2005), in particular. These studies showed that *PYXICEPHALIDAE* and *CACOSTERNIDAE* formed a clade. The close relationship between the two families, as well as other taxa (such as *Strongylopus*), was unexpected but supported by several molecular analyses (Dubois 2005; Van der Meijden *et al.* 2005; Frost *et al.* 2006) that led to the recognition of a larger “Southern African Ranids” clade (sensu Van der Meijden *et al.* 2005). This led Dubois (2005) to place all members of *CACOSTERNIDAE* within the subfamily *PYXICEPHALINAE*. The major analysis of Frost *et al.* (2006) showed that both clades were well supported and were sister-taxa. They recognized both *PYXICEPHALINAE* and *CACOSTERNINAE* and used the old name *PYXICEPHALIDAE* from Bonaparte (1850) as the name of the large clade encompassing both subfamilies. This topology was supported with subsequent analyses of Bossuyt *et al.* (2006), Pyron & Wiens (2011) and Van der Meijden *et al.* (2011), and more recent studies still find a close relationship between the two clades (Bittencourt-Silva *et al.*, 2016; Feng *et al.* 2017; Jetz & Pyron 2018; Cai *et al.* 2019). The recent work of Dubois *et al.* (2021) also corroborated this relationship, but considered the two clades as two families, *PYXICEPHALIDAE* and *CACOSTERNIDAE*, grouped in an epifamily *PYXICEPHALOIDAE*. The relationships of *PYXICEPHALOIDAE* to other *RANOIDEA* are still unclear and unstable, forming a large hexatomy with the epifamilies *CONRAUIDAE*, *ERICABATRACHOIDAE*, *MICRIXALOIDAE*, *RANOIDEA* and *PETROPEDETOIDAE* (Dubois *et al.* 2021). In addition, recent analyses (Lemierre *et al.* 2021) have placed the extinct *Thaumastosaurus* De Stefano, 1903 within the clade, as a member of the *PYXICEPHALIDAE*. *Thaumastosaurus* was long thought to be close to South American hyloids (Roček & Lamaud 1995), but recent analyses incorporating new data, notably on the postcranium (Laloy *et al.* 2013; Báez &

Gómez 2018), placed it as a *RANOIDEA*, close to a clade that includes pyxicephalids and ceratobatrachids. Both pyxicephalids and ceratobatrachids are not sister-taxa, and this result was linked to poor *RANOIDEA* taxonomic sample and convergent hyperossified-linked characters. Recent analyses (Lemierre *et al.* 2021), using an expanded taxonomic sample of *RANOIDEA*, placed *Thaumastosaurus* inside the *Pyxicephaloidea* and *Pyxicephalidae*, as the sister-taxa to a clade composed of the extant *Pyxicephalinae*.

Today, *Pyxicephaloidea* are found in sub-Saharan Africa from Gambia (Western Africa; Channing & Rödel 2019) to Southern Somalia (East range) and south to Cape Province, South Africa (Channing 2001). *Thaumastosaurus* is known in Western Europe from the middle Eocene (around 39.5 Ma; Vasilyan 2018) to late Eocene (around 33.5 Ma; Vasilyan 2018), which represent the only occurrences of the clade outside of its present range.

With the exception of *Thaumastosaurus*, the fossil record for *PYXICEPHALOIDAE* is limited to the Neogene, with the oldest remains attributed to the clade date to the Pleistocene, around 1 Ma (Gardner & Rage 2016). However, molecular age estimates for the clade suggest an origin around the Cretaceous/Paleogene transition (around 60 Ma, according to Feng *et al.* 2017; 62, 87 Ma according to Bittencourt-Silva *et al.* 2016).

2.2. *Pyxicephalidae* Bonaparte 1850 [Lemierre & Laurin], converted clade name.
(RegNum registration number: 571)

2.2.1. Definition

The largest clade containing *Pyxicephalus adpersus* Tschudi, 1838 and *Aubria subsigillata* Duméril, 1856 but not *Cacosternum boettgeri* Boulenger 1882 (*CACOSTERNIDAE*) and *Tomopterna natalensis* Smith, 1849 (*CACOSTERNIDAE*). Abbreviated definition: max total ∇ (*Pyxicephalus adpersus* Tschudi, 1838 and *Aubria subsigillata* Duméril, 1856 ~ *Cacosternum boettgeri* Boulenger 1882, *Tomopterna natalensis* Smith, 1849, and *Petropedetes palmipes* Boulenger, 1905).

