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Supplementary Information for

Evolution of hyperossification expands skull diversity in frogs

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Dataset S1

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Supplementary Methods

Scanning.

All scans were run using a 180kv x-ray tube containing a diamond-tungsten target, with the voltage, current, and detector capture time adjusted for each scan to maximize absorption range for each specimen. Raw x-ray data were processed using GE's proprietary datos|x software version 2.3 to produce a series of tomogram images and volumes, with final voxel resolutions ranging from 1 to 76 µm. The resulting microCT volume files were imported into VG StudioMax version 3.2.4 (Volume Graphics, Heidelberg, Germany), the skull isolated using VG StudioMax's suite of segmentation tools, and then exported as high-fidelity shape files (ply format).

Species sampling.

Of the 158 taxa in our dataset, three scanned museum specimens are only identified to genus: CAS 250653 (*Amietia*), CAS 156600 (*Capensibufo*), and CAS 7265 (*Kassina*). These taxa were treated as *Amietia amietia*, *Capensibufo rosei*, and *Kassina senegalensis* in order to be incorporated into the phylogenetic comparative analyses.

Ancestral state reconstructions.

The models were assigned an equal prior probability using a uniform set-partitioning prior, and the root state frequencies were estimated using a flat Dirichlet prior. The rates of hyperossification gain and loss were drawn from an exponential distribution with a mean of 10 expected character state transitions over the tree. The MCMC was run for 22,000 iterations, the first 2000 iterations were discarded as burn-in, and samples were logged every 10 iterations. Convergence of the MCMC was confirmed by using Tracer v1.6 to ensure that analyses had reached stationarity. The scripts for the analyses are available in the code repository at https://github.com/dpaluh/hyperossification.

Geometric morphometrics.

All three-dimensional geometric morphometric analyses were completed in the R package geomorph version 3.0.3 (1). The scripts and landmark data for all analyses are available in the code repository at https://github.com/dpaluh/hyperossification.

Landmarking. Thirty-six fixed landmarks were digitized on each shape file corresponding to homologous and repeatable points (Fig. S1). Landmarks 1–4 correspond to the foramen magnum, landmarks 5–6 correspond to the posterior extent of the skull roof, landmarks 7–8 correspond to the occipital condyles, landmarks 9–12 correspond to the parasphenoid, landmarks 13–14 correspond to the posterior extent of the jaw joint (quadrate), landmarks 15–16 correspond to the posterior extent of the squamosal (otic ramus), landmarks 17–18 correspond to the anterior extent of the squamosal (zygomatic ramus), landmarks 19–20 correspond to the preorbital process of the maxilla, landmarks 21–22 correspond to the maxillary process of the nasal, landmarks 23–28 correspond to the premaxilla, landmarks 29–30 correspond to the anterior extent of the nasals, landmarks 31–32 correspond to the anterolateral extent of the sphenethmoid (anterior region of skull roof), landmarks 33–34 correspond to the posterolateral extent of the frontoparietal otic flange (posterior region of skull roof), and landmarks 35–36 correspond to the anterior extent of the sphenethmoid. These landmarks were chosen to capture the external shape diversity of frog skulls, and therefore, no landmarks were placed on the elements that form the internal structure of the cranium (e.g., pterygoid, neopalatine, vomer). A future avenue of research is to measure the relative shape and size of these internal elements to test if hyperossification and expansion of the external cranial structures are correlated with the reduction of the internal structures due to an upper limit to the amount of bone that can be invested in the skull, as hypothesized by Trueb (2).

Skull shape diversity and hyperossification. To better characterize skull diversity across all frog families, we tested for phylogenetic signal in shape and centroid size using the Procrustes tangent coordinates. We performed a phylogenetic multivariate analysis of variance (MANOVA) to test if mean shape differed between hyperossified and non-hyperossified taxa to identify the presence or absence of morphological divergence between these two groups. We also estimated morphological disparity and net rates of skull shape evolution for hyperossified and non-hyperossified species to test if there is a significant difference in Procrustes variance and morphological evolutionary rates between these two groups.

Allometry. We conducted a phylogenetic regression to examine the relationship between skull centroid size (the square root of summed squared distances of landmarks from the configuration centroid [3]) and skull shape. A phylogenetic MANOVA was conducted to test if there is a significant interaction between hyperossification and centroid size in influencing skull shape. We also tested for allometric slope differences between hyperossified and non-hyperossified frogs to identify whether there is a different size to shape relationship for hyperossified taxa. A multivariate regression plot was generated to visualize these relationships.

