

Frog limbs in deep time: is jumping locomotion at the roots of the anuran Bauplan?

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Article

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Non-technical Summary

The unique body plan of frogs has been largely conserved from at least 200 Myr, and its evolution from a more generalized tetrapod condition is still poorly understood, in part due to the scarce early fossil record of the group. The origin of the frog body plan has been classically explained as an adaptation to jumping, but recent studies incorporating new data in a phylogenetic context have challenged the popular jumping hypothesis. Here we revisit and test this hypothesis from a paleobiological perspective by integrating limb data from a wide range of extant and fossil frogs. We first explored the evolution of limb proportions from the Jurassic to the Paleogene to understand when the present limb diversity originated and whether, and to what extent, limb proportions have been conserved over the last 200 Myr. We then inferred the locomotor capabilities of extinct species, and from these inferences, we studied the frog locomotor diversity over geological time and reconstructed the ancestral state. The evolution of limb proportions is characterized by an early diversification that was underway in the Jurassic, followed by a repeated evolution of a limited range of limb morphologies that were already explored by the Early Cretaceous. In agreement with this early limb diversity, the Jurassic species were also locomotory diverse, and their inferred locomotor modes do not support the jumping hypothesis. We propose that the patterns found herein of repeated convergent evolution of both limb proportions and locomotor capabilities over geological time hamper any attempt to confidently infer the ancestral locomotion mode, and it therefore might be time to start focusing on other hypotheses on the origin of the frog body plan that are not related to locomotion.

Abstract

The unique body plan of frogs (Lissamphibia: Anura) has been largely conserved from at least 200 Myr, and its evolution from a more generalized tetrapod condition is still poorly understood, in part due to the scarce early fossil record of Salientia, the anuran total-group. The origin of the anuran Bauplan has been classically explained as an adaptation to jumping, but recent studies incorporating new data in a phylogenetic context have challenged the popular jumping hypothesis. Here we revisit and test this hypothesis from a paleobiological perspective by integrating limb data from a wide range of extant and fossil frogs. We first explored the evolution of limb proportions from the Jurassic to the Paleogene to understand when the present limb diversity originated and whether, and to what extent, limb proportions have been conserved over the last 200 Myr. We then inferred the locomotor capabilities of extinct species by phylogenetic flexible discriminant analysis, and from these inferences, we studied the locomotor diversity of frogs over geological time and reconstructed the ancestral state for frog-like salientians. The evolution of limb proportions is characterized by an early diversification that was underway in the Jurassic, followed by a repeated convergence over a limited area of the morphospace that was already explored by the Early Cretaceous. In agreement with this early limb diversity, the Jurassic stem species were also locomotory diverse, and their inferred locomotor modes do not support the jumping hypothesis. We propose that the patterns found herein of repeated convergent evolution of both limb proportions and locomotor capabilities over geological time hamper any attempt to confidently infer the ancestral locomotion mode and, it therefore might be time to start focusing on other hypotheses on the origin of the anuran Bauplan that are not related to locomotion.

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Introduction

Frogs (Lissamphibia: Anura) are taxonomically and ecologically very diverse: with about 7600 living species known to date (Frost 2022), anurans comprise the great majority of extant amphibians and are distributed around the world, with the exception of extreme latitudes and most oceanic islands (Duellman and Trueb 1994; Frost 2022). They live in terrestrial, fossorial, arboreal, and aquatic microhabitats and show a wide range of locomotor capabilities, including hopping, walking, burrowing, swimming, climbing, and long-distance jumping (Duellman and Trueb 1994; AmphibiaWeb 2022). Anurans are also remarkable in their anatomy: in spite of their ecomorphological diversity, they have a very conserved Bauplan encompassing a unique set of skeletal features. Regarding the postcranium, frogs are characterized by a short vertebral column with only six to nine presacral vertebrae, a urostyle as the only postsacral element, elongated ilia, fused zeugopodial elements (i.e., radius + ulna and tibia + fibula), and long hindlimbs with elongated proximal tarsals forming a new segment (Duellman and Trueb 1994; Handrigan and Wassersug 2007).

The origin of this bizarre Bauplan is one of the most intriguing evolutionary transitions in Tetrapoda, and the sparse early fossil record of Salientia (i.e., the total group that includes Anura) offers scant evidence on the matter. The earliest known salientians, the Early Triassic *Czatkobatrachus polonicus* (Evans and Borsuk-Białynicka 1998, 2009) and *Triadobatrachus massinoti* (Piveteau 1936; Rage and Roček 1989), show a combination of derived and plesiomorphic traits (Roček and Rage 2000; Evans and Borsuk-Białynicka 2009; Ascarrunz et al. 2016), which reveals that at least some of the distinctive skeletal features of anurans did not evolve in a concerted manner. A temporal and morphological gap follows these early records: the next oldest fossils that are complete enough to be informative are Jurassic and already present a full frog-like skeleton. These Jurassic taxa, namely the stem species *Prosalirus bitis* (Shubin and Jenkins 1995), *Vieraella herbsti* (Estes and Reig 1973; Báez and Basso 1996), and *Notobatrachus degiustoi* (Reig 1956; Báez and Basso 1996; Báez and Nicoli 2004) and the crown anuran *Rhadinosteus parvus* (Henrici 1998), document that the Bauplan originated at least 200 Myr ago and has remained highly conserved since then (Roček 2000; Handrigan and Wassersug 2007).

The evolution of the anuran Bauplan, in particular that of the morphofunctional complex formed by hindlimbs, ilia, sacrum, and urostyle (Emerson and De Jongh 1980; Jenkins and Shubin 1998; Prikryl et al. 2009; Reilly and Jorgensen 2011; Sigurdson et al. 2012; Jorgensen and Reilly 2013), has been classically explained as an adaptation to saltatory locomotion, either on land (Jenkins and Shubin 1998; Prikryl et al. 2009) or in riparian environments (Gans and Parsons 1966; Handrigan and Wassersug 2007; Essner et al. 2010). However, recent studies that incorporate new data in a phylogenetic context have challenged the popular jumping hypothesis. On one hand, Lires et al. (2016) have shown that, based on comparative postcranial anatomy and quantitative analyses of limb proportions, the Triassic species *Triadobatrachus* was probably not able to leap or jump, but it likely walked by bending the spine laterally and moving the limbs asynchronously like extant salamanders. This result implies that some of the main anuran postcranial characteristics, such as elongated ilia and the humeral anatomy, might have predated the origin of jumping (Lires et al. 2016; Jansen and Marjanović 2022). On the other hand, Reilly and Jorgensen

(2011) recovered the sacro-caudo-pelvic configuration that characterizes extant walker-hopper frogs (i.e., lateral-bender morphology), and not that of jumpers (i.e., sagittal-hinge morphology), as the plesiomorphic state and the general condition in anurans, including the stem species *Prosalirus* and *Notobatrachus*. Furthermore, Herrel et al. (2016) reconstructed the ancestral jump forces for Anura based on data from a range of extant taxa and concluded that early frogs were probably not good at jumping. However, in contrast to Reilly and Jorgensen (2011), these authors propose that the reconstructed ancestral traits are consistent with the phenotype observed in semiaquatic or aquatic frogs, suggesting a possible aquatic origin for the typical anuran postcranium. Taken together, the different lines of evidence point toward disparate evolutionary histories. Nevertheless, in spite of this complex scenario, the idea that the origin of the anuran Bauplan is related to jumping is still widely assumed in recent literature (e.g., Citadini et al. 2018; Reynaga et al. 2018; Senevirathne et al. 2020; Stepanova and Womack 2020).