2.2.2. Etymology

Named after the eponymous genus *Pyxicephalus* Tschudi, 1838. Derived from the ancient Greek *pyxis* ('round' box) and *kephalē* (head).

2.2.3. Reference phylogeny

The primary reference phylogeny is Jetz & Pyron (2018: fig. S1) for the crown-group *PYXICEPHALINAE*, and Lemierre *et al.* (2021: fig. S12) for the relationship between the crown-group and *Thaumastosaurus*. Other recent phylogenies for the crown group include Frost *et al.* (2006: fig. 50) and Pyron & Wiens (2011: fig. 2J).

2.2.4. Composition

The clade encompasses the extant *Pyxicephalus* Tschudi, 1838 and *Aubria* Boulenger, 1917 (forming the crown-group *PYXICEPHALINAE*) and the extinct Eocene *Thaumastosaurus* Stefano, 1903, the last of which is located on the stem of the crown-group.

2.2.5. Diagnostic apomorphies

According to Clarke (1981) and corroborated by Frost *et al.* (2006), the clade is diagnosed by the unique combination of the following apomorphies: [1] presence of enclosed canal for occipital artery (also present in *CERATOPHRYIDAE* for example); [2] well-developed zygomatic ramus of squamosal (longer than its otic ramus and articulated with maxillae; also present in *CERATOBATRACHINAE* for example); [3] well-developed medial ramus of pterygoids overlapping parasphenoid alae (also present in *CERATOBATRACHINAE* for example); [4] cranial exostosis (sensu Trueb 1973; also present in *CERATOPHRYIDAE* for example). Another putative synapomorphy is the anterior extension of the squamosal forming the entire lateral margin of the orbit and in contact anteriorly with the nasal (Lemierre *et al.* 2021).

2.2.6. Synonyms

Approximate synonyms (that implicitly refer to the crown-group to the extent that only extant taxa were mentioned) are *PYXICEPHALINA* Bonaparte, 1850, *PHRYNOPSINAE* Noble, 1931, as mentioned by Loveridge (1936) and Laurent (1946), and *PYXICEPHALINI* Bonaparte, 1850 (used as a valid tribe nomen for the crown-group, see below).

2.2.7. Comments

As mentioned earlier, *PYXICEPHALIDAE* was proposed in the middle of the 19th century (Bonaparte 1850), but rapidly fell into disuse, as numerous ranoids (and other anurans) were considered to be subgenera of *Rana*. Slowly, several subgenera were raised to generic rank (Dubois 1981), as the large genus *Rana* began to be dismantled during the second half of the 20th century.

When *PYXICEPHALIDAE* was erected, it was to accommodate the genus described by Tschudi (1838) a decade earlier, and it only contained this eponymous genus. However, close affinities between *Pyxicephalus* and *Aubria* (first described as *Rana subsigillata* by Duméril in 1856) were first proposed by Procter (1919), who thought that both belonged to the same subgenus of *Rana*, in accordance to a Boulenger's unpublished manuscript on African ranids (see Clarke 1981). These close affinities were also supported by Clarke (1981), who proposed two alternatives, either that *Pyxicephalus* and *Aubria* were congeneric as Procter (1919) had suggested, or that *Aubria* was a sister-taxon to *Pyxicephalus*. A few years later, the second phylogenetic hypothesis (*Aubria* is a sister-taxon to *Pyxicephalus*) was accepted by Dubois (1987), who resurrected *PYXICEPHALIDAE* (~*PYXICEPHALINAE* of Dubois 1987) as a subfamily of *RANIDAE* (which encompassed various taxa previously considered subgenera of *Rana*).