Microhabitat. Previous work has proposed that microhabitat use is correlated with skull shape (2, 4) and that hyperossification may function to prevent evaporative water loss (4, 5). An ideal metric to test the relationship between hyperossification and osmoregulation would be rates of evaporative water loss across taxa (5), but unfortunately, these data are available for very few species. Alternatively, we test if microhabitat use is correlated with skull shape and has a significant interaction with hyperossification after accounting for each main effect using a phylogenetic MANOVA. Microhabitat data for the species in our dataset were largely gathered from Moen et al. (6), IUCN (7), and AmphibiaWeb (8) and divided into four categories: aquatic, arboreal, fossorial, and terrestrial (see Dataset S1 for data and references on individual species). Moen et al. (6) additionally categorized species as semi-aquatic, semi-arboreal, and torrential; these taxa were coded as aquatic, arboreal, and aquatic, respectively, in our analyses. If cranial hyperossification primarily functions to prevent evaporative water loss, we predicted that it should be rare in aquatic frogs but common in burrowing frogs, which often live in highly arid environments.

Feeding biology. Most anurans are considered generalist, gape-limited predators that consume any prey that fits within their mouths, but a subset of species have specialized diets. For example, a specialization of eating termites and ants has repeatedly evolved in frogs (9). Conversely, some frog species have evolved specialized diets that include large, hard prey items, including vertebrates (10). Cranial hyperossification may have evolved in these often large-bodied frogs to strengthen the skull so that it can withstand higher forces during feeding of large prey (2). We identified the diet of frogs in our dataset through a review of the literature (see Dataset S1 for data and references on individual species); species are classified as vertebrate predators if a record of vertebrate predation is known or as invertebrate predators if no records of vertebrate predation exist. Many anuran species lack dietary records (78 of 158 species in our dataset have no published records to our knowledge), and these species were presumed invertebrate predators in our analyses because most frogs are generalist insectivores (10). We additionally classified species as vertebrate predators, invertebrate predators, and unknown diet for the following analyses, which did not influence results (see Table S5, Table S6, Fig. S7). We conducted a phylogenetic MANOVA to test if anuran vertebrate predators and invertebrate predators differ in skull shape and to determine if a significant factor interaction exists between hyperossification and vertebrate predation. The presence or absence of odontoid fangs on the lower jaw was recorded for all specimens in our dataset, as these structures may be associated with a specialized diet that contains a high proportion of large prey (11).

Phragmosis. Phragmotic behavior occurs when an animal uses their head to fill cavities or block holes (12, 13). Anurans that use phragmosis can flex their head at a 90-degree angle relative to their body to the plugging of holes (14). Several frog species use phragmosis in bromeliads, rock crevices, or burrows, and it has been suggested that a close association exists between this behavior and an enlarged hyperossified skull to create an effective barrier against both predators and desiccation (13). We identified frog species that have phragmotic behavior through a review of the literature (Appendix S1, Dataset 1) and conducted a phylogentic MANOVA to test if phragmotic behavior is associated with skull shape and has a significant interaction with the presence of hyperossification.

