JOURNAL OF Evolutionary Biology .ᴀᴄᴇꜱᴇʜ **WILEY**

Two-hundred million years of anuran body-size evolution in relation to geography, ecology and life history

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Abstract

Surprisingly, little is known about body-size evolution within the most diverse amphibian order, anurans (frogs and toads), despite known effects of body size on the physiological, ecological and life-history traits of animals more generally. Here, we examined anuran body-size evolution among 2,434 species with over 200 million years of shared evolutionary history. We found clade-specific evolutionary shifts to new body-size optima along with numerous independent transitions to gigantic and miniature body sizes, despite the upper limits of anuran body size remaining quite consistent throughout the fossil record. We found a weak, positive correlation between a species' body size and maximum latitude and elevation, including a dearth of small species at higher elevations and broader latitudinal and elevational ranges in larger anurans. Although we found modest differences in mean anuran body size among microhabitats, there was extensive overlap in the range of body sizes across microhabitats. Finally, we found that larger anurans are more likely to consume vertebrate prey than smaller anurans are and that species with a free-swimming larval phase during development are larger on average than those in which development into a froglet occurs within the egg. Overall, anuran body size does not conform to geographic and ecological patterns observed in other tetrapods but is perhaps more notable for variation in body size within geographic regions, ecologies and life histories. Here, we document this variation and propose target clades for detailed studies aimed at disentangling how and why variation in body size was generated and is maintained in anurans.

KEYWORDS
Bergmann's rule, development, diet, gigantic, microhabitat, miniature

1 | INTRODUCTION

Body size varies widely among organisms and is deeply entwined with a species' physiology (Reichle, 1968; Savage et al., 2007; White, Phillips, & Seymour, 2006; Zeuthen, 1953), ecology (Wilson, 1975; LaBarbera, 1986; Peters & Peters, 1986; Woodward et al., 2005; Ebenman and Persson 2012; Zinger et al., 2019) and life history (Peters & Peters, 1986; Ebenman and Persson 2012). Tetrapods

have a particularly wide range in body size, prompting numerous hypotheses regarding tetrapod body-size evolution in relation to phylogenetic history (Alroy, 1998; Cooper & Purvis, 2010; Harmon et al., 2010; Landis & Schraiber, 2017), geography (Ashton, 2004; Lomolino, 2005), habitat (Farlow & Planka, 2002; Gearty, McClain, & Payne, 2018; Harrington, De Haan, Shapiro, & Ruane, 2018; Meiri, 2008) and diet (Clauss, Steuer, Müller, Codron, & Hummel, 2013; Costa, Vitt, Pianka, Mesquita, & Colli, 2008; Moen

& Wiens, 2009). As the most diverse amphibian order, anurans (frogs and toads) are particularly suited for testing the relationship between body size and abiotic or biotic factors because they are globally distributed (AmphibiaWeb 2017), have convergently radiated into a variety of microhabitats (Moen, Morlon, & Wiens, 2016; Moen & Wiens, 2017), and have repeatedly evolved distinct life histories (Gomez-Mestre, Pyron, & Wiens, 2012; Meegaskumbura et al., 2015; Portik & Blackburn, 2016). However, most studies focused on anuran body-size evolution only examine tens (Adams & Church, 2008; Ashton, 2002; de Queiroz & Ashton, 2004) or hundreds (Harmon et al., 2010; Lindsey, 1966; Olalla-Tárraga & Rodríguez, 2007) of the ~ 7,000 recognized anuran species (but see Amado, Bidau, & Olalla-Tárraga, 2019). Consequently, we still have a limited understanding of how anuran body size evolves at a macro-evolutionary scale.

Phylogenetic-based hypotheses aim to explain the non-random distribution of body sizes across the tetrapod tree of life, evidenced by clade-specific evolutionary shifts towards new body-size optima (Arévalo, Amador, Almeida, & Giannini, 2018; Harmon et al., 2010; Turner & Nesbitt, 2013). Despite a highly conserved body plan, Anura contains the smallest known tetrapods (<10 mm SVL) as well as relatively large anurans, such as the Helmeted Water Toad *Calyptocephallela gayi*, which can reach 320 mm (AmphibiaWeb 2017). Previous studies investigating miniaturization in anurans have focused on particular lineages and thus use different criteria to identify miniature body size (16 mm—Scherz et al., 2019; 20 mm—Clarke, 1996; 25 mm—Yeh, 2002), while gigantism in anurans has not yet been formally defined. Miniature and gigantic anuran body sizes may emerge intermittently across the phylogeny or they may coincide with clade-specific changes in body-size optima in response to abiotic or biotic factors. Consequently, mapping body size across the anuran phylogeny offers the opportunity to contextualize miniature and gigantic species within the broader evolutionary history and apparent upper and lower limits of anuran body size.

Temperature is one of the most frequently studied abiotic factors in relation to tetrapod body-size evolution. The positive relationship between body size and both latitude and elevation (Bergmann's rule; Bergmann, 1847) is often explained by selection for decreased heat loss via larger surface-area-to-volume ratios at cooler temperatures (Bergmann, 1847). In ectotherms, heat conservation is debated as a selection pressure (Adams & Church, 2008; Partridge & Coyne, 1997; Pincheira-Donoso, Hodgson, & Tregenza, 2008; de Queiroz & Ashton, 2004); however, body size is positively correlated with latitude or elevation in a number of tetrapod ectotherm lineages, including anurans (Table 1), and both evolutionary and developmental plasticity may underlie these relationships. For instance, decreased water or prey availability at higher latitudes may select for larger anuran body sizes (Olalla-Tarraga et al. 2009; Amado et al., 2019; Valenzuela-Sánchez, Cunningham, & Soto-Azat, 2015) because larger bodied anurans desiccate more slowly (e.g. *Scaphiopus couchii*—Newman & Dunham, 1994) and have lower metabolic rates (White et al., 2006). Additionally, developmental plasticity may also contribute to larger body sizes at higher latitude

and elevation because lower temperatures can delay development in ectotherms, leading to increased size at maturity (Angilletta, Steury, & Sears, 2004; Licht, 1975; Ray, 1960) and larger adult body sizes (Pettus & Angleton, 1967). In anurans, previous studies focusing on a subset of total diversity have found mixed support for the relationship between body size and latitude or elevation (Table 1). The most taxonomically comprehensive study to date found a relationship between median body size and potential evapotranspiration in thousands of species (2,761 species); however, their study was geographically restricted to the Americas and does not report the relationship between interspecific body size and latitude (Amado et al., 2019). Thus, characterizing macroevolutionary patterns of anuran body size in relation to latitude and elevation at a global scale is an important first step towards examining these hypotheses.

Ecological factors, including habitat preferences and diet, can also be associated with macroevolutionary patterns of tetrapod body size. For example, body sizes are smaller in volant birds and mammals compared to flightless birds and mammals (Glanz & Montgomery, 1978; Livezey & Humphrey, 1986; Maurer et al., 2004). Additionally, aquatic species have larger body sizes than non-aquatic species in mammals (Gearty et al., 2018), lizards (Meiri, 2008) and crocodiles (Godoy, Benson, Bronzati, & Butler, 2019) and arboreality is associated with longer body sizes in snakes (Harrington et al., 2018). Convergent evolution to occupy particular microhabitats (e.g. aquatic, fossorial, arboreal, etc.) is rampant across the anuran tree of life (Moen et al., 2016; Moen & Wiens, 2017), and these shifts in microhabitat may exert selection pressures on anuran body size. Likewise, diet may also be associated with variation in anuran body size because anurans do not chew their prey and are thus gape limited. Anuran jaw size is positively correlated with body size (Toft, 1980); consequently, larger anurans may be able to exploit prey items that are not available to smaller anurans, thereby resulting in a larger dietary breadth. Alternatively, larger anurans may be more selective in prey and optimize foraging to larger, more nutrient-rich prey items (e.g. *Scaphiopus couchii* – Newman, 1999), a pattern that has also been observed in lizards (Costa et al., 2008) and several vertebrate marine predators (Costa, 2009). A number of studies have found support for a positive correlation between interspecific anuran body size and prey size (Almeria & Nuñeza, 2013; Duellman, 2005; Moen & Wiens, 2009; Newman, 1999; Toft, 1980, 1981; Werner, Wellborn, & McPeek, 1995) as well as interspecific body size and prey type (Ahlm, 2015; Almeria & Nuñeza, 2013; Duré & Kehr, 2001; Lima & Magnusson, 1998; Moen & Wiens, 2009; Simon & Toft, 1991; Werner et al., 1995; Wu, Li, Wang, & Adams, 2005); however, these studies are often limited to particular clades, geographic locations or ecological groups, and thus, the relationship between body size and prey type is uncharacterized at the scale analysed here.

