# Divergent paths, convergent heads: morphological adaptation of head shape to ecological niches in snakes.

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**Abstract**

Morphological convergence—where distantly related species evolve similar traits in response to shared ecological pressures—is a hallmark of adaptive evolution. In snakes, head shape is a key functional trait linked to habitat use and diet, yet the extent and drivers of its convergence across habitat types and diet remain poorly understood. Here, we used geometric morphometric analyses to analyze dorsal head shape from photographs of over 266 snake species, representing ~5% of global snake diversity. Our analyses reveal that head shape variation is only weakly structured by phylogeny and allometry, but shaped by ecological specialization. Morphospace patterns reflect distinct differences in species with different ecologies: fossorial species exhibit compact, broadened heads suited for burrowing; aquatic species show streamlined profiles for hydrodynamic efficiency; and arboreal snakes tend to possess elongated skulls for maneuvering in complex habitats. Terrestrial and semi-fossorial snakes display broad morphospace overlap and an elevated shape disparity highlighting morphological versatility. While diet covaried significantly with head shape, species with similar diets did not exhibit strong morphological convergence. These findings underscore the dominant role of ecology over phylogeny in shaping the evolution of head shape in gape-limited predators like snakes.

**Keywords:** diet; convergence; head shape; habitat use; snakes

## Introduction

The environment shapes animal morphology and selects for traits that increase survival and reproductive success. When facing similar ecological pressures, species often develop similar phenotypes (Esquerré & Keogh, 2016). However, some traits appear more impacted than others by ecology (Deepak et al., 2022). Different factors can explain head shape variation including feeding behavior, sexual selection, and habitat use (Arnold & Pough, 1988; Moon et al., 2019). Species with specialized diets, such as mollusks feeders, may, for example evolve asymmetric mandibles in response to whether snails are left of right wound (Pandelis et al., 2023). Sexual selection may also impact head shape, especially if it impacts mate attraction or competitive ability (Fabre et al., 2016). However, most often a multitude of sometimes conflicting selective pressures drive the evolution of any given trait (Huey & Kingsolver, 1989). Consequently, species inhabiting similar niches may follow distinct evolutionary and morphological pathways (Losos et al., 1998). This is especially true for aquatic snakes facing similar environmental pressures developing different body plans and head shapes (Fabre et al., 2016; Segall et al., 2020; Sheratt et al., 2018). Moreover, despite similar ecological pressures, head shapes may diverge across different clades because other factors such as evolutionary history and niche-specific behaviors also shape morphology (Speed & Arbuckle, 2017; Grundler & Rabosky, 2014).

Snakes are an excellent model system to study morphological convergence because of their ecological versatility (Pyron & Burbrink, 2012) and their reliance on the head to feed as gape-limited predators (Moon et al., 2019). Previous studies have suggested that the evolutionary success of snakes is in large part due to their feeding strategies and trophic specialization (Title et al., 2024). For example, feeding-related morphological evolution is evident in sea snakes, where selective pressures related to foraging mode have resulted in

distinct head shapes (Sherratt et al., 2018). Similarly, homalopsid snakes have evolved unique head shapes driven by the functional demands imposed by the prey they eat (Fabre et al., 2016). Habitat-related selective pressures also influence snake morphology. *Boidae* and *Pythonidae*, for instance, exhibit head shape convergence driven by habitat use (Esquerré & Keogh, 2016).

Previous studies on head shape convergence in snakes have primarily focused on aquatic and fossorial snakes. For instance, aquatic species frequently develop narrow heads with upward-facing eyes and nostrils, features that improve their ability to capture prey, move efficiently through water and spot predators while remaining submerged (Hibbitts and Fitzgerald, 2005; Vincent et al., 2009; Segall et al., 2016, 2020; Deepak et al., 2022). Similarly, burrowing snakes possess robust skulls adapted for digging and streamlined bodies with reduced ventral scales, which help them burrow with minimal friction (Fabre et al., 2016; Herrel et al., 2008). Meanwhile, microcephalic sea snakes exhibit distinct skull shapes linked to developmental changes, representing niche specialization rather than direct functional convergence (Sherratt et al., 2018; Segall et al., 2020).

Our overarching prediction is that snakes inhabiting similar environments or eating similar prey will show morphological convergence. Particularly, we predict that fossorial snakes will exhibit a narrow, V-shaped head facilitating substrate penetration and minimizing the energetic cost of burrowing (Navas et al., 2004). Head shape in fossorial snakes should, however, not be influenced by feeding habits as they mostly feed on small soil invertebrates. Arboreal snakes are predicted to have slender heads to blend in with the environment (i.e. camouflage), except for mollusk specialists that are expected to have blunt heads. Aquatic snakes are expected to express disparity in head shape as they feed on a variety of prey in a variety of underwater habitats. For species that effectively move in different environments

82 (semi-aquatic, semi-arboreal, semi-fossorial) we predict that they will show transitional
83 features. We also predict that greater morphological variation will be observed in snakes that
84 live in transitional habitats and that have non-specialized diets.

85 **Materials and Methods**

86 *Sample and ecological classification*

87 We collected data from 266 species used for habitat use (508 specimens) and 204
88 species for diet (397 specimens). Animals were housed in three European Natural History
89 Museums: the National Museum of Natural History in Paris (97 specimens), the Alexander
90 Koenig Museum in Bonn (316 specimens), and the Museum of Natural Sciences in Brussels
91 (95 specimens). Our measurements were taken from adult specimens whenever possible.
92 However, in some cases, only young individuals were available. For some species (i.e. large
93 pythons and boas), only subadults were measured for practical reasons and the lack of
94 availability of adults (Table S1). Our sampling aimed to encompass the phylogenetic and
95 ecological diversity of snakes, while remaining limited by the availability of specimens in
96 these collections.

97 Based on the literature, eight habitat use categories were determined (Spawls et al.,
98 2002; Whitaker & Captain, 2004; Campbell & Lamar, 2004; Marais, 2004; O'Shea, 2005;
99 Vogel, 2006; Glaw & Vences, 2007; Bartlett & Bartlett, 2009; Das, 2010; O'Shea, 2018;
100 Allen, 2019; Chippaux, 2019; Pietersen et al., 2021; Egan, 2022; Das, 2023). We classified
101 the species into 102 terrestrial, 34 arboreal, 19 aquatic, 6 fossorial, 43 semi-arboreal, 33 semi-
102 aquatic, and 29 semi-fossorial species. We based our ecological categorization on the
103 biomechanical constraints imposed by the environment (Table S2). For instance, similar

hydrodynamic constraints affect both marine and freshwater snakes leading us to group them into the same category.

