Phylogenetic patterns of skeletal morphometrics and pelvic traits in relation to locomotor mode in frogs

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comparative method;
ecological morphology;
locomotion;
morphometrics;
phylogeny.

Abstract
Frogs are one of the most speciose groups of vertebrate tetrapods (> 6200 species) with a diverse array of locomotor behaviours. Despite the impressive diversity in frog locomotor behaviours, there remains a paucity of information on the relationship between skeletal variation and locomotor mode in frogs and the evolutionary patterns in which these relationships are framed across the frog phylogeny. Our current understanding of the evolution of frog locomotion shows that hopping transitioned into jumping within the Neobatrachia where a variety of pelvic/hindlimb length patterns and locomotor niches have appeared, but this has yet to be studied over a broad taxonomic sample of frogs. Although limb length remains as the primary predictor of leaping performance, pelvic and sacral morphometrics have not been quantified in relation to limb proportions, body size and locomotor mode and previous studies have not sampled more than 24 families. We present a large-scale phylogenetic comparison of skeletal morphometrics in relation to locomotor mode in 188 genera from 37 families. Osteological variation in limb/pelvic girdle morphometrics and pelvic traits that are posited to be associated with locomotor mode were analysed to identify which aspects of the frog skeleton are the best descriptors of locomotor mode. Our results, contrary to previous work, reveal that the greatest axis of variation in frogs is represented by the shape of the sacrum with two pelvic morphologies evident in qualitative and quantitative ancestral trait reconstructions. Limb morphology was not significantly different across most locomotor modes, but we identified several outliers in hindlimb phylomorphospace. Patterns of sacral evolution together with hindlimb length outliers reveal how the general bauplan of this successful group of vertebrate tetrapods is constrained, has radiated and has converged on certain phenotypes to fill an array of locomotor modes.

Introduction
The anuran locomotor system is one of the most fascinating among vertebrate tetrapods because it gives rise to an array of locomotor behaviours. Modes of frog locomotion include burrowing, swimming, walking, hopping, jumping, climbing and gliding (Davis, 1965; Emerson, 1979). Despite the diversity in locomotor behaviours, there is surprisingly little information on the relationship between skeletal variation and locomotor mode across frogs. Moreover, the evolutionary patterns that encompass these functional relationships have yet to be described.

Our understanding of the relationship between postcranial skeletal traits and frog locomotion is mostly based on the early work of Rand (1952), Zug (1972, 1978) and Emerson (1979, 1988). Rand (1952) and Zug (1972, 1978) examined jump performance in relation to hindlimb length in disparate taxa and found it to be a good predictor of jump performance within families. Emerson (1979) studied gross dissections of the pelvis (performed on 54 species from 24 families; sensu Frost, 2011) and proposed three functional pelvic-bauplans. The Lateral-bender morphs possess a pelvis with moderately expanded
sacral diapophyses connected to ilial shafts with a loose iliosacral ligament that allows lateral bending and slight fore-aft sliding. It is associated with walking/burrowing/hopping frogs. The *Fore-aft-slider morphs* have greatly expanded sacral diapophyses with no iliosacral attachment allowing greater fore-aft translation of the ilial shafts. Emerson scored this type for some burrower/walker/hoppers, climbers and in the aquatic frogs of the family Pipidae. In the third morph, the sacroiliac movements occur in a different plane. The *Sagittal-hinge morphs* have the anterior margins of the ilial shafts bound to posterodorsally directed cylindrical-diapophyses by a short ligament that limits ilial movement to sagittal bending at the diaphyseal tips. This morph was found mostly in ranoid terrestrial-jumping frogs in her sample. On the basis of a gap in Zug’s and Rand’s relative jumping distances, Emerson (1979, 1988) began to distinguish *hopping* (<9 body lengths) from *jumping* (>9 body lengths per jump) when describing locomotor modes and applied these terms in describing her three pelvic morphs.

Later, Emerson (1988) carried out a multivariate analysis of post-cranial skeletal measurements (on 41 species across 15 families) in relation to locomotor modes. She found that the first three principal axes of variation were driven by hindlimb length, forelimb length and pelvic girdle length, respectively, but there was great overlap of locomotor modes in morphospace. The only clear pattern was for burrower/walker/hoppers to have shorter hindlimbs and longer forelimbs compared with the jumpers that had longer hindlimbs and shorter forelimbs. She concluded that forelimb and hindlimb length described the most variation in frogs is in the shape of the sacrum, the key indicator of proposed leaping ability. However, Emerson did not use skeletal measures of the sacrum, the key indicator of proposed pelvic movements and hence locomotor mode in her previous studies.

More than 25 years after Emerson, Zug and Rand’s work, new studies addressed how skeletal morphology in frogs relates to locomotor function. Gomes et al. (2009) revisited the relationship between hindlimb length and jump performance in a subset of Zug’s (1978) data, but controlled for the effects of phylogeny. The authors found that the relationship of hindlimb length to jumping distance across frogs was largely driven by the pronounced reduction in hindlimb length in numerous burrowing taxa and that differences in jumping ability in the remaining taxa were over a narrow range of distances where taxa from different locomotor modes deviated from the overall trend. Thus, jumping performance is more related to shifts in habitat use rather than being purely hindlimb-size driven, suggesting that other morphological adaptations have contributed to this process. Here again, pelvic measurements were not included.

More recently, Reilly & Jorgensen (2011) revisited pelvic morphology in relation to locomotor mode in the same taxa used by Emerson (1979) with added extant and fossil taxa and a series of new pelvic locomotor traits. This study confirmed Emerson’s three pelvic morphs with some new locomotor traits (sagittal-hinge morphs have dorsal ridges on the ilia and urostyle), but also revealed some new patterns of variation within the lateral-bender and fore-aft-slider morphs. It also showed that the lateral-bender morph is the basal and general condition for frogs and that the sagittal-hinge morph is a derived condition appearing independently several times within the two major lineages of the Neobatrachia (Ranoidea and Hyloidea). This means that walking/hopping is the basal locomotor mode for frogs and sagittal-hinge jumping and fore-aft slider jumping (hyliids) appeared later in crown group taxa.

To date, our understanding of the evolution of frog jumping shows that hopping transitioned into jumping within the Neobatrachia within a mosaic of pelvic/hindlimb length patterns and niche diversification that have yet to be studied over a broad taxonomic sample of frogs. Although hindlimb length remains the primary predictor of leaping performance, pelvic and sacral morphometrics have not been quantified in relation to limb proportions, body size and locomotor mode and previous studies have not sampled more than 24 families (sensu Frost, 2011).