To renew the debate from a paleobiological perspective, here we revisit and test the jumping hypothesis by studying the evolution of limb proportions in frog-like salientians (i.e., the clade formed by Anura + *Prosalirus* + *Vieraella* + *Notobatrachus*; Fig. 1) based on data from 411 extant and 48 fossil species ranging from the Jurassic to the Paleogene. Limb proportions are essential to better understand the ancestral locomotion mode of frogs because: (1) limb anatomy, including proportions, shows a close correlation with the different locomotor behaviors in extant species (e.g., Emerson 1978, 1988; Jorgensen and Reilly 2013; Enriquez-Urzelai et al. 2015; Lires et al. 2016; Citadini et al. 2018; Buttner et al. 2020); and (2) limb proportions can be easily measured in a range of fossil taxa, including the stem forms. In particular, we first explore the evolution of limb proportions over geological time to understand when the present limb diversity originated and whether and to what extent limb proportions have been conserved for the last 200 Myr. We then infer the locomotor capabilities of fossil species by phylogenetic flexible discriminant analysis (pFDA; Motani and Schmitz 2011; Angielczyk and Schmitz 2014), and from these inferences, we study the locomotor diversity of frogs over geological time and reconstruct the ancestral state for frog-like salientians. Finally, based on our results, we discuss the limitations of testing the jumping hypothesis on the origin of the anuran Bauplan and suggest further directions.

Materials and Methods

Taxonomic Sampling

The sampling included 826 adult specimens representing 48 extinct species ranging from the Early Jurassic to the Oligocene, and 411 extant species (Supplementary Table S1). The sample of extant taxa was designed to account for all major clades of frogs and the locomotor diversity within Anura. We included every fossil individual available to us on which the limb linear variables listed in “Measurements and Datasets” could be confidently measured. The stem-anuran *Prosalirus bitis* was also included in spite of the incompleteness of the known individuals because of its evolutionary and temporal relevance. In this case, we combined the measurements of two individuals, scaled proportionally according to the shared preserved elements. *Triadobatrachus* was excluded from the sample because it does not show the full set of autapomorphic traits classically associated

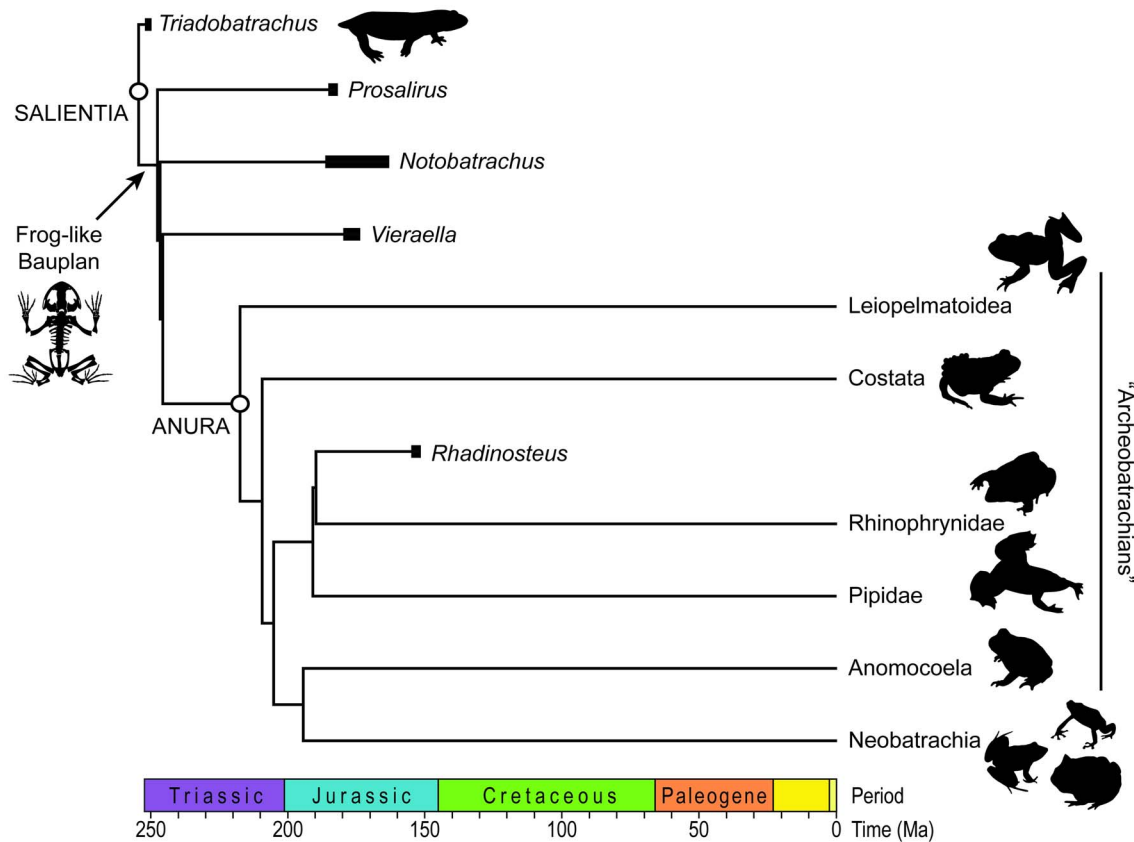


Figure 1. Time-adjusted phylogeny of Salientia showing relevant fossil taxa and major groups of anurans. Extended tips for extinct taxa depict uncertainty of the ages of fossils.

with the anuran Bauplan, and given that its limb proportions are very different from those of other salientians (see Lires *et al.* 2016), its inclusion would disproportionately impact the principal component analyses (PCAs), obscuring relevant patterns among other taxa. The locomotor behavior of *Triadobatrachus* was in fact previously analyzed by some of the authors of the present paper following an approach similar to the one used here, but including salamanders in the sample of extant taxa to deal with the more plesiomorphic morphology of the taxon (Lires *et al.* 2016).