We further use dietary data from the supplementary material of the paper by Title et al. (2024). Categories were modified and regrouped based on the functional constraints imposed by the prey. We define a total of ten dietary groups, including 5 generalists, 4 hard egg feeders, 90 hard prey feeders, 16 invertebrate feeders, 3 mollusk specialists, 2 soft egg specialists, and 83 soft prey eaters (Table S3). In creating these categories, we grouped salamanders, lizards, and fish together as they have cylindrical and flexible bodies and as such should impose similar functional constraints.

*Geometric morphometric data*

For each individual a photo of the head in dorsal view was taken with a Nikon © D3100 camera. Snakes were placed on a grid paper for calibration and scale (1 x 1cm squares; Figure S1A). To perform the geometric morphometric analysis, 25 landmarks and 10 semi-landmarks were selected (Figure S1B) and defined (Table S4). These landmarks and semi-landmarks were based on the literature (Manier, 2004; Mangiacotti et al., 2014; Ruane, 2014; Roth-Monzonetal et al., 2021).

As we based our analysis on landmarks placed on cephalic scales, only species from the colubrid family, including Colubridae, Elapidae, Lamprophiidae, Homalopsidae, Pareidae, Psammophiidae, and Pseudoxyrhophiidae were used. A repeatability test was performed using ten pictures from three individuals of *Lampropeltis californiae* to explore whether the positioning of the head caused variation in landmark placement. Similarly, landmarks were placed ten times on these pictures to evaluate error in landmark placement. Variation in landmark placement due to head positioning as well as landmark placement was limited

(Figure S2). Species were landmarked using the tpsDig software (Rohlf, 2015). The 2D landmark coordinates were imported into R and subjected to a Generalized Procrustes Analysis (GPA; Figure S1C). Species means were then computed from Procrustes-aligned coordinates and used in subsequent analyses. Only species present in both the geometric morphometric dataset and phylogenetic tree were retained. Geometric morphometric analyses were conducted using the *geomorph* package (Adams & Otárola-Castillo, 2013). Semi-landmarks were slid along their tangent directions, minimizing bending energy to optimize their positions.

*Phylogenetic signal*

To evaluate the extent to which shape variation is structured by phylogeny we used the *physignal* function in R from the *geomorph* package (Adams & Otárola-Castillo, 2013). This method is based on a statistical procedure that quantifies the degree of similarity in shape traits among closely related species relative to what would be expected under a null model of trait evolution. The function was run with 1000 iterations to generate a null distribution of phylogenetic signals by randomly reshuffling the phylogenetic tree and comparing the observed signal to the null distribution. A value close to 1 would indicate a strong phylogenetic signal, meaning closely related species exhibit more similar shapes than would be expected by random chance. On the other hand, values significantly less than 1 suggest a weaker phylogenetic signal, indicating that the variation in shape is less influenced by the evolutionary history of the species.

*Allometry*

Allometry was quantified using a phylogenetic generalized least squares (PGLS) model, with shape coordinates as the dependent variable and centroid size as the predictor.

This test aimed to assess size-related variation in shape (i.e., allometry) while accounting for phylogenetic relatedness among species.

*Phylogenetic principal components analysis*

A phylogenetically-informed principal component analysis (PCA) was performed using the *phytools* package (Revell, 2012) to explore shape variation in relation to habitat and diet categories. Eigenvalues were calculated to assess the variance explained by the principal components, and the first two principal components (PC1 & PC2) were visualized. The phylomorphospace was visualized by integrating the pruned phylogenetic tree and the principal component scores, with species colored based on their habitat use and diet using the *ggphylomorpho* function (Barr, 2017).

*Differences between groups*

A phylogenetic multivariate analysis of variance was performed using Procrustes shape coordinates as the dependent variables to test whether habitat or diet groups differed in head shape. The test was run using the *procD.pgls* function from the *geomorph* package (Adams & Otárola-Castillo, 2013).

*Analyses of covariation*

A phylogenetic Two-Block PLS (Partial Least Squares) analysis was carried out using the *phylo.integration* function from the *geomorph* package (Adams & Otárola-Castillo, 2013), to explore whether variation in shape was associated with variation in diet while accounting for shared evolutionary history. We used continuous proportions of prey items (e.g., hard prey, soft prey, invertebrates, etc..), allowing for a finer representation of dietary gradients

171 across species. This matrix was aligned with shape data from Procrustes-aligned landmarks,
172 and phylogenetic relationships were accounted for.

173 *Convergence*

174 To assess morphological convergence among species sharing similar ecological
175 niches, we employed the *search.conv* function from the *RRphylo* package (Castiglione et al.,
176 2019). This method evaluates whether species occupying the same habitat or dietary category
177 exhibit greater phenotypic similarity than expected under a Brownian motion model of trait
178 evolution. The analysis was conducted on a time-calibrated phylogeny and focused on the
179 first two principal components of head shape variation (PC1 and PC2). To ensure statistical
180 robustness, only categories represented by at least three species were retained for analysis
181 (e.g., soft eggs dietary was not included in some analyses as they were less than 3 individuals
182 in this group). The function quantifies convergence by calculating the mean angular distance
183 in trait space between focal taxa and their nearest phenotypic neighbors, both in terms of trait
184 values (ang.state) and their estimated evolutionary timing (ang.state.time). Significant
185 convergence is inferred when observed similarity is greater than expected under neutral
186 evolutionary expectations.

187 *Disparity analysis*

188 We performed a morphological disparity analysis to assess the relationship between
189 shape variation and ecological niches or diet groups while accounting for phylogenetic
190 relationships, using the *morphol.disparity* function from the *geomorph* package (Adams &
191 Otárola-Castillo, 2013). We used Procrustes-aligned shape coordinates (GPA) and tested for
192 differences in morphological disparity across ecological niches and diet categories. A
193 phylogenetically informed disparity analysis was conducted using a permutation-based

resampling method (1000 iterations), enabling robust comparisons of shape variance between habitat types and diet groups.

## Results

### *Phylogenetic signal*

The observed value of K is low for shape (K = 0.0964), indicating a weak phylogenetic signal (Table 1). Furthermore, the result was not statistically significant, suggesting that the morphological shape variation among species is not strongly structured by phylogenetic relationships. This implies that closely related species do not resemble each other more than expected by chance in terms of overall shape.

### *Allometry*

The phylogenetic generalized least squares (PGLS) analysis revealed a statistically significant relationship between shape and centroid size (Table 2). Despite a relatively low proportion of variance explained ($R^2 = 0.027$), the allometric signal in head shape variation was significant ($P < 0.005$).

### *Variation in head shape*

In our principal component analysis, 97% of the variation in head shape is explained by the first two principal components (PC1: 73.39%; PC2: 23.99%; Figure 1). The phylomorphospace of head landmarks reveals structuring of head shape variation among snakes. Fossorial species, characterized by low PC1 and PC2 values, exhibit elongated and broad posterior skulls (Figure 1A). Arboreal and semi-arboreal snakes, by contrast, tend to occupy higher PC1 values and display slender, elongated skulls. Aquatic and semi-aquatic species are more dispersed along PC1, with skulls often appearing streamlined. Terrestrial

216 snakes are widely spread across the morphospace a and semi-fossorial and semi-arboreal
217 species tend to fall in intermediate regions of the morphospace.