This study presents a large-scale comparison of skeletal morphometrics in relation to locomotor mode in 188 genera from 37 families. Variation in skeletal morphometrics and pelvic traits (Reilly & Jorgensen, 2011) were analysed to identify which aspects of the frog skeleton are the best descriptors of locomotor mode and how locomotor mode is conserved and radiates across the frog phylogeny. Covariation among skeletal measurements was assessed using multivariate statistics corrected for phylogeny, and trait evolution was reconstructed using phylogenetic comparative methods. Our results, contrary to previous work, reveal that the greatest axis of variation in frogs is in the shape of the sacrum with the sagittal-hinge morphs being significantly different from all other frogs.

**Materials and methods**

**Taxa and morphometrics**

Skeletal morphometrics were sampled from radiographs of 188 genera (total n = 927, 192 species; three or more adult specimens per genus, see Appendices S1 and S2) using the taxonomy of Frost (2011). The number of genera sampled was based on the availability of taxa in collections with sufficient sample sizes and postural condition of the preserved specimens allowing the uniplanar visualization of limb elements. Specimens were not sexed prior to measurement, thus we used a random mix of male and female frogs for some species.
that we obtained. Preliminary examination of regressions of trait residuals on body length did not reveal any trends suggestive of sexual dimorphism in traits. Measurements of bones from radiographs of wet frog specimens have been shown to accurately reflect measurements taken from the same skeletonized specimens (Simons, 2008). Only specimens fixed flat in a dorsoventral aspect, with limbs and feet extended or neatly folded (Simmons, 2002) were used to provide the same view of all specimens and reduce the effects of parallax. Even in this sample, many of the specimens had poor placement of the manus and its digits during fixation, and thus, the hand was not included in the study. Furthermore, because elements of the pectoral girdle were obscured in radiographs due to other bony and soft tissue densities, no data from this anatomical region were collected. Specimens were placed on a flat surface and radiographed in a dorsoventral view using either X-ray film (Hewlett-Packard Faxitron soft X-ray machine and Kodak Industrex MX125 Film, Eastman Kodak Co., Rochester, NY, USA: 35.6 × 43.2 cm) or on a digital machine (INSPEX 20i digital X-ray system with Kevex PXS10-16W micro-focus X-ray source and Varian PaxScan 4030R panel and software, Varian Medical Systems, Inc., Palo Alto, CA, USA). Radiographs were scanned using an Epson Expression 10000XL scanner at 300 or 600dpi depending on the size of the animal. Osteological dimensions were measured on digitized scans of X-ray images or from digital radiographs in ImageJ.

Specimens ranged in size (SVL) from 8.38 to 138.47 mm, a 16-fold range covering the range of sizes of most frog species. Size was removed prior to statistical analysis by using phylogenetic regressions of LOG10 transformed variables on a LOG10 transformation of body length (sum of the head length & vertebral column length to the tip of the urostyle, [BL]) in the R package PHYTOOLS (Revell, 2009, 2012). Both the ‘lambda’ and ‘Brownian motion’ methods were used to obtain the error structure for the linear model; however, only the lambda results are presented as results differed little and we use lambda in additional analyses below. Body size, measured to the posterior end of the pelvis (SVL) was not used because the ilia readily move under the sacrum in many frogs (Emerson, 1979; Emerson & DeJongh, 1980) and are not uniformly formalin fixed in the same anterior or posterior position relative to the sacrum. This variation in the fore–aft position of the ilia relative to the sacrum also allowed us to identify taxa that exhibit ilial translation on X-rays.

Figure 1 illustrates the measurements on a typical radiograph used in this study [relative sacral width (SW); relative diapophyseal expansion (DE); relative pelvis length (PL); relative forelimb length (FLL); relative hindlimb length (HIND)]. To facilitate comparison with previous studies of limb length and to simplify biological interpretation of the statistics, elements of the hindlimb (lemur; tibiofibula; tibiale/fibulare; metatarsal and phalanges of digit 4) were summed to one value (HIND) as were those for the forelimbs (FLL: humerus; radio-ulna). All morphological variables were LOG10 transformed to meet normality assumptions of statistical tests. Genus-level averages of residuals from the phylogenetic regressions were used as the morphological variables in statistical tests below.

Pelvic type

The X-ray images were used to score the pelvic type (sagittal-hinge vs. non-sagittal-hinge) for each genus using the characters recently identified by Reilly & Jorgensen (2011). Sagittal-hinge pelves have dorsal ridges on the urostyle and ilia, narrow/cylindrical diapophyses and anterior tips of the ilia that align consistently with the anterior aspect of the sacral diapophyses to indicate a tight iliosacral connection. Non-sagittal-hinge taxa have distally expanded sacral diapophyses and were
preserved with the ilia fixed in various positions relative to the anterior edges of the diaphyses indicating that the ilia slide fore–aft along the sacrum. The degree of distal expansion of the sacral diaphyses is a qualitative measure that is not to be confused with the DE morphometric measure corrected for body size. Four characteristics were used to diagnose pelvic type: 1 & 2) presence/absence of dorsal ridges on the urostyle and ilia; 3) distal sacral–diaphyseal expansion (narrow/cylindrical vs. expanded diaphyses); and 4) ilial translation (consistently tight connection vs. presence of fore–aft translation). Taxa that did not possess all four of these traits were scored as non-sagittal-hinge, which includes lateral-bender and fore–aft slider morphs (Emerson, 1979; Reilly & Jorgensen, 2011). Family-level states were based on the predominant pelvic type observed across the genera within each family.

Locomotor modes

Locomotor behaviours were estimated for the sample taxa from the literature (Zug, 1978; Emerson, 1979, 1982; Reilly & Jorgensen, 2011), web resources or personal communications from researchers familiar with the natural behaviours of taxa in question. We scored frog genera as hoppers or jumpers based on Emerson’s (1979, 1988) definition of hopping and jumping (greater than or less than nine body lengths per jump based on jump data or general descriptions of taxa). Hoppers were scored as walker/hoppers (WH) with those known to be fossorial termed burrower/walker/hoppers (BWH). Jumpers were divided into terrestrial (JT) and arboreal (climbing; JA) modes. Family-level locomotor modes were based on the locomotor mode with the greatest number of occurrences among the genera sampled in each family (subfamilies for Hylidae) and are indicated in Fig. 2 [squares = hoppers (WH, BWH); circles = jumpers (JT, JA)]. Aquatic frogs (Family: Pipidae) were not included in this study.

