



General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

High ecomorphological diversity among Early Cretaceous frogs from a large subtropical wetland of Iberia



Grande diversité écomorphologique chez les anoures du Crétacé inférieur d'une vaste zone humide subtropicale d'Ibérie

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ABSTRACT

Anurans are extremely diverse amphibians with a unique *Bauplan*, whose origin, early ecomorphological diversification, and adaptive significance remain elusive. Their early fossil record is improving at an accelerated pace worldwide, but its contribution to these issues is still wanting. Here we explore ecomorphological diversity among Early Cretaceous (Barremian) frogs that inhabited a large subtropical wetland from Iberia by inferring locomotor abilities with a phylogenetic flexible discriminant analysis on data from limb proportions, which strongly correlate with locomotion. The results show a remarkable diversity among these frogs when compared with the extant diversity from this region and from tropical and subtropical wetland assemblages worldwide, encompassing miniature to medium-size jumpers and dedicated swimmers with more extreme proportions than extant ‘archeobatrachians,’ but also more generalized jumping and/or swimming forms. This agrees with the inferred wetland paleoenvironment and the hypothesis regarding early frogs as small poor jumpers or swimmers that evolved their peculiar *Bauplan* in aquatic environments.

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R É S U M É

Les Anoures sont des amphibiens extrêmement divers, avec un *Bauplan* unique, dont l'origine, la diversification écomorphologique première et la signification adaptative restent vagues. Leurs premiers enregistrements fossiles s'améliorent à un rythme accéléré dans le monde entier, mais leur contribution à ces problèmes fait toujours défaut. Ici, nous explorons la diversité écomorphologique chez les anoures du Crétacé inférieur (Barremien) qui vivaient dans une vaste zone humide subtropicale de la péninsule Ibérique, et en déduisons les capacités locomotrices à l'aide d'une analyse discriminante flexible phylogénétique à partir de données sur les proportions des membres, fortement corrélées à la locomotion. Les résultats montrent une diversité remarquable parmi ces anoures par

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rapport à la diversité existante de cette région et à celle d'assemblages de zones humides tropicales et subtropicales du monde entier, cette diversité englobant des sauteurs de taille minuscule à moyenne et des nageurs dédiés, avec des proportions plus extrêmes que celles des « archéobatraciens » existants, mais aussi avec des formes sauteuses et/ou nageuses plus généralisées. Ceci est en accord avec le paléoenvironnement de zone humide inféré et l'hypothèse selon laquelle les premiers anoures sont de petits et médiocres sauteurs ou nageurs qui ont développé leur propre *Bauplan* dans des environnements aquatiques.

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1. Introduction

Anurans make up an extremely taxonomically (> 7000 spp.) and ecologically diverse group of amphibians currently distributed in all continents except Antarctica (Frost, 2019; Wells, 2007). Their peculiar and highly conserved *Bauplan* (Handrigan and Wassersug, 2007) can be traced back in the fossil record at least to the Early Jurassic (Shubin and Jenkins, 1995) and even the Late Triassic (Stocker et al., 2019), and most postcranial morphological diversity within this group, including variation in limb proportions, has frequently been correlated with diverse locomotor abilities and microhabitat use (e.g., Citadini et al., 2018; Emerson, 1978; Enriquez-Urzelai et al., 2015; Jorgensen and Reilly, 2013; Lires et al., 2016; Moen et al., 2015; Wang et al., 2007; Zug, 1972). However, the evolutionary scenario of the origin and early diversification of these morphologies, as well as their adaptive significance, remains elusive, since the long-held hypothesis linking this *Bauplan* with saltatory locomotion in a riparian context (e.g., Gans and Parsons, 1966; Jenkins and Shubin, 1998) has recently been challenged (Ascarrunz et al., 2016; Herrel et al., 2016; Lires et al., 2016; Reilly and Jorgensen, 2011).

It is also unclear how the astonishing ecomorphological diversity that anurans display today has evolved, although the diversification pattern among families has largely been explained by ecological shifts (Moen and Wiens, 2017). According to molecular time estimates, most major anuran clades radiated in the Early Cretaceous (e.g., Pyron, 2014) and, hence, an increased ecomorphological diversification among frogs is expected during this time interval. The Early Cretaceous record of anurans is improving at an accelerated pace with exciting findings taking place worldwide (Báez, 2013; Báez et al., 2009; Dong et al., 2013; Gao and Chen, 2017; Ikeda et al., 2016; Xing et al., 2018), but its integration into other types of data in recovering this diversification pattern is still wanting. It is also noteworthy that, despite the fact that it consists of dozens of specimens in some cases (e.g., Dong et al., 2013), most known Early Cretaceous anuran assemblages to date show low diversity, including in each case one or a few closely related species; yet some remarkable exceptions exist (e.g., Báez et al., 2009).

Outcrops of Barremian age scattered along the Iberian and Montsec Ranges in the northeastern Iberian Peninsula have documented a diverse continental biota that also includes anurans, dwellers of a large wetland system (e.g., Báez and Gómez, 2019; Buscalioni et al., 2018; Gomez et al., 2015). This large wetland system of the Iberian Plate, including a variety of freshwater environments, was at the time part of the western Tethys realm and developed

under a subtropical climate at paleolatitudes around 30°N (Buscalioni and Poyato-Ariza, 2016; Fig. 1A). Three different Iberian localities within this system, namely Santa Maria de Meià (Montsec), Uña, and Las Hoyas (Fig. 1B) have yielded well-preserved and nearly complete anuran specimens (Fig. 1C–H) that have been studied by various authors since they were first discovered (e.g., Báez, 2013, 2016; Báez and Gómez, 2016, 2019; Báez and Sanchiz, 2007; Evans et al., 1995; Fey, 1988; Hecht, 1970; Sanchiz, 1998; Seiffert, 1972; Vergnaud-Grazzini and Wenz, 1975; Villalta, 1954). Noteworthy, the diversity of anurans from these fossil sites has often been underrated, being recognized only two supposedly very similar genera by the turn of the century (Roček, 2000; Sanchiz, 1998). Recent studies on these Iberian fossils have led to revalidating or recognizing additional anuran taxa, considerably increasing the involved taxonomic diversity, but also have furnished detailed accounts of their morphology and a better understanding of their systematic affinities (Báez, 2013; Báez and Gómez, 2016, 2019; Báez and Sanchiz, 2007). This offers the opportunity to study these Early Cretaceous anurans with an ecomorphological approach that might shed some light on the early diversification of the anuran *Bauplan*.

Here we explore the ecomorphological diversity of the Barremian frogs from Iberia, inferring locomotor abilities by means of a phylogenetic flexible discriminant analysis (Motani and Schmitz, 2011) on data from limb proportions, which strongly correlate with locomotor modes (e.g., Enriquez-Urzelai et al., 2015; Lires et al., 2016). In addition, taxonomic and ecomorphological diversity in extinct anurans is contextualized comparing with the extant anuran diversity of the northeastern Iberian Peninsula and selected tropical and subtropical wetlands across the world. Results are also discussed in the context of the paleoenvironmental reconstruction of the Iberian wetland and early evolution of the anuran *Bauplan*.

Institutional abbreviations: MBAm, Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; MNHN, Muséum national d'histoire naturelle, Paris, France; MUPA (formerly MCCM), Museo de Paleontología de Castilla-La Mancha, Cuenca, Spain; PIFUB, Institut für Paläontologie der Freien Universität, Berlin, Germany.

2. Materials and methods

2.1. Taxonomic and phylogenetic nomenclature

Names of extant species, genera, and families (i.e. taxonomic nomenclature) are those of Frost (2019), with the