In contrast to most tetrapod groups, development may exceptionally influence anuran body size at deep phylogenetic scales. Across the amphibian tree of life, anurans have transitioned numerous times from the ancestral condition of having a distinct larval stage during development to the more derived condition 'direct development', in which development into a froglet occurs within the

TABLE 1 Studies evaluating Bergmann's rule in extant tetrapod ectotherms

Support for Bergmann's?	Inter- or Intraspecific?	Clade	No of species	Geographic areas	Study
Yes	Inter	Anurans, urodeles, and snakes	657, 189, 1,222	Worldwide	Lindsey (1966)
	Intra	*Pseudacris triseriata* (boreal chorus frog)	1	Northern Colorado, US	Pettus & Angleton (1967)
	Intra	*Rana sylvatica* (wood frog)	1	Virginia, US	Berven (1982)
	Intra	Anurans and salamanders	16,18	Not specified	Ashton (2002)
	Intra	Turtles	23	Not specified	Ashton & Feldman (2003)
	Intra	Amphibians and turtles	34, 23	Not specified	de Queiroz & Ashton (2004)
	Intra	*Limnodynastes peronii* and *L. tasmaniensis*	2	South Australia	Schäuble (2004)
	Inter	*Liolaemus* lizards	34	South America	Cruz, Fitzgerald, Espinoza, & Schulte Ii (2005)
	Intra	*Schistometopum thomense*	1	São Tomé Island	Measey & Van Dongen (2006)
	Inter/ assemblage-based	anurans	112	Europe and North America	Olalla-Tárraga and Rodríguez (2007)
	Inter/ assemblage-based	anurans	131	Brazilian Cerrado	Olalla-Tárraga et al. (2009)
	Inter/ assemblage-based	*Plethodon* salamanders	44	eastern North America	Olalla-Tárraga et al. (2010)
	Intra	*Bufo andrewsi* (Asiatic toad)	1	western China	Liao & Lu (2012)
	Intra	*Rhinoderma darwinii* (Darwin's frog)	1	Chile	Valenzuela-Sánchez et al. (2015)
	Inter/ assemblage-based	Anurans	2,761	The Americas	Amado et al. (2019)
No	Inter	Lizards and turtles	935, 154	worldwide	Lindsey (1966)
	Intra	Squamates	83	Not specified	Ashton & Feldman (2003)
	Intra	Squamates	83	Not specified	de Queiroz & Ashton (2004)
	Intra	*Rana temporaria* (common frog)	1	Scandinavia	Laugen, Laurila, Jönsson, Söderman, & Merilä (2005)
	Inter/ assemblage-based	Urodeles	153	Europe and North America	Olalla-Tárraga and Rodríguez (2007)
	Inter	*Liolaemus* lizards	26	South America	Pincheira-Donoso et al. (2008)
	Intra and inter	Amphibians	59	United States	Adams & Church (2008)

egg (Gomez-Mestre et al. 2012; Meegaskumbura et al., 2015; Portik & Blackburn, 2016). An upper limit on egg size may limit hatchling and adult body sizes of direct developing species; however, the relationship between direct development and body size is unclear. Blackburn (2008) described a relationship between the evolution of direct development and small body sizes in the ancestor of the genus *Arthroleptis*. Likewise, Zimkus, Lawson, Loader, and Hanken (2012) found a weak correlation but no statistically significant relationship between the evolution of small body size and direct development in Phrynobatrachidae. The largest comparative study of reproductive mode to date (470 species) found that terrestrial-egg-laying species (including both larval and direct developers) were on average smaller than aquatic-egg-laying species (Gomez-Mestre et al., 2012); however, direct developers and larval developers that laid terrestrial eggs did not differ significantly in body size (although direct

developers were smaller on average; Gomez-Mestre et al., 2012). Furthermore, little is known about the relationship between body size and viviparity in anurans, likely due to the limited number of viviparous anuran species. Given the current evidence and limited sampling from previous studies, the relationship between direct development and smaller adult body size in anurans remains uncertain.

Here, we characterize body-size evolution among 2,434 anuran species (35% of extant taxa) across an estimated 200 million years of anuran history (Feng et al., 2017) to test hypotheses of body-size evolution in a phylogenetic framework. We first characterize macroevolutionary patterns in anuran body size by fitting Bayesian models of adaptive evolution to detect significant evolutionary shifts in body size across the anuran tree of life. We also use our distribution of anuran body sizes to examine where the miniature and gigantic anurans are distributed within the anuran phylogeny. We then examine the

body size of extinct anuran taxa in relation to extant taxa to reveal any changes in body size that might have occurred during different eras. Finally, we use phylogenetic comparative methods to quantify the relationships between body-size evolution and latitude, elevation, microhabitat, diet and development mode across the anuran tree of life.

2 | METHODS AND MATERIALS

2.1 | Data collection

We used snout–vent length as our proxy for body size. We collected maximum male, female and overall snout–vent length (regardless of sex) for 2,434 species from the AmphiBIO database (Oliveira, São-Pedro, Santos-Barrera, Penone, & Costa, 2017), secondary references (Allen, Street, & Capellini, 2017; Gingras, Boeckle, Herbst, & Fitch, 2013; Halliday, 2016; Harper et al., 2010; Liao, Zeng, Zhou, & Jehle, 2013; De Lisle & Rowe, 2015; Moen & Wiens, 2009; Nali, Zamudio, Haddad, & Prado, 2014; Wollenberg, Vieites, Glaw, & Vences, 2011; Zamudio, Bell, Nali, Haddad, & Prado, 2016; AmphibiaWeb 2017), as well as a few primary literature sources (Correa et al., 2013; Moen et al., 2016; Moen & Wiens, 2009; Nöllert & Nöllert, 1992). We used latitude and elevation data from Rolland et al. (2018). Fossil data were gathered from Sanchiz (1998), Tietje and Rödel (2018), and Blackburn, Keeffe, Vallejo-Pareja, and Vélez-Juarbe (2020). We collected development mode records (whether a species completes metamorphosis within an egg (direct development), has a free-swimming larval phase (larval development), or completes metamorphosis within the body of the parent (viviparous development)) from secondary references (Lannoo, 2005; Gomez-Mestre et al., 2012; AmphibiaWeb 2017; IUCN, 2017) and the AmphiBIO database (Oliveira et al., 2017). Diet data (whether a species had been recorded eating vertebrates, arthropods, flowers, fruits, leaves and/or seeds) were taken from the AmphiBIO database (Oliveira et al., 2017). Finally, we collected microhabitat data from several secondary references (Moen et al., 2016; Moen & Wiens, 2017; AmphibiaWeb 2017; IUCN, 2017) and used eight microhabitat categories defined by Moen and Wiens (2017): (a) aquatic—almost always in water, (b) arboreal—typically on above-ground vegetation, (c) burrowing—nonbreeding season spent underground or in burrows they have dug, (d) semi-aquatic—partially aquatic and partially terrestrial, (e) semi-arboreal—partially arboreal and partially terrestrial, (f) semi-burrowing—partially burrowing and partially terrestrial, (g) terrestrial—found on the ground, under rocks, or in leaf litter, and (h) torrential—found in high-gradient, fast flowing streams, usually on rocks in the stream or under waterfalls. All data with associated references are in Supplemental Information (Dryad dataset: doi: https://doi.org/10.5061/dryad.1rn8pk0r8).