Comparative methods

For the phylogeny in the following analyses, we used the topology and branch length data of the Pyron & Wiens (2011) tree and trimmed it to match our 188-genera sample (names based on the taxonomy of Frost, 2011). Branch length information was in the format of substitutions per site. Not all species that we measured were included in the Pyron and Wiens study. In these cases, we used a congeneric taxon from their tree to estimate branch length for our taxon. This was carried out for 39 genera (see Appendix S3).

Phylogenetic ANOVA of skeletal measurements

We calculated Pagel’s lambda (Pagel, 1999) for each measured skeletal trait using the R package GEIGER (Harmon et al., 2008) to test for the phylogenetic dependence among skeletal measurements. In addition, we calculated a single lambda value for the five skeletal traits taken together (Freckleton et al., 2002) using PHYTOOLS (Revell, 2012). Values of Pagel’s lambda are estimated with maximum likelihood and normally range from 0 to 1. The estimated lambda for each trait represents the degree to which trait similarity is dependent upon evolutionary history (1 = trait similarity is directly correlated with evolutionary history; 0 = trait similarity is independent of phylogeny). Significant log-likelihood ratio values of these lambda estimates indicates phylogenetic signal in a trait, whereas a nonsignificant value suggests that trait distribution on the phylogeny is not due to evolutionary history.

We used a phylogenetic MANOVA in GEIGER to test for significant differences in trait values among locomotor groups, which would indicate that skeletal traits differ among locomotor modes throughout the phylogeny. To test for differences in locomotor-mode group means for each skeletal measurement, a phylogenetic ANOVA (Garland et al., 1993) was performed in PHYTOOLS (Revell, 2012). Phylogenetic post hoc t-tests (with Holm sequential Bonferroni correction for multiple groups; Holm, 1979; Revell, 2012) were used to identify which locomotor groups were different for each trait while controlling for phylogenetic effects. The procedure for both the phylogenetic ANOVA and MANOVA consists of first calculating the F ratio (Wilks’ λ for MANOVA) of the trait or data set. A trait or data sets are then simulated 1000 times with a Brownian motion model on the phylogeny to obtain the null distribution of the F ratio (and Wilks’ λ). If the test statistic for the data set is greater than the upper 95th percentile of the simulated null distribution, then we find a significant difference in the trait(s) between locomotor modes across the phylogeny.

Finally, we used phylogenetic principal components analysis (PCA) in PHYTOOLS (Revell, 2012) to examine the distribution of locomotor modes and taxa in phylomorphospace. For the phylogenetic PCA, we incorporated estimates of Pagel’s lambda to transform the phylogeny when intermediate degrees of phylogenetic signal were found in the data set. The phylogenetic PCA of morphological trait residuals assesses the covariation of morphological traits and identifies the axes of greatest morphological variation in frogs. Genus-average PC scores were used in a phylogenetic ANOVA (Garland et al., 1993) to test for differences in covariation of morphological traits across locomotor modes, and phylogenetic post hoc t-tests (as above) were used to determine which locomotor groups were different on each PC axis. We plotted family-level averages of PC scores to simplify visualization of taxa in phylomorphospace and consider the location of a taxon in PCA phylomorphospace to represent its morphological bauplan.
Ancestral character reconstructions

Among the skeletal measurements, one trait (DE) explained the greatest amount of variation in frog phylo-morphospace and distinguished between each of the locomotor modes (JT ≠ JA, WH and BWH). Therefore, we reconstructed the evolution of this trait (scored as a two-state trait: small and large diapophyseal expansion; see Results for explanation) using parsimony in Mesquite version 2.74 (Maddison & Maddison, 2010). The family tree used for the reconstruction was trimmed from the genus-level tree (except Hylidae where three subfamilies were retained) resulting in a tree with 39 taxa (see Appendix S4 for family representatives).

In addition, we used parsimony to trace the two-state pelvic type (sagittal-hinge vs. non-sagittal-hinge) through the phylogeny in Mesquite version 2.74 (Maddison & Maddison, 2010) on family-level means.

Results

Pelvic type

Pelvic types for the study taxa are presented in Fig. 2 [circles: sagittal-hinge (black) vs. non-sagittal-hinge (grey)]. Thirty-one of the families (plus two hylid sub-families) are uniformly of one pelvic type and five families contain 75% or more of their genera with one pelvic type (non-sagittal-hinge: Cycloramphidae = 7/9 genera; Hylidae: Hylinae = 22/23; Leiuperidae = 3/4; sagittal-hinge: Dicroglossidae = 4/5; Pyxicephalidae = 5/7). One family (Hemiphractidae) is split such that two genera possess a sagittal-hinge pelvis, whereas the other two genera have a non-sagittal-hinge pelvis (Fig. 2, split symbol). The ancestral character state reconstruction for pelvic type (sagittal-hinge or non-sagittal-hinge) is indi-

Fig. 2 Family-level (subfamilies within the Hylidae) sampling and scoring of locomotor modes (right column of symbols). Analyses were done on genus level (192 total species), then reduced to family level for illustrations. Results for taxon scores for PC1, mostly sacral diapophyseal expansion (left column: black = DE small, grey = DE large) and pelvic type (middle column: black = sagittal-hinge pelvis, grey = non-sagittal-hinge pelvis). Branch colour indicates character state reconstructions for pelvic type and sacral diapophyseal expansion states (grey or black as in symbols), which were identical except for the Leiopelmatidae and Hemiphractidae. Dashed-line branches indicate cases of small diapophyses in non-sagittal-hinge taxa (see text for explanation). The Hemiphractidae thin-black branch shows only the PC1 (DE) reconstruction because genera were equally split on the pelvic traits.
Relative size differences in skeletal elements across locomotor modes

Locomotor modes for study taxa are presented in Fig. 2. The phylogenetic MANOVA indicated that there are significant differences in phylogenetic size-free trait residuals across locomotor modes ($F = 15.628_{3,188}, P = 0.0009$, means listed in Table 1). Post hoc comparisons using phylogenetic ANOVA’s showed that the forelimb (FLL) and pelvic length (PL) relative to body size did not differ across locomotor modes (Table 1). However, there was some differentiation between the locomotor groups in hindlimb length (HIND: $F = 25.996_{3,188}, P = 0.002$), sacrum width (SW: $F = 20.748_{3,188}, P = 0.007$) and diaphyseal expansion (DE: $F = 56.201_{3,188}, P = 0.001$), although not all of the comparisons were significant. Whereas jumping frogs (JA & JT) tend to have relatively longer hindlimbs than WH and BWH frogs, only the comparisons between jumping and BWH frogs were significant (BWH to JT: $P = 0.006$; BWH to JA: $P = 0.030$). Jumping frogs have relatively narrow sacral widths as compared with BWH and WH frogs, but only the comparison between BWH and JT frogs was significant ($P = 0.018$).