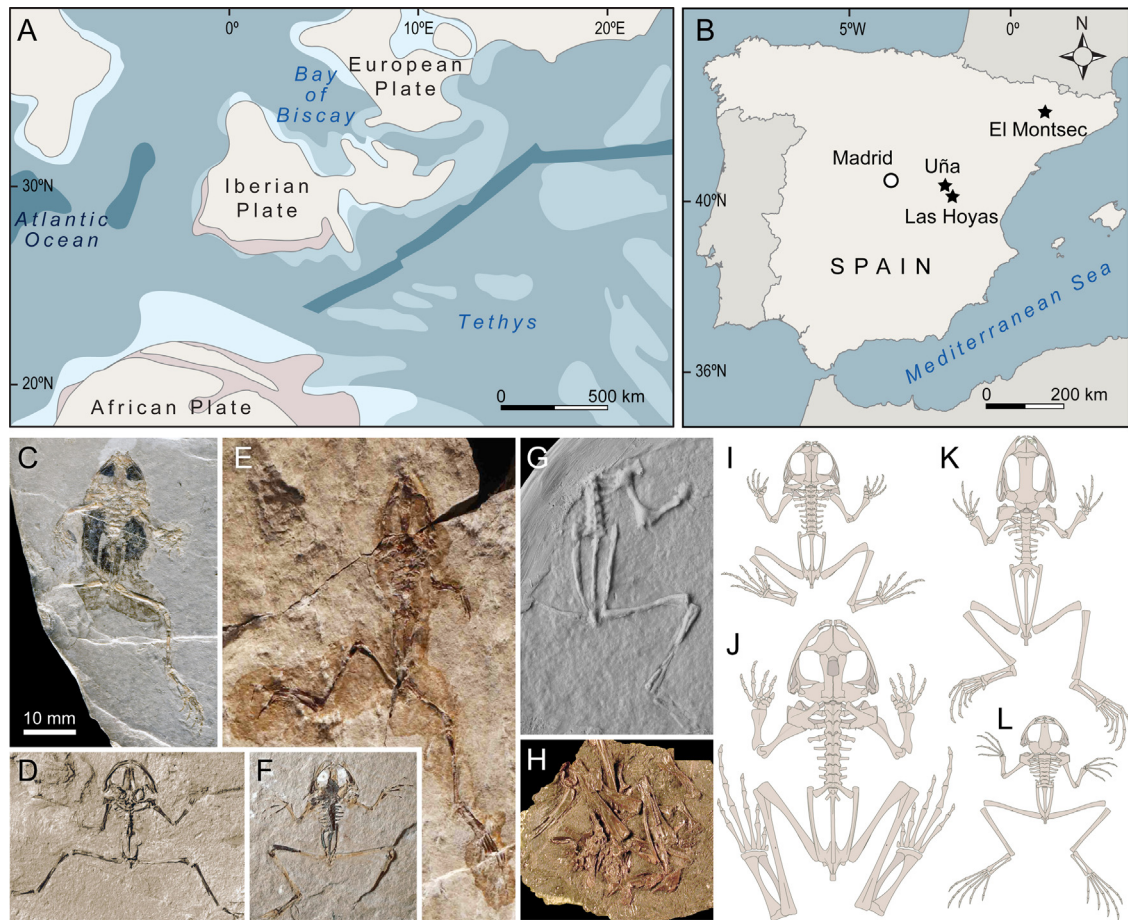


Fig. 1. Provenance, fossils, and anatomy of Early Cretaceous frogs from the Iberian wetland. **A.** Paleogeographic map of the Iberian Plate during the Barremian–Aptian (modified form [Gerdes et al., 2010](#)). **B.** Current location of the Barremian fossil sites in the Iberian Peninsula. **C–H.** Photographs of representative fossils: **C.** *Eodicoglossus santonjae* (MNHN 4723, Holotype); **D.** *Neusibatrachus wilfert* (MB.Am.1469a, Holotype); **E.** *Iberobatrachus angelae* (MUPA-LH 15999b); **F.** *Gracilibatrachus avallei* (MUPA-LH 21171b, Holotype); **G.** *Gen. et sp. indet.* (MUPA-LH 11392); **H.** *Wealdenbatrachus jucarensis* (PIFUB 101/U70V, Holotype). **I–L.** Restorations of selected taxa: **I.** *Eodicoglossus santonjae*; **J.** *Wealdenbatrachus jucarensis*; **K.** *Iberobatrachus angelae*; **L.** *Gracilibatrachus avallei*. **I–K** are based on [Báez and Gómez \(2019\)](#). **C–L** are to the same scale.

Fig. 1. Provenance, fossiles et anatomie de grenouilles du Crétacé inférieur de la région humide d'Espagne. **A.** Carte paléogéographique de la plaque Ibérique pendant le Barrémien–Aptien (modifié d'après [Gerdes et al., 2010](#)). **B.** Localisation actuelle des sites fossilifères barrémiens de la péninsule Ibérique. **C–H.** Photographies de fossiles représentatifs : **C.** *Eodicoglossus santonjae* (MNHN 4723, holotype) ; **D.** *Neusibatrachus wilfert* (MB.Am. 1469a, holotype) ; **E.** *Iberobatrachus angelae* (MUPA-LH 15999b) ; **F.** *Gracilibatrachus avallei* (MUPA-LH 21171b, holotype) ; **G.** *Gen. et sp. indet.* (MUPA-LH 11392) ; **H.** *Wealdenbatrachus jucarensis* (PIFUB 101/U70V, holotype). **I–L.** Restauration de taxa sélectionnés ; **I.** *Eodicoglossus santonjae* ; **J.** *Wealdenbatrachus jucarensis* ; **K.** *Iberobatrachus angelae* ; **L.** *Gracilibatrachus avallei*. **I–K** sont basés sur [Báez et Gómez \(2019\)](#). **C–L** sont à la même échelle.

exception of *Silurana*, following [Gómez \(2016\)](#). We have generally referred to the main anuran clades (i.e. the phylogenetic nomenclature) following the definitions of [Frost et al. \(2006\)](#), but used Pipanura (sensu [Ford and Cannatella, 1993](#)) for the clade composed of Xenoanura plus Acosmanura, and Pipimorpha (sensu [Ford and Cannatella, 1993](#)) for the stem-based clade including Pipidae. The taxonomy and systematic relationships of the extinct taxa studied in this paper are based on recent studies ([Báez, 2013, 2016](#); [Báez and Gómez, 2016, 2019](#); [Báez and Sanchiz, 2007](#); [Gómez, 2016](#)).

2.2. Taxonomic sampling

To date, Barremian anurans from Iberia represent at least five valid genera and species, namely

Eodicoglossus santonjae [Villalta, 1954](#), *Wealdenbatrachus jucarensis* [Fey, 1988](#), *Neusibatrachus wilfert* [Seiffert, 1972](#), *Gracilibatrachus avallei* [Báez, 2013](#), and *Iberobatrachus angelae* [Báez, 2013](#), which in turn document at least three major radiations of ‘archeobatrachian’ (i.e. non-neobatrachian) anurans ([Báez and Gómez, 2016, 2019](#); [Table 1](#)). We sampled fossils representing these taxa, but also two other specimens with sufficient anatomical detail to be ascribed at some systematic level. In view of our present aims, we studied only those fossils representing adult individuals and providing data on skeletal limb proportions. The identification and stratigraphic and geographic provenance of these specimens are indicated in [Table 1](#). For the estimation of locomotor capabilities of these extinct frogs, we sampled 34 extant ‘archeobatrachian’ species ([Supplementary Material 1](#)). In addition, we

Table 1

Systematics and provenance of the fossil specimens included in the analyses.

Tableau 1

Systématique et provenance des spécimens fossiles inclus dans les analyses.

Taxon	Specimen	Locality	Horizon	Major radiation	References
<i>Eodiscoglossus santonjae</i>	MNHN 4723. Holotype	Santa Maria de Meià (Montsec), Lleida Province	La Pedrera de Rúbies Lithographic Limestones Fm. (early Barremian)	Stem Lalagobatrachia	Báez, 2013; Báez and Gómez, 2016, 2019
<i>Neusibatrachus wilferti</i>	MB.Am.1469a, b. Holotype (formerly PIFUB 33 A, B)	Santa Maria de Meià (Montsec), Lleida Province	La Pedrera de Rúbies Lithographic Limestones Fm. (early Barremian)	Basal Pipimorpha	Báez and Sanchiz, 2007; Gómez, 2016
<i>Iberobatrachus angelae</i>	MUPA-LH 15999 a, b	Las Hoyas, Cuenca Province	La Huérguina Fm (late Barremian)	Costata	Báez, 2013; Báez and Gómez, 2019
<i>Gracilibatrachus avallei</i>	MUPA-LH 21171 a, b. Holotype	Las Hoyas, Cuenca Province	La Huérguina Fm (late Barremian)	Basal Pipimorpha	Báez, 2013; Gómez, 2016
Gen. et sp. indet.	MUPA-LH 11392	Las Hoyas, Cuenca Province	La Huérguina Fm (late Barremian)	Stem (or basal) Pipanura ^a	Báez, 2016; Báez and Gómez, 2019; ROG pers. observ.
<i>Wealdenbatrachus</i> sp.	MUPA-LH 7990	Las Hoyas, Cuenca Province	La Huérguina Fm (late Barremian)	Stem Lalagobatrachia	Báez and Gómez, 2019; Evans et al., 1995; Sanchiz, 1998
<i>Wealdenbatrachus jucarensis</i>	PIFUB 101/U70 I–V. Restoration by Báez and Gómez (2019)	Uña, Cuenca Province	La Huérguina Fm (late Barremian)	Stem Lalagobatrachia	Báez and Gómez, 2019

^a The affinities of MUPA-LH 11392 are based on the combination of eight presacral vertebrae with imbricated neural arches, ribs fused to the transverse processes, moderately dilated sacral diapophyses, urostyle having small transverse processes, a moderately long scapula lacking crest on its leading margin, and long ilia lacking well-developed dorsal crests.

sampled skeletons of extant anuran species that currently inhabit northeastern Spain (Lobo et al., 2016), as well as tropical and subtropical wetlands of South (Ingaramo et al., 2012; Valério et al., 2016) and North America (Dixon et al., 2011), Africa (Sinsch et al., 2012), and Asia (Rais et al., 2012; Roy and Dey, 2015; Schoppe and Cervancia, 2009), in order to contextualize the taxonomic and ecological diversity of the Barremian frogs from Iberia (Supplementary Material 1). Although frog-bearing levels from Montsec have been regarded as early Barremian whereas those from Uña and Las Hoyas as late Barremian (De Vicente and Martín-Closas, 2013; Fregenal-Martínez et al., 2017), we pooled fossils from these three localities to make these comparisons. It is noteworthy that *Eodiscoglossus*, represented in Montsec by *E. santonjae*, and *Wealdenbatrachus*, represented in Uña by *W. jucarensis*, have both been identified among the anurans from Las Hoyas (Báez, 2013; Buscalioni and Poyato-Ariza, 2016; Sanchiz, 1998). Only the pipimorph *Neusibatrachus wilferti* from Montsec has not yet been identified among the fossils from Las Hoyas, from which the pipimorph *Gracilibatrachus* has been described instead, but its presence at this locality cannot be ruled out.

2.3. Osteological data

For each individual, we took length measurements of five major limb bones following Lires et al. (2016: fig. 2): humerus (Hu), radio-ulna (RU), femur (Fe), tibiofibula (TF), and fibular (Tar). Analyses were done on species means when two or more individuals per species were available. Measurements were either taken from photographs with ScreenCaliper, Version 4.0 (Iconico, New York), 3D models with MeshLab 2016 (Cignoni et al., 2008), or dry skeletons with a manual digital caliper (0.01 mm error). It

has been shown that these different data sources provide reliable, equivalent measurements (Jorgensen and Reilly, 2013; Lires et al., 2016). All limb proportions used in the analyses are available in Supplementary Material 1.

2.4. Locomotor modes

Following most previous approaches on frog eco-morphology (e.g., Citadini et al., 2018; Emerson, 1978; Enriquez-Urzelai et al., 2015; Jorgensen and Reilly, 2013; Lires et al., 2016), we typified each extant species as having a primary locomotor mode related to displacement behaviors, but we did not consider microhabitat preferences (i.e. aquatic/terrestrial/arboreal) nor other behavioral patterns related to substrate use, such as burrowing. Three major locomotor categories were recognized: jumpers (J), swimmers (Sw), and walker/hoppers (WH). We acknowledge that this is a gross categorization of anuran locomotion and there is not always a clear-cut classification of species into a single mode, but we followed this approach in view of the support for similar classification schemes used by previous studies on the same type of data (e.g., Enriquez-Urzelai et al., 2015; Lires et al., 2016). Locomotor modes of extant species were obtained from the literature (e.g., Emerson, 1978, 1988; Enriquez-Urzelai et al., 2015; Lires et al., 2016; Taigen et al., 1982; Zug, 1972) or Web resources (AmphibiaWeb, 2018) and are listed in Supplementary Material 1.