Measurements and Datasets

We measured the length of the humerus, radioulna, femur, tibiofibula, and proximal tarsals and the maximum lengths of the metacarpal and metatarsal arches (Fig. 2), expanding the raw datasets of Lires *et al.* (2016) and Gómez and Lires (2019) in the number of taxa and limb variables. In line with these previous studies, measurements did not include the epiphyses and were taken from dry skeletons using a manual digital caliper, digital photographs with ScreenCaliper (v. 4.0; Iconico, New York), or 3D models with MeshLab (v. 2016.12; Cignoni *et al.* 2008). From these measurements, limb proportions were calculated relative to the total length of all fore- and hindlimb bones considered (i.e., the sum of the seven length variables; referred to hereafter as “total dataset”). To include *Prosalirus* and other fossil taxa in which the metapodial arches (i.e., metacarpals and metatarsals) cannot be measured, a reduced dataset was produced in which the proportions were calculated excluding these measurements. For those species represented by more than one individual, the

mean values were taken. We conducted the analyses on both the complete and reduced datasets, but we only report and discuss the results of the former, except when noted, because it is more informative. Both datasets and the results from the reduced dataset are available in the Supplementary Material.

Locomotor Modes

We classified extant species according to three main locomotor categories: jumpers (J), swimmers (Sw), and walker-hoppers (WH) (Supplementary Table S1). Given that the main goal of the locomotor study was to test whether the jumping mode is plesiomorphic for frog-like salientians (i.e., the salientian clade excluding *Triadobatrachus* and *Czatkobatrachus*), and following most previous approaches on frog ecomorphology (e.g., Emerson 1978; Jorgensen and Reilly 2013; Enriquez-Urzelai *et al.* 2015; Lires *et al.* 2016; Citadini *et al.* 2018), we typified each extant species as having a primary locomotor mode related to displacement behaviors, but we did not consider microhabitat or substrate preferences (i.e., aquatic/terrestrial/arboreal) or other behavioral patterns related to substrate use (e.g., burrowing or climbing; Toledo *et al.* 2012). Regarding climbing taxa, these have previously been regarded as arboreal walkers and/or jumpers by other authors (e.g., Emerson 1978; Jorgensen and Reilly 2013). We acknowledge that this is a gross categorization of anuran locomotion and that 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.*

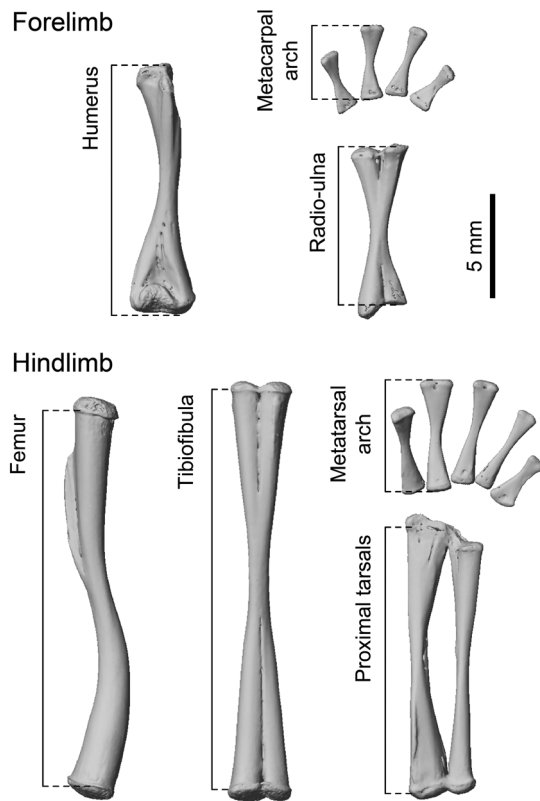


Figure 2. Linear measurements of forelimb and hindlimb bones.

2016). Locomotor modes of extant species were obtained from the literature (e.g., Emerson 1979; Jorgensen and Reilly 2013; Enriquez-Urzelai et al. 2015) or Web resources (e.g., AmphibiaWeb 2022) and are listed in Supplementary Table S1.

Phylogeny

A time-calibrated phylogeny was assembled using the topology of Pyron (2014) as a backbone tree and adding the fossil taxa and extant species not considered in that study by hand (tree files available in the Supplementary Material). The addition of taxa was made conservatively in agreement with complementary recent phylogenetic studies and expert taxonomic assignments (Báez 2013; Dong et al. 2013; Marjanović and Laurin 2014; Báez and Gómez 2016, 2019; Gómez 2016). We calculated the length of the branches leading to extinct taxa using the youngest possible age of fossils according to the numerical ages of Cohen et al. (2013, updated) and following previous approaches (i.e., Marjanović and Laurin 2008, 2014; Angielczyk and Schmitz 2014), assigning a minimum time interval (herein 1 Myr).

Morphospace of Limb Proportions

To summarize the diversity of limb morphology, we constructed morphospaces by PCAs on the correlation matrices of the two datasets (Fig. 3, Supplementary Fig. S1, Supplementary Table S2). From the resulting coordinates, plots were generated for distinct time periods (Fig. 4, Supplementary Figs. S2, S3) to visualize changes in this diversity over geological time. To better understand the evolution of limb proportions, we performed an

ancestral state reconstruction of PC 1, PC 2, and PC 3 using the function *fastAnc* of the R (v. 4.1.2; R. Core Team 2021) package *phytools* (v. 1.0.3; Revell 2012) and plotted the values corresponding to the last common ancestor of frog-like salientians on the PCA (Fig. 3, Supplementary Fig. S1). Additionally, phylogenetic morphospaces were built by superimposing the phylogenetic topology on the PCAs (Supplementary Figs. S4, S5) using the *phylogenetic morphospace* function in *phytools* (v. 1.0.3; Revell 2012).

Locomotor Modes in the Morphospace, Phylogenetic Multivariate Analysis of Variance (MANOVA), and pFDA

To test whether limb morphology is related to locomotor mode, we: (1) visually evaluated whether species with a shared locomotor mode group together in the morpho and phylogenetic morphospaces; and (2) performed phylogenetic MANOVAs and pairwise comparisons from each dataset using the functions *lm.rpp* and *pairwise* in the R package *RRPP* (v. 1.1.2; Collyer and Adams 2018, 2019; Supplementary Table S3).

In addition, to better illustrate the widespread convergence of limb morphologies related to locomotor modes observed in the morpho- and phylogenetic morphospaces, we plotted the locomotor modes of extant taxa on the tree and overlaid a continuous ancestral state reconstruction of PC 1 and PC 2 (Supplementary Figs. S6, S7) using the *contMap* function in the R package *phytools* (v. 1.0.3; Revell 2012).