The greatest difference among locomotor modes was in the relative size of diaphyseal expansion. The ranges of mean residuals across locomotor modes (Table 1) showed that diaphyseal expansion was five times more variable across frogs than the other four traits. BWH and WH frogs tended to have relatively greater diaphyseal expansion than jumping frogs, although the only significant difference was that JT frogs had a smaller diaphyseal expansion than the three other locomotor modes (JT to BWH: $P = 0.006$; JT to WH: $P = 0.006$; JT to JA: $P = 0.008$).

Morphological trait covariation and bauplan differences across locomotor modes

The variance explained by principal components and the loadings of size-free trait residuals are presented in Table 2. Phylogenetic ANOVA’s for differences of PC scores among locomotor modes are presented in Table 3. The first principal component explained 65.1% of the variation in the data set and was highly correlated with diaphyseal expansion (DE loading: $-0.99$) and sacral width and pelvic length to a lesser degree (SW: $-0.45$; PL: $-0.48$). It was not surprising then that PC1 revealed significantly less diaphyseal expansion in JT frogs compared with the other three locomotor modes (Table 2), as we found in the univariate tests. Locomotor modes did not differ on the remaining PC axes. The second axis described 15.8% of the variation and was represented mainly by hindlimb length (HIND loading: 0.93) and forelimb length to a lesser degree (FLL: 0.43).

The distribution of locomotor modes on PCs 1 and 2 is presented in Fig. 3 (Data S1). To visualize frog distributions for the entire data set, we plotted the family-level means for PC scores and coded them by their family-level locomotor modes. Given the PC loadings, this represents a relative diaphyseal expansion (PC1) by relative hindlimb length (PC2) phylomorphospace. Statistical results of ANOVA’s on PC scores indicate that the only significant differences across frog locomotor modes is that the JT frogs had relatively smaller diaphyseal expansion for their size than the other locomotor modes (PC1). Scores on PC2 were not significantly different across locomotor modes, but do appear to be

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**Table 1** Differences in size-corrected residuals of pelvic and limb traits across locomotor modes in frogs based on phylogenetic ANOVA’s of 188 genera. Locomotor modes (mean ± 1 SE) grouped by lines are not significantly different (Holm sequential Bonferroni-corrected post hoc tests).

<table>
<thead>
<tr>
<th>Trait/PC-value</th>
<th>BWH</th>
<th>WH</th>
<th>JA</th>
<th>JT</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>DE $P &lt; 0.001$</td>
<td>0.077 ± 0.018</td>
<td>−0.052 ± 0.044</td>
<td>−0.106 ± 0.029</td>
<td>−0.325 ± 0.012</td>
<td>0.402</td>
</tr>
<tr>
<td>Pagel’s $\lambda = 1.0$</td>
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<tr>
<td>HIND $P = 0.002$</td>
<td>−0.004 ± 0.009</td>
<td>−0.001 ± 0.010</td>
<td>0.050 ± 0.007</td>
<td>0.050 ± 0.007</td>
<td>0.084</td>
</tr>
<tr>
<td>Pagel’s $\lambda = 1.0$</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>SW $P = 0.007$</td>
<td>0.028 ± 0.006</td>
<td>0.017 ± 0.011</td>
<td>−0.035 ± 0.010</td>
<td>−0.039 ± 0.006</td>
<td>0.067</td>
</tr>
<tr>
<td>Pagel’s $\lambda = 0.78$</td>
<td></td>
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<tr>
<td>PL $P = 0.079$</td>
<td>0.023 ± 0.007</td>
<td>−0.017 ± 0.009</td>
<td>0.001 ± 0.005</td>
<td>−0.030 ± 0.005</td>
<td>0.053</td>
</tr>
<tr>
<td>Pagel’s $\lambda = 0.76$</td>
<td></td>
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<tr>
<td>FLL $P = 0.284$</td>
<td>−0.002 ± 0.005</td>
<td>0.031 ± 0.008</td>
<td>−0.006 ± 0.005</td>
<td>−0.004 ± 0.007</td>
<td>0.037</td>
</tr>
<tr>
<td>Pagel’s $\lambda = 0.51$</td>
<td></td>
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<tr>
<td>Pagel’s $\lambda$ for combined traits = 0.91</td>
<td></td>
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</tbody>
</table>
reflecting some of the differences in hindlimb length revealed by the univariate tests (Table 1). Hindlimb length tended to be greater in jumping frogs (JA & JT), but this is affected by outliers in JT, JA and BWH locomotor modes. The significantly shorter BWH hindlimb length (relative to JA & JT frogs) is apparent in the PC2 family distribution.

To understand some of the variation in this phylomorphospace, we plotted zones delimiting patterns of variation on PC1 and PC2. On PC1, we plotted the mean ± 1 SD for JT frogs (vertical dashed lines: –0.329 ± 0.088 SD in Figs 3–6). We considered any taxon to the left of the JT mean plus 1 SD on PC1 to have a small diapophyseal expansion and those to the right (>1 SD) to have significantly larger diapophyseal expansion, resulting in two discrete character states for diapophyseal expansion. These character states are mapped on the phylogeny (Fig. 2) as black (small diapophyseal expansion) or grey (large diapophyseal expansion) symbols, respectively, and the ancestral character states are reconstructed in Figs 2, 4–6 using corresponding branch colours. This PC1 character reconstruction was identical to the pelvic-type reconstruction except for two families (Leiopelmatidae and Hemiphractidae).

To identify outliers on PC2, we plotted the mean ± 1 SD for the PC2 scores of all taxa combined (horizontal dashed lines: 0.004 ± 0.067 in Figs 3–6). Although locomotor groups could not be statistically distinguished from one another on PC2, 32 of the 37 frog families examined fell within one standard deviation of the mean on this axis and visible gaps separated outliers (Fig. 2). Thus, we considered taxa outside one standard deviation of the PC2 mean to be outliers exhibiting extremely long or short hindlimbs relative to body size.