2.5. Morphospace of limb proportions and locomotor modes

Prior to statistical analyses, we performed a Principal Component Analysis (PCA) in R 3.3.0 (R Core Team,

2016) based on the size-corrected limb data. This provided a morphospace to summarize the diversity in limb proportions in the studied Barremian frogs and among the sampled ‘archeobatrachian’ anurans, allowing a relatively straightforward interpretation of the relation between limb proportions and locomotor modes. In addition, we evaluated if fossils fell within the shape space of ‘archeobatrachians’ as defined by the 95% confidence interval on the first two PCA axes. If extant species with the same locomotor mode clustered together in distinct regions of this morphospace and fossils were more or less within the range of extant forms, this would allow one to use this set of ‘archeobatrachians’ to infer locomotor modes in the studied extinct taxa.

2.6. Phylogenetic flexible discriminant analysis

We inferred locomotor modes for the Barremian anurans by means of a phylogenetic flexible discriminant analysis (pFDA; Motani and Schmitz, 2011) in R 3.3.0 (R Core Team, 2016), as has been implemented by Schmitz and Motani (2011) and Angielczyk and Schmitz (2014). In contrast to standard discriminant analyses, pFDA accounted for phylogenetic covariance when predicting a categorical variable (locomotor mode) based on continuous variables (the five limb bone linear measurements). Classification rules were derived from the combinations of those continuous variables that best discriminate between groups (i.e. ‘discriminant functions’) and were established with a training dataset of species having known locomotor modes. Extinct taxa were then assigned to groups by posterior probabilities calculated for each test sample. Prior to visualization and statistical analyses, we corrected the data for size by using the proportional length of each bone among the sum of the five measured elements per individual, since scaling against snout-vent length (svl) would introduce more error, and we focused on limb proportions alone. Taking into account the putative phylogenetic relationships of the involved extinct taxa, classification rules were established on a training set of 34 extant ‘archeobatrachian’ species, whose sampling is completely balanced for locomotor modes. In order to account for phylogenetic covariance during the classification of fossils, a time-adjusted phylogenetic tree (Fig. 2) was assembled in Mesquite Version 3.31 (Maddison and Maddison, 2011). The backbone tree of extant species was derived from the already calibrated topology of Pyron (2014), with a few remaining extant species added by hand based on prominent systematic accounts (e.g., Frost, 2019). To this backbone, extinct taxa were added by hand with a conservative approach, according to our current knowledge based on recent studies (Báez, 2013; Báez and Gómez, 2016, 2019; Dong et al., 2013; Gómez, 2016; Marjanović and Laurin, 2014). The length of branches leading to extinct taxa were derived directly from the youngest possible age of fossils following the numerical ages of Cohen et al. (2013, updated) and assigning internodes a minimum time interval (1 Myr herein) following previous approaches (Angielczyk and Schmitz, 2014; Marjanović and Laurin, 2008, 2014). Classification rules were established at an optimal Pagel’s lambda value that maximizes a correlation

between morphological variables and locomotor mode, which was estimated following the approach of Schmitz and Motani (2011), although we explored classifications under different values of Pagel’s lambda across its full range as a sort of sensitivity analysis.

2.7. Comparisons between Barremian and extant frog assemblages

In order to contextualize our results for the extinct frogs from Montsec, Uña, and Las Hoyas in the northeastern Iberian Peninsula, we compared their taxonomic, phylogenetic, morphological and ecological diversity to that of the anuran assemblage that today inhabit this same region (Lobo et al., 2016; Supplementary Material 1). Also, as these localities document a large wetland system developed under a subtropical climate during the Barremian (Buscalioni and Poyato-Ariza, 2016), we compared the data with some frog assemblages from tropical and subtropical wetlands from different continents (Supplementary Material 1). The number of families, major radiations, and a measure of the phylogenetic diversity (Faith, 1992) represented in each assemblage were used as proxies of taxonomic and phylogenetic diversity, whereas known or inferred locomotor modes were used as proxies of ecological diversity. Phylogenetic diversity was estimated through the calculation of the phylogenetic diversity index (Faith, 1992) using the Stratigraphic Tools of Mesquite (Josse et al., 2006) on a time-adjusted tree including all extant species represented on the assemblages mainly derived from that of Pyron (2014) and following the aforementioned approach (Supplementary Material 2). For meaningful comparisons between the Barremian and extant assemblages, this index was scaled according to the tree depth (in Ma) represented in each sub-tree (Supplementary Materials 1, 2). A more quantitative approach regarding ecomorphological diversity was performed on morphological data, which consisted of standardized limb proportions as well as standardized values of ratios within (RU/Hu; TF/Fe) and between (forelimb/hindlimb) limbs and of svl of extinct and extant taxa (Supplementary Material 1). The svl of extinct species were derived from the total length of the skeleton of nearly complete specimens or reliable restorations (Table 1; Fig. 1C–L; Supplementary Material 1), whereas those of extant species correspond either to the mean adult svl obtained from the literature (Trochet et al., 2014) or to the actual svl of adult specimens. Comparisons were made through calculation of the sum of variances (SOV) using the dispRity R package (Guillerme, 2018) in R 3.3.0 (R Core Team, 2016). Differences in disparity were considered significant by non-overlapping 95% confidence intervals, which were calculated by bootstrapping each group 1000 times. To account for the difference in sample size, which was almost negligible, the samples were rarefied to the smallest sample size.

3. Results

Our results show that ‘archeobatrachian’ anurans with the same locomotor mode clump together with very little overlap in more or less distinct domains of the

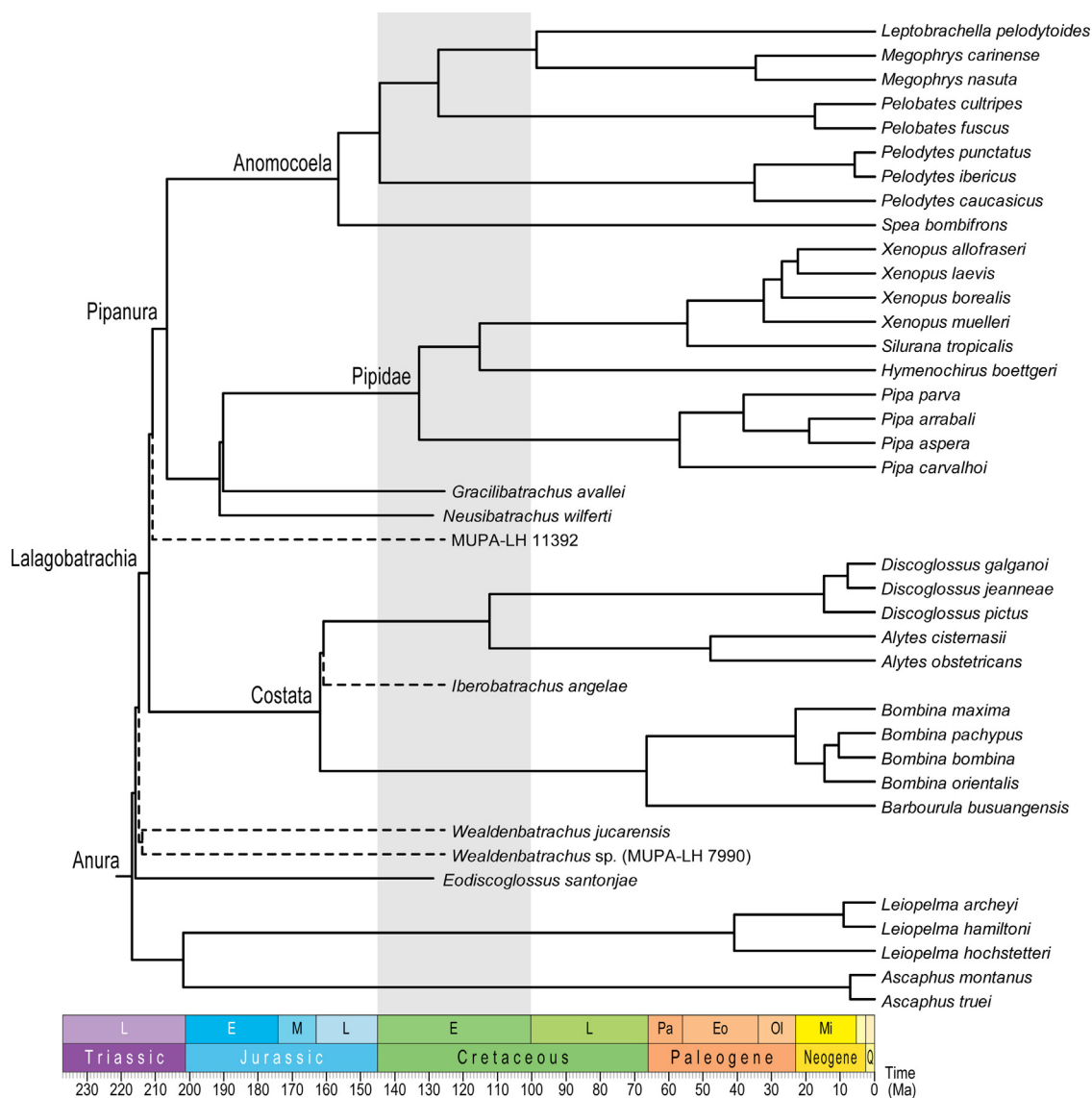


Fig. 2. Time-adjusted phylogeny of 'archeobatrachian' frogs. Tree used to account for phylogenetic covariance in the phylogenetic flexible discriminant analysis (Motani and Schmitz, 2011), depicting the putative relationships of Early Cretaceous frogs from the Iberian wetland. See text for further details.
Fig. 2. Phylogénie, ajustée au temps, de grenouilles « archéobatrachiennes ». Arbre utilisé en prenant en compte la covariance phylogénétique dans l'analyse discriminante flexible phylogénétique (Motani et Schmitz, 2011), décrivant les relations putatives entre grenouilles du Crétacé inférieur dans la zone humide Ibérique. Voir le texte pour plus de détails.

morphospace defined by the first two PCA axes (Fig. 3A), which together represent more than 86% of the total variance (PC1: 63.36%, PC2: 22.76%). This indicates that species with different locomotor modes tend to have different limb proportions. Most jumpers and swimmers show negative values of the PC1 associated with comparatively short forelimbs and long hindlimbs, but most jumpers and swimmers clearly differ in the PC2, which relates to jumpers often having tibiofibulae that are clearly longer than the femora and longer proximal tarsals than swimmers. In contrast, walker/hoppers are restricted to positive values of the PC1, having relatively longer forelimbs and shorter hindlimbs with respect to jumpers and swimmers, and all but burrowing specialists show positive values of PC2. The departure

of burrowing species (e.g., *Pelobates* spp.) from most walkers/hoppers mainly relates to the fact that the femur is clearly longer than the tibiofibula.

