

FROG ORIGINS: INFERENCES BASED ON ANCESTRAL RECONSTRUCTIONS OF LOCOMOTOR PERFORMANCE AND ANATOMY

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Herrel, A., Moureaux, C., Laurin, M., Daghfous, G., Crandell, K., Tolley, K. A., Measey, G. J., Vanhooydonck, B., Boistel, R. (2016): Frog origins: inferences based on ancestral reconstructions of locomotor performance and anatomy. – Fossil Imprint, 72(1-2): 108–116, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Frogs are the most species-rich and ecologically diverse group of amphibians and are characterized by a unique body plan including long legs, elongated ilia, and fused caudal vertebrae. Stem anurans such as *Triadobatrachus* or *Czatkobatrachus* have been suggested to have used jumping or hopping as part of their locomotor repertoire based on their anatomy. The earliest known true frog, *Prosalirus bitis* was suggested to have been a proficient jumper. However, data on jumping performance in frogs have never been used to attempt reconstruction of ancestral features at the base of the radiation. Here we provide data on jumping performance (forces and acceleration) in 20 species of extant frogs including representatives of most of the early radiating clades. We next use ancestral character value inferences to assess ancestral features. Our analyses suggest that frog ancestors were of small to medium size, had relatively short limbs, produced rather low jump forces, yet were capable of relatively high acceleration. Given the short limbs and low forces, the unique frog bauplan with a reduced vertebral column and a mobile ilio-sacral joint may not have been an adaptation for powerful jumping.

Key words: Anura, locomotion, forces, anatomy, jumping

Received: December 6, 2015 | Accepted: April 8, 2016 | Issued: August 15, 2016

Introduction

Frogs are characterized by a unique bauplan that sets them apart from other amphibians. Unique features of anurans include elongated hind limbs, an elongation of the iliac shaft, a transformation of the caudal skeleton into a rod-like urostyle, and the development of a mobile sacro-iliac joint (Emerson 1979, Jenkins and Shubin 1998). The ecological context driving the evolution of this unique morphology has been debated and aquatic, riparian, and terrestrial origins have all been suggested (Gans and Parsons 1966, Lutz and Rome 1994). Modern frogs show a diversity of locomotor modes despite their specialized anatomy,

including hoppers, jumpers, swimmers, burrowers, and arboreal walkers (Emerson 1978, Wells 2007). Moreover, morphological convergence has been observed in species with similar ecologies (Moen et al. 2013) suggesting that anatomy reflects the locomotor environment of these animals. Additionally, differences in jumping performance have been demonstrated in frogs with different ecologies (Zug 1978).

Stem anurans such as *Triadobatrachus* KUHN, 1962 or *Czatkobatrachus* EVANS et BORSUK-BIALYNICKA, 1998 have been suggested to have used jumping or hopping as part of their locomotor repertoire based on their forelimb anatomy,

which shares several features with anatomically modern frogs (Sigurdson et al. 2012). Based on the anatomy of the frog-like deltoid attachment of the scapula, Sigurdson and co-authors suggested that these frogs used their forelimbs to absorb landing forces. The lack of use of forelimbs during landing observed in primitive frogs such as *Ascaphus* STEJNEGER, 1899 or *Leiopelma* FITZINGER, 1861 (Essner et al. 2010) was consequently interpreted as a derived feature of this group. The Early Jurassic *Prosalirus bitis* SHUBIN et JENKINS, 1995 has also been suggested to have been a proficient jumper based on the anatomy of its pelvic girdle (Shubin and Jenkins 1995, Jenkins and Shubin 1998). These authors proposed an important role of the sacro-iliac articulation in allowing frogs to transmit forces from the appendicular to the axial system, thus helping create a powerful jump. A review of the pelvic and thigh musculature in frogs (Přikryl et al. 2009) suggested that terrestrial jumping may have been the primitive mode of locomotion from which other locomotor modes were subsequently derived. Moreover, they argued in favor of the importance played by the ilio-sacral articulation and associated musculature in the development of a jumping locomotor mode.