**Table 2** Loadings, per cent variance explained by each PC axis, and eigenvalues for each of the morphological traits used in the phylogenetic PCA.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residual SW</td>
<td>–0.4511</td>
<td>0.1506</td>
<td>0.8025</td>
<td>0.0387</td>
<td>–0.3579</td>
</tr>
<tr>
<td>Residual DE</td>
<td>–0.9947</td>
<td>0.0360</td>
<td>–0.0735</td>
<td>–0.0605</td>
<td>–0.0020</td>
</tr>
<tr>
<td>Residual PL</td>
<td>–0.4798</td>
<td>0.2553</td>
<td>–0.1166</td>
<td>0.8317</td>
<td>0.0053</td>
</tr>
<tr>
<td>Residual FLL</td>
<td>–0.2294</td>
<td>0.4296</td>
<td>0.5021</td>
<td>–0.0169</td>
<td>0.7143</td>
</tr>
<tr>
<td>Residual HIND</td>
<td>0.2960</td>
<td>0.9322</td>
<td>–0.1479</td>
<td>–0.1003</td>
<td>–0.1062</td>
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<tr>
<td>Percent variation</td>
<td>65.1</td>
<td>15.8</td>
<td>8.5</td>
<td>5.7</td>
<td>4.8</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>0.0436</td>
<td>0.0106</td>
<td>0.0056</td>
<td>0.0037</td>
<td>0.0032</td>
</tr>
</tbody>
</table>

**Table 3** Differences in phylogenetic PC scores across locomotor modes in frogs based on phylogenetic ANOVA’s of 188 genera. Locomotor modes (mean ± 1 SE) grouped by lines are not significantly different (Holm sequential Bonferroni-corrected post hoc tests).

<table>
<thead>
<tr>
<th>Axis/P-value</th>
<th>BWH</th>
<th>WH</th>
<th>JA</th>
<th>JT</th>
</tr>
</thead>
<tbody>
<tr>
<td>PC 1</td>
<td>0.089 ± 0.018</td>
<td>–0.045 ± 0.044</td>
<td>–0.113 ± 0.029</td>
<td>–0.329 ± 0.012</td>
</tr>
<tr>
<td>P &lt; 0.001</td>
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<tr>
<td>PC 2</td>
<td>–0.019 ± 0.008</td>
<td>0.006 ± 0.012</td>
<td>0.033 ± 0.008</td>
<td>0.013 ± 0.007</td>
</tr>
<tr>
<td>P = 0.375</td>
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<td>PC 3</td>
<td>0.012 ± 0.006</td>
<td>0.040 ± 0.010</td>
<td>–0.021 ± 0.008</td>
<td>0.022 ± 0.007</td>
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<td>P &gt; 0.255</td>
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variation in the multivariate phylomorphospace of the frog skeleton (Tables 1 and 2). In both the univariate (Table 1) and multivariate (Table 3) analyses, JT frogs had significantly smaller diaphyseal expansion compared with the remaining three locomotor modes. In fact, a small diaphyseal expansion is generally a good predictor of the JT locomotor mode. All JT families (except Hylidae: Pelodryadinae) were within one standard deviation of the JT mean on PC1 (Fig. 3) and had a sagittal-hinge pelvic (Fig. 2). This included independent transitions to JT modes with narrow sagittal-hinge pelves in two ranoid and three hyloid families (Fig. 2). Pelodryadinae (Litoria nasuta) is the only JT group with large diaphyseal expansion and a non-sagittal-hinge pelvis. A second finding, contrary to previous work (Emerson, 1988), is that relative hindlimb length did not play a major role in frog skeletal variation across most frogs. Hindlimb length was not significantly different between most locomotor mode comparisons (Table 1). The notable exceptions were that BWH frogs had relatively shorter hindlimbs than both JA and JT frogs. Although HIND was the primary variable driving PC2 (Table 2), this axis only accounted for a small percentage of the variation and exhibited no significant differences among the locomotor modes (Table 3). Using one standard deviation of PC2 scores as a cut-off revealed one derived shorter-hindlimb BWH family, one derived long-hindlimb BWH (Pelodytidae) and four jumping families (2 JT and 2 JA) among the longer HIND outliers (Fig. 3).

The dominant contribution of diaphyseal expansion in frog phylomorphospace (i.e. the observation of small or large diaphyseal expansion on PC1) is matched by the dichotomy in sagittal-hinge vs. non-sagittal-hinge pelvic types. This is congruent with Emerson’s (1979) separation of sagittal-hinge (narrow; rod like; tightly connected) from lateral-bender and Reilly & Jorgensen’s (2011). The leioptlamatids and heleophrynids are found on the left and the alytids occupy the centre of the plot indicating small-to-moderate diaphyseal expansion and average relative hindlimb lengths. The Palearctic alytids occupy the middle of the PC plot (on the origin), suggesting that they are representative of the average anuran phenotype with average-sized diaphyses and average hindlimb lengths. These frogs are walker–hoppers and known for their forward burrowing (Brown & Crespo, 2000), but their central position in phylomorphospace reveals nothing about their limbs or pelvis that would indicate any morphological specialization for this behaviour. Heleophrynidae is the outgroup to Neobatrachia and lies between the Leiopelmataidae and Alytidae on the plot, retaining the average bauplan and WH mode.

In addition to families in this central phylomorphospace region, the basal taxa have evolved at least three more different morphologies. First, the Middle American rhinophrynids and Nearctic scaphiopodids have convergently evolved larger diaphyseal expansion and relatively shorter hindlimbs, which appears to relate to their ecology. Both taxa also converged on a strategy of spending much of their life underground and emerging from their burrows only to forage and breed (Pearson, 1955).

Second, the Bombinatoridae and Megophryidae have converged into similar large diaphyseal expansion space. The former family has spread over the Palearctic region, but the megophryids are the most speciose group of basal frogs (156 species) and have radiated across the
Fig. 4 Patterns of diapophyseal expansion (PC1) and hindlimb length (PC2) in basal frog taxa. Phylomorphospace phylogenies are used only to illustrate family-level relationships; branch lengths/orientations do not represent amount or direction of evolutionary change in the plot. Distinctions set up in Fig. 3 for PC1 and PC 2 delineate small vs. large diapophyseal expansion and outliers in relative hindlimb length indicated as long (+) on the phylogeny. Black branches on the phylogeny indicate transitions from a large diapophyseal expansion with non-sagittal-hinge pelvic traits to a small diapophyseal expansion with sagittal-hinge pelvic traits. Dashed-line branches indicate cases of small diapophyses in non-sagittal-hinge taxa (see text for explanation).