2.2 | Data analysis

All phylogenetic analyses were performed within R version 3.4 (R Core Team 2017) using a time-calibrated phylogeny of amphibians (Pyron, 2014a,2014b) that we trimmed to the 2,434 species within our phenotypic data set using the R packages *phytools* (Revell, 2012) and *geiger* (Harmon, Weir, Brock, Glor, & Challenger, 2007). For the following analyses, we used a species' maximum recorded body size (measured as snout–vent length, SVL) because we were interested in a species' potential body size regardless of sex. However, when only maximum female SVL or maximum male SVL were analysed results were qualitatively similar for most analyses (see Table S1). For all analyses, we used the natural log of a species' SVL.

We first used *bayou* (Uyeda & Harmon, 2014) to detect significant shifts in body size without specific *a priori* hypotheses of body-size evolution while accounting for phylogenetic relationships among species. *Bayou* uses Bayesian reversible jump methods to fit multi-optima Ornstein–Uhlenbeck (OU) models of continuous character evolution. We ran two MCMC chains in parallel for ten million generations each, sampling every 100 generations. We discarded the first 30% of each chain as burn-in and then assessed run convergence using Gelman's R-statistic (Gelman & Rubin, 1992) and by plotting and comparing the branch posterior probabilities of detected shifts to new body-size optima. We then combined the chains and compared models that included these *bayou* shifts in mvMORPH, using AICc comparisons to determine which shifts estimated in *bayou* significantly improved the fit of an OUM model in mvMORPH. We first determined whether a model with shifts (OUM) versus a model with a single evolutionary optimum (OU) or a model with Brownian motion (BM) was a better fit to our data. After comparing AICc among evolutionary models of Brownian motion and a single OU optimum, we continuously added OU regimes in order of posterior probability support from our combined *bayou* chains until the addition of regimes was not supported (based on a decrease in AICc). We report transitions in body-size optima that had > 44% posterior probability from our combined chains because these thirteen optima all improved the fit of our OU models in mvMORPH based on AICc (Table S2).

To visualize the phylogenetic distribution of miniature and gigantic anuran species relative to our detected *bayou* shifts in body-size evolution, we used existing criteria for defining miniature species and used the miniature criteria to inform an anuran gigantism threshold. Previous studies have defined lineage-specific thresholds for miniature anuran species, and we chose the most conservative size threshold of those previously published for miniature species (16 mm; Scherz et al., 2019). As we found no agreed upon definition for gigantic anurans, we determined how far the miniature threshold (16 mm) deviated from the mean anuran snout–vent length on a log scale (mean SVL log(mm) = 3.809). We then used this difference to dictate a minimum threshold for gigantic anuran body sizes. We ultimately defined miniature and gigantic anuran body sizes as below 16 mm and above 127 mm, respectively (Figure S2).

We performed phylogenetic least-squares (PGLS) analyses to test for an association between a species' SVL (in log(mm)) and latitude (minimum, maximum and range), elevation (minimum, maximum and range), microhabitat (aquatic, arboreal, burrowing, terrestrial and torrent), presence/absence of vertebrate prey in diet,

or development mode (direct, and larval), while accounting for phylogeny. Variance-inflation factors calculated in R did not reveal multicollinearity between our explanatory variables (all VIFs were less than five (VIF_{max} = 1.22) as recommended in Ringle, Wende, and Becker (2015). We ran PGLS models using the R package *caper* (Orme et al., 2018) to test the relationship between SVL and our various geographic, ecological and life-history variables and obtain adjusted R-squared values for these relationships. All PGLS analyses were run with phylogenies trimmed from Pyron (2014a,2014b) to the species for which we had both SVL and independent variable data. We performed PGLS analyses with the natural log of each species' maximum SVL as our dependent variable and one of the independent variables, while estimating phylogenetic signal (lambda) in the residual error simultaneously with the regression parameters (Revell, 2010). For latitudinal range, we observed heteroscedasticity in the phylogenetically corrected residual plots and corrected for this by using a square root transformation of latitudinal range in all relevant analyses. Diagnostic plots for all reported PGLS analyses are in Supplemental Figures S12-S16. For microhabitat, we calculated least-square means of body size for each microhabitat category from our PGLS analyses using the R package *lsmeans* (Lenth, 2016).

Finally, although we have no *a priori* hypotheses to guide multiple regression tests, we explore a few preliminary analyses to determine whether interactions among the factors tested (latitude, elevation, microhabitat and development mode) revealed redundancy in those variables' abilities to explain body-size variation. Similar to above, we performed PGLS analyses in the R package *caper* (Orme et al., 2018) with the natural log of each species' maximum SVL as our dependent variable and two or more of the independent variables, while estimating phylogenetic signal (lambda) in the residual error simultaneously with the regression parameters (Revell, 2010). We ran one PGLS analysis with latitudinal and elevational range as independent variables. We ran a second PGLS analysis with maximum latitudinal and maximum elevation as independent variables. We ran a third PGLS analysis with latitudinal range, elevational range, microhabitat and development mode (excluding viviparous species) as independent variables. No multiple regressions were performed with diet data because diet was known for such a limited number of species in comparison with other factors.

3 | RESULTS

3.1 | Overall patterns of anuran body-size evolution

Body size (snout–vent length; SVL) varied by 32-fold among the 2,434 species in our study. Species' maximum body size ranged from 10.7 mm SVL (*Brachycephalus didactylus*) to 320 mm SVL (*Calyptocephallela gayi* and *Conraua goliath*; figure with species names in Figure S1), and the natural log of SVL was normally distributed (Figure S2). In our *bayou* analyses, we found thirteen shifts in anuran SVL that were supported by model comparisons within mvMORPH (Figure 1; Table S1). Although including all 13 shifts

improved the fit of our OU models in mvMORPH, the *bayou* posterior probabilities for shifts eight through 13 were < 70% and should therefore be interpreted with caution. The shifts we detected encompass 14 anuran families, with some shifts occurring at the root of families (Conrauidae and Myobatrachidae) or genera (*Leptodactylus*; Figure 1; Table 2). Most evolutionary shifts were to larger SVLs from the root estimate body size of 56.4 mm (Figure 1; Table 2): four shifts were towards 'gigantic' evolutionary optima (>127 mm), and five shifts were towards larger body-size optima ranging from 69–92 mm. Only four of the thirteen estimated shifts in body-size were towards optima smaller than the root estimate (shifts with yellow to light-green colours in Figure 1) and none were towards 'miniature' evolutionary optima, although the shift encompassing Brachycephalidae and Eleutherodactylidae (yellow clade in Figure 1; 21.76 mm SVL; Table 2) is only slightly larger than previously used criteria for defining miniaturization in some studies of anuran body size (20 mm–Clarke, 1996).

Our data set included 33 miniature species (< 16 mm SVL) and 70 gigantic species (>127 mm SVL; Figure 1). Bufonidae had the greatest number of gigantic species (20 of the 199 bufonid species in this study), while Brachycephalidae had the greatest number of miniature species (10 of the 23 *Brachycephalus* species in this study). Although there are miniature and gigantic anurans within the thirteen clades of anurans with estimated shifts in SVL optima, the distribution of miniature or gigantic anurans across the phylogeny is not always associated with overall shifts in body-size evolution detected by our *bayou* analyses (Figure 1).

3.2 | Fossil record

We compared the body sizes of 49 anuran species from the fossil record with the body sizes of extant taxa. Only two anuran species from the fossil record had body sizes outside the range of extant taxa (*Beelzebufo ampinga*—425 mm, *Caudiverbera parodii*—350 mm). Thirty-three of these extinct species belong to extant families (including *B. ampinga* and *C. parodii*), and we found that thirteen extinct species from seven families (Alytidae—3:80, 87, and 200 mm; Ceratophrynidae—1:425 mm; Leiopelmatidae—3:80, 80 and 150 mm; Pelobatidae—3:100, 110 and 156 mm; Pelodytidae—1: 53mm; Scaphiopodidae—1:100 mm; Telmatobidae—1:350 mm) had body sizes greater than all extant species in the corresponding family (Figure 2).