218 In terms of diet, species consuming soft-bodied prey (e.g., snakes, lizards) generally
219 exhibit higher PC1 values, associated with elongated and narrower heads (Figure 1B; Figure
220 2). Conversely, species feeding on harder prey (e.g., rodents, birds, mollusks) are found in the
221 lower range of PC1 and often exhibit broader, more robust skulls. Mollusk specialists and
222 other durophagous feeders show this trend most strongly. PC2 variation also reflects dietary
223 adaptations: species with lower PC2 values, such as soft-prey specialists and generalists, tend
224 to have narrower skulls, while invertebrate feeders cluster around broader and more robust
225 head shapes. Deformation grids show that many species exhibit a combination of longer,
226 narrower snouts with posterior skull widening—contributing to the shared V-shaped
227 morphology in fossorial, semi-aquatic, and some hard-prey specialists (Figure 1). Overall,
228 generalist feeders and species with diverse prey types occupy wide, overlapping regions of the
229 morphospace, indicating that head shape in snakes is shaped by a complex interplay between
230 habitat use and dietary specialization.

231 *Differences between habitat groups*

232 The MANOVA indicates significant differences between habitat groups in head shape
233 (Table 3). When adding $Log_{10}$-transformed centroid size as a covariate, we found significant
234 effects of habitat, centroid size and the interaction between the two (Table 3). The interaction
235 between habitat and centroid size was also significant. Moreover, post-hoc pairwise
236 comparisons further revealed that fossorial snakes, as well as semi-fossorial, differ
237 significantly from all ecological groups (Table 4). Additionally, semi-aquatic and semi-
238 arboreal differ from terrestrial snakes in head shape.

239 *Differences between diet groups*

240 There was a trend toward head shape differentiation among diet groups, based on
241 dominant dietary regimes, as revealed by the phylogenetic MANOVA (Table 5). When
242 adding $Log_{10}$-transformed centroid size as a covariate, this tendency remained. Centroid size
243 did differ between dietary groups, while interactions were not significant (Table 5). Post hoc
244 pairwise comparisons indicated a significant difference in head shape between species
245 consuming hard prey and those consuming soft prey ($P < 0.05$; Table 6). There were trends
246 observed between hard prey and soft eggs feeders ($P = 0.090$), as well as between
247 invertebrates and soft eggs feeders ($P = 0.092$).

248 *Analyses of covariance*

249 Our results revealed a significant covariation between head shape and habitat use (r-
250 PLS = 0.38, Z = 2.67, $P < 0.01$), as well as between head shape and diet (r-PLS = 0.59, Z =
251 3.82, $P < 0.05$) (Table 7). This indicates that species occupying different habitat types or
252 relying on different dietary resources differ in head shape. Specifically, the distribution of
253 species along the first PLS axis suggests that morphological variation is aligned with
254 ecological gradients (Figure 3). Aquatic and fossorial species appear to cluster separately
255 from arboreal or terrestrial taxa, reflecting adaptive morphological specializations for
256 swimming, burrowing, or climbing. In the case of diet, species that consume hard prey tend to
257 separate from those feeding primarily on soft-bodied prey or eggs, suggesting that cranial
258 shape variation may be driven by biomechanical demands related to prey processing (Figure
259 4).

260 *Convergence*

261 The convergence test results revealed contrasting patterns in morphological evolution
262 depending on whether species were grouped by habitat use or diet (Table 8). Among habitat
263 groups, strong evidence for morphological convergence was found within aquatic and
264 fossorial species. These two groups showed significantly lower mean angles of phenotypic
265 distance (ang.state = 58.46 and 11.29, respectively; $P < 0.01$ for both). These results were also
266 supported by the timing-based convergence metric, indicating that the convergent traits
267 evolved synchronously within these clades (ang.state.time = 331.51 and 98.38 respectively; $P$
268 $< 0.01$ for both groups). In contrast, no significant convergence was detected within the other
269 habitat groups, such as terrestrial, arboreal, semi-arboreal, semi-aquatic, or semi-fossorial
270 species (Table 8). While some of these groups (e.g., arboreal or semi-aquatic) showed
271 moderately low angles of phenotypic distance, the results were not statistically significant.

272 No dietary group showed statistically significant morphological convergence, although
273 Mollusks approached the lowest angle values (ang.state = 53.65, $P = 0.165$), hinting at
274 possible trends that did not reach significance, potentially due to the very small sample size.
275 All other dietary groups—including hard prey, soft prey, invertebrates, and hard egg
276 specialists—exhibited non-significant convergence metrics. Timing-based convergence
277 likewise yielded no significant patterns, indicating that when morphological similarities were
278 observed, they did not evolve at the same time across lineages.

279 *Disparity analysis*

280 Our findings indicate that semi-fossorial species exhibit the highest morphological
281 disparity (0.0122; Table 9). Aquatic species displayed the second highest score in
282 morphological disparity (0.0116). Moderate levels of disparity were observed in the following
283 categories: terrestrial species (0.0112) and semi-arboreal species (0.0111). Conversely,
284 fossorial species (0.0108), semi-aquatic species (0.0108) and arboreal species (0.0087)

demonstrated the lowest non-zero variances. Pairwise absolute differences reveal that the greatest differences occur between aquatic and arboreal species (0.003), as well as between arboreal and semi-fossorial species (Table S5). However, pairwise absolute differences among the other habitat types remain small and statistically non-significant (Table S6).

Our findings further indicated that species consuming soft prey exhibit the highest morphological disparity (0.018; Table 9). Species consuming hard prey and mollusk displayed notable morphological disparity (0.011 and 0.0085 respectively). Moderate levels of disparity were observed in generalist species (0.0071), invertebrate feeders (0.0088) and hard-egg consumers (0.0086). Conversely, soft-egg consumers (0.0025) demonstrated the lowest non-zero variances. Pairwise absolute differences confirm that soft-prey consumers exhibit significantly higher morphological disparity compared to most other dietary categories, particularly soft-egg, mollusk, and hard-egg consumers (Table S7). Yet, pairwise absolute differences and significance levels among the other diet categories remain minimal and non-significant, except marginally for the comparison between soft-prey and soft-egg consumers (Table S8).