However, the affinities of *PYXICEPHALIDAE* to other *RANOIDEA* remained unclear, at least until the application of molecular phylogenetics to anurans (Frost *et al.* 2006) and ranoids (Dubois 2005; Scott 2005; Van der Meijden *et al.* 2005), in particular. These studies showed that *PYXICEPHALIDAE* belongs to a large clade of 'southern African Ranids' (sensu Van der Meijden *et al.* 2005). Following these results, Dubois (2005) proposed to expand *PYXICEPHALIDAE* (~*PYXICEPHALINAE* of Dubois 2005) to encompass cacosternins taxa. Frost *et*

al. (2006) analysis led to the restriction of *PYXICEPHALINAE* to its eponymous genus and *Aubria*. In their recent monograph, Dubois *et al.* (2021) considered the latter clade as a family, and retained the name *PYXICEPHALIDAE* Bonaparte, 1850 as the valid nomen. As mentioned earlier, a recent study recovered the extinct *Thaumastosaurus* as a *PYXICEPHALIDAE* (Lemierre *et al.* 2021).

Pyxicephalidae are known in the fossil record since the middle Eocene, around 39.5 Ma, with the geologically oldest remains attributed to *Thaumastosaurus* (Lemierre *et al.* 2021). *Thaumastosaurus* extends up to the late Eocene, around 33.5 Ma. There is a large gap in the fossil record of *Pyxicephalidae* after the Eocene; the next oldest remains attributed to are from the late Pleistocene (around 12 000 years; Robbins *et al.* 1996) and attributed to the crown-group *Pyxicephalinae*.

2.3. *Pyxicephalinae* Bonaparte, 1850 [A. Lemierre, M. Laurin], converted clade name (RegNum registration number: 572)

2.3.1. Definition

The smallest clade containing *Pyxicephalus adspersus* Tschudi, 1838 and *Aubria subsigillata* Duméril, 1856 but not *Thaumastosaurus* De Stefano, 1903. Abbreviated definition: min crown ∇ (*Pyxicephalus adspersus* Tschudi, 1838 and *Aubria subsigillata* Duméril, 1856 ~ *Thaumastosaurus servatus* Filhol, 1877).

2.3.2. Etymology

Named after the eponymous genus *Pyxicephalus* Tschudi 1838. Derived from the ancient Greek *pyxis* ('round' box) and *kephalē* (head).

2.3.3. Reference phylogeny

The primary reference phylogeny is Jetz & Pyron (2018, fig. S1), with a majority of taxa within the clade represented. Other recent phylogenies for *PYXICEPHALINAE* include Frost *et al.* (2006: fig. 50) and Pyron & Wiens (2011: fig. 2J).

2.3.4. Composition

The clade encompasses the extant *Pyxicephalus* Tschudi, 1838 and *Aubria* Boulenger, 1917.

2.3.5. Diagnostic apomorphies

Pyxicephalinae can be characterized using the following combination of skeletal synapomorphies, recovered in the analyses of Lemierre *et al.* (2021): [1] alary process of premaxillae oriented dorsally; [2] development of fang-like laminar projection on anterior portion of dentaries; [3] articulation for lower jaw located posterior to occiput.

2.3.6. Synonyms

Synonyms are the same as for *Pyxicephalidae*, as most authors used both names to refer to a clade composed only of extant taxa.

2.3.7. Comments

The clade is endemic to Sub-Saharan Africa, from Gambia (Western Africa; Channing and Rödel 2019) to Southern Somalia (East range) and south to Cape Province, South Africa (Channing 2001), with various *Pyxicephalus* taxa having the widest geographical range (Channing & Rödel 2019).

The genus *Pyxicephalus* is represented by some of the largest extant anurans (the various taxa are dubbed the African bullfrog) and are known to be very aggressive and voracious eaters, eating anything that they can manage to capture. They are notably known for preying on small vertebrates (small anurans, squamates, rodents) and are even capable of subduing and eating small birds (Branch 1976). This genus is also known to be consumed for its flesh by local inhabitants of southern Africa (for an example in Namibia, see Okeyo *et al.* 2015) and this practice has been recorded for at least 12 000 years, with the oldest remains attributed to *Pyxicephalus* being burnt, indicating that the frogs had been cooked and eaten (Robbins *et al.* 1996, 2009).