3.3 | Body-size evolution, latitude and elevation

We used phylogenetic least-squares (PGLS) to examine the relationship between latitude, elevation, and body size for 1,358 species. Although most species occur at lower latitudes (Figure 3a), *Rana temporaria*, *R. arvalis* and *Bufo bufo* can be found at latitudes more than 65 degrees from the equator. We found a positive relationship between body size and maximum latitude ($F_{1,1,356}$ = 39.88, *p* < .001, adjusted
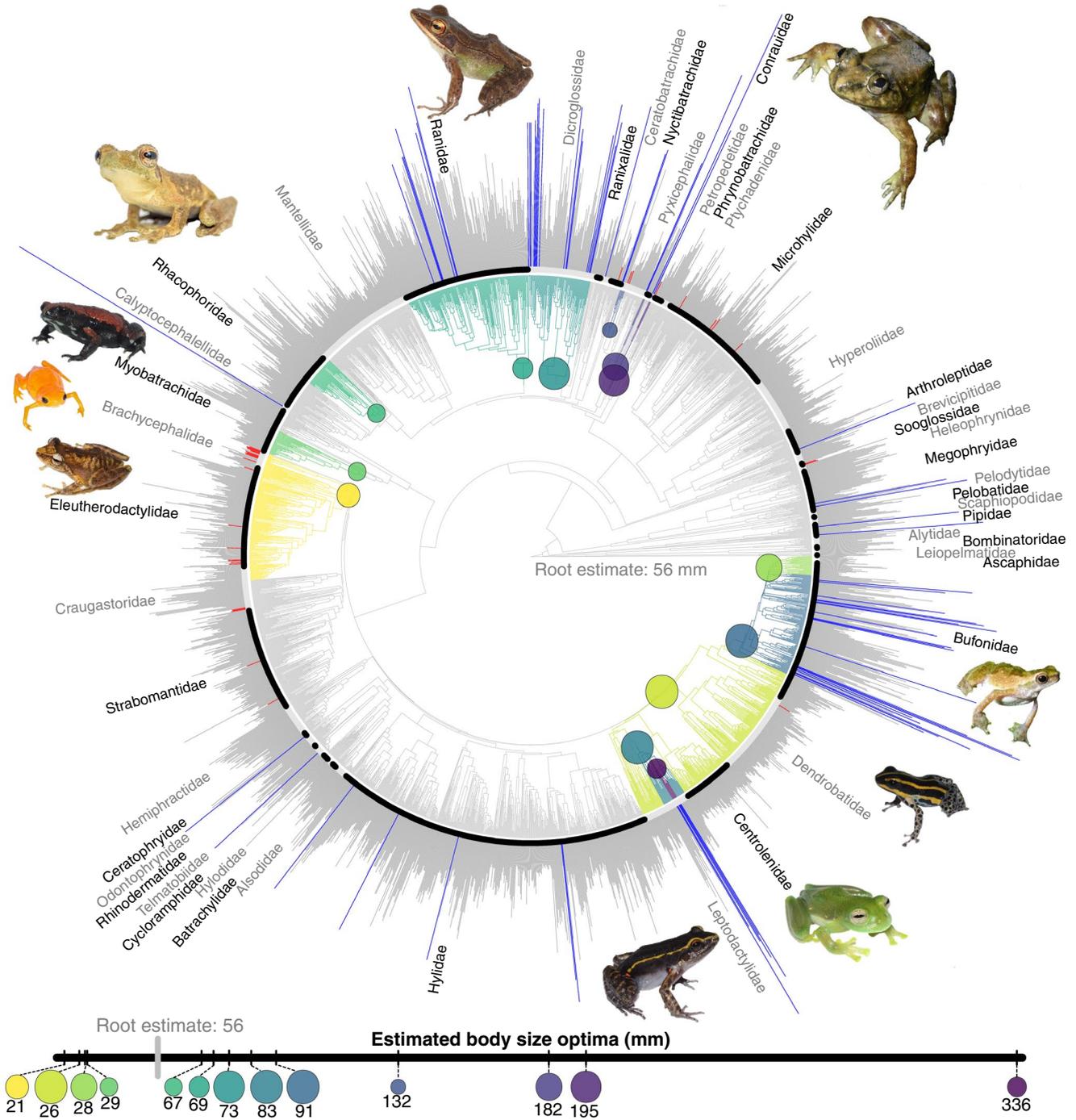
FIGURE 1 Shifts in body-size evolution detected among 2,434 anuran species. A phylogeny (trimmed from Pyron, 2014a,2014b) of all species included in this study with maximum body size of each species represented by the length of the bars on the perimeter of the tree. Although bar lengths represent body size in millimetres, analyses were performed with the natural log of a species' maximum body size. Miniature (< 16 mm, red) and gigantic (> 127 mm, blue) species' bars are coloured. Branches within the phylogeny are coloured based on estimated shifts in body-size evolution found in our *bayou* analyses. Colors adapted from *viridis* R package (Garnier 2018). *bayou* regime is listed in the legend, and the posterior probability of each shift is indicated by the size of the coloured circle. The grey and black bands around the tree perimeter indicate demarcations between families that have more than one species within this phylogeny. In clockwise order, anuran photographs from select families within estimated shifts in body size evolution—eleutherodactylid (*Eleutherodactylus portoricensis*) credit: Alberto Lopez; brachycephalid (*Brachycephalus ephippium*) credit: C. Guilherme Becker; myobatrachid (*Pseudophryne coriacea*) credit: RC Bell; rhacophorid (*Chiromantis rufescens*) credit: Christian Irian; ranid (*Amnirana albolabris*), conrauid (*Conraua crassipes*) and bufonid (*Nectophryne batesii*) credit: Bryan Stuart; dendrobatid (*Ranitomeya sirensis*), centrolenid (*Teratohyla midas*), and leptodactylid (*Lithodytes lineatus*) credit: Ivan Prates

TABLE 2 Summary of body-size optima found in *bayou* analyses with posterior probability, shift level (primary = an optima shift away from background variance, secondary = a shift within a primary optima, tertiary = a shift within a secondary optima), families included in the optima, estimated body-size optima, within-optima average body size and 95% confidence interval

Posterior probability	Shift level	Families included	Estimated optima	Average body size ± 95% confidence interval (mm)
97.8	Secondary	Bufonidae	91.50	86.20 ± 7.22
97.7	Primary	Allophrynidae Bufonidae Centrolenidae Dendrobatidae Leptodactylidae	26.52	28.76 ± 1.15
96.7	Secondary	Allophrynidae Leptodactylidae	83.26	65.47 ± 9.26
93.5	Primary	Dicroglossidae	73.26	81.48 ± 8.61
91.5	Primary	Conrauidae	194.47	189.75 ± 102.84
79.6	Primary	Pyxicephalidae	181.98	161.67 ± 86.43
78.9	Tertiary	Bufonidae	28.47	35.04 ± 4.74
69.7	Primary	Brachycephalidae Eleutherodactylidae	21.76	32.88 ± 2.32
61.3	Primary	Ranidae	69.41	79.17 ± 4.20
57.7	Tertiary	Leptodactylidae	336.37	176.07 ± 32.30
53.5	Primary	Myobatrachidae	29.21	29.64 ± 2.34
53.1	Primary	Rhacophoridae	66.84	66.19 ± 7.11
44.8	Primary	Pyxicephalidae	131.69	100.71 ± 28.38

R-squared = 0.028, slope = 6.4 e^{-3}, slope SE = 1.0 e^{-3}; Figure 3a) but not minimum latitude ($F_{1,1,356} = 3.73$, $p = .054$, slope = -2.4 e^{-3}, slope SE = $1.2e^{-3}$; Figure 3a) among species. We also found a positive relationship between a species' latitudinal range and maximum body size ($F_{1,1,356} = 97.41$, $p < .001$, adjusted R-squared = 0.066, slope = 9.3 e^{-3}, slope SE = 9.7 e^{-4}; Figure 3a). Latitudinal range explained about six per cent of body-size variation, and maximum latitude explained only three per cent of body-size variation, reflecting wide ranges in body size across latitudes. The weak positive association between body size and latitude and latitudinal ranges is largely the result of species with smaller body size being abundant at lower latitudes and with smaller latitudinal ranges. The fewer anuran species found at higher latitudes and with wide latitudinal ranges are often medium or large in body size.