We inferred locomotor modes for the 48 extinct salientian species by pFDA (Motani and Schmitz 2011; Angielczyk and Schmitz 2014) based on the limb data of the 411 extant taxa. pFDA is a statistical method that predicts a categorical variable from a set of continuous variables while accounting for the phylogenetic covariance of the data. In pFDA, as in standard discriminant analysis, classification rules are calculated by combinations of continuous variables that best discriminate among groups in a training dataset for which the categorical variables are known. These rules are then used to assign groups to those samples without a group membership by posterior probabilities (Angielczyk and Schmitz 2014). In this study, limb proportions are the continuous variables, locomotor modes are the categorical ones (i.e., groups), and the proportions of extant taxa are used as the training set to classify the fossil taxa.

We conducted pFDA on each dataset (Table 1, Supplementary Tables S4, S5) based on the R scripts of Motani and Schmitz (2011) available at <https://github.com/lSchmitz/phylo.fda>. Following Angielczyk and Schmitz (2014), we performed the pFDA on a branch-length transformed tree at the optimal Pagel's lambda (i.e., at which the correlation between limb morphology and locomotor mode is maximized) and a range of ± 0.2 of that value. We used the proportion of each locomotor mode in the training set (i.e., extant taxa) as prior probabilities (Supplementary Table S6). The performance of the resulting classification rules was estimated as the proportion of correct classifications obtained when applying these rules to the training set (i.e., cross-validation; Table 2, Supplementary Tables S8, S9).

Ancestral Locomotor Mode Reconstruction

We estimated the ancestral locomotor mode of the frog-like salientians from the known modes of extant anurans and those inferred for extinct species by pFDA under optimal lambda. Locomotor modes inferred from the complete dataset were preferred, when available, over those inferred using the reduced

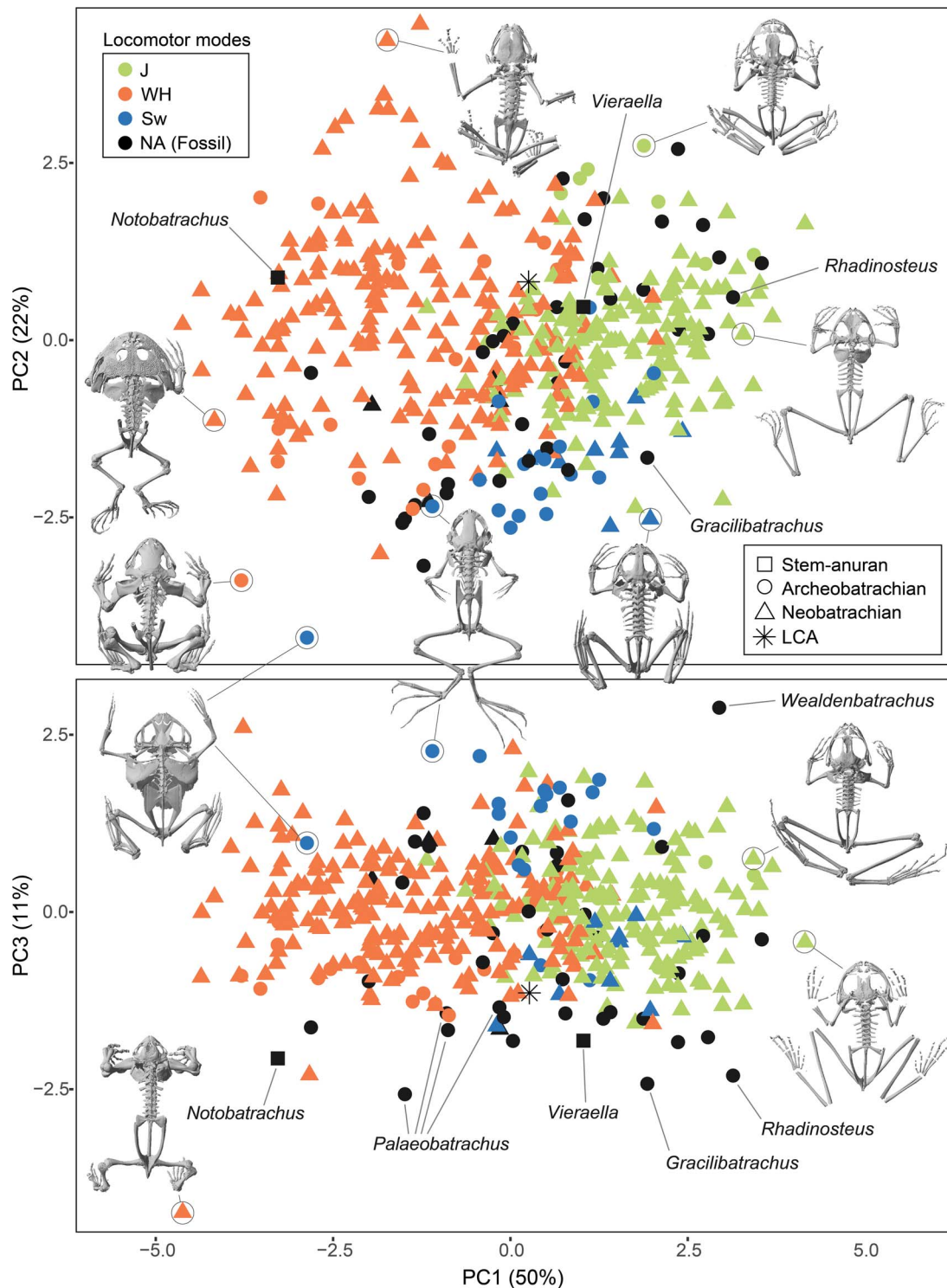


Figure 3. Morphospace of limb proportions constructed from the species averages of the full set of variables (shown in Fig. 2). Abbreviations: J, jumping; LCA, last common ancestor of frog-like salientians; NA, locomotor mode unknown, used for fossil taxa and LCA; Sw, swimming; WH, walking-hopping.

one. Only classifications with a probability higher than 0.8 were taken into account. The ancestral reconstruction was made by maximum likelihood (Fig. 5, Supplementary Fig. S6) and parsimony (Fig. 5, Supplementary Fig. S9) using the R packages *ape* (v. 5.6.1; Paradis and Schliep 2019) and *phangorn* (v. 2.8.1; Schliep 2011), respectively.