The Barremian anurans from Iberia show diverse limb proportions, some of which overlap extant 'archeobatrachian' species in the morphospace, whereas others occupy somewhat distinctive areas, although most still within the 95% confidence interval of extant forms in the PC1–PC2 morphospace (Fig. 3A), calling for caution when interpreting inferences for these particular taxa. Most of these fossils are located in the morphospace closer to extant jumpers and swimmers than to walkers/hoppers, some having proportions more similar to those of particular neobatrachians than to any extant 'archeobatrachian' species

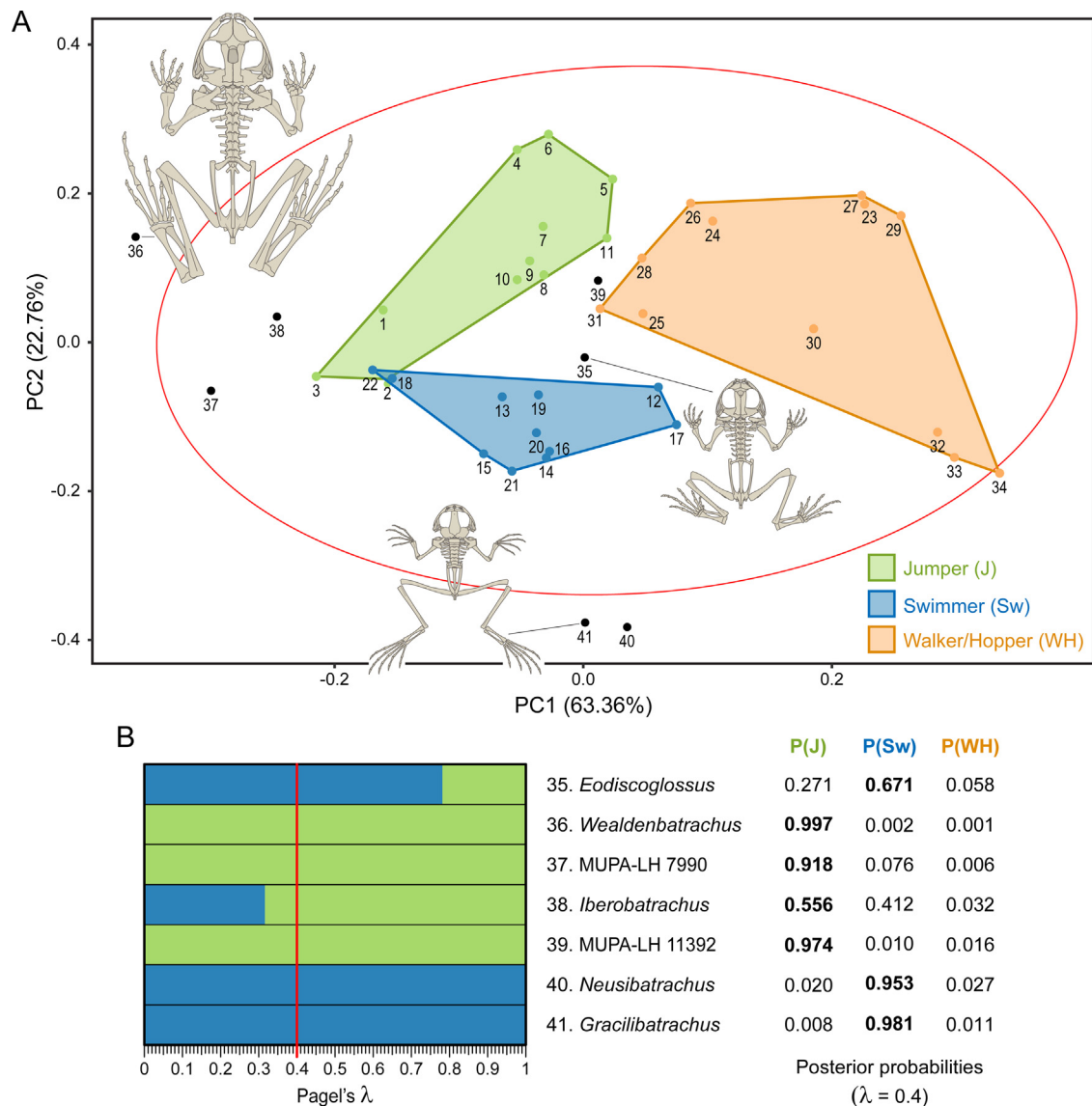


Fig. 3. Limb proportions and locomotor modes in Barremian frogs from Iberia and extant 'archeobatrachian' species. **A.** Morphospace of limb proportions derived from the PCA on species means, where the locomotor modes of extant taxa are depicted in different colors and those of extinct taxa by black dots, highlighting the anatomy of the selected taxa. The 95% confidence interval for all extant taxa is indicated in red. **B.** Classification of extinct taxa based on the phylogenetic flexible discriminant analysis (Motani and Schmitz, 2011) under all values of Pagel's lambda and posterior probabilities under its optimal value. Numbers identifying taxa are explained in [Supplementary Material 1](#).

Fig. 3. Proportions des membres et modes locomoteurs chez les grenouilles du Barrémien d'Espagne et les espèces « archéobatrachiennes » actuelles. **A.** Morpho-espaces des proportions de membres, dérivés de l'analyse en composantes principales sur moyennes d'espèces où les modes locomoteurs de taxa actuels sont représentés par des couleurs différentes et ceux des taxa éteints par des points noirs, en mettant l'accent sur l'anatomie de taxa sélectionnés. L'intervalle de confiance de 95 % pour tous les taxa actuels est indiqué en rouge. **B.** Classification des taxa éteints, basée sur l'analyse discriminante flexible phylogénétique (Motani et Schmitz, 2011), avec toutes les valeurs lambda de Pagel et les probabilités postérieures sous leur valeur optimale. Les numéros indiquant les taxa sont expliqués dans le [matériel supplémentaire 1](#).

([Supplementary Material 1](#)). For instance, *Wealdenbatrachus jucarensis* shows extreme negative values of PC1, whereas the pipimorphs *Neusibatrachus* and *Gracilibatrachus* show extreme negative values of PC2. Conversely, *Eodiscoglossus santoniae* and MUPA-LH 11392 plot almost in the center of the PC1–PC2 morphospace, in between extant species with different locomotor modes, which might suggest that their limb proportions are rather generalized.

Application of the pFDA classification rules with the estimated optimal Pagel's lambda (0.4) results in four extinct species classified as jumpers and the remaining three as swimmers, with high posterior probabilities (>95%) in most cases ([Fig. 3B](#)). Moreover, those classifications with high posterior probabilities at optimal lambda do not vary across the entire range of lambda values, including classification of the pipimorphs *Neusibatrachus* and *Gracilibatrachus* as swimmers and

Wealdenbatrachus jucarensis, MUPA-LH 7990, and MUPA-LH 11392 as jumpers. It has to be noted that, in spite of its seemingly generalized limb proportions, MUPA-LH 11392 is consistently classified as a jumper, which relies on the fact that the distance to the centroid of jumpers is consistently shorter than those of other locomotor groups. In contrast, *Eodiscoglossus* and *Iberobatrachus* are classified at optimal lambda with relatively low posterior probabilities (<70%) as swimmer and jumper, respectively, but their classification vary across the range of lambda, being alternatively classified as swimmers at low values and jumpers at high values. Fossils were never classified as hopper/walkers with the classification rules derived from the pFDA, disregarding the value of lambda (Fig. 3B).

The fossil frogs from the Iberian Plate represent at least five distinct genera, namely the already known *Eodiscoglossus*, *Gracilibatrachus*, *Iberobatrachus*, *Neusibatrachus*, and *Wealdenbatrachus*, but MUPA-LH 11392 certainly represents an additional one. In turn, these taxa might represent at least five families (although they are not defined yet) and four major radiations of ‘archeobatrachian’ anurans: stem lalagobatrachians, costatans, stem (or alternatively basal) pipanurans, and basal pipimorphs (Báez, 2013, 2016; Báez and Gómez, 2016, 2019; Gómez, 2016; Supplementary Material 1; Table 1; Fig. 2). Conversely, sampled tropical and subtropical assemblages represent between three to seven families and two to five major radiations each, being ‘archeobatrachian’ anurans largely unrepresented (Supplementary Material 1; Fig. 4A). In addition, the inferred phylodiversity encompassed by this Barremian assemblage rivals or even surpasses the current anuran phylodiversity of the Iberian region and of sampled tropical and subtropical assemblages across the world (Supplementary Material 1; Fig. 4A). In ecological terms, the Barremian assemblage is similar to the sampled extant wetland assemblages in that each encompasses swimmers and is rich in jumpers, but differs from the latter in lacking walker/hoppers and in having a larger proportion of swimmers (Fig. 4A). The ecomorphological disparity calculated by SOV on the standardized limb proportions (Fig. 4B) and the standardized ratios plus svl (Fig. 4C) is statistically similar between extinct and most extant assemblages, although the latter is somewhat higher for the Barremian assemblage. The Barremian wetland encompasses taxa not only with diverse limb proportions, but also of different size classes ranging from the miniature adult pipimorphs (20 mm svl) to the medium-size *Wealdenbatrachus jucarensis* (50 mm svl), which barely resembles in size and proportions some extant species of *Discoglossus*.