## Discussion

Our analyses demonstrate that snake head shape variation is not primarily governed by phylogenetic relatedness or body size, but rather reflects adaptations to ecological contexts and feeding strategies. The weak and statistically non-significant phylogenetic signal (K = 0.0964) indicates that closely related species do not resemble each other in head shape more than expected by chance. This supports the idea that ecological and functional demands may override phylogenetic constraints, enabling repeated and independent morphological adaptations across lineages. Similar patterns have been observed by da Silva et al. (2018), who reported convergent skull shapes in aquatic and fossorial snakes regardless of

phylogenetic affiliation, emphasizing the influence of habitat-driven functional demands. Likewise, da Silva et al. (2017) found that trophic specialization drove significant cranial divergence among Neotropical snakes with limited phylogenetic signal, suggesting that diet, like habitat, can supersede phylogenetic inertia. On the other hand, Esquerré and Keogh (2016) found a moderate phylogenetic influence on head shape in Australian elapids, though ecological divergence still played a key role—highlighting potential clade-specific variation in the balance between constraint and adaptation. Although our allometric test revealed a statistically significant relationship between centroid size and shape, the effect was small ($R^2 = 0.025$), suggesting that body size alone explains little of the head shape variation. This decoupling indicates that selection acts more directly on cranial morphology than on ody size (da Silva et al., 2018).

The distribution of species in morphospace reinforces this interpretation. Ecological specialization corresponds to distinct regions of cranial variation, especially among fossorial, arboreal, and semi-aquatic species. Fossorial snakes, with their V-shaped and posteriorly broadened skulls, occupy a unique morphospace region—consistent with mechanical requirements for head-first burrowing and maneuvering through confined spaces (da Silva et al., 2018; Strong et al., 2020; Pandelis et al., 2023). Arboreal and semi-arboreal species exhibit slender, elongated skulls, which likely facilitate navigation and prey capture in structurally complex habitats (Herrel et al., 2008; Klaczko et al., 2016). Similarly, aquatic and semi-aquatic species often show streamlined cranial shapes associated with reduced hydrodynamic drag (Segall et al., 2016 – 2020; Deepak et al., 2022).

The phylogenetic MANOVA confirmed significant overall differences in head shape among habitat groups, with fossorial and semi-fossorial species showing distinct morphologies compared to most others. This pattern highlights the strong biomechanical

constraints imposed by a subterranean lifestyle. Interestingly, semi-fossorial species exhibited the highest disparity among all habitat types. This elevated variation may stem from their intermediate ecological position, requiring adaptations to both surface and subsurface environments. Variability in substrate type, time spent underground, and degrees of cranial reinforcement or kinesis could contribute to this morphological diversity (Herrel et al., 2008; da Silva et al., 2018; Tingle et al., 2024).

Aquatic species displayed relatively high morphological disparity, likely reflecting the broad ecological diversity of aquatic environments and the wide array of prey types these snakes exploit. This is consistent with findings from Segall et al. (2016, 2020) and Deepak et al. (2022) who showed that aquatic snakes adapted to different flow regimes, prey sizes, and foraging strategies often evolve distinct cranial morphologies. Water acts both as a biomechanical constraint and a driver of morphological diversification (Sherratt et al., 2018). In contrast, fossorial species displayed more moderate disparity levels, which may reflect stronger functional constraints linked to a fully subterranean lifestyle. Such species often converge toward compact, reinforced head shapes adapted to head-first burrowing, thereby limiting morphological variation. In arboreal snakes, stability during strikes and secure navigation along narrow, flexible supports may favor streamlined, stable cranial morphologies (Klaczko et al., 2016; Alencar et al., 2017). Similarly, semi-aquatic species may face conflicting selective pressures between aquatic locomotion and terrestrial maneuverability, potentially resulting in conservative morphologies shaped by functional compromise (Sherratt et al., 2018; Segall et al., 2020).

Dietary specialization also contributes meaningfully to head shape variation. Species feeding on soft-bodied prey such as snakes, amphibians, or fish often display elongated, narrow heads—likely facilitating the consumption of these prey. In contrast, snakes that

consume hard or bulky prey, including mammals, birds, or shelled invertebrates, possess broader, more robust skulls adapted to gripping and processing resistant prey. In 2019, Perkins & Eason showed that sympatric water snake species exhibited head shapes matching their dietary preferences: narrow heads were associated with fish diets, and broad heads with amphibians. Generalists spanned a wide morphospace, reflecting cranial versatility and behavioral plasticity (Deepak et al., 2022; Pandelis et al., 2023). Soft-prey consumers exhibited the highest morphological disparity, likely reflecting the variety of functional solutions for handling elongate, mobile prey (Segall et al., 2020; Pandelis et al., 2023). In contrast, mollusk and soft-egg specialists clustered tightly in morphospace, suggesting convergence toward a limited set of biomechanically effective forms for durophagy (Pandelis et al., 2023).

Convergence analyses further illuminate the strong influence of habitat-driven functional constraints. Significant morphological convergence was detected among fossorial and aquatic species, likely reflecting parallel adaptations to movement through compact substrates or fluid environments (Herrel et al., 2008; Segall et al., 2016). Similarly, our detection of convergence among fossorial taxa supports the view that dealing with resistant media—whether water or soil—can lead to similar head shapes across distantly related lineages. In contrast, we did not detect significant convergence among dietary groups. Although species consuming similar prey types often exhibited analogous head shapes, these patterns lacked statistical support for convergence. This contrasts with findings such as Perkins and Eason (2019), who documented strong diet-morphology correlations in sympatric species. The broader inconsistency may be due to variability in foraging behavior, strike mechanics, or ecological context across clades, limiting the emergence of shared morphological optima. Furthermore, lineages may face developmental or functional constraints that shape divergent cranial solutions to similar dietary challenges (Segall et al.,

382 2020; Pandelis et al., 2023). The exclusion of underrepresented groups, such as mollusk
383 feeders or egg specialists, from our convergence analyses may also limit our ability to detect
384 certain trends.

385 Taken together, our findings reinforce the growing consensus that habitat use and
386 dietary specialization play significant but distinct roles in shaping the evolution of head shape
387 in snakes. Environments imposing strong biomechanical constraints, such as arboreal and
388 fossorial habitats, clearly shape cranial form. However, diet—especially differences in prey
389 hardness and body shape—exerts an even stronger and more consistent influence on cranial
390 morphology across lineages, as highlighted by the PLS analysis. The pronounced covariation
391 among head shape, habitat, and diet underscores that ecological specialization involves a
392 dynamic interplay of selective pressures, with both habitat use and feeding ecology jointly
393 driving morphological evolution in snakes.