3. Concluding remarks

The *Pyxicephaloidea*, *Pyxicephalidae* and *Pyxicephalinae* are here converted in the phylogenetical nomenclatural system. We also took the opportunity to formally include the extinct *Thaumastosaurus* in two nomina. Although the phylogenetical position of *Thaumastosaurus* has strong support, its exclusion from *Pyxicephaloidea* would render *Pyxicephalidae* and *Pyxicephalinae* synonyms. As mentioned earlier, a large geographical and stratigraphic gap exist between *Thaumastosaurus* and the other *Pyxicephalidae*, and undescribed extinct taxa from Africa might fill these gaps. As an example, the recently described *Rocekophryne ornata* Rage *et al.*, 2021 from the lower Eocene of Algeria is considered a *RANOIDEA* with osteological characters similar to *Thaumastosaurus*. In addition, *R. ornata* shares several osteological synapomorphies with the *Pyxicephaloidea* (presence of an open groove for the occipital arteria pathway and ornamented pars facialis of the maxilla). This taxon could represent the oldest *Pyxicephaloidea* and would fill part of the geographical gap of the clade. Phylogenetical analyses are needed to confirm this hypothetic position.

As this work is based on our recent phylogenetical analyses of an extinct stem-*PYXICEPHALINAE*, we did not convert the *CACOSTERNIDAE*. The conversion of this family could be addressed in a more complete study of the relationships between the various genera of *CACOSTERNIDAE*.

To conclude, this work on the conversion of *PYXICEPHALOIDEA*, *PYXICEPHALIDAE* and *PYXICEPHALINAE* is only a first step toward the conversion of the numerous anuran clade nomina, as no study has yet converted **SALIENTIA** or **ANURA**, or various less inclusive clades, except for those converted here.

All definitions of names following the phylogenetical nomenclature system are stored in the RegNum website: <https://www.phyloregnum.org>.

4. References

- Báez, A. M. & Gómez, R. O. (2018) Dealing with homoplasy: osteology and phylogenetic relationships of the bizarre neobatrachian frog *Baurubatrachus pricei* from the Upper Cretaceous of Brazil. *Journal of systematic Palaeontology*, **16**: 279–308.
- Bittencourt-Silva, G. B., Conradie, W., Siu-Ting, K., Tolley, K., Channing, A., Cunningham, M., Farooq, H., Menegon, M. & Loader, S. (2016) The phylogenetic position and diversity of the enigmatic mongrel frog *Nothophryne* Poynton, 1963 (Amphibia, Anura). *Molecular Phylogenetics and Evolution*, **99**: 89–102.
- Bonaparte, C. (1850) *Conspectus Systematum. Herpetologiae et Amphibiologiae*, Brill. Leiden: 1 pl.
- Bossuyt, F., Brown, R. M., Hillis, D. M., Cannatella, D. C. & Milinkovitch, M. C. (2006) Phylogeny and biogeography of a cosmopolitan frog radiation: Late Cretaceous diversification resulted in continent-scale endemism in the family Ranidae. *Systematic Biology*, **55**: 579–594.
- Boulenger, G. A. (1882) *Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum*. Second edition. London (Taylor & Francis): 1–530.
- Boulenger, G. A. (1887) Descriptions of new reptiles and batrachians in the British Museum (Natural history), part III. *Annals and Magazine of natural History*, (5), **20** (115): 50–53.
- Boulenger, G. A. (1905). Descriptions of new West-African frogs of the genera *Petropedetes* and *Bulua*. *Annals and Magazine of natural History*, (7), **15** (87): 281–283.
- Boulenger, G. A. (1906) Descriptions of new batrachians discovered by Mr. G. L. Bates in South Cameroon. *Annals and Magazine of natural History*, (7), **17** (7): 317–323.
- Boulenger, G. A. (1917) Sur la conformation des phalangettes chez certaines grenouilles d’Afrique. *Compte rendu hebdomadaire des Séances de l’Académie des Sciences*, Paris, **165**: 989–990.
- Boulenger, G. A. (1918) Aperçu des principes qui doivent régir la classification des espèces du genre *Rana*. *Bulletin de la Société zoologique de France*. **43**: 111–121.
- Boulenger, G. A. (1920a) A monograph of the South Asian, Papuan, Melanesian and Australian frogs of the genus *Rana*. *Records of the Indian Museum*, **20**: 1–226.
- Boulenger, G. A. (1920b) A monograph of the American frogs of the genus *Rana*. *Proceeding of the American Academy of Arts and Sciences*, **55** (9): 413–480.
- Branch, W. R. (1976) Two exceptional food records for the African Bullfrog, *Pyxicephalus adspersus* (Amphibia, Anura, Ranidae). *Journal of Herpetology*, **10** (3): 266–268.
- Cai, Y.-Y., Shen, S.-Q., Lu, L.-X., Storey, K. B., Yu, D.-N. & Zhang, J.-Y. (2019) The complete mitochondrial genome of *Pyxicephalus adspersus*: high gene rearrangement and phylogenetics of one of the world’s largest frogs. *PeerJ*, **7** [e7532].
- Cantino, P. D. & Queiroz, K. de (2020) *International Code of Phylogenetic Nomenclature (PhyloCode): a phylogenetic code of biological nomenclature*. Boca Raton, Florida (CRC Press): 1–189 pp.
- Channing, A. (2001) *Amphibians of central and southern Africa*. Ithaca, NY (Cornell University Press): 1–496.
- Channing, A. & Boycott, R. C. (1989) A new frog genus and species from the mountains of the southwestern Cape, South Africa (Anura: Ranidae). *Copeia*, **1989** (2): 467–471.
- Channing, A. & Rödel M.-O. (2019) *Field guide to the frogs & other amphibians of Africa*. Cape Town, South Africa (Struik Nature): 1–395.
- Clarke, B. T. (1981) Comparative osteology and evolutionary relationships in the African Raninae (Anura Ranidae). *Monitore zoologico italiano*, (n.s.), suppl. **15**: 285–331.