Elevational distributions in our data set ranged from sea level to 5,538 metres (Figure 2b). Again, most species occur at lower elevations, but *B. maculatus*, *Atelopus ignescens* and *Scutiger boulengeri* can be found at elevations exceeding 5,000 m. We found a positive relationship between body size and maximum elevation (F$_{1,1,356}$ = 12.76, $p = .005$, adjusted R-squared = 0.009, slope = 3.6 e^{-5}, slope SE = 1.0 e^{-5}; Figure 3b); however, maximum elevation explained less than one per cent of body-size variation. We also found a negative relationship between body size and minimum elevation ($F_{1,1,356} = 30.53$, $p < .001$, adjusted R-squared = 0.021, slope = -8.9 e^{-5}, slope SE = 1.6 e^{-5}; Figure 3b) and a positive relationship between a species' elevation range and maximum body size ($F_{2,1,356} = 51.96$, $p < .001$, adjusted R-squared = 0.036, slope = 0.06 slope SE = 5.7 e^{-3}; Figure 3b); however, both minimum and maximum elevation explained a small percentage of body-size variation. Among altitudinal variables tested, elevation range explained the largest proportion of variation but still only accounted for four per cent of body-size variation. The positive associations between body size and maximum elevation and

elevational range result from smaller anurans being absent at higher latitudes and generally having lower latitudinal ranges.

Our multiple regression analyses reveal that when analysed together, maximum latitude and elevation both retained a significant relationship with maximum SVL (overall model: $F_{2,1,355} = 23.28$, $p < .001$, adjusted R-squared = 0.033; maximum latitude: $t_{1,1,355} = 5.76$, $p < .001$, slope = 5.95 e^{-3}, slope SE = 0.28; maximum elevation: $t_{1,1,355} = 2.52$, $p = .012$, slope = 2.55 e^{-5}, slope SE = 1.01 e^{-5}), and together, these variables explained three per cent of body-size variation, which is slightly more than maximum latitude or elevation explained alone. When latitude and elevation range were analysed in a multiple regression, only latitudinal range continued to show a significant relationship with maximum SVL (overall model: $F_{2,1,355} = 50.98$, $p < .001$, adjusted R-squared = 0.070; latitude range: $t_{1,1,355} = 14.54$, $p < .001$, slope = 3.94, slope SE = 0.27; elevation range: $t_{1,1,355} = 1.93$, $p = .054$, slope = 2.37 e^{-5}, slope SE = 1.23 e^{-5}). Furthermore, when a species' latitude range, microhabitat and development mode were analysed together in relation to a species' maximum SVL, latitude range continued to show significant relationships with maximum SVL (overall model: $F_{11,951} = 8.52$, $p < .001$, adjusted R-squared = 0.088; latitude range: $t_{1,951} = 8.42$, $p < .001$, slope = 4.15, slope SE = 0.28).

3.4 | Body-size evolution associated with microhabitat and diet

We analysed variation in body size among 1,720 anuran species that occupy eight categories of microhabitat (aquatic, arboreal, burrowing, semi-aquatic, semi-arboreal, semi-burrowing, terrestrial and torrential) using PGLS and found very little evidence that body size varied in association with microhabitat in a meaningful way
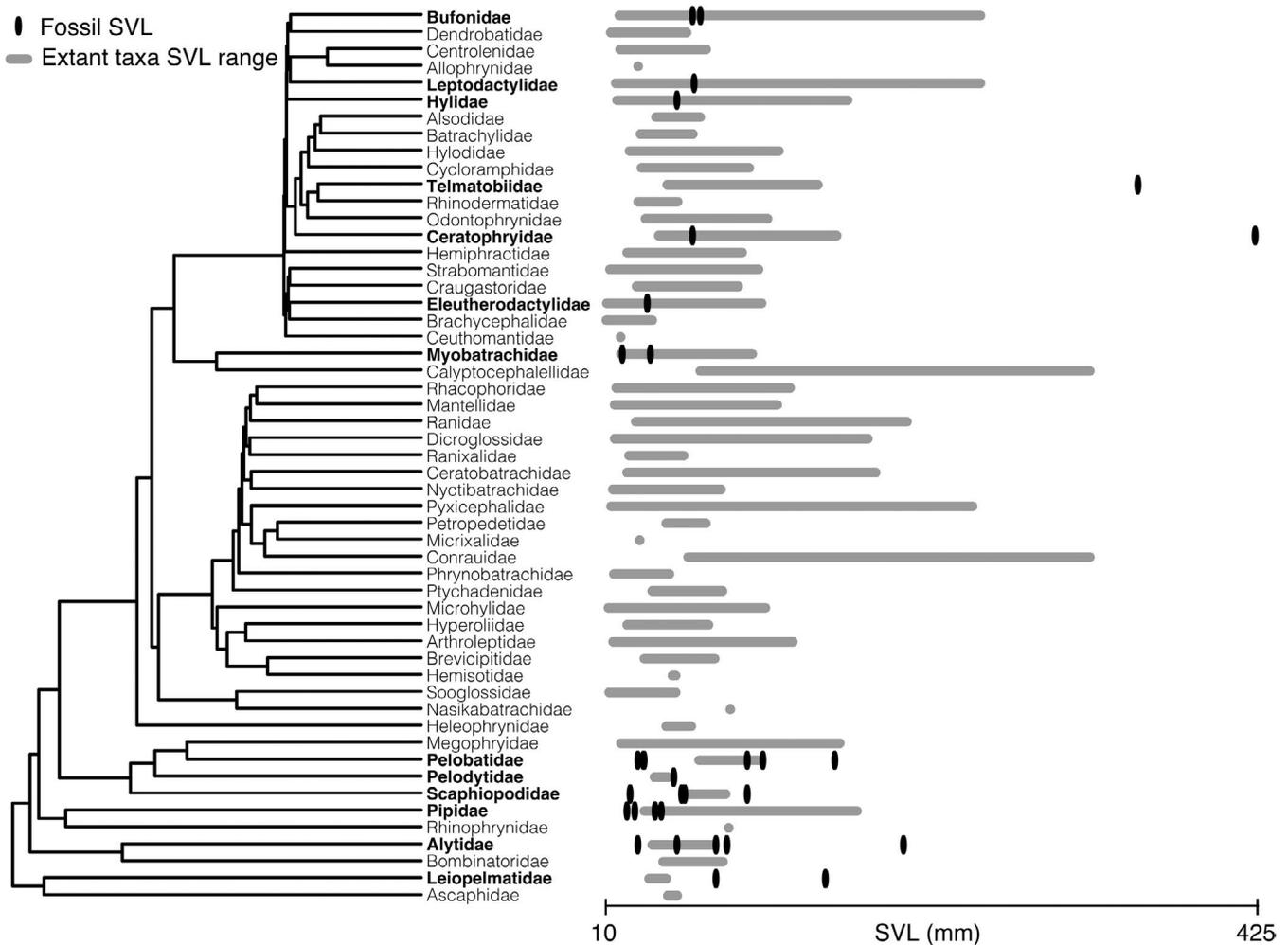
FIGURE 2 The phylogenetic distribution of fossil records that have been identified to extant families. A phylogeny (trimmed from Pyron, 2014a,2014b) displaying the relationships among families. The range of extant taxa body sizes (snout–vent lengths; SVLs) in each family is represented by the grey bar, and fossil records are represented by black points

($F_{7,1712}$ = 4.75, p < .001, adjusted R-squared = 0.015; Figure 4a). Although there was a significant association, microhabitat explained less than two per cent of body-size variation. Generally, more small species are found in arboreal, semi-arboreal and terrestrial microhabitats. The two largest species in our data set (*Calyptocephallela gayi* and *Conraua goliath*), which are each 70 mm longer in SVL than the next largest species, are aquatic and semi-aquatic; however, gigantic species (maximum SVLs > 127 mm) can be found in all microhabitats except torrential. By contrast, all the miniature species (<16 mm SVL) are found in arboreal, semi-arboreal, terrestrial or unknown microhabitats. Our multiple regression analysis revealed that when a species' latitude range, elevation range, microhabitat and development mode were analysed together in relation to a species maximum SVL, microhabitat retained a significant relationship with maximum SVL (overall model: $F_{11,951}$ = 8.52, p < .001, adjusted R-squared = 0.088; microhabitat: $F_{7,951}$ = 2.75, p = .007).