However, based on the fact that during development the muscles associated with the modified sacro-iliac joint mature after frogs have already assumed their typical locomotor mode, Fabrezi and co-authors (2014) argued that these modifications are not needed for jumping per se. Additionally, Reilly and Jorgensen (2011), based on a re-analysis of pelvic morphology across a broad sample of frogs, suggested that the lateral bender, walker/hopper morphology of the pelvic girdle is basal for frogs and that long distance jumping must be considered as a derived feature which evolved convergently in different frog lineages (see also Jorgensen and Reilly 2013, Reilly et al. 2015, 2016). Here we use measurements of jumping performance in extant frogs to reconstruct jumping performance at the base of the anuran tree, specifically focusing on jumping forces and acceleration as these are the traits most likely under selection (Emerson 1978). To do so we measured jump forces in 20 species of frogs with an emphasis on basal clades as these are especially insightful in reconstructing ancestral states (see also Robovska-Havelkova et al. 2014).

Materials and methods

Animals

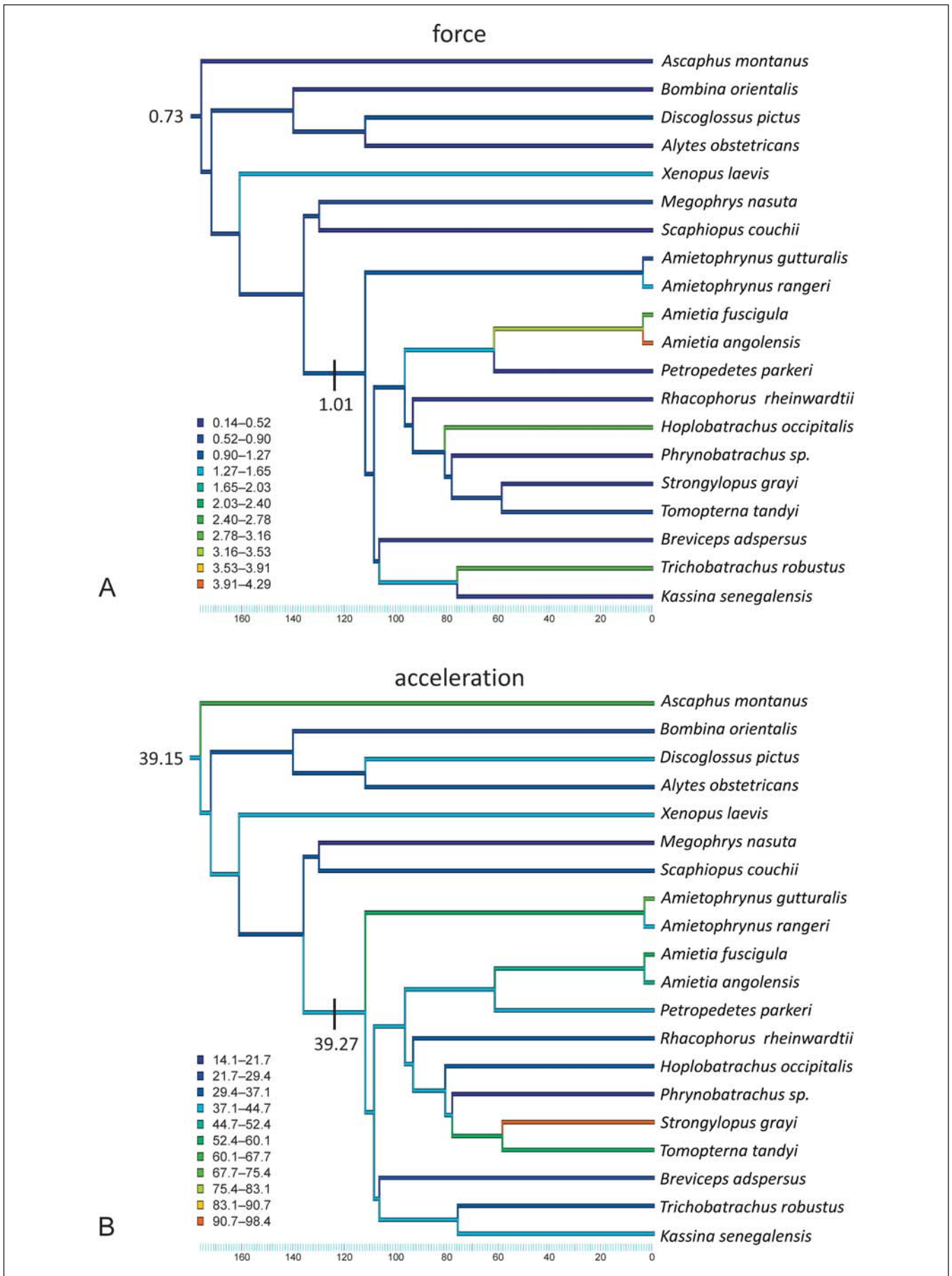
Jumping performance was measured in 104 individuals from 20 species of extant frogs (Table 1) at the lab in Paris or in the field. Between one and 32 individuals per species were tested. Animals captured in the field were induced to jump, measured, and released at the exact site of capture within 24 hours. In addition to measuring jump forces, every individual was measured using digital calipers (Mitutoyo, Kawasaki, Kanagawa, Japan; ± 0.01 mm). The following body dimensions were quantified: body length as the straight-line distance from the posterior margin of the cloaca to the tip of the snout; the length of the femur, the tibia, the foot, and the longest toe (see Herrel et al. 2012).