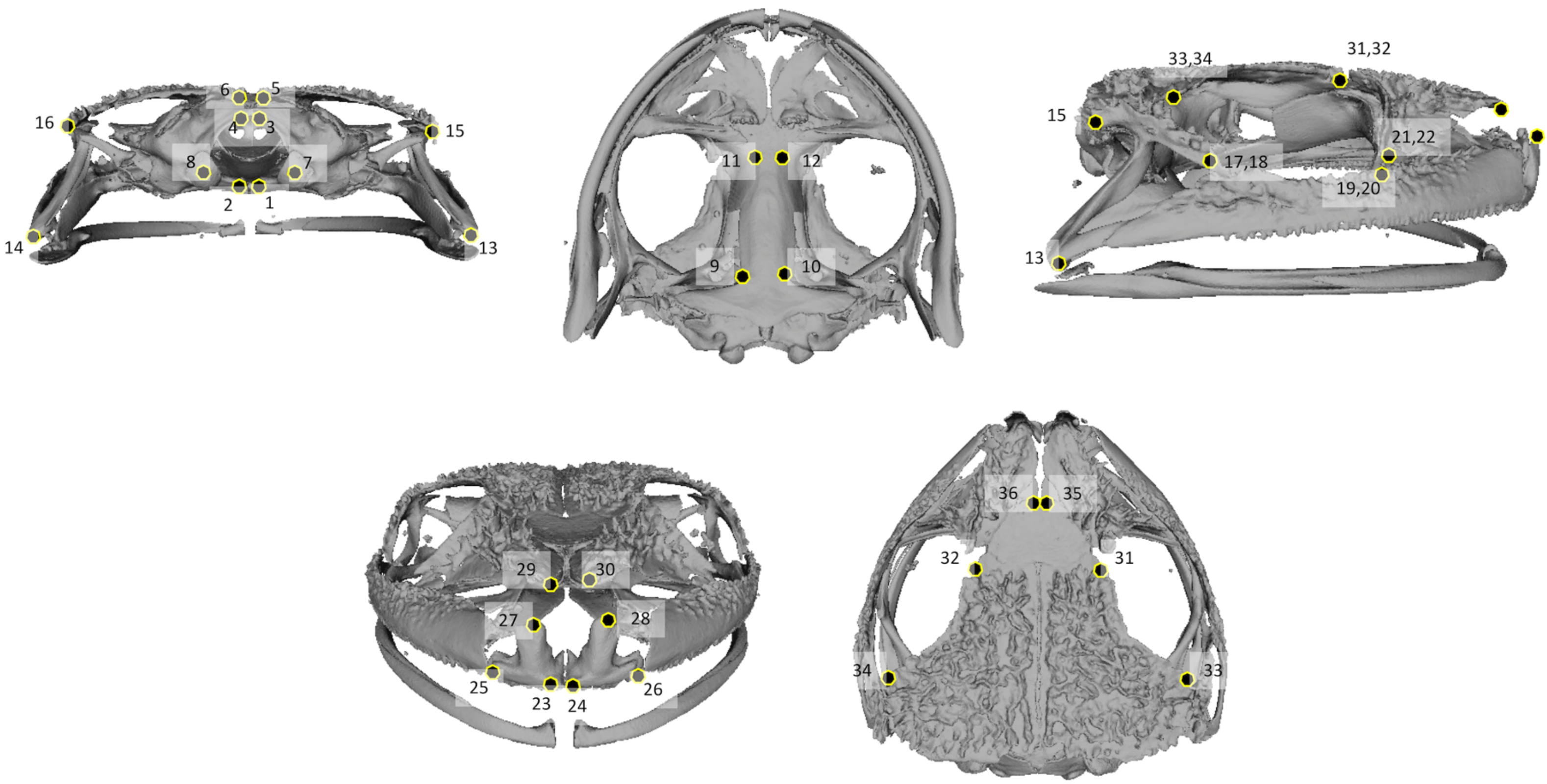

Figure S1. Thirty-six fixed landmarks digitized onto each specimen. See Supplementary Methods for description of landmark points.