394 Beyond analytical methods, a number of biological and data-driven limitations should
395 be acknowledged. First, the categorization of ecological niches remains somewhat coarse and
396 potentially subjective. For example, semi-fossorial species may share more ecological traits
397 with terrestrial than fully fossorial snakes, and semi-aquatic species vary widely in their
398 dependence on aquatic environments (Esquerré & Keogh, 2016; Silva et al., 2017).
399 Incorporating quantitative ecological data—such as habitat features (e.g., branch density, soil
400 compaction, water salinity) or substrate use (e.g., frequency of use of forest soil, mud, or tree
401 species)—could refine these categories and better capture the ecological continuum
402 (Manjarrez et al., 2017; Tingle et al., 2024). Second, although our dietary classifications are
403 grounded in empirical data, they could be enhanced by integrating quantitative prey traits—
404 such as size and hardness—that more accurately represent the functional challenges faced by
405 predators, rather than relying solely on prey shape (Vincent et al., 2009; Da Silva et al., 2018).

406 For instance, both birds and frogs may be categorized as soft prey, yet their ecologies and
407 physical properties differ markedly, potentially requiring distinct feeding adaptations (Segall
408 et al., 2020; Deepak et al., 2022). Understanding the functional properties of prey would thus
409 provide more nuanced insights into head shape evolution. Furthermore, the inclusion of
410 behavioral variables—such as foraging strategy or strike kinematics—would significantly
411 strengthen the link between morphology and ecological function (Herrel et al., 2008; Segall et
412 al., 2016; Moon et al., 2019). These traits are likely to interact with head shape in complex
413 ways that are not fully captured by static ecological or dietary categories alone. Additionally,
414 focusing on taxonomically or ecologically specialized clades (e.g., snail-eaters, egg
415 specialists) could shed light on extreme morphological adaptations that illustrate more clearly
416 how head shape evolves under strong selective pressure (Pandelis et al., 2023; Palci et al.,
417 2024).

418 Our study underscores the complex and multifactorial nature of head shape evolution
419 in snakes, driven more by ecological function than phylogenetic history or allometry.
420 Building on this, Moon et al. (2019) emphasize the remarkable adaptability of the snake
421 feeding system, noting that head morphology reflects not only dietary and ecological
422 demands, but also performance constraints like gape limitation, strike kinematics, and prey
423 handling strategies. They highlight how head shape plays a central role in functional
424 performance—such as strike accuracy, hydrodynamics, and force generation—yet also
425 caution that our understanding remains limited by the narrow taxonomic and ecological scope
426 of most studies. To address this, future research should aim for a more integrative approach—
427 linking head morphology with detailed data on strike mechanics, bite force, and prey-handling
428 behaviors across ecological contexts. For instance, striking behaviors vary between aquatic
429 and terrestrial environments, and bite performance has only been measured in a few species,
430 suggesting that much remains to be explored (Bartolon et al., 2013; Penning, 2017; Moon et

al., 2019). Prey manipulation could have a significant effect on the overall morphology of snakes, and could be of great interest in understanding the adaptability of certain niches to different prey items (Crotty & Jane, 2017). Furthermore, intraspecific variation in feeding plasticity (Manjarrez et al., 2017; Bonnet et al., 2020; Ortiz-Medina et al., 2022), as well as ontogenetic (Lopez et al., 2013; Patterson et al., 2022) and sexual dimorphism (Borczyk et al., 2021; Shine & Goiran, 2021) in head shape and diet, could further illuminate the selective pressures shaping head form. Expanding datasets to include internal morphology, muscle architecture, and functional performance metrics would not only validate the ecological relevance of head shape variation but also test longstanding hypotheses about convergence and specialization in snake evolution. In doing so, we can build a more mechanistic understanding of how morphology translates into ecological success.

## Conclusion

Our findings reveal that snake head shape is shaped less by phylogenetic relatedness or body size and more by ecological function and dietary specialization. Morphological variation in cranial form reflects repeated, and often convergent, adaptations to environmental demands such as burrowing, climbing, or swimming, as well as to prey capture and processing. This is especially apparent in fossorial and semi-aquatic snakes, where head shapes align with biomechanical requirements like substrate penetration or hydrodynamic efficiency, and in durophagous species, which exhibit robust skulls for handling hard prey. Despite a weak phylogenetic signal and minimal allometric influence, we detected strong associations between head shape and ecological context, reinforced by disparity patterns and PLS analyses. Intriguingly, high morphological disparity within narrow ecological categories—such as fossorial and aquatic niches—suggests the evolution of multiple functional solutions to similar environmental challenges, likely shaped by fine-scale habitat variation, prey diversity, or biomechanical constraints.

Our use of cephalic scale-based morphometrics offers a pragmatic and ecologically relevant proxy for head shape in large comparative datasets, but we recognize its limitations. Internal cranial architecture, muscle arrangement, and soft tissue all contribute to ecological performance and remain largely unexplored in this context. Moving forward, a more integrative approach—incorporating performance data (e.g., bite force, strike dynamics), behavioral traits (e.g., foraging strategy, prey handling), and finer-scale ecological metrics—will be essential for linking form to function. Investigating intraspecific variation, ontogeny, and sexual dimorphism can further illuminate how head shape evolves under diverse selective pressures. By bridging morphology with performance and behavior, future research can deepen our understanding of how ecological demands shape evolutionary trajectories, not only in snakes but across vertebrate lineages navigating similar functional landscapes.

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## References

Adams, D. C., & Otárola-Castillo, E. (2013). Geomorph: An r package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, *4*(4), 393–399.

Alencar, L. R. V., Martins, M., Burin, G., & Quental, T. B. (2017). Arboreality constrains morphological evolution but not species diversification in vipers.

Allen, L. R. (2019). *Venomous Snakes of Australia and Oceania*. CSIRO Publishing.

Arnold, S. J., & Pough, F. H. (1983). Allometry and the evolution of gape-limited predation in snakes. *American Naturalist*, 121(2), 151–170.

Barr , W. A. (2017). ggphylomorpho, version 0.2.

Bartlett, R. D., & Bartlett, P. P. (2009). *Guide and Reference to the Snakes of Western North America (North of Mexico) and Hawaii*. University Press of Florida

Bartolon, G., Stepp-Bolling, C., Jackson, K., Kley, N., & Brainerd, E. (2013). To Crush or to Engulf Your Victim: a biomechanical trade-off in lizards versus snakes. *American Naturalist* (Vol. 66).

Bonnet, X., Brischoux, F., Briand, M., & Shine, R. (2021). Plasticity matches phenotype to local conditions despite genetic homogeneity across 13 snake populations. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1943).

Borczyk, B., Paśko, Ł., Kusznierz, J., & Bury, S. (2021). Sexual dimorphism and skull size and shape in the highly specialized snake species, *Aipysurus eydouxii* (Elapidae: Hydrophiinae). *PeerJ*, *9*.

Campbell, J. A., & Lamar, W. W. (2004). *The Venomous Reptiles of the Western Hemisphere*. Cornell University Press.

Castiglione, S., Serio, C., Tamagnini, D., Melchionna, M., Mondanaro, A., di Febbraro, M., Profico, A., Piras, P., Barattolo, F., & Raia, P. 2019. A new, fast method to search for morphological convergence with shape data. *PLoS ONE*, *14*(12).