4. Discussion

Limb proportions in sampled ‘archeobatrachians’ correlate well with locomotion, as has previously been observed in diverse anurans (Emerson, 1988; Enriquez-Urzelai et al., 2015; Jorgensen and Reilly, 2013; Lires et al., 2016; Zug, 1972), which allowed us to infer the locomotor abilities in extinct taxa. The extinct frogs from the Iberian wetland, which show diverse limb proportions but more typical of jumpers or swimmers, were classified accordingly by the pFDA rules. Some classifications do not depart

from expectation, as in the cases of the pipimorph taxa or *Wealdenbatrachus*. The pipimorphs *Neusibatrachus* and *Gracilibatrachus*, which are part of the stem of the highly aquatic pipids (Báez, 2013; Báez and Sanchiz, 2007; Gómez, 2016), are consistently inferred as swimmers, in agreement with the aquatic lifestyle inferred on the basis of several skeletal features other than limb proportions (Báez, 2013; Gómez and Pérez-Ben, 2019). Also concurring with previous suggestions mainly based on limb proportions and ilial morphology (Báez and Gómez, 2019), specimens of *Wealdenbatrachus* are invariably classified as jumpers.

On the contrary, the locomotor behaviors of the remaining Barremian frogs from Iberia have not been advanced previously, but some remarks have previously been made on their hindlimb proportions. In this regard, *Iberobatrachus* has been considered more similar to *Wealdenbatrachus* than to *Eodiscoglossus*, although differences in their proximal tarsals have been stressed (Báez, 2013; Báez and Gómez, 2019). In line with these previous observations, *Iberobatrachus* is classified as a jumper under most analytical conditions, yet many of these classifications are with posterior probabilities only marginally over 50% and swimming as the primary locomotor mode should not be dismissed. It is also noteworthy that *Iberobatrachus* clearly differs from *Wealdenbatrachus* in having proportionally shorter hindlimbs relative to svl (although this feature was not part of our analyses; Fig. 1J, K) and in lacking a well-developed dorsal crest on the ilial shaft, which has been interpreted as indicative of different locomotor abilities (Báez and Gómez, 2019). Crested ilia characterize many, but not all, proficient jumpers among neobatrachian anurans, though they are only present in species of *Discoglossus* among extant ‘archeobatrachian’ jumpers (Gómez and Turazzini, 2016; Přikryl et al., 2009; Reilly and Jorgensen, 2011), which are known to exert lower jump forces than neobatrachians (Herrel et al., 2016). Therefore, the sole lack of a dorsal crest on the ilium cannot be taken as evidence against jumping locomotion. In any case, it is possible that the uncertainty in the classification might indicate that both jumping and swimming were important parts of the locomotor repertoire of *Iberobatrachus*, which would agree with semiaquatic habits, although a more thorough scrutiny of its anatomy and the integration of additional data from extant taxa will be needed to elucidate this issue.

The osteology of *Eodiscoglossus santonjae* has recently been revised in detail; its generalized limb proportions have been regarded as part of its overall plesiomorphic morphology (Báez and Gómez, 2016). This appears to be confirmed by our limb data, as *Eodiscoglossus* plot almost at the centroid of the ‘archeobatrachian’ morphological diversity between extant species of the three different locomotor modes considered herein (Fig. 3A). However, this taxon is classified as a swimmer under most analytical conditions, yet with relatively low posterior probabilities, being otherwise classified as a jumper. This is interesting, since generalized limb proportions might imply an all-purpose morphology capable to cope with different demands imposed by diverse microhabitats (e.g., Soliz et al., 2017; Tulli et al., 2016). Among the locomotor and other substrate-related behaviors of anurans, however, *Eodiscoglossus* does not

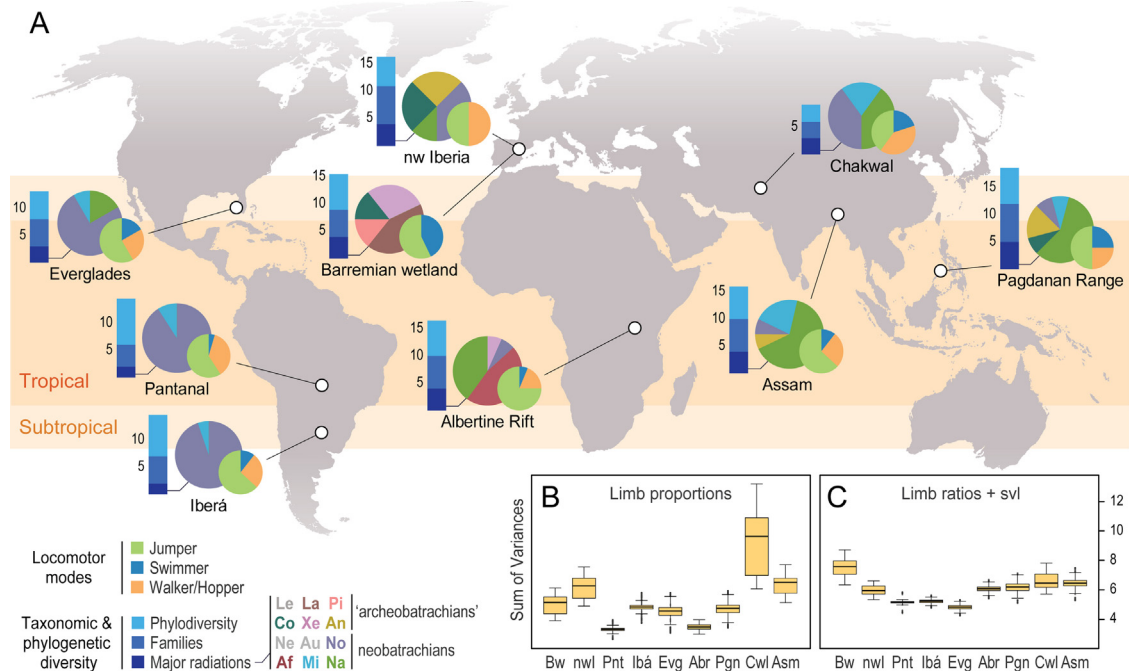


Fig. 4. Taxonomic, phylogenetic and ecomorphological diversity of the Barremian Iberian wetland, the extant Iberian frog assemblage, and tropical and subtropical wetlands. **A.** Map showing the location and diversity of the assemblages. **B–C.** Boxplots comparing ecomorphological diversity by means of the sum of variances calculated on standardized limb proportions (**B**) and limb ratios plus svl (**C**). The data is available in [Supplementary Materials 1–2](#). Major radiations abbreviations in **A**: Af, Afrobatrachia; An, Anomocoela; Au, Australobatrachia; Co, Costata; La, stem Lalagobatrachia; Le, Leiopelmatidae + Ascaphidae; Mi, Miobatrachidae; Na, Natatanura; Ne, basal neobatrachians; No, Nobleobatrachia; Pi, stem or basal Pipanura; Xe, Xenoanura. Assemblages abbreviations in **B–C**: Abr, Albertine Ridge; Asm, Assam; Bw, Barremian wetland; Cwl, Chakwal; Evg, Everglades; Ibá, Iberá; nwl, northwestern Iberia; Pgn, Pagdanan Range; Pnt, Pantanal.

Fig. 4. Diversité taxonomique, phylogénétique et écomorphologique des assemblages de grenouilles barrémiennes de la zone Ibérique humide, de grenouilles ibériques actuelles et de celles de zones humides tropicales et subtropicales. **A.** Carte montrant la localisation et la diversité des assemblages. **B–C.** Diagrammes de relevés comparant la diversité écomorphologique au moyen de la somme des variances calculées sur des proportions standardisées de membres (**B**) et des rapports de membres plus svl (**C**). Les données sont disponibles en [matériel supplémentaire 1–2](#). Principales abréviations de radiations en **A**: Af, Afrobatrachia; An, Anomocoela; Au, Australobatrachia; Co, Costata; La, branche Lalagobatrachia; Le, Leiopelmatidae; Mi, Miobatrachidae; Na, Natatanura; Ne, Néobatrachiens de base; No, Nobleobatrachia; Pi, branche ou Pipanura de base; Xe, Xenoanura. Abréviations d'assemblages en **B–C**: Abr, chaîne d'Albertine; Asm : Assam; Bw, zone humide barrémienne; Cwl, Chakwal; Evg, Everglades; Ibá, Ibérie; nwl, Ibérie nord-occidentale; Pgn, alignement de Pagdanan; Pnt, Pantanal.

seem to be able to jump long distances, walk fast or burrow effectively. Most walker/hoppers that also burrow exhibit stout, proportionally short hindlimbs and feet with a more or less hypertrophied prehallux (Emerson, 1976; Fabrezi et al., 2017), whereas *Eodiscoglossus* shows only a tiny ossified prehallux, despite having a hypertrophied prepollex (Báez and Gómez, 2016). Also, it has not the comparatively long forelimbs and short hindlimbs of efficient fast-walkers relative to other anurans (Reynaga et al., 2018). Therefore, in this case the ambiguity in the classification might indicate that *Eodiscoglossus* was a semiaquatic unspecialized swimmer with some jumping capability, although this remains to be tested with additional data.