Fig. 5 Patterns of diapophyseal expansion (PC1) and relative hindlimb length (PC2) in the Ranoidea. Phylomorphospace phylogenies are used only to illustrate family-level relationships; branch lengths/orientations do not represent amount or direction of evolutionary change in the plot. Distinctions set up in Fig. 3 for PC1 and PC 2 delineate small vs. large diapophyseal expansion and outliers in relative hindlimb length indicated as short (−) on the phylogeny. Black branches on the phylogeny indicate transitions from a large diapophyseal expansion with non-sagittal-hinge pelvic traits to a small diapophyseal expansion with sagittal-hinge pelvic traits. The Natatanura have shifted to small diapophyses and a sagittal-hinge pelvis even when locomotor mode changes back to BWH, whereas the Allodapanura retain large diapophyses with one transition to the small state and sagittal-hinge pelvis. Note that limb length is uniformly average in the Ranoidea except in Brevicipitidae (−).
lush forests and streams of southern and Southeast Asia (Wells, 2006). These frogs are characterized by walking and hopping behaviour, but are not good jumpers or effective burrowers. Instead, they rely on their mimicry of forest floor leaves to escape visual predators (Duellman & Trueb, 1986; Wells, 2006).

Third, the pelodytids, Palearctic sister group to the megophryids, have evolved both more expanded diapophyses and longer hindlimbs. The occurrence of long instead of short hindlimbs in the Pelodytidae makes them perhaps the most derived BWH frog, and functional data are needed to understand the role of their long legs in burrowing.

Rhinophrynidae together with the fully aquatic species of the family Pipidae (excluded from this analysis) make up the extant families in the Xenoanuran lineage. Although pipids were not used in the current morphometric analysis, a few general points about their pelvic morphology are worth discussion. The entire skeleton of both groups is dense and robust (pers. observation), and the short hindlimbs found in \textit{Rhinophrynus} paired with strong bones allow it to dig deep into soil where it spends most of its life aestivating in Neotropical savannah or consuming ants and termites in its burrows (Trueb & Gans, 1983). Pipids have extremely expanded bony diapophyses in addition to many other derived
skeletal traits, and the extreme fore–aft motion of the pipid pelvis as described by Palmer (1960) was used as a model for Emerson’s fore–aft slider morph pelvis. In our preliminary analyses that included three pipid taxa, they had average HIND values, but mapped well to the right of the Bombinatoridae, Megophryidae and Pelodytidae for diaphyseal expansion in Fig. 4. Pipids were omitted from our analysis because incomplete taxon sampling (n = 3; Pipa; Silurana; Xenopus) coupled with a novel locomotor mode (aquatic) violated test assumptions, which state that the number of observations within a group should be greater than the number of dependent variables (> 5 in this case; Tabachnick & Fidell, 1996). However, with our knowledge of pipid diaphyseal morph, it appears that at least three different basal families have independently developed very large diaphyseal expansion – one radiation in southeast Asia and Europe (Pelodytidae), one in northern Asia and Europe (Bombinatoridae) and one aquatic radiation in Africa and South America (Pipidae).

Ranoidea

Figure 5 shows evolution of locomotor modes and family placement in phylomorphospace in the Ranoidea. Based on the identical pelvic type and sacral expansion reconstructions for the Ranoidea, the common ancestor of the Natatanura shifted to a JT locomotor mode with a small diaphyseal expansion and sagittal-hinge type pelvis while retaining average relative hindlimb lengths. This major African radiation has maintained a rather constrained position of the frog phylomorphospace, but the radiation into the cosmopolitan Ranidae appears to be moving to somewhat longer relative hindlimb-length phylomorphospace. The sagittal-hinge pelvis and JT locomotion has dominated the group, whereas the BWH locomotor mode has reappeared in the family Ceratobatrachidae (and some pyxicephalids and dicroglossids, see below). Concordant with their BWH behaviour, these families are trending towards larger diaphyses although they are still within the JT range, but all the ceratobatrachids and most of the pyxicephalids and dicroglossids retain sagittal-hinge pelvic characters. Some genera in both the Pyxicephalidae (2/7 genera in our sample) and the Dicroglossidae (1/5 genera in our sample) have lost components of the sagittal-hinge system and are BWH frogs. In the Pyxicephalidae, Tomopterna and Cacosternum have lost the ilial ridges and have ilial translation on the sacrum. In the Dicroglossidae, the genus Sphaerotheria also clearly has ilial translation on the sacrum and is a BWH frog, but retains its ilial and urostyle ridges.

Finally, in the Natatanura, there is a shift to arboreality in the Rhacophoridae with no shift in the JT sagittal-hinge frog bauplan. Instead, the rhacophorids have developed expanded toe pads, intercalary cartilages and other derived phalanx morphologies concordant with their arboreal habits (Liem, 1970; Manzano et al., 2007; Kamermans & Vences, 2009). In fact, the convergence in external morphology between the phylogenetically disparate hylid and rhacophorid tree frogs can be so extreme that one must examine phalanx and pectoral girdle morphology for correct family-level placement (Kamermans & Vences, 2009). We suggest that rhacophorid sagittal-hinge pelvis morphology can also help to differentiate these natatanurans from the hylids.

The Allodapanura is dominated by the cosmopolitan Microhyliidae with ~500 species and more genera (68) than any other frog family. This massive frog radiation, along with the Hemisotidae has retained average hindlimb lengths, a non-sagittal-hinge pelvis and straddle the BWH group mean for PC1. The BWH mode is the most common for the microhyliids with many taxa using shallow refuges under leaves, stones or other forest debris. Although some genera are forward or backwards burrowers that spend life underground (Emerson, 1976), there does not appear to be strong selection for shorter hindlimbs or wider sacral expansion observed in some burrowing basal taxa and in the hylids. Even the hemisotids, which possess derived skull and pectoral girdle morphology for unique forward-burrowing behaviors (Emerson, 1976) lack any major changes in hindlimb length or pelvic traits. The Brevicipitidae is the only family in our allodapanuran sample to evolve shorter hindlimbs and larger diaphyseal expansion, which appears to be related to its more specialized burrowing function.

The remaining families in our allodapanuran sample (Hyperoliidae and Arthroleptidae) share a common ancestor that shifted to small diaphyseal expansion and a sagittal-hinge pelvis. However, the Arthroleptidae are terrestrial jumpers, whereas the Hyperoliidae (and leptopelid arthroleptids) are arboreal jumpers similar to the Asian tree-frog family Rhacophoridae in developing climbing adaptations in the manus and pes (Manzano et al., 2007; Kamermans & Vences, 2009).