Phylogenetic framework

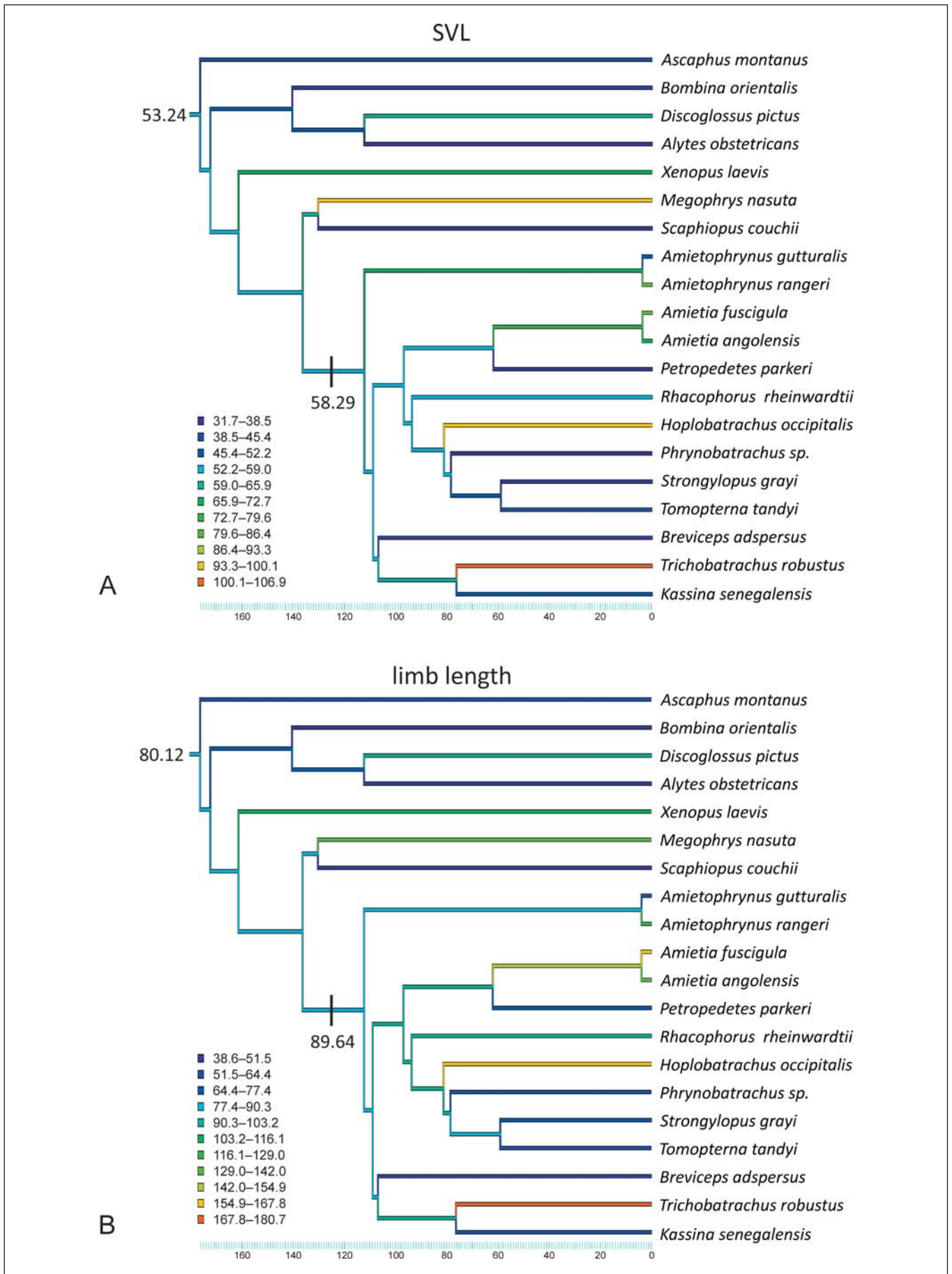
For comparative analysis, a timetree was compiled from the literature. The topology and branch lengths reflect mostly Bossuyt and Roelants (2009), although information from the fossil record was also used (e.g. Marjanović and Laurin 2014). The absolute age of fossils was estimated using a recent geological timescale (Gradstein et al. 2012). The branch immediately under a fossil is assumed to occupy at least a whole geological age (most of which lasted between 2 and 12 Ma), which accounts for the uncertainty regarding their true age, and (partly) for the fact that a clade is necessarily somewhat older than its oldest known fossil record. Lissamphibian phylogenies more recent than Bossuyt and Roelants (2009) have been published, notably the tip dating study by Pyron (2011), but these typically have fewer anuran terminal taxa. Alternatively, we could have used only those with estimated node ages, which unfortunately would eliminate other recent studies from consideration (e.g., Frost et al. 2006, Pyron and Wiens 2013). However, these more recent studies are generally congruent with Bossuyt and Roelants (2009). We placed minimal time constraints into the tree based on the age of the oldest fossil belonging to each clade and molecular ages (Laurin et al. 2009). In the latter case, we used the lower (most recent) boundary of the 95% confidence interval (CI) of the node ages as minimal constraint (Laurin et al. 2009). This calibration scheme, along with use of the Stratigraphic Tools (<http://mesquiteproject.org/packages/stratigraphicTools/> developed by Josse et al. in 2006) for Mesquite (<https://mesquiteproject.wikispaces.com/> developed by Maddison and Maddison), can be used to stretch the branch lengths (within certain limits) over the whole tree in an objective (standardized) manner that allows branch lengths to reflect evolutionary time. To do this, the minimal terminal and/or internal branch lengths can be increased using the Stratigraphic Tools. This can be useful when the phylogenetic independent contrasts are not standardized adequately over the initial tree. The terminals representing time constraints were pruned after standardization had been achieved, prior to character optimization.