- De Stefano, G. (1903) I sauri del Quercy appartenenti alla collezione Rossignol. *Atti della Società italiana di Scienze naturali*, **4**: 382–418.
- Dubois, A. (1981) Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens Anoures) du Monde, avec identification de leurs espèces-types: conséquences nomenclaturales. *Monitore zoologico italiano*, (n.s.), suppl. **15**: 225–284.
- Dubois, A. (1982) Notes sur la classification des Ranidae (Amphibiens, Anoures). *Bulletin mensuel de la Société linnéenne de Lyon*, **61** (10): 305–352.
- Dubois, A. (1983) Classification et nomenclature supragénérique des Amphibiens Anoures. *Bulletin mensuel de la Société linnéenne de Lyon*, **52**: 270–276.
- Dubois, A. (1987) Miscellanea taxinomica batrachologica (I). *Alytes*, **5**: 7–95.
- Dubois, A. (1992) Notes sur la classification des Ranidae (Amphibiens, Anoures). *Bulletin mensuel de la Société linnéenne de Lyon*, **61**: 305–352.
- Dubois, A. (1994) Phrynobatrachinae Laurent, 1941 (Amphibia, Anura): proposed conservation. *Bulletin of zoological Nomenclature*, **51** (3): 240–246.
- Dubois, A. (2005) Amphibia Mundi. 1.1. An ergotaxonomy of recent amphibians. *Alytes*, **23**: 1–24.
- Dubois, A., Ohler, A. & Pyron, R. A. (2021) New concepts and methods for phylogenetic taxonomy and nomenclature in zoology, exemplified by a new ranked cladonomy of recent Amphibians (Lissamphibia). *Megataxa*, **5** (1): 1–738.
- Duméril, A. H. A. (1856) Note sur les Reptiles du Gabon. *Revue et Magasin de Zoologie pure et appliquée*, **2**: 553–562.
- Duméril, A. H. A. & Bibron, G. (1841) *Erpétologie générale ou Histoire naturelle complète des Reptiles*. Volume **8**. Paris (Roret): 1–792.
- Feng, Y.-J., Blackburn, D. C., Liang, D., Hillis, D. M., Wake, D. B., Cannatella D. C. & Zhang, P. (2017) Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. *Proceedings of the national Academy of Sciences*, **114**: E5864–E5870.
- Filhol, H. 1877. *Recherches sur les phosphorites du Quercy: Etude des fossiles qu'on y rencontre et spécialement des mammifères*. Paris (Librairie de l'Académie de médecine): 690 pp.
- Frazão, A., H. R. da Silva & Russo, C. A. de M. (2015) The Gondwana breakup and the history of the Atlantic and Indian Oceans unveils two new clades for early Neobatrachian diversification. *PLoS One*, **10** [e0143926].
- Frost, D. R., Grant, T., Faivovich, J., Bain, R. H., Haas, A., Haddad, C. F. B., de Sá, R. O., Channing, A., Wilkinson, M., Donnellan, S. C., Raxworthy, C. J., Campbell, J. A., Blotto, B. L., Moler, P., Drewes, R. C., Nussbaum, R. A., Lynch, J. D., Green, D. M. & Wheeler, W. C. (2006) The Amphibian Tree of Life. *Bulletin of the American Museum of natural History*, **297**: 1–291.
- Gardner, J. D. & Rage, J.-C. (2016) The fossil record of lissamphibians from Africa, Madagascar, and the Arabian Plate. *Palaeobiodiversity and Palaeoenvironments*, **96**: 169–220.
- Hewitt, J. (1919) *Anhydrophryne rattrayi*, a remarkable new frog from Cape Colony. *Records of the Albany Museum, Grahamstown*, **3**: 182–189.
- Hewitt, J. (1925) On some new species of reptiles and amphibians from South Africa. *Records of the Albany Museum, Grahamstown*, **3**: 343–368.
- Hewitt, J. (1926) Descriptions of new and little-known lizards and batrachians from South Africa. *Annals of the South African Museum*, **20**: 413–431.
- Hewitt, J. & Methuen, P. A. (1912) Descriptions of some new Batrachia and Lacertilia from South Africa. *Transactions of the royal Society of South Africa*, **3**: 107–111.