Results

Morphospace

The first axis of variation in limb proportions (i.e., PC 1; 50% of the total variance; Supplementary Table S2) is related to the relative length of fore versus hindlimbs; PC 2 (22%; Supplementary

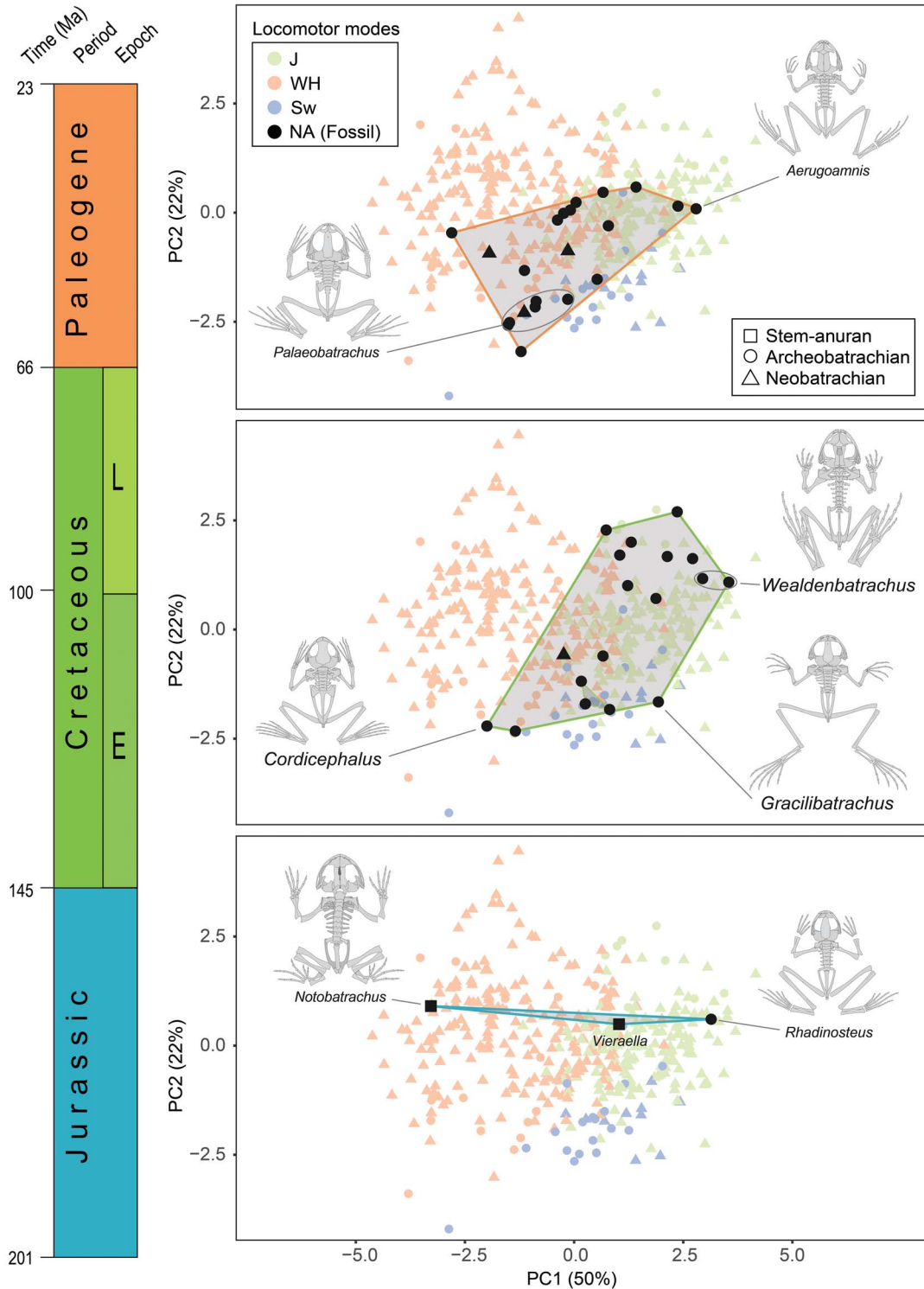


Figure 4. Detail of morphospace occupation over geological time. Extant taxa in the background for reference and fossil species of each Period in black. Abbreviations: J, jumping; NA, locomotor mode unknown, used for fossil taxa; Sw, swimming; WH, walking-hopping.

Table S2) is instead linked to the autopod (i.e., the mesopodium [wrist and ankle] plus digits): species with negative values are characterized by short proximal tarsals and long metatarsals and metacarpals (Fig. 3, Supplementary Table S2). PC 3 (11%; Supplementary Table S2) is mainly composed of hindlimb

variables: negative values correspond to long femora and short proximal tarsals and metatarsals (Fig. 3).

The different regions of the morphospace have been repeatedly explored by distantly related clades. This pattern of convergence is clearly observed not only in the phylomorphospace

Table 1. Classification of fossil species by phylogenetic flexible discriminant analysis (pFDA) using the total dataset and the optimal lambda value, except *Prosalirus*, for which the reduced data set was used. Abbreviations: J, jumping; LM, locomotor mode; Sw, swimming; WH, walking-hopping.

	LM	p_J	p_{Sw}	p_{WH}
<i>Prosalirus</i>	Sw	0.007	0.903	0.091
<i>Notobatrachus</i>	WH	0	0.001	0.999
<i>Vieraella</i>	Sw	0.365	0.541	0.093
<i>Rhadinosteus</i>	J	0.939	0.04	0.021

(Supplementary Fig. S4) and the ancestral reconstruction of PC 1 and PC 2 on the phylogeny (Supplementary Figs. S6, S7), but also in the broad overlap between “archeobatrachians” and neobatrachians (Fig. 3). Fossil species are within the range of the extant ones, with some exceptions over PC 3 (see “Discussion”; Fig. 3). The inferred PC values of the last common ancestor of frog-like salientians also fall within the range of extant frogs (Fig. 3).

Locomotor Modes: Relationship with Limb Morphology, Inference in Fossils, and Ancestral State Reconstruction

Jumpers, swimmers, and walker-hoppers occupy distinctive regions of the morphospace, but also overlap to different degrees (Fig. 3). Walker-hoppers and jumpers differ in the relative length of their fore- and hindlimbs (i.e., over PC 1): walker-hoppers have forelimbs that are similar in length to or even longer than hindlimbs, whereas hindlimbs are characteristically much longer than forelimbs in jumpers. Swimmers tend to have intermediate

Table 2. Classification of extant species by phylogenetic flexible discriminant analysis (pFDA) using the total dataset and the optimal lambda value. A, Raw number of species. B, Diagonal: percentage of species with the locomotor mode (LM) of the column correctly classified as such; off-diagonal: percentage of species with the LM of the column misclassified under the LM of the row. C, Diagonal: percentage of species classified under the LM of the row that actually have this LM; off-diagonal: percentage of species misclassified under the LM of the row that actually have the LM of the column. Abbreviations: J, jumping; Sw, swimming; WH, walking-hopping.