Taken together, our results suggest that among these Early Cretaceous frogs, there were some jumpers and swimmers having more extreme limb proportions than extant 'archeobatrachian' species, but also species having more generalized limb proportions with varying degrees of jumping and swimming abilities, typical of aquatic and semiaquatic frogs (Emerson, 1978, 1988; Soliz et al., 2017). Interestingly, this ecomorphological structure with good representation of aquatic or likely semiaquatic jumping

and swimming species matches the expectation given that the depositional environments might have been part of a large subtropical wetland system extending across northeastern Iberia (Buscalioni et al., 2018; Buscalioni and Poyato-Ariza, 2016). It is most similar in ecomorphological structure to that from Pagdanan Range on the Philippine archipelago among the extant wetland assemblages surveyed (Fig. 4) and contrasts with that of the frog assemblage currently inhabiting northeastern Iberia, which is dominated by terrestrial jumpers and walker/hoppers, dwelling borders of swamps or temporary ponds developed under more temperate and drier climatic and environmental conditions (AmphibiaWeb, 2018; Trochet et al., 2014). Additional comparisons with the extant assemblages further stress the remarkable taxonomic and ecomorphological diversities represented among Barremian fossils, which, despite the intrinsic biases of the fossil record, equal or even surpass present-day values of taxonomic, phylogenetic, and ecomorphological diversity (Supplementary Material 1; Fig. 4). The high ecomorphological disparity depicted by fossils, encompassing jumpers and dedicated swimmers plus jumper/swimmer

putatively semiaquatic generalists of different size classes, certainly agrees with previous observations on these anurans (Báez and Gómez, 2019; Buscalioni and Poyato-Ariza, 2016) as well as with the paleoenvironmental reconstruction of northeastern Iberia as a complex subtropical wetland during the Barremian (Buscalioni et al., 2018; Fregenal-Martínez and Buscalioni, 2009). This large wetland system constituted a heterogeneous environment with diversity of intermingled aquatic, semiaquatic, and terrestrial microhabitats (Buscalioni et al., 2018; Buscalioni and Poyato-Ariza, 2016; Gomez et al., 2015) and might support a high diversity of anurans and other components of the biota from the Iberian Plate by providing a mosaic of available niches (Provete et al., 2014; Tews et al., 2004).

It is also noteworthy that the Barremian assemblage is exclusively made up of 'archeobatrachian' taxa, whereas extant assemblages worldwide are largely dominated by neobatrachians and only a few 'archeobatrachian' groups may be part of subtropical or tropical wetlands, namely a few bombinatorid costatans, pipid xenoanurans, and megophryid anomocoelans (Supplementary Material 1; Fig. 4A). The current scenario is not surprising, since 'archeobatrachians' represent only 4% of all extant anuran species (Frost, 2019). This, coupled with the observed pattern in the morphospace of limb proportions showing some Barremian fossils falling outside the hulls defined by extant 'archeobatrachians' (Fig. 3A), indicates that the extant taxonomic and ecomorphological 'archeobatrachian' diversity has become impoverished. Early Cretaceous assemblages from Laurasian continents other than that from Iberia also lack neobatrachians, whose diversification was well underway then as it is evidenced by the anurofauna from the Aptian Crato Formation of Brazil (Báez et al., 2009) and as it is inferred based on molecular time estimates (e.g., Pyron, 2014). Despite Neobatrachians reached a widespread distribution across most Gondwanan continents by the end-Cretaceous, they remained absent from Iberia and most other Laurasian terrains (Báez et al., 2012; Gao and Chen, 2017; Ikeda et al., 2016; Xing et al., 2018; this study), which reinforces the hypothesis of an origin and early diversification of these anurans in Gondwana (Báez et al., 2009, 2012) and suggests some geographical isolation from Laurasian landmasses during most of the Cretaceous.

The frogs from the Barremian Iberian wetland are amongst the earliest well-known representatives of some major crown-group radiations, providing valuable data on the early ecomorphological diversification of anurans. The origin of the anuran *Bauplan* has traditionally been linked with saltatory locomotion (e.g., Gans and Parsons, 1966; Jenkins and Shubin, 1998), although this view has recently been challenged on different grounds (Ascarrunz et al., 2016; Herrel et al., 2016; Lires et al., 2016; Reilly and Jørgensen, 2011). Alternatively, a walker/hopper locomotion has been proposed as the primitive anuran condition in some recent studies (e.g., Ascarrunz et al., 2016; Jørgensen and Reilly, 2013; Reilly and Jørgensen, 2011), although the latter did not consider swimming as a discrete locomotion category in their analyses. It is surprising, though, that among the Barremian frogs from Iberia none was classified here as walker/hopper, whereas jumpers are well represented. However, these jumpers either appear

to be generalists or similar in size and proportions to extant *Discoglossus*, which produced low jump forces most often associated with swimming than jumping in most studied anurans (Herrel et al., 2016). Moreover, dedicated swimmers are also well represented in this Early Cretaceous assemblage, and swimming abilities are also expected for the remaining taxa, including those consistently classified as jumpers, since almost every extant anuran shows some swimming capability (Emerson and De Jongh, 1980; Peters et al., 1996; Soliz et al., 2017), though species distantly related or with different ecologies might swim rather differently (Nauwelaerts and Aerts, 2002; Robovska-Havelková et al., 2014). In this regard, general similarities in limb proportions and kinematics between swimming and jumping frogs have previously been acknowledged (Emerson and De Jongh, 1980; Lires et al., 2016; Nauwelaerts et al., 2007; Peters et al., 1996; Soliz et al., 2017; but see Robovska-Havelková et al., 2014), and there are many wetland-dweller neobatrachians that excel at both types of locomotion (Nauwelaerts et al., 2007; Soliz et al., 2017). However, recent work on jumping performance across the anuran tree demonstrated that 'archeobatrachian' jumpers do not really excel in jumping locomotion as they exert only low jump forces in comparison to jumping neobatrachians (Herrel et al., 2016). Frogs from the Barremian of Iberia exclusively represent miniature to medium-size 'archeobatrachians' with jumping and/or swimming abilities in a large and complex wetland, depicting a scenario compatible with the hypothesis regarding early frogs as small poor jumpers or swimmers that made their peculiar *Bauplan* in aquatic environments evolve (Herrel et al., 2016).

5. Conclusions

The Early Cretaceous frogs from the Iberian wetland exhibit a remarkable taxonomic, phylogenetic, and ecomorphological diversity, encompassing miniature to medium-size 'archeobatrachians' with varying degrees of jumping and swimming abilities, indicating a Konservat-Lagerstätte preservation of this wetland anuran assemblage (Buscalioni and Poyato-Ariza, 2016). In addition, this assemblage rivals modern tropical and subtropical wetlands here surveyed, which have relatively high species richness representing up to five major anuran radiations, whereas most temperate frog communities encompasses less than a handful of syntopic species (Sinsch et al., 2012; Wells, 2007). This further highlights the subtropical nature of this Iberian wetland and suggests that it could be an ancient anuran biodiversity hotspot. It would be of interest also to investigate other less spectacular Early Cretaceous frog assemblages to grasp a better panorama of the early phylogenetic and ecomorphological diversification of crown-group anurans and assess if frogs were also part of the Cretaceous Terrestrial Revolution (Lloyd et al., 2008).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2019.07.005>.