Force plate recordings

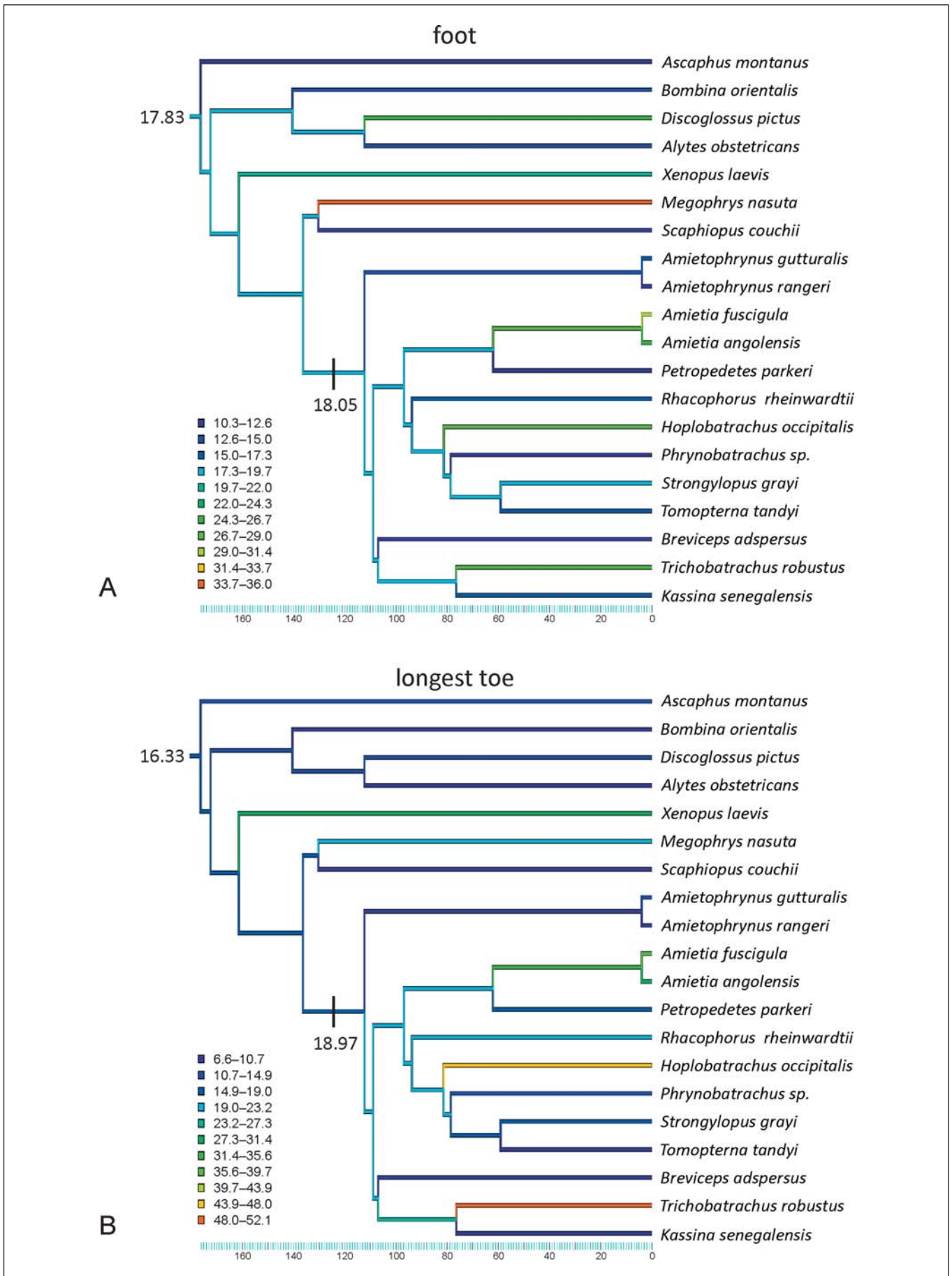
Maximal jump forces for all species except *Ascaphus* were measured using a piezo-electric force platform (Kistler Squirrel force plate; ± 0.1 N) as described previously (Herrel et al. 2014). The force platform was connected to a charge amplifier (Kistler Charge Amplifier type 9865) and forces were recorded at 500 Hz using Bioware software (Kistler). Forces for *Ascaphus* were recorded at the flight lab of the University of Montana, Missoula using a Bertec Corporation (Columbus, Ohio) Force plate (model 3190121-060104138) and signals were recorded using 'Chart' and exported to Excel. Frogs were placed individually on the force plate, allowed to rest for a few seconds and then induced to jump by us unexpectedly clapping our hands behind the frog. This elicited escape responses from the individuals. Frogs were caught and placed back on the force plate as many times as possible during the 60 second recording time. Three jump sessions of 60 seconds that typically involved three to five jumps were recorded for each individual totaling between nine and over twenty jumps. Although jump forces are



Text-fig. 1. Ancestral character value reconstruction for A) the peak resultant force during jumping, and B) the peak jumping acceleration. Branch lengths are proportional to time and the reconstructed values (numbers next to arrows) are indicated at the base of the Anura and at the base of the Neobatrachia (vertical line). Red colors indicate high trait values and blue colors lower trait values.



Text-fig. 2. Ancestral character value reconstruction for A) body length, and B) limb length. Branch lengths are proportional to time and the reconstructed values (numbers next to arrows) are indicated at the base of the Anura and at the base of the Neobatrachia (vertical line). Red colors indicate high trait values and blue colors lower trait values.



Text-fig. 4. Ancestral character value reconstruction for A) foot length, and B) the length of the longest toe. Branch lengths are proportional to time and the reconstructed values (numbers next to arrows) are indicated at the base of the Anura and at the base of the Neobatrachia (vertical line). Red colors indicate high trait values and blue colors lower trait values.

repeatable across trials (see also Herrel et al. 2014), only the single most forceful jump data was used for further analyses as we were interested in maximal jumping performance. Forces in X, Y and Z-directions were extracted using the Kistler Bioware software and the total resultant force (i.e. the vector sum of the X, Y and Z forces) was calculated for each individual after body mass was subtracted from the Z-force. This force was then divided by body mass to calculate the peak acceleration during jumping. We focus here on forces and acceleration as these best reflection a frog's ability to get away from a predator (i.e. its acceleration) and are thus the most likely traits under selection in frogs (Emerson 1978).