A	True LM		
Predicted LM	J	Sw	WH
J	145	7	19
Sw	3	17	9
WH	13	4	188
B	True LM		
Predicted LM	J	Sw	WH
J	90.06	25.00	8.80
Sw	1.86	60.71	4.17
WH	8.07	14.29	87.04
C	True LM		
Predicted LM	J	Sw	WH
J	84.80	4.09	11.11
Sw	10.34	58.62	31.03
WH	6.34	1.95	91.71

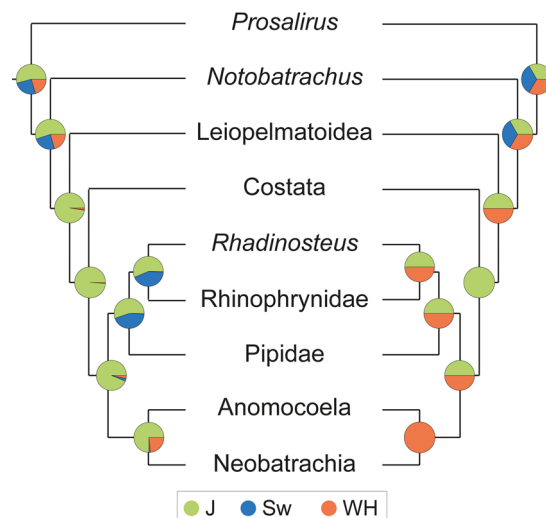


Figure 5. Locomotor modes of selected nodes reconstructed from the full set of limb variables (shown in Fig. 2) using maximum likelihood (left) and maximum parsimony (right). Abbreviations: J, jumping; Sw, swimming; WH, walking-hopping.

limbs with respect to walker-hoppers and jumpers, overlapping greatly with both groups over PC 1, although less so over PC 2 due to the characteristically longer metapodia of pipids and paradoxical frogs (Turazzini and Gómez 2023), which are highly aquatic clades well represented in the sample (Fig. 3). The overlap of swimmers is particularly extensive with jumpers, to the point that Sw and J modes are the only pair that are not recovered as significantly different in the pairwise analyses (Supplementary Table S3). In agreement with these results, only 60.7% of swimmers are classified as such in our training sample (i.e., extant taxa), and conversely, only 58.6% of taxa classified as Sw do actually belong to that locomotor mode (Table 2). In contrast, the cross-validation success is high for walker-hoppers and jumpers: they are correctly classified as such in 90% and 87% of the cases, respectively; 91.7% and 84.8% of taxa classified as WH and J do belong to these groups (Table 2).

All limb variables have similar loadings in the discriminant functions obtained by pFDA (Supplementary Table S7); within this limited range, the largest loadings are those of metacarpal length in one function and metatarsal length in the other. The relevance of metapodia in distinguishing groups is also reflected in the generally higher misclassification rate of the reduced dataset, in which metapodial variables are excluded. In particular, the exclusion of the metapodia greatly reduces the probability of correctly distinguishing swimmers and jumpers (Supplementary Table S9).

The use of different lambda values does not significantly change the cross-validation success (Table 2, Supplementary Table S8) and impacts the classification of three of the 42 fossil species of the total dataset, including the stem-salientian *Vieraella herbsti*, which is alternatively recovered as Sw under the optimal lambda, but as J under optimal -0.02 (Table 1, Supplementary Table S4). The complete classification results of fossils by pFDA are presented in Supplementary Tables S4 and S5.

Regarding the ancestral locomotor capacities of frog-like salientians, none of the three modes is retrieved unambiguously as the most parsimonious ancestral state. In contrast, jumping is obtained as the most probable ancestral mode when using the maximum-likelihood approach ($p_J = 0.54$; $p_{Sw} = 0.25$; $p_{WH} =$

0.20). The inferences retrieved for the entire tree are available in Supplementary Figures S6–S9.

Discussion

Evolution of Limb Proportions

Whereas the Triassic *Triadobatrachus* has limbs with intermediate proportions between anurans and salamanders (Lires et al. 2016), our data show that from the Jurassic on, limbs of fossil salientians are within the range documented in extant frogs (Fig. 3). Only over PC 3 do some fossil taxa lie slightly outside the range of living anurans, with relatively long femora and short proximal tarsals and metatarsals that partially resemble the ancestral condition (i.e., inferred from salamanders and *Triadobatrachus*). The group of species located in this peripheral position over PC 3 includes the Jurassic *Notobatrachus degiustoi* and *Vieraella herbsti*, the only stem salientians (Fig. 1) for which the full set of variables can be measured. This position in the morphospace indicates that their proportions might represent an intermediate grade between the ancestral configurations and modern anuran proportions. However, because the salientian Jurassic record is still very sparse and the available data indicate that homoplasy is widespread in the group, the possibility that they evolved from salientian forms with shorter femora and longer proximal tarsals not yet represented in the fossil record cannot be completely ruled out. In this regard, similar proportions have evolved convergently in pipimorphs and pelobatids ranging from the Jurassic to the Oligocene, which indicates that proportional long femora and short proximal tarsals and metatarsals are, at least in these latter cases, a derived state.

Limb proportions were already diversified by the Jurassic, pointing toward an earlier origin of the salientian Bauplan. This evidence is consistent with recent calibrated molecular phylogenies that recover the origin of Anura in the Late Triassic (Feng et al. 2017; Hime et al. 2021) and with the presence of *ilia* that might be closely related to the crown-group in the Late Triassic Chinle Formation (Stocker et al. 2019).

According to our sample of Jurassic taxa (i.e., stem-anurans and the xenonuran *Rhadinosteus parvus*; Supplementary Table S1), the documented early limb diversification was mainly related to variation in the relative lengths between fore- and hindlimbs (i.e., PC 1; Fig. 4). By the Early Cretaceous, limb proportions were further diversified in relation to the autopod (i.e., PC 2 and PC 3; Fig. 4, Supplementary Fig. S2), linked to a phylogenetically more diverse fossil record encompassing a number of pipimorphs, a clade with characteristically long metapodia (Trueb 1996; Wuttke and Poschmann 2010; Gómez 2016).

It is worth noting that the fossil diversity shown in this study predominantly encompasses “archeobatrachians” (Fig. 4; Supplementary Table S1), whereas neobatrachians are poorly represented in the sample due to their scant record of articulated specimens with well-preserved limbs. Molecular time estimates (e.g., Pyron 2014) and the anurofauna from the Aptian Crato Formation of Brazil (Báez et al. 2009) show that the neobatrachian diversification was well underway during the Early Cretaceous (e.g., Pyron 2014; Feng et al. 2017; Jetz and Pyron 2018; Hime et al. 2021). Hence, it is expected that at least from the Early Cretaceous on, limb diversity was probably greater than what we have documented in our fossil sample. This bias is particularly accentuated after the Cretaceous/Paleogene boundary, the time when the species-rich Hyloidea, Microhylidae, and Natatanura,

the three Neobatrachian clades comprising about 88% of extant anurans, underwent a rapid diversification (Feng et al. 2017; Jetz and Pyron 2018; Hime et al. 2021).