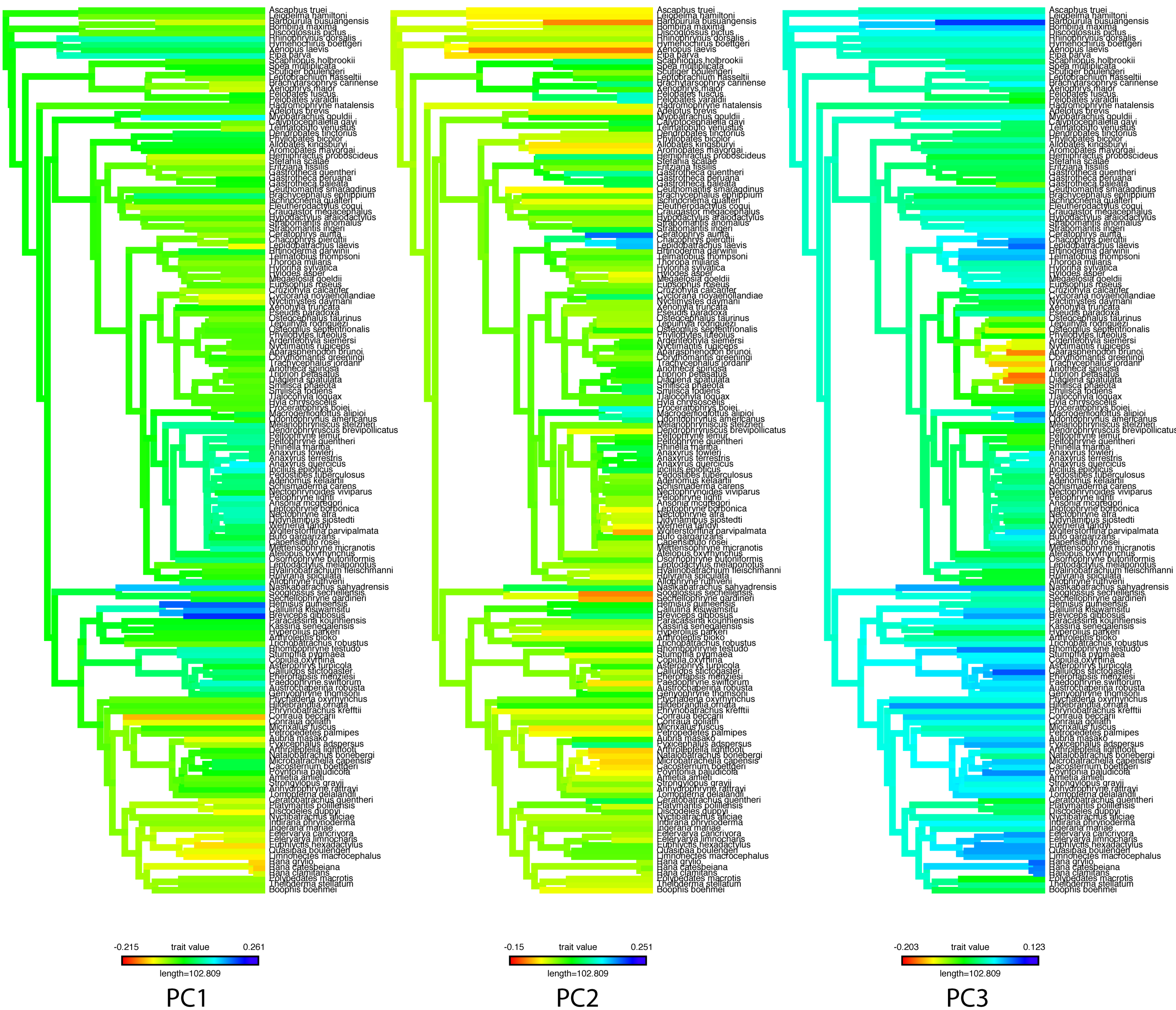

Figure S2. Contmap (15) maximum likelihood ancestral state reconstructions of skull shape PC scores on the trimmed phylogeny of Jetz and Pyron (16).

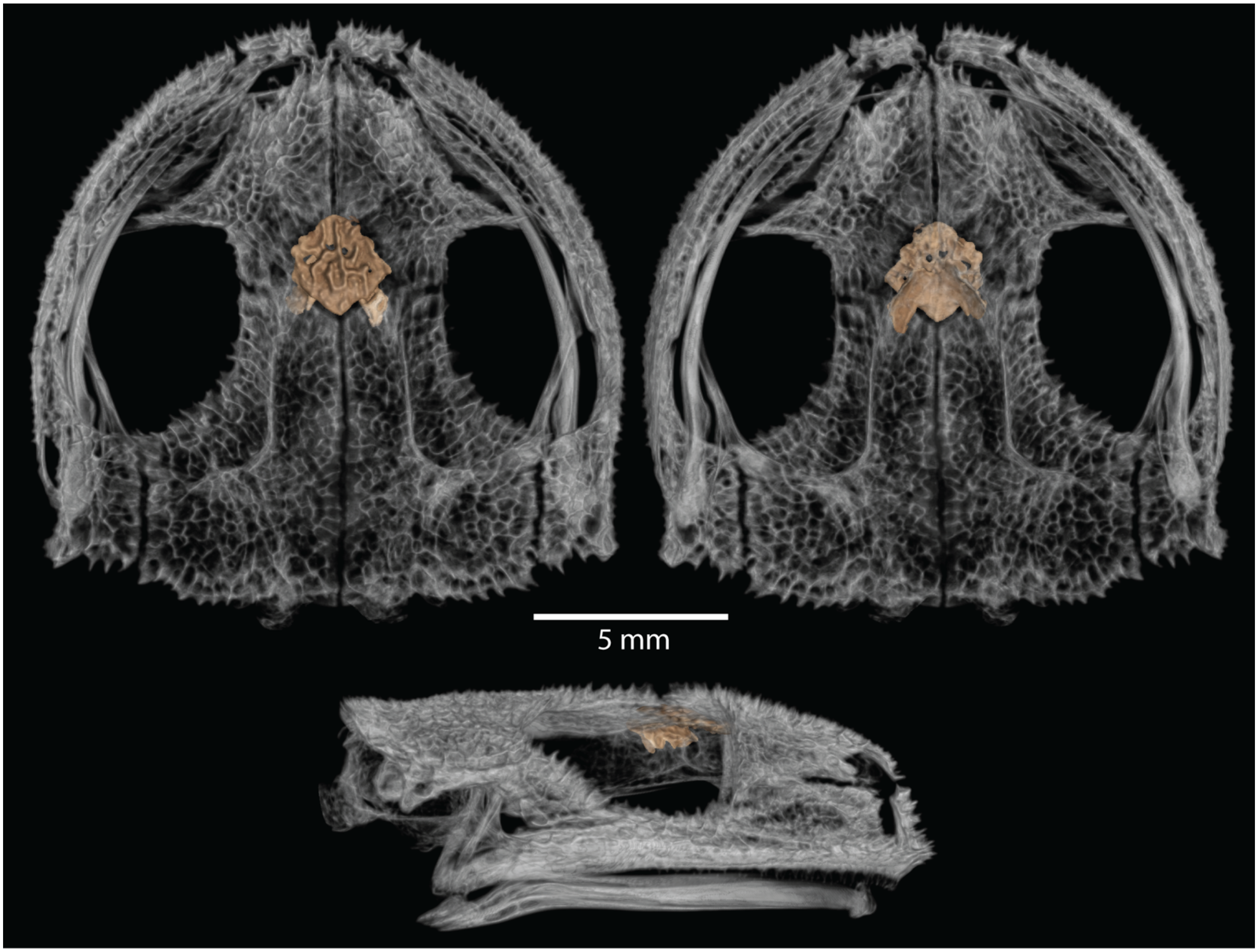

Figure S3. Dermal sphenethmoid of *Gastrotheca galeata* (KU 219765). The dermal sphenethmoid, an unpaired diamond-shaped bone that lies between the nasals and frontoparietal and covers the endochondral sphenethmoid, is found in several of the casque-headed hylids (*Aparasphenodon*, *Corythomantis*, *Itapotihyla*, *Osteocephalus*, *Osteopilus*, *Trachycephalus*, *and Triprion* [13, 17]), and we have verified its suspected presence in *G. galeata* (18).