We analysed diet data of 629 anuran species in relation to maximum body size. Arthropod prey were recorded in all but five of the 629 species' diets, vertebrate prey were recorded in 59 species' diets, and plant material (flowers, fruits, leaves or seeds) was only recorded

in 23 species' diets. We found anurans with larger body sizes are more likely to have vertebrates documented in their diet than species with smaller body sizes when accounting for phylogenetic relationships ($F_{1,627}$ = 53.38, p < .001, adjusted R-squared = 0.077; Figure 4b), although having a vertebrate recorded in a species' diet only explained seven per cent of body-size variation. The smallest anuran with a vertebrate recorded in its diet was *Afrixalus fornasini* with a snout–vent length of 40 mm.

3.5 | Body-size evolution and development mode

We analysed development mode (direct development, larval development and viviparity) among 2,228 species of anuran that ranged in body size from the smallest to largest species in our data set (10.7—320 mm SVL). All four species categorized as viviparous in this study (*Nectophrynoides minutus, Nec. tornieri, Nec. viviparus, Nimbaphrynoides occidentalis*) were within the family Bufonidae, while larval and direct developing species were found throughout the frog phylogeny (Figure 5). Body sizes of larval developing, direct
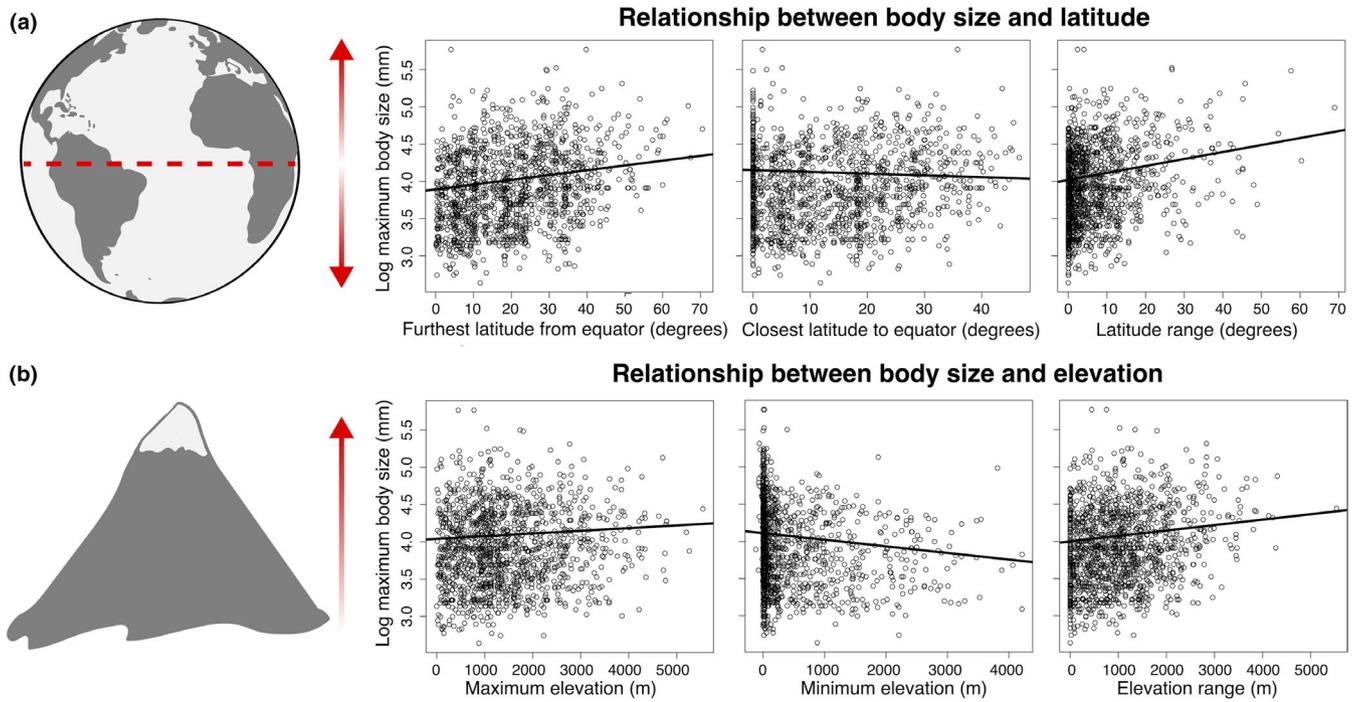
FIGURE 3 Relationship between body size and latitude and elevation among anuran species. (a) Scatter plots depicting the relationship between a species' maximum body size and latitudinal maximum, minimum and range. Regression lines from the corresponding PGLS analyses overlay the points in each plot. (b) Scatter plots depicting the relationship between a species' maximum body size and elevational maximum, minimum and range. Regression lines from the corresponding PGLS analyses overlay the points in each plot. To most clearly predict and allow interpretation of the raw data, elevation range is plotted without the square root transformation that avoids heteroscedasticity and is reported in the results text
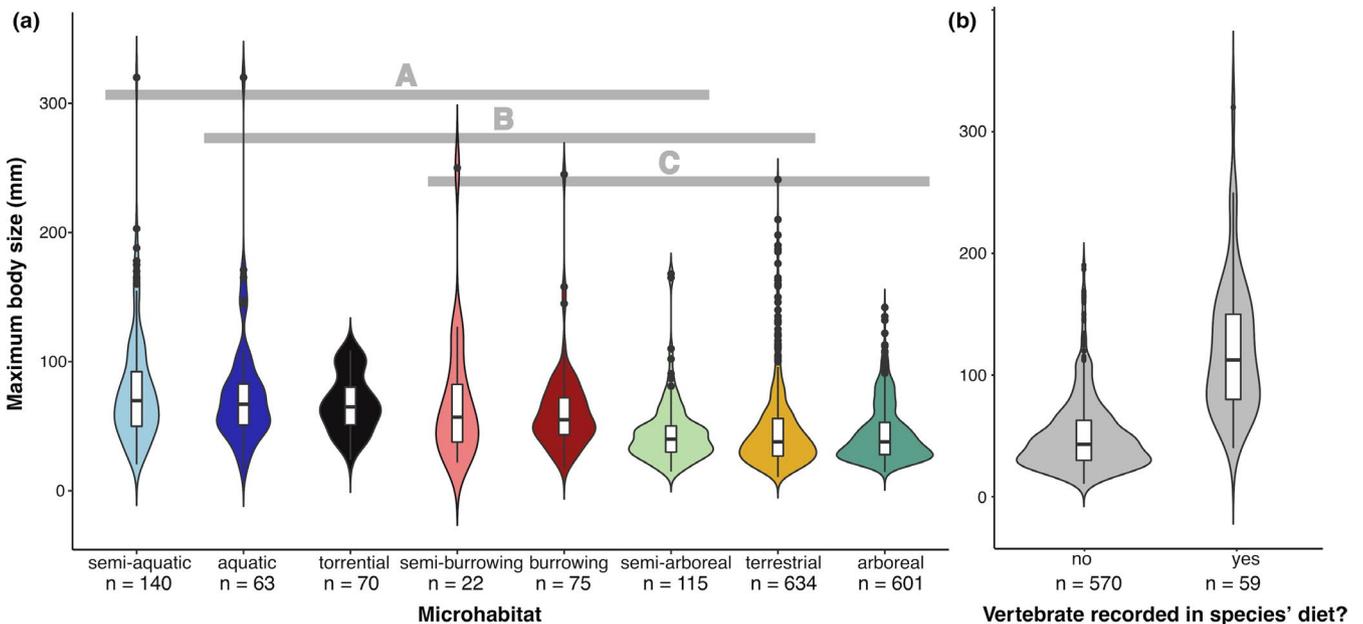
FIGURE 4 Relationship between body size and microhabitat and diet in anuran species. (a)—A violin plot depicting differences in body size among microhabitats with significantly different least-square means groups indicated by the grey, lettered bars. Microhabitats are ordered by average body size from largest to smallest. Colours adapted from the Wes Anderson R package (Ram & Wickham, 2018). (b) A violin plot comparing the maximum body sizes of species with and without vertebrates recorded in their diet. Although the y axis of both plots shows body size in millimetres, analyses were performed with the natural log of a species' maximum body size
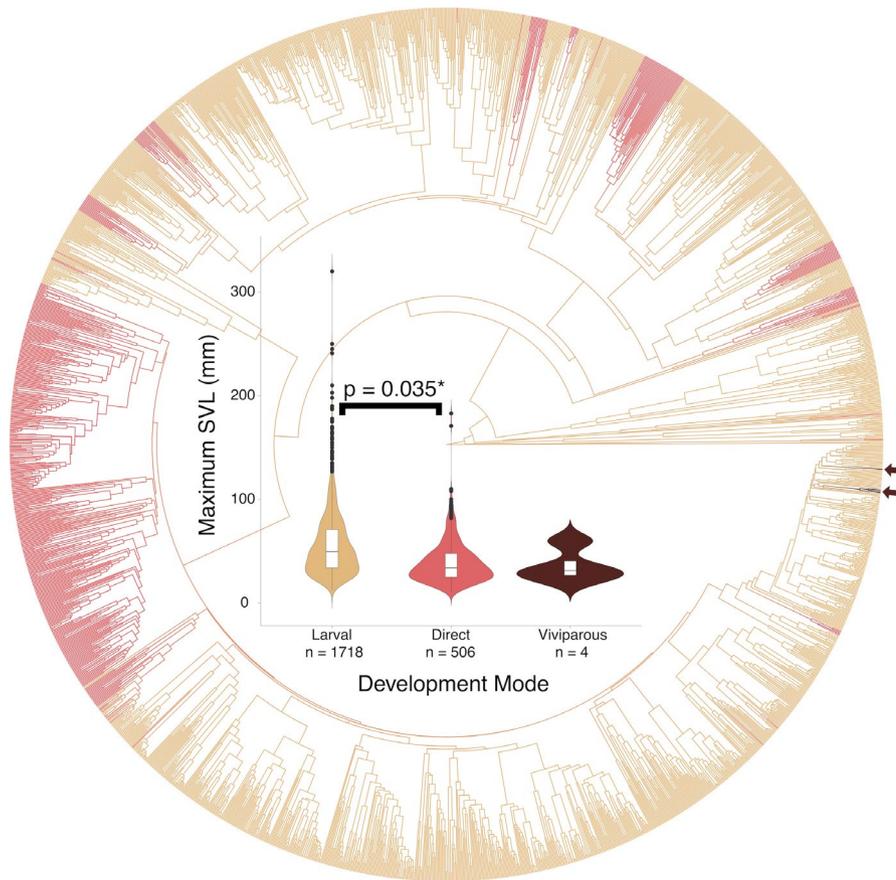
FIGURE 5 The phylogenetic distribution of development mode among 2,228 anuran species and its relationship with body size. A phylogeny (trimmed from Pyron, 2014a, b) displaying the relationships among larval developing species (tan), direct developing species (pink) and viviparous species (dark red with arrows). The box plot shows the range of body sizes among species in each development mode category with the results from our PGLS analysis comparing body sizes between larval and direct developers. Although the box plot's y axis shows body size in millimetres, analyses were performed with the natural log of a species' maximum body size. Colours adapted from the Wes Anderson R package (Ram & Wickham, 2018)