References

- AmphibiaWeb, 2018. Information on Amphibian Biology and Conservation (accessed 15 December 2018) <http://amphibiaweb.org>.
- Angielczyk, K.D., Schmitz, L., 2014. Nocturnality in synapsids predates the origin of mammals by over 100 million years. *Proc. R. Soc. B* 281, 20141642, <http://dx.doi.org/10.1098/rspb.2014.1642>.
- Ascarrunz, E., Rage, J.-C., Legreneur, P., Laurin, M., 2016. *Triadobatrachus massinoti*, the earliest known lissamphibian (Vertebrata: Tetrapoda) re-examined by ICT-Scan, and the evolution of trunk length in batrachians. *Contrib. Zool.* 85, 201–234, <http://dx.doi.org/10.1163/18759866-08502004>.
- Báez, A.M., 2013. Anurans from the Early Cretaceous Lagerstätte of Las Hoyas, Spain: new evidence on the Mesozoic diversification of crown-clade Anura. *Cretaceous Res.* 41, 90–106, <http://dx.doi.org/10.1016/j.cretres.2012.11.002>.
- Báez, A.M., 2016. Saliencia. In: Poyato-Ariza, F.J., Buscalioni, A.D. (Eds.), *Las Hoyas: A Cretaceous Wetland. A Multidisciplinary Synthesis after 25 Years of Research on an Exceptional Fossil Lagerstätte from Spain*, Friedrich Verlag, Munich, pp. 143–150.
- Báez, A.M., Gómez, R.O., 2016. Revision of the skeletal morphology of *Eodiscoglossus santoniae* an early Cretaceous frog from northeastern Spain, with comments on its phylogenetic placement. *Foss. Imprint* 72, 67–77, <http://dx.doi.org/10.14446/FI.2016.67>.
- Báez, A.M., Gómez, R.O., 2019. Redescription of the overlooked basal frog *Wealdenbatrachus* reveals increased diversity among Early Cretaceous anurans. *Cretaceous Res.* 99, 14–29, <http://dx.doi.org/10.1016/j.cretres.2019.02.006>.
- Báez, A.M., Sanchiz, B., 2007. A review of *Neusibatrachus wilferti*, an Early Cretaceous frog from the Montsec Range, northeastern Spain. *Acta Palaeontol. Pol.* 52, 477–487.
- Báez, A.M., Moura, G.J.B., Gómez, R.O., 2009. Anurans from the Lower Cretaceous Crato Formation of northeastern Brazil: implications for the early divergence of neobatrachians. *Cretaceous Res.* 30, 829–846, <http://dx.doi.org/10.1016/j.cretres.2009.01.002>.
- Báez, A.M., Gómez, R.O., Ribeiro, L.C., Martinelli, A.G., Teixeira, V.P., Ferraz, M.L., 2012. The diverse Cretaceous neobatrachian fauna of South America: *Uberabatrachus carvalhoi*, a new frog from the Maastrihtian Marília Formation, Minas Gerais, Brazil. *Gondwana Res.* 22, 1141–1150, <http://dx.doi.org/10.1016/j.gr.2012.02.021>.
- Buscalioni, A.D., Poyato-Ariza, F.J., 2016. Las Hoyas: a unique Cretaceous ecosystem. In: Khosla, A., Lucas, S. (Eds.), *Cretaceous Period: Biotic Diversity and Biogeography*. N.M., Mus. Nat. Hist. Sci. Bull. 71, 51–62.
- Buscalioni, A.D., Martín-Closas, C., Delvene, G., Munt, M.C., Barral, A., Tinner-Grellet, G., Gomez, B., Daviero-Gomez, V., Chamero, B., 2018. Taphonomy and palaeoecology in the upper Barremian of the SW Iberian chain (Spain): a model to compare taxonomy and diversity of biotas from different coeval basins. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 490, 305–324, <http://dx.doi.org/10.1016/j.palaeo.2017.11.009>.
- Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., Ranzuglia, G., 2008. Meshlab: An Open-Source Mesh Processing Tool. Eurographics Italian Chapter Conference, Salerno. The Eurographics Association, pp. 129–136, <https://doi.org/10.2312/LocalChapterEvents/ItalChap/ItalianChapConf2008/129-136>.
- Citadini, J.M., Brandt, R., Williams, C.R., Gomes, F.R., 2018. Evolution of morphology and locomotor performance in anurans: relationships with microhabitat diversification. *J. Evol. Biol.* 31, 371–381, <http://dx.doi.org/10.1111/jeb.13228>.
- Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2013. *The ICS International Chronostratigraphic Chart*. *Episodes* 36, 199–204.
- De Vicente, A., Martín-Closas, C., 2013. Lower Cretaceous charophytes from the Serranía de Cuenca, Iberian Chain: taxonomy, biostratigraphy and palaeoecology. *Cretaceous Res.* 40, 227–242, <http://dx.doi.org/10.1016/j.cretres.2012.07.006>.
- Dixon, A.D., Cox, W.R., Everham, E.M., Ceilley, D.W., 2011. Anurans as biological indicators of restoration success in the Greater Everglades ecosystem. *Southeast. Nat.* 10, 629–647, <http://dx.doi.org/10.1656/058.010.0404>.
- Dong, L., Roček, Z., Wang, Y., Jones, M.E.H., 2013. Anurans from the Lower Cretaceous Jehol Group of Western Liaoning, China. *PLoS One* 8, e69723, <http://dx.doi.org/10.1371/journal.pone.0069723>.
- Emerson, S.B., 1976. Burrowing in frogs. *J. Morphol.* 149, 437–458, <http://dx.doi.org/10.1002/jmor.1051490402>.
- Emerson, S.B., 1978. Allometry and jumping in frogs: helping the twain to meet. *Evolution* 32, 551–564, <http://dx.doi.org/10.2307/2407721>.
- Emerson, S.B., 1988. Convergence and morphological constraint in frogs: variation in postcranial morphology. *Fieldiana Zool.* 43, 1–19.
- Emerson, S.B., De Jongh, H.J., 1980. Muscle activity at the iliosacral articulation of frogs. *J. Morphol.* 166, 129–144, <http://dx.doi.org/10.1002/jmor.1051660202>.
- Enriquez-Urzela, U., Montori, A., Llorente, G.A., Kaliontzopoulou, A., 2015. Locomotor mode and the evolution of the hindlimb in western Mediterranean anurans. *Evol. Biol.* 42, 199–209, <http://dx.doi.org/10.1007/s11692-015-9311-1>.
- Evans, S.E., McGowan, G., Milner, A.R., Sanchiz, B., 1995. IV.4. Amphibians. In: Meléndez, M.N. (Ed.), *Las Hoyas. A lacustrine KonservatLagerstätte*, Cuenca, Spain. In: *Proc. 11 Int. Symp. on Lithographic Limestones. Field Trip Guide Book*. Ediciones de la Universidad Autónoma de Madrid, Madrid, pp. 51–53.
- Fabrezi, M., Goldberg, J., Chuliver Pereyra, M., 2017. Morphological variation in anuran limbs: constraints and novelties. *J. Exp. Zool. B: Mol. Dev. Evol.* 328, 546–574, <http://dx.doi.org/10.1002/jez.b.2753>.
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10, [http://dx.doi.org/10.1016/0006-3207\(92\)91201-3](http://dx.doi.org/10.1016/0006-3207(92)91201-3).
- Fey, B., 1988. Die Anurenfauna aus der Unterkreide von Uña (Ostspanien). *Berl. Geowiss. Abh. Reihe A/Band* 103, 1–99.
- Ford, L.S., Cannatella, D.C., 1993. The major clades of frogs. *Herpetol. Monogr.* 7, 94–117, <http://dx.doi.org/10.2307/1466954>.
- Fregenal-Martínez, M.A., Buscalioni, A.D., 2009. Las Hoyas konservatLagerstätte: a field-trip to a Barremian subtropical continental (wetland) ecosystem. In: Alcalá, L., Royo-Torres, R. (Eds.), *Mesozoic Terrestrial Ecosystems in Eastern Spain*. *Fundamental* 14, 133–152.
- Fregenal-Martínez, M., Meléndez, N., Muñoz-García, M.B., Elez, J., De la Horra, R., 2017. The stratigraphic record of the Late Jurassic–Early Cretaceous in the Alto Tajo, Serranía de Cuenca region (Iberian Ranges, Spain): genetic and structural evidences for evidences and a new lithostratigraphical proposal. *Rev. Soc. Geol. España* 30, 113–142.
- Frost, D.R., 2019. Amphibian Species of the World: An Online Reference. Vers. 6.0. American Museum of Natural History, New York, <http://research.amnh.org/herpetology/amphibia/index.plp> (accessed 9 January 2019).
- 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.T., Raxworthy, C.J., Capbell, 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. *Bull. Am. Mus. Nat. Hist.* 297, 1–370 ([https://doi.org/10.1206/0003-0090\(2006\)297\[0001:TATOL\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2)).
- Gans, C., Parsons, T.S., 1966. On the origin of the jumping mechanism in frog. *Evolution* 20, 92–99, <http://dx.doi.org/10.2307/2406151>.