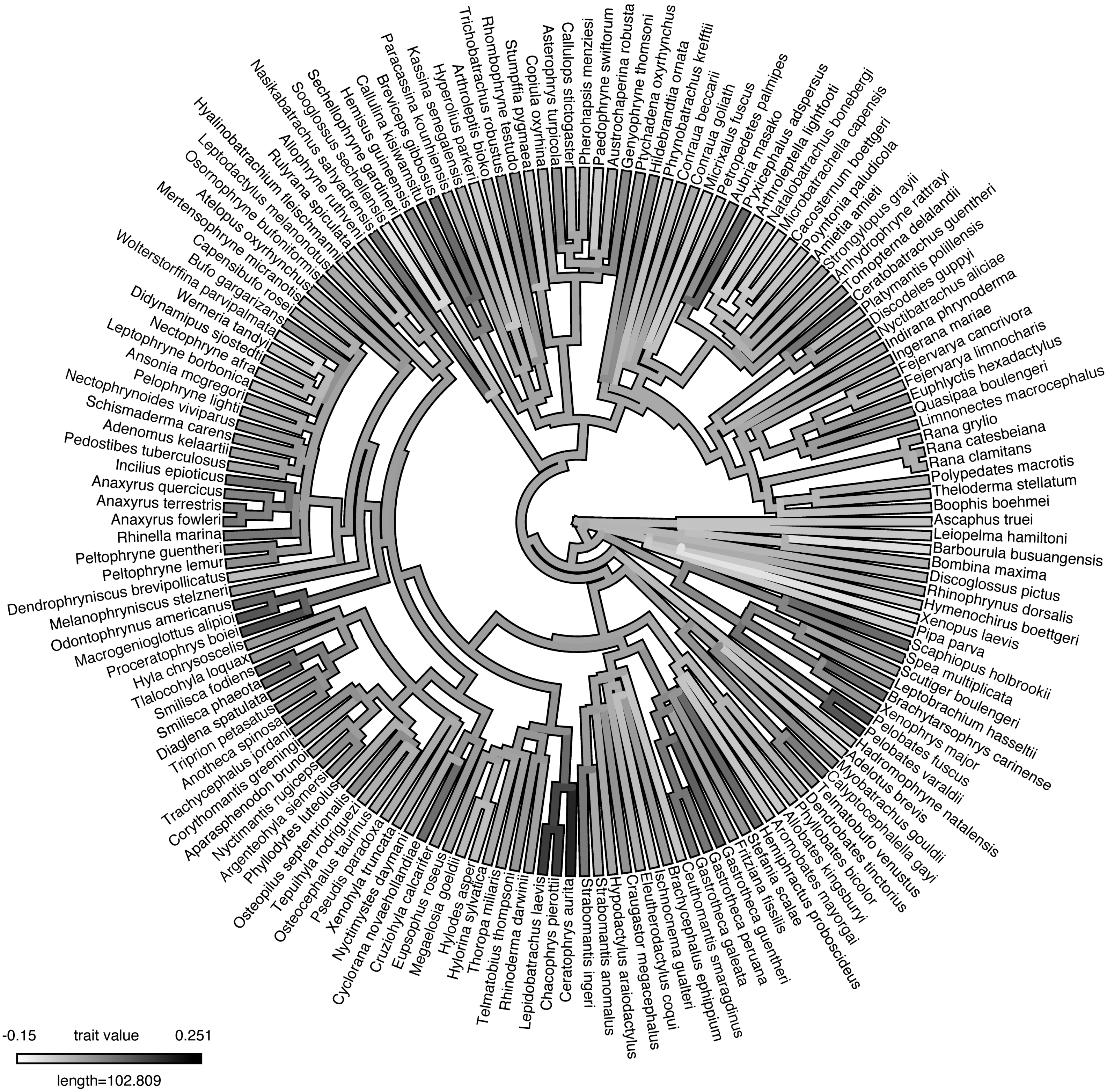

Figure S4. Trimmed phylogeny of Jetz and Pyron (16) from Fig. 1 with tip names.