Ancestral character state reconstruction

We calculated species means for forces, body length, hind limb length, and hind limb segment lengths. Next, we used Mesquite (V. 3; <https://mesquiteproject.wikispaces.com/> developed by Maddison and Maddison) to calculate ancestral character states using squared change parsimony with the dated phylogeny described above.

Results

Our ancestral character state reconstructions suggest that the ancestor of Anura was relatively small (ca. 53 mm snout-vent length), had relatively short legs, which produced rather low jump forces but relatively higher acceleration (Text-figs 1, 2). The short legs in the ancestor are mostly due to short femur, tibia and longest toe (Text-figs 3, 4). Neobatrachian frogs are characterized by significantly higher jump forces, longer hind limbs and slightly lower acceleration, possibly due to their larger body size and the scaling of force relative to mass (Text-figs 1, 2). Our ancestral character state reconstructions further suggest at least three independent origins of species that evolved high jump forces and accelerations (Text-fig. 1). Large body size evolved independently at least three times among the species in our data set and is not confined to the Neobatrachia (Text-fig. 2A). Long limbs, however, evolved mostly within the Neobatrachia with at least three independent groups showing long limbs (Text-fig. 2B). These long limbs are due to evolution in the length of different segments in different groups with some showing long femora, yet other long tibiae, or toes (Text-figs 3, 4). Interestingly, the *Megophrys nasuta* (SCHLEGEL, 1858) evolved long feet in addition to a relatively long tibia and femur but has short toes and relatively poor jumping performance (Table 1).

Discussion

As in any other study, our interpretation of the ancestral character state is limited by taxon sampling. The greater the extant diversity is sampled, the better the inferences on ancestral nodes will be. Given that we sampled only 20 out of the 4000 plus species of frogs our analysis is clearly limited. However, despite the apparent paucity of taxa in our study, our sampling does include representatives of nearly all early radiating lineages rather than the three to four taxa included in some other papers (Reilly et al. 2015, 2016).

These taxa are especially important in inferring ancestral nodes and as such our estimates are likely to be more robust than what would be assumed based on the limited sampling. Moreover, our ancestral character state reconstructions correspond reasonably well to what is known about the anatomy of fossil taxa. For example the earliest known anuran, the Jurassic *Prosalirus bitis*, had a femur and tibiofibula length of around 16 mm, only somewhat shorter than the estimated 22–23 mm in our analyses. Similarly, *Prosalirus* SHUBIN et JENKINS, 1995 had a body length between 45 and 50 mm, which is again somewhat shorter than our estimates (Shubin and Jenkins 1995, Jenkins and Shubin 1998). The earliest stem anuran *Triadobatrachus* was larger (about 10 cm SVL) but had markedly short femora (about 19 mm; Rage and Roček 1989, Roček and Rage 2000). The slightly later stem anuran *Czatkobatrachus* was smaller (about 5 cm) but no hind limb elements are so far known (Evans and Borsuk-Bialynicka 1998, Roček and Rage 2000). However, the exquisitely preserved Jurassic *Notobatrachus degiustoi* REIG, 1956 (Baez and Nicoli 2004, 2008) was much larger than *Prosalirus* and *Czatkobatrachus* suggesting that the basal-most anurans may have rapidly evolved larger body sizes. Overall, the available fossil data suggest a relative decrease in body size but increase in relative limb length from *Triadobatrachus* to more crown-ward stem-anurans like *Prosalirus* (see Evans and Borsuk-Bialynicka 1998) followed by a subsequent evolution of taxa with larger body size, such as *Notobatrachus* REIG, 1956.