Chippaux, J.-P. (2019). *Snakes of Central and Western Africa*. Johns Hopkins University Press.

Crotty, T. L., & Jayne, B. C. (2014). Trade-offs between eating and moving: what happens to the locomotion of slender arboreal snakes when they eat big prey? *Biological Journal of the Linnean Society*, 114, 446-458.

da Silva, F. O., Fabre, A. C., Savriama, Y., Ollonen, J., Mahlow, K., Herrel, A., Müller, J., & Di-Poï, N. (2018). The ecological origins of snakes as revealed by skull evolution. *Nature Communications*, *9*(1).

Das, I. (2010). *A Field Guide to the Reptiles of South-East Asia*. New Holland Publishers.

Das, I. (2023). *Snakes of South-East Asia*. Bloomsbury Publishing.

Deepak, V., Gower, D. J., & Cooper, N. (2022). Diet and habit explain head-shape convergences in natricine snakes. *Journal of Evolutionary Biology*, *36*(2), 399–411.

Egan, D. (2022). *Snakes of the Middle East*. Bloomsbury Wildlife.

Esquerré, D., & Scott Keogh, J. (2016). Parallel selective pressures drive convergent diversification of phenotypes in pythons and boas. *Ecology Letters*, *19*(7), 800–809.

Fabre, A.-C., Bickford, D., Segall, M., & Herrel, A. (2016). The impact of diet, habitat use, and behaviour on head shape evolution in homalopsid snakes. *Biological Journal of the Linnean Society,* 118, 634-647.

Glaw, F., & Vences, M. (2007). *A Field Guide to the Amphibians and Reptiles of Madagascar*. Vences & Glaw Verlag.

Grundler, M. C., & Rabosky, D. L. (2014). Trophic divergence despite morphological convergence in a continental radiation of snakes. *Proceedings of the Royal Society B: Biological Sciences*, 281(1795), 20140413.

Herrel, A., Huyghe, K., Vanhooydonck, B., Backeljau, T., Breugelmans, K., Grbac, I., van Damme, R., & Irschick, D. J. (2008). Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource.

Hibbitts, T. J., & Fitzgerald, L. A. (2005). Morphological and ecological convergence in two natricine snakes.

Huey, R. B., & Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution*, 4(5), 131-135.

Klaczko, J., Sherratt, E., & Setz, E. Z. F. (2016). Are diet preferences associated to skulls shape diversification in xenodontine snakes? *PLoS ONE*, *11*(2).

López, M. S., Manzano, A. S., & Prieto, Y. A. (2013). Ontogenetic variation in head morphology and diet in two snakes (Viperidae) from Northeastern Argentina. *Journal of Herpetology*, *47*(3), 406–412.

Lettoof, D. C., Parkin, T., Jolly, C. J., de Laive, A., & von Takach, B. (2023). Snake life history traits and their association with urban habitat use in a tropical city. *Urban Ecosystems*, *26*(2), 433–445.

Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K., & Rodríguez-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, 279(5359), 2115–2118.

Mangiacotti, M., Giansanti, A., & Sacchi, R. (2014). Geometric morphometrics reveals inter- and intraspecific shape variation in head morphology of European lacertid lizards. *Zoologischer Anzeiger*, 253(2), 83–93.

Manier, M. K. (2004). Geographic variation in the long-nosed snake, *Rhinocheilus lecontei* (*Colubriade*): beyond the subspecies debate. In *Biological Journal of the Linnean Society*, 83, 65-85.

Manjarrez, J., Macías Garcia, C., & Drummond, H. (2017). Morphological convergence in a Mexican garter snake associated with the ingestion of a novel prey.

Manjarrez, J., Pacheco-Tinoco, M., & Venegas-Barrera, C. S. (2017). Intraspecific variation in the diet of the Mexican garter snake Thamnophis eques. *PeerJ*, *2017*(11).

Marais, J. (2004). *A Complete Guide to the Snakes of Southern Africa*. Struik Publishers.

Moon, B. R., Penning, D. A., Segall, M., & Herrel, A. (2019). Feeding in Snakes: Form, Function, and Evolution of the Feeding System (pp. 527–574).

Navas, C. A., Antoniazzi, M. M., Jared, C., & Kohlsdorf, T. (2004). Morphological and physiological specialization for digging in amphisbaenians, an ancient lineage of fossorial vertebrates. *Journal of Experimental Biology*, 207(14), 2433–2441.

Ortiz-Medina, J. A., Cedeño-Vázquez, J. R., González-Solís, D., & Mata-Silva, V. (2022). Intraspecific Variation in Diet Composition and Morphology of Yucatecan Cantils (*Agkistrodon russeolus* Gloyd 1972 [Serpentes: Viperidae]). *Herpetologica*, *78*(4), 244–252.

O'Shea, M. (2005). *Reptiles et Amphibiens*. Delachaux et Niestlé.

O'Shea, M. (2018). *The Book of Snakes: A Life-Size Guide to Six Hundred Species from Around the World*. University of Chicago Press.

Palci, A., Lee, M. S. Y., Aubret, F., & Sherratt, E. (2024). Multiple Paths to a Larger Mouth: Morphological Divergence in Two Island Populations of Australian Tiger Snakes (Notechis scutatus). *Evolutionary Biology*.

Pandelis, G. G., Grundler, M. C., & Rabosky, D. L. (2023). Ecological correlates of cranial evolution in the megaradiation of dipsadine snakes. *BMC Ecology and Evolution*, *23*(1).

Patterson, M., Wolfe, A. K., Fleming, P. A., Bateman, P. W., Martin, M. L., Sherratt, E., & Warburton, N. M. (2022). Ontogenetic shift in diet of a large elapid snake is facilitated by allometric change in skull morphology. *Evolutionary Ecology*, *36*(4), 489–509.

Penning, D. A. (2017). The scaling of bite force and constriction pressure in kingsnakes (*Lampropeltis getula):* Proximate determinants and correlated performance. *Integrative Zoology*, *12*(2), 121–131.

Perkins, M. W., & Eason, P. K. (2019). The relationship of head morphology and diet among three sympatric watersnake species. *Amphibia Reptilia*, *40*(1), 65–77.

Pietersen, D. W., Conradie, W., & Branch, W. (2021). *Snakes and Other Reptiles of Zambia and Malawi*. Struik Nature.

Pyron, R. A., & Burbrink, F. T. (2012). Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution*, *66*(1), 163–178.

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology & Evolution, 3, 217–223.