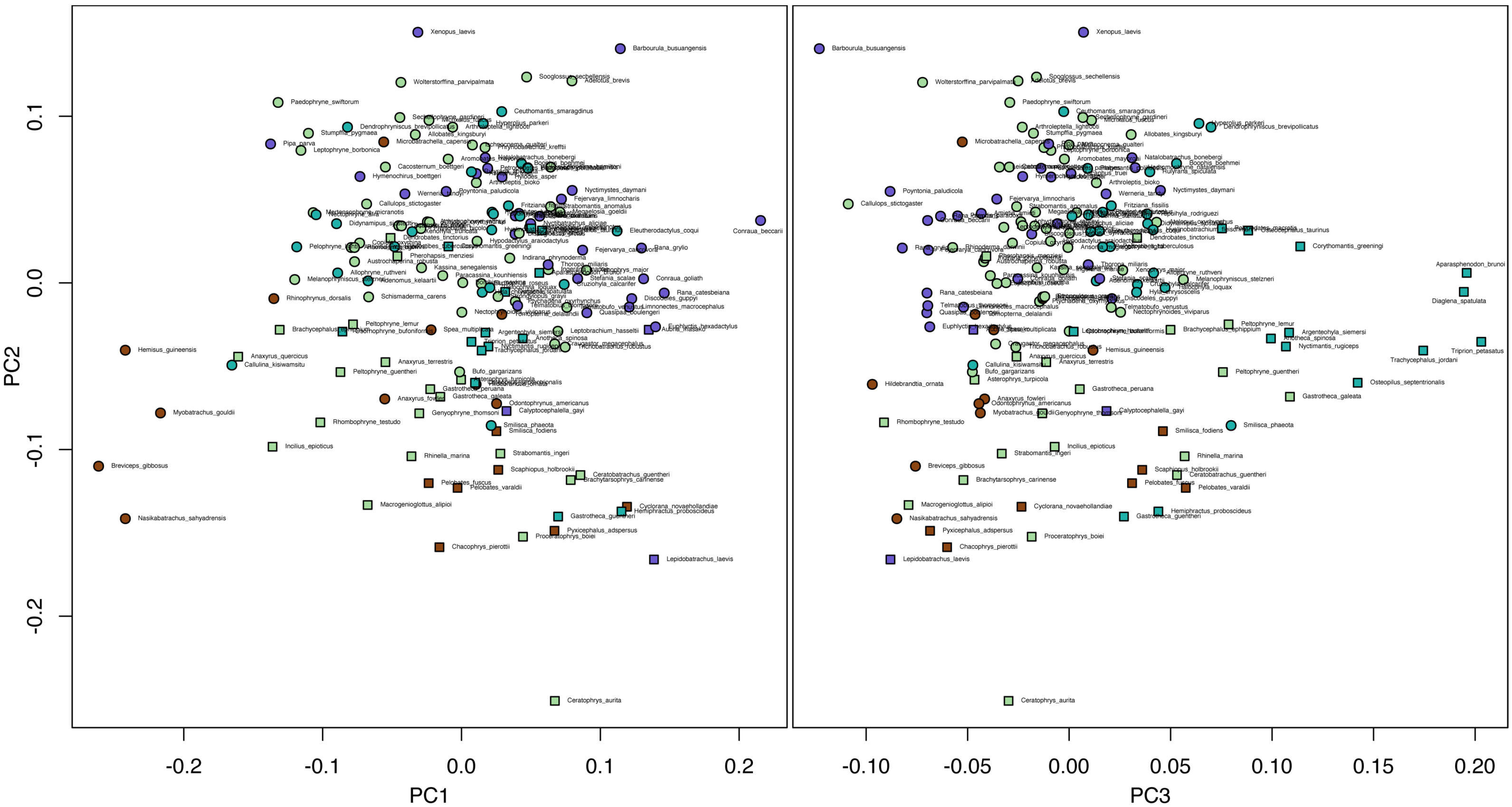

Figure S5. PCA plots from Fig. 2.1 and 2.2 with taxon names.