- Jetz, W. & Pyron, R. A. (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature, Ecology & Evolution*, **2**: 850–858.
- Laloy, F., Rage, J. C., Evans, S. E., Boistel, R., Lenoir, N. & Laurin, M. (2013) A re-interpretation of the Eocene anuran *Thaumastosaurus* based on microCT examination of a ‘mummified’ specimen. *PLoS One*, **8** [e74874].
- Largen, M. J. (1991) A new genus and species of petropedetine frog (Amphibia Anura Ranidae) from high altitude in the mountains of Ethiopia. *Tropical Zoology*, **4**: 139–152.
- Laurent, R. F. (1941) Contribution à l’ostéologie et à la systématique des Ranides africains. Première note. *Revue de Zoologie et de Botanique africaines*, **34**, ‘1940’: 74–96.
- Laurent, R. F. (1946) Mises au point dans la taxonomie des Ranides. *Revue de Zoologie et de Botanique africaines*, **39**: 336–338.
- Laurent, R. F. (1953) Reptiles et Batraciens récemment parvenus au Musée royal du Congo belge. *Bulletin du Cercle zoologique congolais*, **21**: 21–29.
- Laurin, M., Arntzen, J. W., Báez, A. M., Bauer, A. M., Damiani, R., Evans, S. E. *et al.* (2020a) Amphibia. In: K. de Queiroz, P. D. Cantino & J. A. Gauthier (ed.), *Phylonyms: an implementation of PhyloCode*, Boca Raton, Florida (CRC Press): 765–771.
- Laurin, M., Arntzen, J. W., Báez, A. M., Bauer, A. M., Damiani, R., Evans, S. E. *et al.* (2020b) Lissamphibia. In: K. de Queiroz, P. D. Cantino & J. A. Gauthier (ed.), *Phylonyms: an implementation of PhyloCode*, Boca Raton, Florida (CRC Press): 773–778.
- Lemierre, A., Folie, A., Bailon, S., Robin N. & Laurin, M. (in press) From toad to frog, a CT-based reconsideration of *Bufo servatus*, an Eocene anuran mummy from Quercy (France). *Journal of Vertebrate Paleontology*, **41** (3) [e1989694].
- Loveridge, J. P. (1936) Scientific results of an expedition to rain forest regions in eastern Africa VII. Amphibians. *Bulletin of the Museum of comparative Zoology*, **79**: 369–430.
- Noble, G. K. (1931) *The biology of the Amphibia*. New York & London (McGraw-Hill Book Company): 1–600.
- Okeyo, D. O., Kandjenogo, L. & Kashea, M. M. (2015) Harvesting and consumption of the giant African bullfrog, a delicacy in northern Namibia. In: K. C. Chinsebu, A. Cheikhyoussief, D. Mumbengegwi, M. Kandawa-Schilz, C. D. Kasanda, & L. Kazembe (ed.), *Indigenous knowledge of Namibia*, Windhoek, Namibia (UNAM Press): 205–219.
- Parry, R. (1982) A revision of southern African *Pyxicephalus* Tschudi (Anura: Ranidae). *Annals of the Natal Museum*, **25**: 281–292.
- Pallas, P. S. (1771) *Reise durch verschiedene Provinzen des Russischen Reichs*. Theil **1**. Saint-Petersburg (Gedruckt bey der Kayserlichen Academie der Wissenschaften): 1–504.
- Poynton, J. C. (1963) Descriptions of southern African amphibians. *Annals of the Natal Museum*, **15**: 319–332.
- Poynton, J. C. & Broadley, G. (1985) Amphibia Zambesiaca 2. Ranidae. *Annals of the Natal Museum*, **27**: 115–181.
- Procter, M. J. B. (1919) On the skull and affinities of *Rana subsigillata* A. Dum. *Proceedings of the zoological Society of London*, **89**: 21–27.
- Pyron, R. A. & Wiens, J. J. (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, **61**: 543–583.
- Queiroz, K. de, Cantino, P. D. & Gauthier, J. A. (2020) *Phylonyms: a companion to the PhyloCode*. Boca Raton, Florida (CRC Press): 1–1352.
- Rage, J.-C. (2016) Frogs (Amphibia, Anura) from the Eocene and Oligocene of the Phosphorites du Quercy (France). An overview. *Fossil Imprint*, **72** (1–2): 53–66.
- Rage, J.-C., Adaci, M., Bensalah, M., Mahboubi, M., Marivaux, L., Mebrouk, F. & Tabuce, R. (2021) Latest early-middle Eocene deposits of Algeria (Glib Zegdou, HGL50) yield the