Rohlf, F. J. (2015). tpsDig, version 2.0

Roth-Monzón, A. J., Devitt, T. J., Ríos-Muñoz, C. A., Parra-Olea, G., Campbell, J. A., & Flores-Villela, O. (2021). Geographic Variation in the Green Rat Snake *Senticolis triaspis* (Squamata: Colubridae): Evidence from Mitochondrial DNA, Morphology, and Niche Modeling. *Ichthyology and Herpetology*, *109*(4), 1026–1035.

Ruane, S. (2015). Using geometric morphometrics for integrative taxonomy: An examination of head shapes of milksnakes (genus Lampropeltis). *Zoological Journal of the Linnean Society*, *174*(2), 394–413.

Segall, M., Cornette, R., Fabre, A. C., Godoy-Diana, R., & Herrel, A. (2016). Does aquatic foraging impact head shape evolution in snakes? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1837).

Segall, M., Cornette, R., Godoy-Diana, R., & Herrel, A. (2020). Exploring the functional meaning of head shape disparity in aquatic snakes. *Ecology and Evolution*, *10*(14), 6993–7005.

Sherratt, E., Rasmussen, A. R., & Sanders, K. L. (2018). Trophic specialization drives morphological evolution in sea snakes. *Royal Society Open Science*, *5*(3).

Shine, R., & Goiran, C. (2021). Sexual dimorphism in size and shape of the head in the sea snake *Emydocephalus annulatus* (Hydrophiinae, Elapidae). *Scientific Reports*, *11*(1).

Silva, F. M., Prudente, A. L. da C., Machado, F. A., Santos, M. M., Zaher, H., & Hingst-Zaher, E. (2017). Aquatic adaptations in a Neotropical coral snake: A study of morphological convergence. *Journal of Zoological Systematics and Evolutionary Research*, *56*(3), 382–394.

Spawls, S., Howell, K., Drewes, R., & Ashe, J. (2002). *A Field Guide to the Reptiles of East Africa: Kenya, Tanzania, Uganda, Rwanda, and Burundi*. A&C Black Publishers.

Speed, M. P., & Arbuckle, K. (2017). Quantification provides a conceptual basis for convergent evolution. *Biological Reviews*, *92*(2), 815–829.

Strong, C. R. C., Palci, A., & Caldwell, M. W. (2020). Insights into skull evolution in fossorial snakes, as revealed by the cranial morphology of *Atractaspis irregularis* (Serpentes: Colubroidea). *Journal of Anatomy*, *238*(1), 146–172.

Title, P. O., Singhal, S., Grundler, M. C., Costa, G. C., Alexander Pyron, R., Colston, T. J., Grundler, M. R., Prates, I., Stepanova, N., H Jones, M. E., Q Cavalcanti, L. B., Colli, G. R., Di-Poï, N., Donnellan, S. C., Moritz, C., Mesquita, D. O., Pianka, E. R., Smith, S. A., Vitt, L. J., & Rabosky, D. L. (n.d.). The macroevolutionary singularity of snakes. *Science,* 383, 918-923.

Vincent, S. E., Brandley, M. C., Herrel, A., & Alfaro, M. E. (2009). Convergence in trophic morphology and feeding performance among piscivorous natricine snakes. *Journal of Evolutionary Biology*, *22*(6), 1203–1211.

Vogel, G. (2006). *Venomous Snakes of Asia*. Edition Chimaira.

Whitaker, R., & Captain, A. (2004). *Snakes of India: The Field Guide*. Draco Books.

Table 1: Blomberg's K values and significance.

| | K | *P* |
|---|---|---|
| Shape | 0.0964 | 0.9071 |

620 Table 2: Summary of the allometric test results using a phylogenetic generalized least squares
621 (PGLS) model with log-transformed centroid size as the predictor of shape. The table reports
622 the degrees of freedom (Df), sums of squares (SS), F statistic, effect size (Z), and associated
623 p-value (*P*) for the regression.

| | Df | SS | $R^2$ | F | Z | r | *P* |
|---|---|---|---|---|---|---|---|
| Centroid size | 1 | 4.12 | 0.027 | 6.82 | 2.63 | 0.16 | $P < 0.05$ |

624

625 Table 3: Results of the phylogenetic MANCOVA and MANOVA testing the effect of habitat
626 use on shape with and without accounting for allometry. The table presents the degrees of
627 freedom (Df), sum of squares (SS), mean squares (MS), proportion of explained variance
628 ($R^2$), F-statistic (F), and p-value.

| | Df | SS | MS | $R^2$ | *F* | *P* |
|---|---|---|---|---|---|---|
| MANCOVA | | | | | | |
| Habitat | 6 | 24.94 | 4.16 | 0.13 | 6.72 | $P < 0.05$ |
| Centroid size | 1 | 2.91 | 2.91 | 0.01 | 4.71 | $P < 0.05$ |
| Interaction | 6 | 11.46 | 1.91 | 0.06 | 2.73 | $P < 0.05$ |
| MANOVA | | | | | | |
| Habitat | 6 | 24.94 | 4.16 | 0.13 | 6.33 | $P < 0.05$ |

629

630 Table 4: Results of the Tukey post hoc test for pairwise comparisons of morphological
631 disparity across niche groups. The table presents the effect size (d), upper confidence limit at
632 95% (UCL 95%), Z-score (Z), and p-value for each comparison.

| Comparison | d | UCL (95%) | Z | *P* |
|---|---|---|---|---|
| Fossorial – aquatic | 0.17 | 0.13 | 2.20 | $P < 0.05$ |
| Fossorial – arboreal | 0.17 | 0.13 | 2.17 | $P < 0.05$ |
| Fossorial – semi-aquatic | 0.18 | 0.13 | 2.28 | $P < 0.05$ |
| Fossorial – semi-arboreal | 0.17 | 0.13 | 2.25 | $P < 0.05$ |
| Fossorial – semi-fossorial | 0.20 | 0.13 | 2.40 | $P < 0.05$ |
| Fossorial – terrestrial | 0.18 | 0.13 | 2.23 | $P < 0.05$ |
| Semi-fossorial - arboreal | 0.07 | 0.06 | 2.12 | $P < 0.05$ |
| Semi-fossorial – semi-aquatic | 0.09 | 0.07 | 2.34 | $P < 0.05$ |
| Semi-fossorial – semi-arboreal | 0.06 | 0.05 | 1.94 | $P < 0.05$ |
| Semi-fossorial – terrestrial | 0.09 | 0.04 | 2.91 | $P < 0.05$ |
| Semi-aquatic – terrestrial | 0.08 | 0.06 | 2.35 | $P < 0.05$ |
| Semi-arboreal – terrestrial | 0.05 | 0.05 | 1.89 | $P < 0.05$ |

633

634 Table 5: Results of the phylogenetic MANCOVA and MANOVA testing the effect of diet on
635 head shape. The table presents the degrees of freedom (Df), sum of squares (SS), mean
636 squares (MS), proportion of explained variance ($R^2$), F-statistic (F), and p-value.