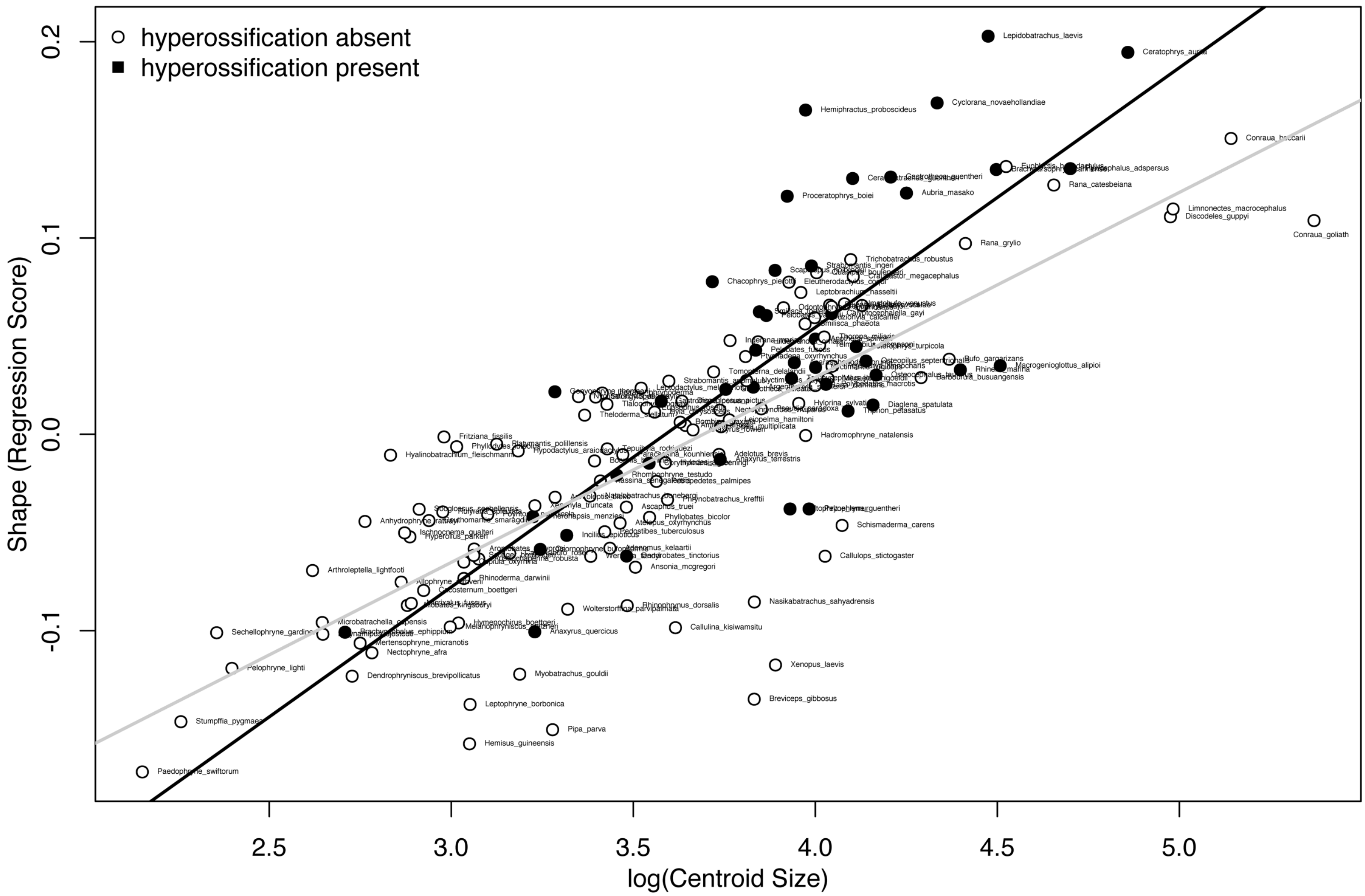

Figure S6. Regression plot from Fig. 3 with taxon names.