- richest and most diverse fauna of amphibians and squamate reptiles from the Palaeogene of Africa. *Paleovertebrata*, **44** (1) [e1].
- Robbins, L. H., Murphy, M. L., Stevens, N. J., Brook, G. A., Ivester, A. H., Haberyan, K. A., Klein, R. G., Milo, R., Stewart, K. M., Matthiesen, D. G., & Winkler, A. J. (1996) Palaeoenvironment and archaeology of Drotzky's Cave: western Kalahari Desert, Botswana. *Journal of archaeological Science*, **23**: 7–22.
- Robbins, L. H., Campbell, A. C., Murphy, M. L., Brook, G. A., Mabuse, A. A., Hitchcock, R. K., Babutsi, G., Mmolowa, M., Stewart, K.M., Steele, T. E., Klein, R. G. & Appleton, C. C. (2009). Mogapelwa: archaeology, palaeoenvironment and oral traditions at Lake Ngami, Botswana. *South African archaeological Bulletin*, **64**: 13–32.
- Roček, Z. & Lamaud P. (1995) *Thaumastosaurus bottii* De Stefano, 1903, an anuran with Gondwanan affinities from the Eocene of Europe. *Journal of Vertebrate Paleontology*, **15**: 506–515.
- Rödel, M.-O. (2000) *Herpetofauna of West Africa*. Volume **1**. *Amphibians of the West African savanna*. Frankfurt/Main (Edition Chimaira): 1–335.
- Scott, E. (2005) A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. *Cladistics*, **21**: 507–574.
- Smith, A. (1849) *Illustrations of the zoology of South Africa, consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa in the years 1834, 1835 and 1836...* *Reptilia*. London (Smith, Elder & Co.): appendix 1–28.
- Trueb, L. (1973) Bones, frogs and evolution. In: J. L. Vial (ed.), *Evolutionary biology of the Anurans, Contemporary research on major problems*, Columbia (University of Missouri Press): 65–133.
- Tschudi, J. J. (1838) Classification der Batrachier, mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. *Mémoires de la Société des Sciences naturelles de Neuchâtel*, **2**: 1–100.
- Van der Meijden, A., Vences, M., Hoegg, S. & Meyer, A. (2005) A previously unrecognized radiation of ranid frogs in Southern Africa revealed by nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **37**: 674–685.
- Van der Meijden, A., Crottini, A., Tarrant, J., Turner, A. & Vences, M. (2011) Multi-locus phylogeny and evolution of reproductive modes in the Pyxicephalidae, an African endemic clade of frogs. *African Journal of Herpetology*, **60**: 1–12.
- Van Dijk, D. E. (1966) Systematic and field keys to the families, genera and described species of southern African anuran tadpoles. *Annals of the Natal Museum*, **18**: 231–286.
- Vasilyan, D. (2018) Eocene Western European endemic genus *Thaumastosaurus*: new insights into the question “Are the Ranidae known prior to the Oligocene?” *PeerJ*, **6** [e5511].
- Wake, D. B. (2020) Caudata. In: K. de Queiroz, P. D. Cantino & J. A. Gauthier (ed.), *Phylonoms: an implementation of PhyloCode*. Boca Raton, Florida (CRC Press): 785–787.
- Wake, M. H. (2020) Gymnophiona. In: K. de Queiroz, P. D. Cantino & J. A. Gauthier (ed.), *Phylonoms: an implementation of PhyloCode*. Boca Raton, Florida (CRC Press): 779–783.
- Yuan, Z.-Y., Zhang, B.-L., Raxworthy, C. J., Weisrock, D. W., Hime, P. M., Jin, J.-Q., Lemmon, E. M., Lemmon, A. R., Holland, S. D., Kortyna, M. L., Zhou, W.-W., Peng, M.-S., Che, J., & Prendini, E. (2019) Natatanuran frogs used the Indian Plate to step-stone disperse and radiate across the Indian Ocean. *National Science Review*, **6**: 10–14.