Our results show that the ancestral condition for frogs may correspond to a small-bodied animal with relatively short legs, low jumping forces, but possibly reasonably high accelerations. Note, however, that our estimates of forces and accelerations are based on the reconstructions of both traits independently. In reality, forces and accelerations are tightly linked and the accelerations vary principally depending on the forces exerted relative to the animal's body mass. Extant leiopelmatid frogs show an alternate leg swimming pattern (Abourachid and Green 1999, but see Nauwelaerts and Aerts 2002) and do not use their forelimbs for dissipating landing forces (Essner et al. 2010, Reilly et al. 2015, 2016). This combination of features suggests that frog-like jumping may have evolved in a semi-aquatic riparian habitat where this behavior could have been used to escape towards the water, and where controlled landing was of less importance (Gans and Parsons 1965, Essner et al. 2010). Semi-aquatic locomotor modes have been inferred for early discoglossids with a more specialized jumping life-style being assigned to early neobatrachians only (Venczel and Szentesi 2012). This corroborates the idea that long distance terrestrial jumping is essentially a derived trait (Reilly and Jorgensen 2011). Field observations of jumping in leiopelmatids show that they jump only occasionally (Reilly et al., 2015) suggesting that early frogs may indeed not have been good jumpers. This is supported by our analyses suggesting that basal frogs had relatively short limbs and produced only low jump forces. Within the Neobatrachia REIG, 1958, however, the evolution of high jumping forces appears to have gone hand in hand with the evolution of long limbs with several independent evolutionary events leading up to high-performance jumping.

This then prompts the question as to whether early anurans such as *Prosalirus* were indeed proficient jumpers as has been previously suggested (Shubin and Jenkins 1995,

Table 1: Maximum resultant jump forces and limb dimensions for species used in the analysis.

	N	maximum resultant force (N)	acceleration (ms ⁻²)	body length (mm)	limb length (mm)	femur (mm)	tibia (mm)	foot (mm)	longest toe (mm)
<i>Alytes obstetricans</i> (LAURENTI, 1768)	5	0.143 ± 0.06	33.34 ± 8.87	32.01 ± 5.42	44.14 ± 7.55	11.57 ± 1.56	12.86 ± 2.18	13.13 ± 2.17	6.58 ± 1.78
<i>Amietia angolensis</i> (BOCAGE, 1866)	3	3.910 ± 1.19	47.74 ± 13.78	85.52 ± 11.75	153.30 ± 19.50	43.32 ± 6.37	44.55 ± 6.45	24.65 ± 2.83	40.78 ± 4.30