Two main patterns are observed in extant anurans. First, even though the real past diversity is underrepresented and our sample of extant taxa is much larger and phylogenetically more diverse than the fossil one, the region of the morphospace occupied by extant species is largely restricted to that of fossils. Second, the different regions of the morphospace have been repeatedly explored by non-closely related species (Fig. 3, Supplementary Figs. S4, S6, S7). Consequently, when the distribution of taxa in the limb morphospace is analyzed over geological time, the general pattern that emerges is that after an early morphological diversification that was already underway in the Jurassic, the evolution of limbs is marked by repeated convergence over a range of proportions that had already been largely explored by the Early Cretaceous (Fig. 4). These findings are in line with those of Moen et al. (2016), who found that the evolution of the general body form in anurans is also characterized by a remarkable degree of morphological conservation, alongside widespread convergence (related to microhabitat), even among phylogenetically distant clades that diverged as far back as 150 Ma. Numerous previous works on biomechanics (e.g., Herrel et al. 2016) and macroevolutionary anatomical patterns in anurans (e.g., Citadini et al. 2018; Buttner et al. 2020; Stepanova and Womack 2020; Petrović et al. 2021) have shown that locomotion, together with microhabitat, has been a major driver of diversification and convergence in anuran limb evolution. Our results agree with these previous findings: (1) taxa are distributed in the limb morphospace according to their locomotor modes (Fig. 3), at least partially; and (2) cross-validation errors from pFDA are rather small (Table 2).

The question of why only a subset of the theoretically possible limb proportions has actually evolved in the last 200 Myr of evolution of salientians might be addressed from at least two complementary perspectives. On the one hand, given that adaptive pressures related to locomotor modes seem to be a key driver in the evolution of limb proportions, limb configurations associated with low locomotor efficiency in the available ecological space might have been negatively selected in a consistent manner over the evolution of Salientia. Likewise, other selective pressures on limbs might act on other biological aspects, such as feeding (e.g., prey manipulation; Gray et al. 1997) or mating (e.g., amplexus; Duellman 1992). On the other hand, intrinsic developmental processes might have constrained limb evolution. The evolution of the unique anuran Bauplan involved profound changes in development, among which the most evident are the evolution of the tadpole and a drastic metamorphosis (Duellman and Trueb 1994). The fact that the entire anuran skeleton has been remarkably conserved in spite of the ecological diversity of the group suggests that these radical developmental changes might have imposed tight constraints on the skeletal system as a whole, including the limbs. In this regard, the rampant convergence at deep temporal scales observed in both body form (Moen et al. 2016) and limb proportions could be attributed to the limited ways available to respond to selection due to such constraints, which are inherent to the clade (Wake 1991; Moen et al. 2016). Other constraints underlying the conservation and convergence of the appendicular morphology might be related to plesiomorphic developmental processes in limb patterning. Specifically, recent studies have shown that the macroevolutionary diversity of limb proportions in amniotes is also limited to certain areas of the morphospace and that this distribution can be predicted

by interactions between activating and inhibitory signals that would modulate the proximo-distal limb patterning sequence in tetrapods (Young 2013; Young *et al.* 2015). Preliminary studies by C.M.P.-B. suggest that the macroevolutionary patterns of limb proportions in anurans also agree with the predictions of the developmental model tested in amniotes. Interestingly, the proximo-distal sequence in which limb elements develop might have not only biased limb proportions toward certain directions but might have also impacted the rates of limb evolution in frogs (Stepanova and Womack 2020). A hypothesis originally delineated for mammals proposes that later-developing bones are subjected to reduced developmental constraints, which might confer them more freedom to evolve in response to selection pressures (Weisbecker 2011; Martín-Serra *et al.* 2015; Stepanova and Womack 2020). In agreement with this hypothesis, it has been shown that the distal limb elements (*i.e.*, later-developing bones) of frogs show higher evolutionary rates compared with the more proximal ones (Stepanova and Womack 2020).

Locomotor Modes over Geological Time

The results of the pFDA and the distribution of species in the morphospace show that limb proportions represent valuable evidence to discuss locomotor modes in extinct salientians. Even though locomotor groups partially overlap in the morphospace (Fig. 3) and differences in proportions between jumpers and swimmers are not statistically significant (Supplementary Table S3), the cross-validation error rates obtained for the training sample (*i.e.*, extant anurans) in the pFDA are rather small, even between swimmers and jumpers (Table 2, Supplementary Table S8). Swimming is the most challenging locomotor mode when trying to infer locomotion from limb morphology, because swimmers have intermediate proportions between walker-hoppers and jumpers. In contrast, walker-hoppers and jumpers with more extreme limb configurations tend to be correctly classified. Importantly, the inference of locomotor modes from limb proportions is applicable to the fossil taxa sampled herein because they are largely within the range documented in extant anurans. Moreover, there is no evidence that the functional relationship between limb morphology and locomotor behavior was different in fossils with respect to living species, because the postcranial skeleton of extinct taxa is very similar to that of living anurans.

The three locomotor modes might have already been present in the Jurassic. *Notobatrachus* is recovered in an area of the morphospace PC 1–PC 2 only shared with walker-hopper extant anurans, far from the overlap zone with the Sw and J modes (Fig. 3). This is in turn reflected in a high pFDA posterior probability (*i.e.*, $p_{WH} = 0.999$; Table 1). Furthermore, Reilly and Jorgensen (2011), in their comprehensive study on the pelvic system morphology, have shown that the ilio-sacral configuration of *Notobatrachus* is consistent with walking-hopping locomotion. In contrast, the classification of *Prosalirus* and *Vieraella* as swimmers is not as well supported. Importantly, *Prosalirus* lacks preserved metatarsi, which are a main feature in the morphological diversification of swimmers (*i.e.*, over PC 2 of the full set of variables; Fig. 3, Supplementary Table S2). Furthermore, in contrast to our results, *Prosalirus* was interpreted as a jumper in its original description (Shubin and Jenkins 1995; Jenkins and Shubin 1998) and was later recovered as a walker-hopper according to its ilio-sacral morphology (Reilly and Jorgensen 2011). *Vieraella* is recovered as Sw with a rather low posterior probability ($p_{Sw} = 0.54$), which is consistent with its intermediate position over

PC 1 and PC 2 (Fig. 3). In addition, it presents the leiopelmatoid-like type of sacral diapophyses (Báez and Basso 1996) that Reilly and Jorgensen (2011) linked to walker-hoppers, although this species was not considered in their study. The xenouuran *Rhadinosteus*, the only crown-anuran sampled for the Jurassic, is classified as J ($p_J = 0.94$; Table 1). Its postcranial anatomy has not been previously described in relation to jumping, but it has been noted that it lacks the burrowing and swimming specializations typical of extant xenouurans (*i.e.*, *Rhinophrynus* and pipids, respectively; Henrici 1998). Regarding the pelvic morphology, the ilium resembles that of *Prosalirus* (R.O.G., personal observation), but the poor preservation of the sacrum makes it difficult to classify the species in the terms of Reilly and Jorgensen (2011).