developing and viviparous species overlapped, with larval developers having the largest range (*Microhyla superciliaris* and *Stumpffia pygmaea* 12 mm – *Calyptocephallela gayi* and *Conraua goliath* 320 mm), direct developers having a slightly smaller body-size range (*Brachycephalus didactylus* 10.7 mm – *Leptodactylus vastus* 250 mm), and the four viviparous species covering the narrowest body-size range (*Nectophrynoides minutus* 22 mm – *N. viviparous* 60 mm). We tested for an association between maximum body size and development mode, excluding the viviparous species (due to the very small number of viviparous species), and found that species with larval development have larger maximum body sizes than direct developing species ($F_{1,2,222} = 4.48$, $p = .035$, adjusted R-squared = 0.002). However, direct development explains less than one per cent of body-size variation. Furthermore, when a species' latitudinal range, microhabitat and development mode (excluding viviparous species) were analysed together in relation to a species maximum SVL, development mode no longer had a significant relationship with maximum SVL (overall model: $F_{11,951} = 9.12$, $p < .001$, adjusted R-squared = 0.077; development mode: $F_{2,967} = 0.83$, $p = .437$).

4 | DISCUSSION

We report 32-fold variation in body size over the estimated 200 million years (Feng et al., 2017) of evolutionary history connecting the 2,434 anuran species in this study. Our analysis of clade-specific

shifts in body-size evolution supported multiple shifts to larger body-size optima, including several towards 'gigantic' evolutionary optima (>127 mm), with only a few shifts to smaller body-size optima, none of which fell below the 'miniature' (< 16 mm) threshold. With regard to anuran body sizes at the extremes, we found that miniature and gigantic species were dispersed in numerous families across the anuran tree of life and were not always associated with the shifts detected in our *bayou* analysis. In addition, we found weak associations between a species' body size and its geographic distribution, ecology and development mode. Although testing for interactions among these factors is beyond the scope of this study, we note that these interactions may be important and that certain factors (elevation and development mode) lose significant relationships with body size when analysed in a multiple regression. In sum, anurans do not show strong geographic and ecological body-size patterns observed in other tetrapod clades (Bergmann's rule, differences among habitat use, and diet type) and instead show striking body-size variation across latitudes, elevations, and among ecological and life-history variables.

4.1 | Evolutionary limits at the extremes of anuran body size

Although maximum body size in anurans varies from 10.7 to 320 mm (approx. 0.10 – 3,250 g; Almeida-Santos, Siqueira, Van Sluys, &

Rocha, 2011; AmphibiaWeb 2017), the range of anuran body sizes is dwarfed by that displayed in other tetrapod groups of similar age (mammals: common ancestor ~ 218 mya—Foley, Springer, & Teeling, 2016, <2 g – 907,185 g—Cooper & Purvis, 2010; lizards: common ancestor ~ 200 mya—Zheng & Wiens, 2016, 17 mm – 1,540 mm—Meiri, 2008) and even clades that emerged much more recently (birds: common ancestor ~ 95 mya—Claramunt & Cracraft, 2015, 2 g – 100,000 g—Bokma, 2002). Yet, miniature anurans push the lower limits of tetrapod body size and include the smallest known tetrapods (e.g. *Brachycephalus didactylus* and other very small species battling for the title). These tiny tetrapods potentially benefit from crypsis or the ability to occupy niches that demand smaller body sizes; however, miniature anurans also face physical constraints that result in the loss or reduction of structures (Hanken & Wake, 1993; Yeh, 2002). For instance, the genus *Bracycephalus* encompasses many miniature species that have lost digits (Yeh, 2002). By contrast, although many species across the anuran tree of life could be recognized as anuran 'giants' using our proposed criteria, the largest representatives from other tetrapod groups are much larger than the largest anurans (Mieri 2008; Olson et al., 2009; Smith et al., 2010). Thus, although we detected multiple evolutionary shifts to larger body sizes and 'giants' in several families, anurans appear to have a stricter upper body-size limit compared to other major tetrapod clades. It is unclear what dictates the upper body-size limit of anurans but the families Pyxicephalidae and Conrauidae are excellent candidates for future studies investigating anuran upper body-size limits because these families contain the largest anuran species and show shifts to the largest evolutionary body-size optima.