<i>Amietia fuscigula</i> (DUMÉRIL et BIBRON, 1841)	2	2.801 ± 0.73	54.39 ± 19.17	74.33 ± 10.85	144.21 ± 19.07	37.90 ± 3.55	44.69 ± 3.79	28.06 ± 4.37	33.56 ± 7.36
<i>Amietophrynus gutturalis</i> (POWER, 1927)	3	0.799 ± 0.36	69.58 ± 9.67	47.84 ± 7.07	63.86 ± 8.13	16.38 ± 2.41	18.40 ± 2.02	18.92 ± 3.12	10.16 ± 1.94
<i>Amietophrynus rangeri</i> (HEWITT, 1935)	2	1.341 ± 1.81	41.68 ± 0.91	83.48 ± 2.42	116.52 ± 6.63	31.54 ± 1.29	34.00 ± 2.10	29.75 ± 2.19	21.23 ± 1.05
<i>Ascaphus montanus</i> (MITTLEMAN et MYERS, 1949)	5	0.399 ± 0.07	63.07 ± 11.64	39.55 ± 4.73	63.87 ± 6.95	17.79 ± 2.69	19.98 ± 1.40	11.69 ± 1.30	14.40 ± 1.93
<i>Bombina orientalis</i> (BOULENGER, 1890)	7	0.148 ± 0.04	23.77 ± 6.77	37.94 ± 3.05	48.17 ± 4.56	12.66 ± 1.43	13.66 ± 2.03	14.70 ± 1.64	7.15 ± 1.19
<i>Breviceps adpersus</i> (PETERS, 1882)	3	0.279 ± 0.13	26.48 ± 2.89	36.77 ± 5.08	38.60 ± 7.69	11.54 ± 2.43	9.03 ± 2.58	11.41 ± 2.55	6.63 ± 0.13
<i>Discoglossus pictus</i> (OTTH, 1837)	7	1.084 ± 0.69	39.15 ± 7.85	59.57 ± 16.22	95.13 ± 24.05	23.36 ± 6.12	31.11 ± 7.98	26.22 ± 6.70	14.44 ± 3.79
<i>Hoplobatrachus occipitalis</i> (GÜNTHER, 1858)	9	2.840 ± 1.01	32.94 ± 3.61	98.30 ± 11.29	165.15 ± 18.41	45.20 ± 6.07	45.08 ± 5.13	27.74 ± 3.63	47.12 ± 4.24
<i>Kassina senegalensis</i> (DUMÉRIL et BIBRON, 1841)	1	0.284	40.50	45.82	53.08	14.46	15.25	15.04	8.33
<i>Megophrys nasuta</i> (SCHLEGEL, 1858)	3	0.667 ± 0.14	17.25 ± 4.95	98.03 ± 6.55	134.21 ± 14.51	39.51 ± 3.82	37.86 ± 4.49	33.70 ± 4.02	23.14 ± 2.43
<i>Petropedetes parkeri</i> (AMIET, 1983)	7	0.202 ± 0.08	43.58 ± 8.76	37.19 ± 3.42	68.31 ± 4.27	18.68 ± 0.92	21.94 ± 1.37	12.03 ± 0.72	15.66 ± 2.48
<i>Phrynobatrachus</i> sp.	1	0.188	14.06	31.67	61.25	16.65	19.55	10.31	14.74
<i>Rhacophorus reinwardtii</i> (SCHLEGEL, 1840)	2	0.395 ± 0.21	32.39 ± 8.67	53.95 ± 7.15	98.255 ± 9.19	28.92 ± 1.89	29.31 ± 2.77	16.94 ± 3.02	23.10 ± 1.51
<i>Scaphiopus couchii</i> (BAIRD, 1854)	4	0.175 ± 0.08	29.57 ± 5.68	34.51 ± 3.77	43.83 ± 4.15	12.31 ± 1.49	12.33 ± 1.41	11.26 ± 1.26	7.93 ± 1.17
<i>Strongylopus grayii</i> (SMITH, 1849)	1	0.353	90.72	37.19	77.14	20.51	23.58	17.74	15.31
<i>Tomopterna tandyi</i> (CHANNING et BOGART, 1996)	6	0.544 ± 0.12	57.61 ± 17.13	43.08 ± 5.44	57.65 ± 8.10	16.51 ± 1.65	16.46 ± 2.49	16.55 ± 2.44	8.14 ± 1.82
<i>Trichobatrachus robustus</i> (BOULENGER, 1900)	1	3.130	29.50	100.1	167.8	41.60	50.00	28.20	48.00
<i>Xenopus laevis</i> (DAUDIN, 1802)	32	1.423 ± 0.32	39.96 ± 9.21	71.8 ± 9.19	114.13 ± 9.54	30.90 ± 3.84	31.71 ± 3.32	21.31 ± 1.96	30.22 ± 3.22