Submitted: 24 February. Accepted: ***. Published: ***.
Corresponding Editor: Alain Dubois.

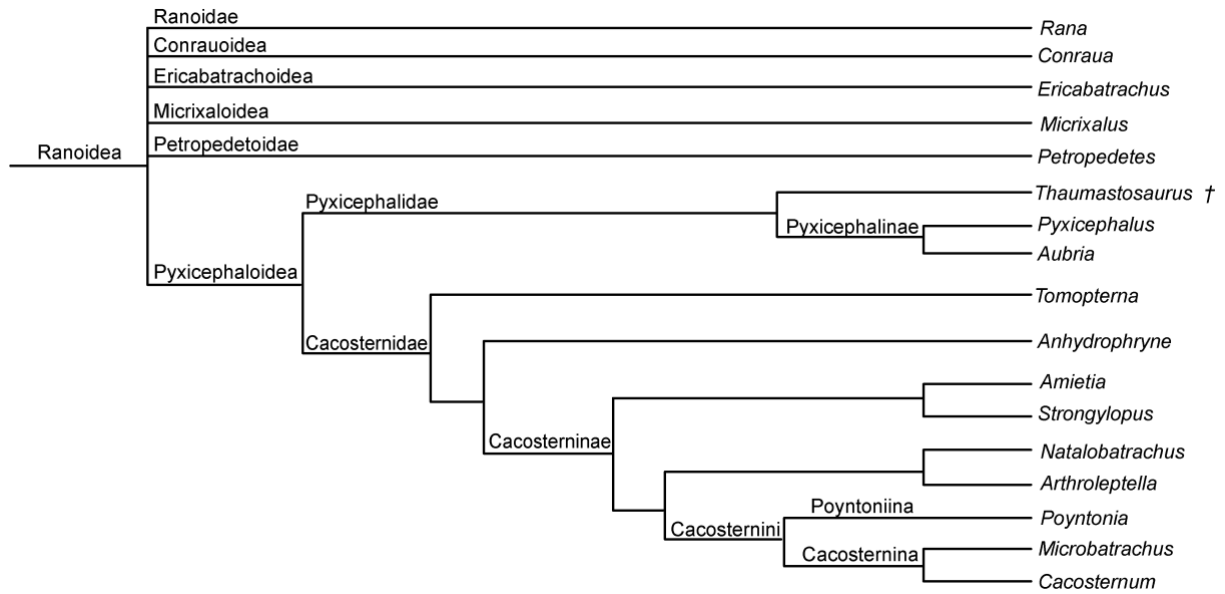


FIGURE 1. Simplified phylogeny of the *Pyxicephaloidea* modified from the phylogeny of Dubois et al (2021). Position of *Thaumastosaurus* has been inferred from Lemierre et al (2021). Terminal taxa are at the generic level and † represents an extinct taxon.