Hylidea

Patterns of locomotor evolution in the Hylidea are illustrated in Fig. 6. The Hylidea is the most morphologically diverse group of frogs and is limited to new world distributions except for the Australobatrachians, Australo-Papuan distribution of the pelodyridnine hylids and the cosmopolitan bufonids.

There is a series of WH taxa possessing large diaphyseal expansion and a non-sagittal-hinge pelvis that retain the primitive condition from the outgroup Heleophrynidae. These include the Brachycephalidae and three families in the Leptodactyliformes (Ceratophryidae; Cycloramphidae; Leiuperidae) that trend towards small sacral diaphyses (see below).

There are three kinds of hylid burrowers. The basal Australobatrachia are BWH frogs with average
diapophyseal expansion and non-sagittal-hinge pelvic traits. Within this group, the Limnodynastidae have shorter relative hindlimb lengths than the rest of the hylodean taxa and their sister, Myobatrachidae has evolved even shorter hindlimbs and fossorial habits shared by the rhinophrynids and brevicepitids in this general phylomorphospace. The third BWH frog group is the Bufonidae, which has radiated worldwide and maintains average hindlimb lengths, but differs in having evolved a larger diapophyseal expansion.

Hyloid JT frogs

There are four different JT hyloids that possess small diapophyseal expansion and a sagittal-hinge pelvis. Two are found in the Terrarana, a diverse group of direct-developing Neotropical frogs (~900 species, about a sixth of all frog species; Gonzalez-Voyer et al., 2011; Hedges et al., 2008). The Eleutherodactylidae, Strabomantidae and Craugastoridae maintain the condition from a common ancestor that evolved small diapophyses, sagittal-hinge pelvic traits and a JT locomotor mode. Eleutherodactylidae and Strabomantidae represent one type of hyloid JT frog with morphologies strikingly similar to nataianuran JT frogs. However, the Craugastoridae represent a second form of hyloid JT frog, unique in having also evolved extremely long relative hindlimb length.

Within the Leptodactyliformes, two other families (the Leptodactylidae and Dendrobatidae) have also shifted to small diapophyses, sagittal-hinge pelvic traits and a JT locomotor mode. Leptodactylids and the leiuiperids share similar diapophyseal space (although Leiuiperidae lies outside of JT diapophyseal space), but only the Leptodactylidae gained the other sagittal-hinge traits; the leiuiperids retain smooth ilia and urostyles with a moveable sacroiliac joint consistent with WH locomotion. The Dendrobatidae are the fourth JT hyloid family average lies in a PC space that just parallels one taxon from the pelodryadinine hylids, Litoria nasuta. Although externally this frog would appear similar to a ranid JT frog, internally, it retains a pelvis typical of most hylids with a large diaphyseal expansion and non-sagittal-hinge pelvic traits. However, it differs in several regards. Litoria nasuta is terrestrial rather than arboreal, has the second longest relative hindlimb length of any frog that we measured (first is a bufonid, Leptophryne borbonica) and has gained the common name ‘Rocket Frog’ due to its exceptional jump performance (55.2 body lengths per jump; James & Wilson, 2008) used to evade predators. This frog outperformed ranid taxa in Zug’s study by four-fold distance and they accomplished this with expanded diapophyses and a non-sagittal-hinge pelvis, suggesting that extreme hindlimb length alone can be a major factor in determining jump performance. Finally, although a terrestrial frog, it retains remnants of the hylid toe pad configuration.

Hyloid tree frogs

There are four kinds of hyloid tree frogs and they are dominated by large diapophyseal expansion and non-sagittal-hinge pelvic traits (except the hemiphractids, which have a mix of pelvic traits).

Two tree frog types are found in the Hylidae, a family that includes about one sixth of all frog species. Hylids possess intercalary cartilages between their distal and penultimate phalanges that aid in climbing. Most hylid taxa are arboreal jumpers and outperform most terrestrial frogs (Zug, 1978). The Hylinae, a subfamily that contains the majority of the hylid taxa, are characterized by strikingly average body types with moderately expanded diapophyses and average hindlimb lengths (Fig. 6). Thus, this type of generic hyloid tree-frog pelvis differs little from a basal WH condition in phylomorphospace. The Phyllomedusinae makes up the second type of hylid that has a slightly larger diapophyseal expansion. In addition to jumping, these arboreal frogs are capable walkers (Duellman, 1968) and their slightly longer hindlimbs and hypothesized increase in lateral-bending ability potentially afforded by greater diapophyseal expansion may support this behaviour.

The Centrolenidae comprise the third type of tree frog, found in the Leptodactyliformes. Frogs of this family retain the moderate diapophyseal expansion and non-sagittal-hinge pelvic traits, but have evolved very long relative hindlimb length. The centrolenids are convergent with the Pelodryadinae in both pelvic and hindlimb phylomorphospace. Unfortunately, there are no jump-performance data to compare with the Pelodryadinae to test the hypothesis that extreme hindlimb length alone can be a major factor in determining jump performance.

The fourth hyloid tree frog is in the family Hemiphractidae. Although this Neotropical group is united by reproductive behaviour (Duellman and Trueb, 1986), we found pelvic traits to be unevenly distributed among genera. Although all are scored as arboreal jumpers, two of the four genera we sampled (Flectronotus and Gastrotheca) had non-sagittal-hinge pelvic traits, whereas the other two (Hemiphractus and Stefania) clearly had a full component of sagittal-hinge traits. The family average lies in a PC space that just puts them in the small diapophyseal expansion category with long hindlimbs. However, when separated, the non-sagittal-hinge Flectronotus and Gastrotheca (arboreal taxa) are placed nearer hyline phylomorphospace with average diapophyseal expansion and HIND, whereas Hemiphractus and Stefania (more terrestrial/
scansorial taxa) are placed much closer to the Craugastoridae (small DE and long HIND). Difference in phylomorphospace and pelvic states appear to be signalling some differences in this family that may be related to difference in both jumping performance and locomotor modes, both of which require further study.