- Gao, K.Q., Chen, J., 2017. A new crown-group frog (Amphibia: Anura) from the Early Cretaceous of northeastern Inner Mongolia, China. *Am. Mus. Novitates* 3876, 1–39.
- Gerdes, K.D., Winefield, P., Simmons, M.D., Oosterhout, Van C., 2010. The influence of basin architecture and eustasy on the evolution of Tethyan Mesozoic and Cenozoic carbonate sequences. *Geol. Soc., London, Special Publ.* 329, 9–41, <http://dx.doi.org/10.1144/SP329.2>.
- Gomez, B., Daviero-Gomez, V., Coiffard, C., Martín-Closas, C., Dilcher, D.L., 2015. *Montsecchia*, an ancient aquatic angiosperm. *Proc. Natl. Acad. Sci. U S A* 112, 10985–10988, <http://dx.doi.org/10.1073/pnas.1509241112>.
- Gómez, R.O., 2016. A new pipid frog from the Upper Cretaceous of Patagonia and early evolution of crown-group Pipidae. *Cretaceous Res.* 62, 52–64, <http://dx.doi.org/10.1016/j.cretres.2016.02.006>.
- Gómez, R.O., Pérez-Ben, C., 2019. Fossils reveal long-term continuous and parallel innovation in the sacro-caudo-pelvic complex of the highly aquatic pipid frogs. *Front. Earth Sci.* 7, 56, <http://dx.doi.org/10.3389/feart.2019.00056>.
- Gómez, R.O., Turazzini, G.F., 2016. An overview of the ilium of anurans (Lissamphibia, Salientia), with a critical appraisal of the terminology and primary homology of main ilial features. *J. Vert. Paleontol.* 36, e1030023, <http://dx.doi.org/10.1080/02724634.2015.1030023>.
- Guillermé, T., 2018. dispRity: a modular R package for measuring disparity. *Methods Ecol. Evol.* 9, 1755–1763, <http://dx.doi.org/10.1111/2041-210X.13022>.
- Handrigan, G.R., Wassersug, R.J., 2007. The anuran *Bauplan*: a review of the adaptive, developmental, and genetic underpinnings of frog and tadpole morphology. *Biol. Rev.* 82, 1–25, <http://dx.doi.org/10.1111/j.1469-185X.2006.00001.x>.
- Hecht, M.K., 1970. The morphology of *Eodiscoglossus*, a complete Jurassic Frog. *Am. Mus. Novitates* 2424, 1–17.
- Herrel, A., Moureaux, C., Laurin, M., Daghfous, G., Crandell, K., Tolley, K.A., Measey, J.G., Vanhooydonck, B., Boistel, R., 2016. Frog origins: inferences based on ancestral reconstructions of locomotor performance and anatomy. *Foss. Imprint* 72, 108–116, <http://dx.doi.org/10.14446/fi.2016.108>.
- Ikeda, T., Ota, H., Matsui, M., 2016. New fossil anurans from the Lower Cretaceous Sasayama Group of Hyogo Prefecture, Western Honshu, Japan. *Cretaceous Res.* 61, 108–123, <http://dx.doi.org/10.1016/j.cretres.2015.12.024>.
- Ingaramo, M.R., Etchepare, E.G., Álvarez, B.B., Porcel, E., 2012. Riqueza y composición de la fauna de anuros en la región oriental de la Reserva Natural Provincial Esteros del Iberá, Corrientes, Argentina. *Rev. Biol. Trop.* 60, 759–769, <http://dx.doi.org/10.15517/RBT.V60I2.3996>.
- Jenkins, F., Shubin, N., 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. *J. Vert. Paleontol.* 18, 495–510, <http://dx.doi.org/10.1080/02724634.1998.10011077>.
- Jorgensen, M.E., Reilly, S.M., 2013. Phylogenetic patterns of skeletal morphometrics and pelvic traits in relation to locomotor mode in frogs. *J. Evol. Biol.* 26, 929–943, <http://dx.doi.org/10.1111/jeb.12128>.
- Josse, S., Moreau, T., Laurin, M., 2006. Stratigraphic Tools for Mesquite. <http://mesquiteproject.org/packages/stratigraphicTools/>.
- Lires, A.I., Soto, I., Gómez, R.O., 2016. Walk before you jump: new insights on frog locomotion from the oldest known salientian. *Palaeobiology* 42, 612–623, <http://dx.doi.org/10.1017/pab.2016.11>.
- Lloyd, G.T., Davis, K.E., Pisani, D., Tarver, J.E., Ruta, M., Sakamoto, M., Hone, D.W., Jennings, R., Benton, M.J., 2008. Dinosaurs and the Cretaceous terrestrial revolution. *Proc. Royal Soc. B* 275, 2483–2490, <http://dx.doi.org/10.1098/rspb.2008.0715>.
- Lobo, J.M., Martínez-Solano, I., Sanchiz, B., 2016. A review of the palaeoclimatic inference potential of Iberian Quaternary fossil batrachians. *Palaeobiodivers. Palaeoenviron.* 96, 125–148, <http://dx.doi.org/10.1007/s12549-015-0224-x>.
- Maddison, W.P., Maddison, D.R., 2011. Mesquite: A Modular System for Evolutionary Analysis, Version 3. 31 (accessed 22 June 2018) <http://mesquiteproject.org>.
- Marjanović, D., Laurin, M., 2008. Assessing confidence intervals for stratigraphic ranges of higher taxa: the case of Lissamphibia. *Acta Palaeontol. Pol.* 53, 413–432, <http://dx.doi.org/10.4202/app.2008.0305>.
- Marjanović, D., Laurin, M., 2014. An updated paleontological timetree of lissamphibians, with comments on the anatomy of Jurassic crown-group salamanders (Urodela). *Hist. Biol.* 26, 535–550, <http://dx.doi.org/10.1080/08912963.2013.797972>.
- Moen, D.S., Wiens, J.J., 2017. Microhabitat and climatic niche change explain patterns of diversification among frog families. *Am. Nat.* 190, 29–44, <http://dx.doi.org/10.1086/692065>.
- Moen, D.S., Morlon, H., Wiens, J.J., 2015. Testing convergence versus history: convergence dominates phenotypic evolution for over 150 million years in frogs. *Syst. Biol.* 65, 146–160, <http://dx.doi.org/10.1093/sysbio/syv073>.
- Motani, R., Schmitz, L., 2011. Phylogenetic versus functional signals in the evolution of form-function relationships in terrestrial vision. *Evolution* 65, 2245–2257, <http://dx.doi.org/10.1111/j.1558-5646.2011.01271.x>.
- Nauwelaerts, S., Aerts, P., 2002. Two distinct gait types in swimming frogs. *J. Zool.* 258, 183–188, <http://dx.doi.org/10.1017/S0952836902001292>.
- Nauwelaerts, S., Ramsay, J., Aerts, P., 2007. Morphological correlates of aquatic and terrestrial locomotion in a semiaquatic frog, *Rana esculenta*: no evidence for a design conflict. *J. Anat.* 210, 304–317, <http://dx.doi.org/10.1111/j.1469-7580.2007.00691.x>.
- Peters, S.E., Kamel, L.T., Bashor, D.P., 1996. Hopping and swimming in the leopard frog, *Rana pipiens*: I. Step cycles and kinematics. *J. Morphol.* 230, 1–16 ([https://doi.org/10.1002/\(SICI\)1097-4687\(199610\)230:1<1::AID-JMOR1>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1097-4687(199610)230:1<1::AID-JMOR1>3.0.CO;2-N)).
- Přikryl, T., Aerts, P., Havelková, P., Herrel, A., Roček, Z., 2009. Pelvic and thigh musculature in frogs (Anura) and origin of anuran jumping locomotion. *J. Anat.* 214, 100–139, <http://dx.doi.org/10.1111/j.1469-7580.2008.01006.x>.
- Provete, D.B., Gonçalves-Souza, T., Garey, M., Martins, I.A., Rossa-Feres, D.C., 2014. Broad-scale spatial patterns of canopy cover and pond morphology affect the structure of a Neotropical amphibian metacommunity. *Hydrobiologia* 734, 69–79, <http://dx.doi.org/10.1007/s10750-014-1870-0>.
- Pyron, R.A., 2014. Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Syst. Biol.* 63, 779–797, <http://dx.doi.org/10.1093/sysbio/syu042>.
- R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>.
- Rais, M., Baloch, S., Rehman, J., Anwar, M., Hussain, I., Mehmood, T., 2012. Diversity and conservation of amphibians and reptiles in North Punjab, Pakistan. *Herpetol. Bull.* 122, 16–25.
- Reilly, S.M., Jorgensen, M.E., 2011. The evolution of jumping in frogs: morphological evidence for the basal anuran locomotor condition and the radiation of locomotor systems in crown group anurans. *J. Morphol.* 272, 149–168, <http://dx.doi.org/10.1002/jmor.10902>.
- Reynaga, C.M., Astley, H.C., Azizi, E., 2018. Morphological and kinematic specializations of walking frogs. *J. Exp. Zool. A: Ecol. Integr. Physiol.* 329, 87–98, <http://dx.doi.org/10.1002/jez.2182>.
- Robovska-Havelková, P., Aerts, P., Roček, Z., Přikryl, T., Fabre, A.-C., Herrel, A., 2014. Do all frogs swim alike? The effect of ecological specialization on swimming kinematics in frogs. *J. Exp. Biol.* 217, 3637–3644, <http://dx.doi.org/10.1242/jeb.109991>.
- Roček, Z., 2000. Mesozoic anurans. In: Heatwole, H., Carroll, R.L. (Eds.), *Amphibian Biology 4*. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp. 1295–1351.
- Roy, J.K., Dey, M., 2015. Studies on anuran diversity and threats to the herpetofauna on Assam University Campus, Northeast India. *Hamadryad* 37, 104–110.
- Sanchiz, B., 1998. Salientia. In: Wellnhofer, P. (Ed.), *Encyclopedia of Palaeoherpetology*. Verlag Dr. Friedrich Pfeil, Munich, pp. 1–275.
- Schmitz, L., Motani, R., 2011. Response to comment on 'Nocturnality in dinosaurs inferred from scleral ring and orbit morphology'. *Science* 334, 1641–1642, <http://dx.doi.org/10.1126/science.1208489>.
- Schoppe, S., Cervancia, M., 2009. Herpetological surveys along Paganan Range and Dumarán Island, Northern Palawan, Philippines. *Hamadryad* 34, 95–106.
- Seiffert, J., 1972. Ein Vorläufer der Froschfamilien Palaeobatrachidae und Ranidae im Grenzgebiet Jura-Kreide. *N. Jahrb. Mineral., Geol., Paläontol.* 1972, 120–131.
- Shubin, N.H., Jenkins, F.A., 1995. An Early Jurassic jumping frog. *Nature* 377, 49–52.
- Sinsch, U., Lümekemann, K., Rosar, K., Schwarz, C., Dehling, M., 2012. Acoustic niche partitioning in an anuran community inhabiting an Afromontane wetland (Butare, Rwanda). *Afr. Zool.* 47, 60–73, <http://dx.doi.org/10.1080/15627020.2012.11407524>.
- Soliz, M., Tulli, M.J., Abdala, V., 2017. Osteological postcranial traits in hylid anurans indicate a morphological continuum between swimming and jumping locomotor modes. *J. Morphol.* 278, 403–417, <http://dx.doi.org/10.1002/jmor.20651>.
- Stocker, M.R., Nesbitt, S.J., Kligman, B.T., Paluh, D.J., Marsh, A.D., Blackburn, D.C., Parker, W.G., 2019. The earliest equatorial record of frogs from the Late Triassic of Arizona. *Biol. Lett.* 15, 20180922, <http://dx.doi.org/10.1098/rsbl.2018.0922>.

- Taigen, T.L., Emerson, S.B., Pough, F.H., 1982. Ecological correlates of anuran exercise physiology. *Oecologia* 52, 49–56, <http://dx.doi.org/10.1007/BF00349011>.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92, <http://dx.doi.org/10.1046/j.0305-0270.2003.00994.x>.
- Trochet, A., Moulherat, S., Calvez, O., Stevens, V., Clobert, J., Schmeller, D., 2014. A database of life-history traits of European amphibians. *Biodivers. Data J.* 2, e4123, <http://dx.doi.org/10.3897/BDJ.2.e4123>.
- Tulli, M.J., Cruz, F.B., Kohlsdorf, T., Abdala, V., 2016. When a general morphology allows many habitat uses. *Integr. Zool.* 11, 473–489, <http://dx.doi.org/10.1111/1749-4877.12193>.
- Valério, L.M., Dorado-Rodrigues, T.F., Chupel, T.F., Penha, J., Strüssmann, C., 2016. Vegetation structure and hydroperiod affect anuran composition in a large neotropical wetland. *Herpetologica* 72, 181–188, <http://dx.doi.org/10.1655/Herpetologica-D-14-00069.1>.
- Vergnaud-Grazzini, C., Wenz, S., 1975. Les discoglossidés du Jurassique supérieur du Montsech (Province de Lérida, Espagne). *Ann. Paleontol. (Vertébrés)* 61, 19–36.
- Villalta, J.F.de., 1954. *Novedades paleomastológicas desde el último cursillo (1952)*. II Cursillo Internacional Paleontología, Museo de Sabadell, Sabadell, Spain.
- Wang, Y., Jones, M.E.H., Evans, S.E., 2007. A juvenile anuran from the Lower Cretaceous Jiufotang Formation, Liaoning, China. *Cretaceous Res.* 28, 235–244, <http://dx.doi.org/10.1016/j.cretres.2006.07.003>.
- Wells, K.D., 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago.
- Xing, L., Stanley, E.L., Bal, M., Blackburn, D.C., 2018. The earliest direct evidence of frogs in wet tropical forests from Cretaceous Burmese amber. *Sci. Rep.* 8, 8770, <http://dx.doi.org/10.1038/s41598-018-26848-w>.
- Zug, R.G., 1972. Anuran locomotion: structure and function. I. Preliminary observations on relation between jumping and osteometrics of appendicular and postaxial skeleton. *Copeia* 4, 613–624, <http://dx.doi.org/10.2307/1442720>.