The presence of both jumpers and swimmers is more certain in the Early Cretaceous. In particular, *Wealdenbatrachus*, classified herein as a jumper with a high posterior probability ($p_J = 0.98$; Supplementary Table S4) consistent with the results of Gómez and Lires (2019), has previously been proposed to be an efficient long-distance jumper based not only on its long hindlimbs, but also on its iliac anatomy (Báez and Gómez 2019). Likewise, some early Cretaceous taxa were almost undoubtedly swimmers: pipimorphs such as *Cratopipa* and *Cordicephalus* are classified as swimmers ($p_{Sw} = 0.96$ and 0.84 , respectively; Supplementary Table S4) and present postcranial features of extant pipids that have been classically linked to their aquatic lifestyle (*e.g.*, robust hindlimbs, proportionally long fingers in hands and feet, expanded sacral diapophyses; Cannatella and Trueb 1988; Trueb 1996; Báez *et al.* 2012; Cannatella 2015; Gómez and Pérez-Ben 2019; Turazzini and Gómez 2023).

In summary, the Mesozoic phylogenetic and morphological diversification of salientians correlates with the evolution of locomotor diversity during this period. During the Jurassic, even though the distinction between swimmers and jumpers is not clear, both walker-hopper (*i.e.*, *Notobatrachus*) and non-walker-hopper modes might have already been present. It is very likely that swimming and jumping behaviors had already evolved by the Early Cretaceous linked to the limb diversification toward other dimensions of the morphospace documented for that time (*i.e.*, PC 2).

Evolution of the Salientian Bauplan in Relation to Jumping Locomotion

In recent years, the classical view that the anuran Bauplan evolved in relation to jumping has been challenged by novel evidence and a renewed discussion of the issue from an updated phylogenetic perspective (see “Introduction”). In line with these studies, our findings cast further doubts on the jumping hypothesis, because: (1) none of the stem-salientians are recovered as a jumper specialist; (2) the last common ancestor of all frog-like salientians is recovered in an area of the morphospace where the locomotor modes overlap (Fig. 3); and (3) accordingly, jumping is not unequivocally inferred as the ancestral state for this clade (Fig. 5). More importantly, independent of the specific locomotor abilities inferred herein, the patterns observed in the morphospace together with the phylogenetic distribution of locomotor modes in extant taxa (Supplementary Figs. S6–S9) reveal fundamental shortcomings in testing this hypothesis not only from limb proportions, but probably from any other evidence.

The most evident hurdle is obtaining confident inferences of locomotor modes in fossil taxa, even under the (reasonable) assumption that the correlation between skeletal morphology and function observed in living anurans can be extrapolated to

forms that diverged 200 Ma. When such inferences are made from limb proportions, the main problems, as discussed earlier, are that locomotor modes overlap to some extent in the limb morphospace and that the resulting classifications are not necessarily consistent with evidence from other parts of the skeleton (e.g., the pelvic system morphology). However, it remains possible that other new or still underexplored approaches, such as bone micro-anatomy, may provide more reliable insights into the locomotor modes of fossil frogs in the future.

The second, and in our view the most important, issue is to what extent the morphology and locomotion of both fossil and living forms are useful to reconstruct the ancestral locomotor mode of frog-like salientians and, in turn, to test whether jumping is a synapomorphy of this clade. On the one hand, the distribution of species in the (phylo)morphospace (Fig. 3, Supplementary Figs. S4, S6–S7), where closely related species can occupy very different regions (e.g., the myobatrachids *Myobatrachus gouldii* and *Crinia georgiana* with a PC 1 values of -4.6 and 2.5 , respectively), and the large disparity already documented in the Jurassic (Fig. 4) reveal that limb proportions are highly evolvable and have been so since the early days of salientians. Consequently, it is not clear whether the limbs of the oldest and early divergent taxa with the full Bauplan are actually representative of the plesiomorphic state of frog-like salientians, as discussed above for *Notobatrachus* and *Vieraella*.

On the other hand, independent of the evolutionary pace of the different skeletal structures and the correlation between osteology and locomotor behavior used to make inferences in fossils, the phylogenetic distribution of locomotor modes among extant taxa (Fig. 3, Supplementary Figs. S4, S6–S9) reveals that this trait is also highly evolvable: the evolution of locomotor modes is signed by repeated convergence, with multiple transitions from WH and J to any of the other modes, even among closely related taxa (e.g., within the genus *Ranoidea*). Therefore, even if new early stem forms with a clear jumping morphology were discovered, and jumping was thus reconstructed as the ancestral state, the high evolvability of locomotor modes would still hamper any conclusion regarding the origin of the Bauplan in relation to jumping. Likewise, hypothetical new “intermediate” fossils (i.e., without the full set of anuran features, like *Triadobatrachus*) would also be uninformative due to the limitations of inferring a behavior as specialized as anuran jumping from anatomical configurations that are not represented in the modern taxa.

In contrast to these impediments and uncertainties, it is clear that salientians evolved from forms with undulatory locomotion (either temnospondyls [e.g., Anderson 2008; Kligman et al. 2023] or lepospondyls [e.g., Marjanović and Laurin 2019]) and that, based on *Triadobatrachus*, at least some of the unique features of the anuran Bauplan are likely to have evolved before the origin of jumping (Lires et al. 2016). In addition, it is a fact that living anurans are functionally and ecologically very diverse in spite of their conserved anatomy and that within this diversity, jumping locomotion, although widespread, is not the rule (Fig. 3, Supplementary Fig. S8). Furthermore, species can show not one but a repertoire of locomotory movements, such as arboreal frogs that climb and jump (Reilly and Jorgensen 2011) or some hylids and ranids, which are good jumpers and swimmers (Nauwelaerts et al. 2007; Soliz et al. 2017). In this context, after weighing this evidence and the limitations of inferring the ancestral locomotor mode, we wonder how fruitful it is to keep discussing the origin of the anuran Bauplan in relation to jumping. After all, anurans are not only unique in their adult morphology, but

also, and maybe more profoundly, in their development (e.g., Handrigan and Wassersug 2007), which is marked by a biphasic life cycle with a free-living tadpole and a complex metamorphosis. Tadpoles are under very different selective pressures than post-metamorphic individuals (Roelants et al. 2011), and it has even been suggested that the bizarre adult morphology of frogs is the default “by-product” of evolutionary processes that acted on the larval stage during the early evolution of the clade (Altig 2006). In spite of this, it is still poorly understood to what extent adult anatomy is the result of constraints imposed by metamorphosis and the tadpole stage. Taking this into account, we think that a shift of focus from a functional to a developmental perspective would renew the debate on the origin of the Bauplan and might shed new light on the matter.

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