**Does hindlimb length relate to jumping distance?**

Across the range of average hindlimb lengths, we see similar jumping performance in terms of body lengths per jump [Ranidae, 12.5; Dendrobatidae, 11.7; Eleutherodactylidae, 11.0; Hylinae, 14.6; Microhylidae, 10.8 (family means from Zug, 1978)]. The uniformity of jumping performance across the five taxa mentioned above spanning three sagittal-hinge and two non-sagittal-hinge groups suggests that pelvic type does not relate to a difference in jumping performance. However, in the Hylidae, differences in jumping performance between the average relative hindlimb hyline (14.6) and the long-legged *Litoria nasuta* (Pelodyridinae, 55.2) provides evidence that longer hindlimbs result in greater jumping distance, especially given their similar pelvic configurations. Data on the long-legged outliers (craugastorids, hemiphractids, centrolenids) are needed to further inform this observation and understand the relationship between longer relative hindlimb lengths and better jumping performance across pelvic types.

There appears to be a relationship between hindlimb length and body mass that affects jumping performance in frogs of similar relative hindlimb lengths. For example, within the 12 species of ranids studied by Zug (1978), four had mean relative jumping distances less than nine (technically hoppers) and eight were jumpers ranging from 9.5–18.6 body lengths per jump. Thus, there is a doubling of jumping performance within the fairly static bauplan of this genus. From local species studies, we know that jumping performance can be predicted by simple ballistics, muscles are operating under predictable effects of body size and temperature and jumping power exceeds power available from muscles and therefore energy storage systems are in play in the limbs (Marsh, 1994; Roberts et al., 2011). Yet, more comparative studies are needed to identify what is different about ranid hindlimbs across a two-fold difference in jump distance and among other taxa as well. For example, shorter jumping performance in bufonids (4.2 body lengths/jump) and *Bombina* (3.8) compared with ranids (12.5) was posited to be related to intrinsic differences in muscle fibre composition and lower overall muscle mass (Marsh, 1994; Choi & Park, 1996). However, the microhylids with hindlimbs similar to the bufonids (Figs 5 and 6) have the same jump distance (10.8 body lengths/jump) and average mechanical power output per kilogram as the ranids (Marsh, 1994). How do their legs move them twice as far as bufonids?

Clearly, more comparative work is needed on the details of hindlimb design and relative hindlimb length in relation to body size and jumping distance in frogs. It seems that some taxa have indeed shifted to much longer hindlimbs, but they have not been the models used for the study of frog jumping physiology and energy-storage mechanisms. It is probable that frogs with different ecological demands for jumping in their overall locomotor mode will differ in relative hindlimb lengths, muscle architecture, energy-storage mechanisms, fibre-type distribution, motor patterns and limb kinematics – all of which are needed to serve their locomotor needs (James et al., 2007).

**Frog morphometrics and locomotor modes**

For this initial family-level analysis, we chose to follow Emerson’s early work by using four generalized locomotor-mode categorizations based on the primary behaviour we could collect from the literature. Until a more rigorous quantitative behavioural system for defining frog locomotor modes emerges, this system remains useful. However, there is still a paucity of jumping-distance data and behavioural locomotor data for most frog species. Even with these simple locomotor modes, we made several important observations on the distribution of frog bauplans.

First, the shape of the frog sacrum gives us the most insight into differences among locomotor modes. The expanded sacrum, non-sagittal-hinge WH and BWH frogs are basal, remain viable across the frog phylogeny and provide the stock from which all other pelvic types have evolved. Second, the dichotomy we found in pelvic morphs (small DE: sagittal-hinge vs. large DE: non-sagittal-hinge) relates to a clear separation of locomotor modes, as all JT families were the former (except the subfamily, Pelodyridinae) and the WH/BWH frogs are the latter. Therefore, there appears to be strong selection for a small diaphyseal expansion and the sagittal-hinge traits in frogs that evolve into generalized terrestrial jumpers (except Pelodyridinae) as they appear in concert regardless of phylogenetic origin. However, these traits do not limit frogs to the JT mode (at least in the Ranoidea) where both sagittal-hinge radiations have spawned sagittal-hinge arboreal taxa (Rhacophoridae and Hyperoliidae). Furthermore, the sagittal-hinge pelvis *per se* is not related to better jumping performance. Third, hindlimb length was the next most relevant morphological character to frog locomotion, but it exhibits far less variation than the sacrum. Most frogs have the same relative hindlimb lengths in relation to their body size. Shorter limbs were always associated with more fossorial habits. Although most tree frogs (Hyloidea and Ranoidea) have average relative hindlimb length, the moderately high outliers included two of the four hyloid tree-frog radiations. The Craugastoridae and Pelodyridinae were identified
as the most derived frogs in terms of their relatively long hindlimbs and JT mode, and they seem to share a new locomotor niche. Forelimb length and pelvic length were conserved across frogs.

Although Emerson characterized the different frog pelvic types, there still remain many morphological deviations from these that have yet to be defined or studied in the context of locomotor function. The present set of traits we used to define the non-sagittal-hinge pelvis does not distinguish between Emerson’s lateral-bender and fore–aft slider morphs, which she distinguished by attachment points of the dorsal ligament connecting the ilial shafts to the sacrum. We could not score ligaments from radiographs, but our findings from numerous dissections suggest that Emerson’s ligament trait is an oversimplification biased in part by the derived condition in the pipids. It is clear that the hyloids are more similar to lateral benders than pipids, and work is underway to quantify morphological differences among the non-sagittal-hinge pelves. In addition, as Emerson (1982) noted and we noticed in our survey, there are additional characteristics of the transverse processes on the posterior presacral vertebrae, the postero-dorsal angle of the sacral diapophyses and aspects at the anterior of the urostyle that clearly distinguish non-sagittal-hinge from sagittal-hinge pelves.

Finally, the function of the different pelvic designs is not understood. The hypotheses for a lateral-bending, fore–aft sliding or sagittal-hinge pelvis (Emerson & DeJongh, 1980) have not been tested and variation in muscle architecture and motor patterns across pelvic types or locomotor modes has not been described. The ecological relevance of locomotor mode has not been investigated and landing dynamics have only recently begun to be studied (Essner et al., 2010; Gillis et al., 2010). These and other studies assessing how different frog taxa move in various habitats and under different environmental pressures may eventually help to explain how this diverse group of amphibians has been able to fill so many ecological niches with such radical transformation in pelvic design.

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References


Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Specimens examined.

Appendix S2 Proportion of familial diversity examined.

Appendix S3 Substitute taxa used.

Appendix S4 Family representatives for ancestral character reconstruction.

Data S1 Genus-level data set.

Data deposited at Dryad: doi: 10.5061/dryad.d03nf

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