Table entries are means ± standard deviations. N = number of individuals.

Jenkins and Shubin 1998). Even stem anurans like *Triadobatrachus* have been suggested to be jumpers or hoppers based on their forelimb anatomy (Sigurdson et al. 2012). However, our data suggest that the earliest frogs most likely did not excel in jumping and showed relatively low jump forces. Accelerations reconstructed at the base of the anuran tree are somewhat higher, however. This suggests that other locomotor behaviors such as swimming, often associated with lower forces than jumping (Nauwelaerts and Aerts 2003), may provide alternative possible locomotor contexts for the origin of the unique derived frog bauplan. The absence of the use of the forelimbs for braking during landing in the semi-aquatic and basal leioepelmatids supports this idea. From an aquatic origin the step to a riparian habitat where the same behavior would be equally useful in escaping from predators would be relatively small. This may then have set the stage

for the evolution of specialized terrestrial long-distance jumping.

In summary, our results show that the anuran ancestor was of small size and a mediocre jumper with somewhat higher acceleration, and medium-length legs. These traits correspond to a phenotype typically associated with semi-aquatic or aquatic frogs and suggest a possible aquatic origin for the typical frog bauplan, in contrast to what is often suggested. It is clear, however, that specialized high-power jumping did not originate before the origin of the Neobatrachia. Moreover, it is likely that this behavior originated independently several times. More extensive sampling across the anuran tree is needed to improve our ancestral character state estimates, but we hope that the data set presented here will provide the impetus for future researchers to do so.

Acknowledgements

Financial support was provided by ANR MOBIGEN to AH (ANR-09-PEXT-003) and a MNHN ATM grant from the 'Biodiversité actuelle et fossile' program to AH.

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