Over historic time periods, we found that limits on anuran body size appear to have changed very little relative to other groups of tetrapods (e.g. mammals; Smith et al., 2010). Only two extinct anuran species were larger than any extant taxa in our study (*Beelzebufo ampinga* and *Caudiverbera parodii*) and no extinct taxa were smaller, though fossils of miniature anurans would be harder to find and identify. *Beelzebufo ampinga* and *C. parodii* are estimated to be from different eras (*B. ampinga*—Mesozoic, Late Cretaceous; *C. parodii*—Cenozoic, Miocene), giving no clear indication that a particular time allowed for or selected for larger body size in the evolutionary history of frogs. Although the anuran fossil record is rather limited, we found that thirteen extinct species (from seven families) were larger than extant species within their same family. Therefore, we see little evidence for changes in overall body size throughout the evolution of anurans, but body-size ranges within families may have fluctuated over time.

4.2 | Anuran body size shows a positive but scattered correlation with latitude, elevation and distribution

Latitude and elevation only explained a small proportion of the variation in anuran body size, indicating that other evolutionary,

environmental or ecological factors are likely having a larger impact on anuran body-size evolution. Similar to many previous studies investigating Bergmann's rule in anurans, we found that maximum body size in anurans is positively correlated with both the maximum latitude and maximum elevation at which species occur (Amado et al., 2019; Ashton, 2002; Lindsey, 1966; Olalla-Tárraga, Diniz-Filho, Bastos, & Rodríguez, 2009; Olalla-Tárraga & Rodríguez, 2007); however, these relationships were relatively weak. Among our latitudinal and elevational measures, latitude and elevation range explained the most variation in maximum body size (although still only six and four per cent, respectively), indicating that larger species inhabit broader ranges of latitudes and elevations than smaller species do. Our results and those from other studies with more limited geographic sampling underscore that anuran body size is shaped by many factors beyond simply latitude and elevation. For instance, phylogenetic analyses of anuran body size in the Americas that accounted for climatic variables such as annual precipitation and potential evapotranspiration explained up to 23 per cent of body-size variation (Amado et al., 2019). Bufonids exhibited shifts to both smaller and larger body-size optima in our analysis, occur in a range of latitudes, elevations and climates, and exhibited stronger relationships between maximum body size, latitude and elevation than what we found more generally among anurans in this study (Figure S17). It may be more appropriate to investigate previous hypotheses about body-size evolution with respect to latitude, elevation and climate within lineages such as bufonids to limit potentially confounding clade-specific patterns present across the entire order.

4.3 | Anuran body size varies with respect to microhabitat and diet

Habitat and diet both show relationships with body size in other tetrapods, and anurans are no exception. However, there is considerable overlap in anuran body sizes among our microhabitat categories and the relationship between size and microhabitat is largely driven by a propensity for smaller anurans to be terrestrial and arboreal. Although small anurans are found in every microhabitat, the vast majority (89%) of smaller-than-average anurans (<52 mm) in our data set are either arboreal, semi-arboreal or terrestrial. Likewise, the slightly larger average body sizes of aquatic anurans are in part due to the largest aquatic and semi-aquatic anurans being more than double the size of the largest arboreal species. Although frogs of most body sizes can be found in most microhabitats, and microhabitat explains less than two per cent of body-size variation in our data set, the observation that the two largest extant anurans are aquatic and semi-aquatic poses some interesting hypotheses. For anurans, aquatic habitats may be a release from ecological, locomotor or climatic constraints that dictate stricter upper body-size limits in other microhabitats. Furthermore, the very modest association between anuran body size and microhabitat may be stronger when other biotic and abiotic factors, such as prey availability and microclimate, are accounted for. Families Bufonidae, Hylidae and Pyxicephalidae

could be particularly useful for detailed comparisons among closely related species given their variation in body size and microhabitat use.

Almost all the anuran species in our data set prey on arthropods; however, the presence of vertebrate prey in the diet was positively associated with larger body size. This pattern is consistent with changes in prey items seen across anuran ontogeny (Blackburn & Moreau, 2006; Flowers & Graves, 1995) as well as optimal foraging theory, which predicts that animals will choose the optimal prey types available (based on nutrition, handling times and other factors; reviewed in Pyke, Pulliam, & Charnov, 1977). Studies in lizards and marine vertebrate predators found similar support for optimal foraging theory as body size increased (Costa, 2009; Costa et al., 2008). Surprisingly, 23 species had records of plant material (flowers, fruits, leaves or seeds) in their diets. Plant material in anuran stomach contents is largely thought to be by-catch (Whitaker, Rubin, & Munsee, 1977), although there is at least one species, *Xenohyla truncata*, that eats fruit in the wild and is able to subsist on fruit in the laboratory (da Silva, de Britto-Pereira, Caramaschi, & de Britto-Pereira, 1989). Thus, plant consumption in anurans is currently too poorly documented to make any strong conclusions about anuran herbivory. Field studies of diet relative to prey availability, systematic surveys of museum specimen gut contents, and DNA barcoding of gut contents could help determine whether the relationship between larger body size and presence of different prey types found here is the result of optimal foraging or simply incomplete knowledge of anuran diets.

4.4 | The relationship between body-size evolution and development mode

We found a very weak association between development mode and body size across deep evolutionary scales, with development mode explaining less than one per cent of body-size evolution. Anurans have transitioned from having a distinct larval stage during development to direct development (in which development into a froglet occurs within the egg) numerous times (Gomez-Mestre et al., 2012; Meegaskumbura et al., 2015; Portik & Blackburn, 2016), and Hanken and Wake (1993) previously proposed a relationship between direct development and miniaturization. Of our 33 miniature species (<16 mm), 26 are direct developers, five are larval developers, and two have undocumented development modes. This pattern supports a strong association between direct development and miniaturization in Anura, despite many direct developers reaching much larger body sizes. Additionally, when looking among frogs of all sizes, we found larger adult body sizes associated with larval development and smaller adult body sizes associated with direct development, consistent with trends found in previous studies (Blackburn, 2008; Gomez-Mestre et al., 2012; Zimkus et al., 2012). However, given the very small amount of variation in body size explained by development mode, the strong overlap in body sizes of species with differing developmental modes, and the lack of a significant relationship between body size and development mode when accounting for other factors, it does not appear that evolutionary transitions to direct development directly affect body-size evolution (e.g. by limiting size at metamorphosis).

5 | CONCLUDING REMARKS

Overall, we identified clade-specific shifts in body-size evolution across the anuran tree of life as well as many transitions to gigantic anuran body sizes. While the upper limits of body size across anurans were largely consistent through deep time, two extinct species defy upper body-size limits of extant taxa and we point out eleven additional extinct species that exceed extant body sizes within their respective families. Finally, we found that anuran body size is very weakly correlated with latitude, altitude, microhabitat, predation on vertebrates, and development mode, with any given factor only explaining a small amount of anuran body-size variation. Although our study cannot conclusively identify the mechanisms that generated these patterns of body size over the last 200 million years, we comprehensively test a number of long-standing hypotheses regarding anuran body-size evolution and nominate several lineages for future studies on how and why body size varies across the anuran tree of life.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
MCW contributed to the conception of the study, data collection, data analysis and writing. RCB contributed to the conception of the study and writing.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/jeb.13679.

DATA AVAILABILITY STATEMENT
Data deposited at Dryad: https://doi.org/10.5061/dryad.1rn8pk0r8.

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SUPPORTING INFORMATION

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