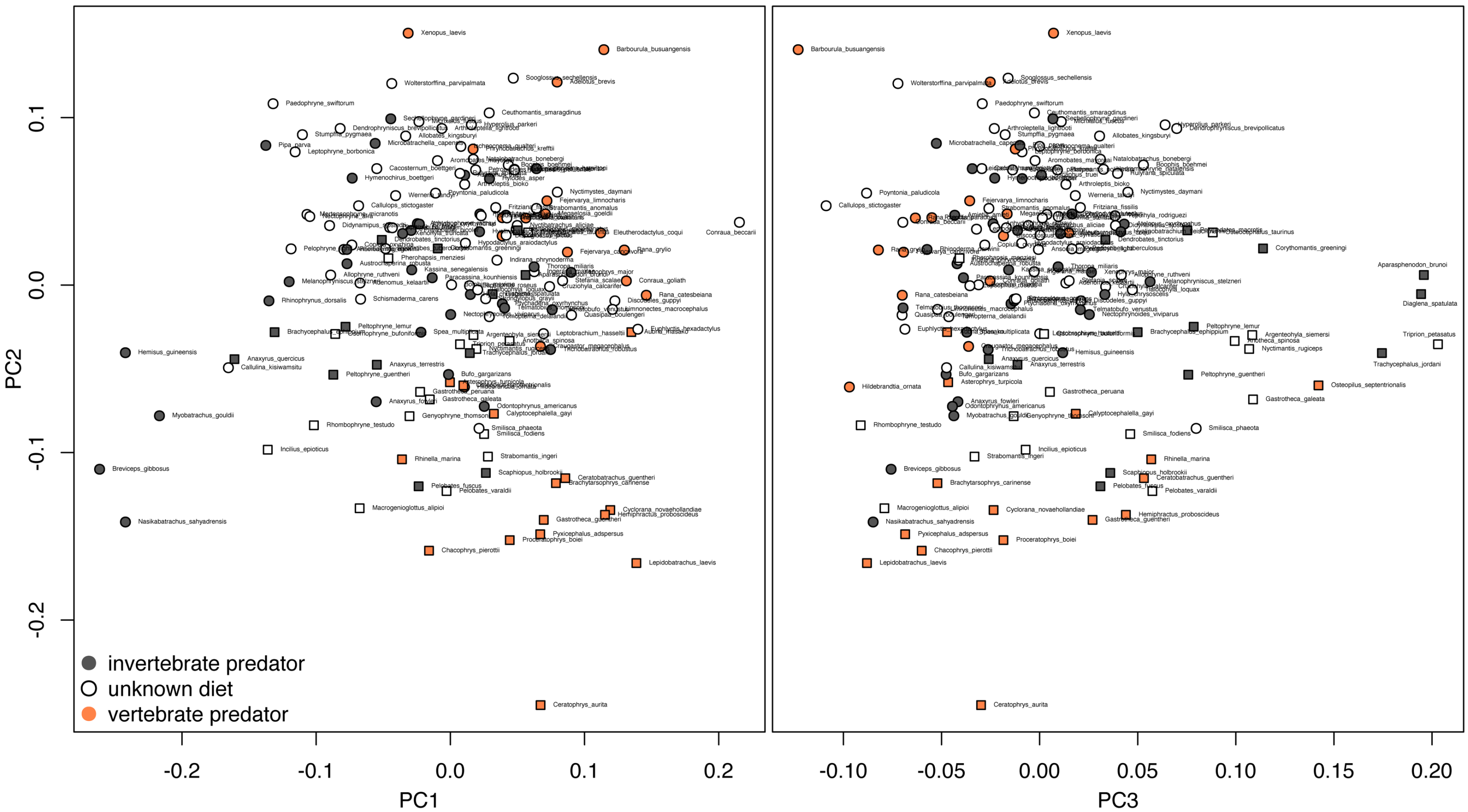

Figure S7. PCA plots from Fig. 2.3 and 2.4 with points colored by diet states of invertebrate predator, unknown diet, and vertebrate predator.

Table S1. Posterior probability and Bayes Factors for the five Markov models of phenotypic character evolution sampled in the reversible-jump MCMC ancestral state reconstructions.

		Bayes factors			
Model	Model posterior probability	0 to 1 irreversible	1 to 0 irreversible	1-rate	2-rate
0 to 1 irreversible	0	-	5	0	0.01
1 to 0 irreversible	0	0.2	-	0	0
1-rate	0.91	729.4	3647	-	10.45
2-rate	0.09	69.8	349	0.1	-

Table S2. Post hoc pairwise comparison *P* values for microhabitat and skull shape.

	aquatic	arboreal	fossorial	terrestrial
aquatic	1.00	*	*	*
arboreal	**0.005**	1.00	*	*
fossorial	**0.000**	**0.000**	1.00	*
terrestrial	**0.008**	**0.033**	**0.001**	1.00

Table S3. Post hoc pairwise comparison *P* values testing for factor interaction between hyperossification and microhabitat influencing skull shape after accounting for each main effect. Significant differences in skull shape were found between hyperossified aquatic frogs and multiple other groups, but there are only 3 hyperossified aquatic frogs in our dataset.

	no.aqu	no.arb	no.fos	no.ter	yes.aqu	yes.arb	yes.fos	yes.ter
no.aquatic	1.00	*	*	*	*	*	*	*
no.arboreal	0.953	1.00	*	*	*	*	*	*
no.fossorial	0.251	0.388	1.00	*	*	*	*	*
no.terrestrial	0.985	0.964	0.084	1.00	*	*	*	*
yes.aquatic	**0.029**	**0.044**	**0.0369**	**0.038**	1.00	*	*	*
yes.arboreal	0.694	0.443	0.184	0.526	**0.006**	1.00	*	*
yes.fossorial	0.951	0.954	0.893	0.938	0.133	0.216	1.00	*
yes.terrestrial	0.197	0.360	0.774	**0.036**	**0.007**	**0.008**	0.942	1.00

Table S4. Post hoc pairwise comparison *P* values testing for factor interaction between hyperossification (hyperossified, H; nonhyperossified, NH) and diet (invertebrate or vertebrate predator) influencing skull shape after accounting for each main effect.

	NH.invert_predator	NH.vert_predator	H.invert_predator	H.vert_predator
NH.invert_predator	1	*	*	*
NH.vert_predator	0.866	1	*	*
H.invert_predator	0.973	0.514	1	*
H.vert_predator	0.068	**0.000**	0.0586	1

Table S5. Post hoc pairwise comparison *P* values for diet (invertebrate predator, vertebrate predator, unknown diet) and skull shape.

	invert_predator	unknown	vert_predator
invert_predator	1	*	*
unknown	0.119	1	*
vert_predator	**0.000**	**0.000**	1

Table S6. Post hoc pairwise comparison *P* values testing for factor interaction between hyperossification (hyperossified, H; nonhyperossified, NH) and diet (invertebrate predator, vertebrate predator, unknown diet) influencing skull shape after accounting for each main effect.

	NH.invert	NH.unknown	NH.vert_	H.invert	H.unknown	H.vert
NH.invert_predator	1	*	*	*	*	*
NH.unknown	0.180	1	*	*	*	*
NH.vert_predator	0.641	0.925	1	*	*	*
H.invert_predator	0.598	0.961	0.467	1	*	*
H.unknown	0.924	0.407	0.386	**0.025**	1	*
H.vert_predator	0.254	0.134	**0.000**	**0.005**	0.302	1

Dataset S1. Species and specimens examined in this study with associated data and references. File available at https://github.com/dpaluh/hyperossification

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