| | Df | SS | MS | $R^2$ | *F* | *P* |
|---|---|---|---|---|---|---|
| MANCOVA | | | | | | |
| Diet | 5 | 6.78 | 1.36 | 0.04 | 1.99 | 0.083 |
| Centroid size | 1 | 5.85 | 5.85 | 0.04 | 8.59 | $P < 0.05$ |
| Interaction | 5 | 5.75 | 1.15 | 0.04 | 1.69 | 0.141 |
| MANOVA | | | | | | |
| Diet | 5 | 6.78 | 1.36 | 0.05 | 1.89 | 0.089 |

637

638 Table 6: Results of the Tukey post hoc test for pairwise comparisons of morphological
639 disparity across diet groups. The table presents the effect size (d), upper confidence limit at
640 95% (UCL 95%), Z-score (Z), and p-value (p.value) for each comparison. Significant p-
641 values are denoted by an asterisk (*).

| Comparison | d | UCL (95%) | Z | *P* |
|---|---|---|---|---|
| Hard prey – Soft prey | 0.04 | 0.04 | 2.08 | $P < 0.05$ |
| Hard prey – Soft egg | 0.16 | 0.21 | 1.46 | 0.090 |
| Invertebrates – Soft eggs | 0.16 | 0.20 | 1.40 | 0.092 |

642

643 Table 7: Results of the two-block partial least squares (PLS) analysis assessing the
644 relationship between morphology and habitat use and morphology and diet while accounting
645 for phylogeny. The table reports the correlation coefficient from the PLS analysis (r-PLS), the
646 standardized effect size (Z-score), and the associated p-value.

| | r-PLS | Effect size | *P* |
|---|---|---|---|
| Habitat | 0.38 | 2.67 | $P < 0.01$ |
| Diet | 0.59 | 3.82 | $P < 0.01$ |

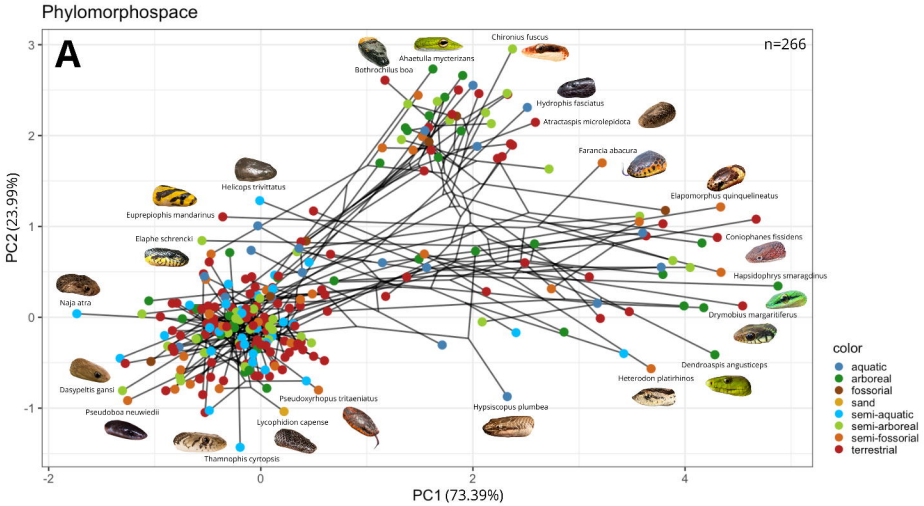
647

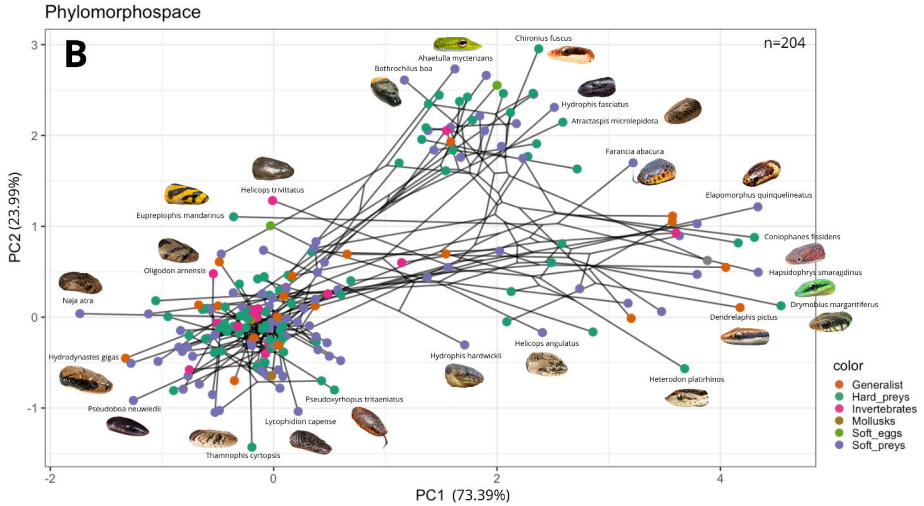
Table 8: Results of the convergence test. State1 and state2 correspond to pair of ecological groups being compared. The mean angles of phenotypic distance are reported using ang.state (state) and the test of convergence with timing of diversification using ang.state.time (time), with the corresponding p-values.

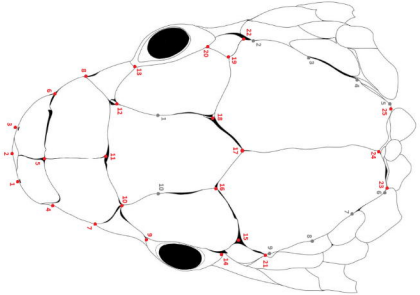
| | State | *P* | Time | *P* |
|---|---|---|---|---|
| Niche | | | | |
| terrestrial | 90.31 | 0.736 | 518.63 | 0.984 |
| arboreal | 85.40 | 0.087 | 478.54 | 0.271 |
| semi-arboreal | 91.41 | 0.886 | 507.65 | 0.715 |
| aquatic | 58.46 | $P < 0.01$ | 331.51 | $P < 0.01$ |
| semi-aquatic | 85.42 | 0.078 | 538.57 | 0.937 |
| fossorial | 11.29 | $P < 0.01$ | 98.38 | $P < 0.01$ |
| semi-fossorial | 90.73 | 0.563 | 525.32 | 0.850 |
| Diet | | | | |
| Hard eggs | 102.42 | 0.640 | 532.97 | 0.604 |
| Hard prey | 89.35 | 0.443 | 491.36 | 0.290 |
| Invertebrates | 87.85 | 0.304 | 508.23 | 0.621 |
| Mollusks | 53.65 | 0.165 | 448.20 | 0.372 |
| Soft prey | 88.04 | 0.155 | 501.86 | 0.616 |

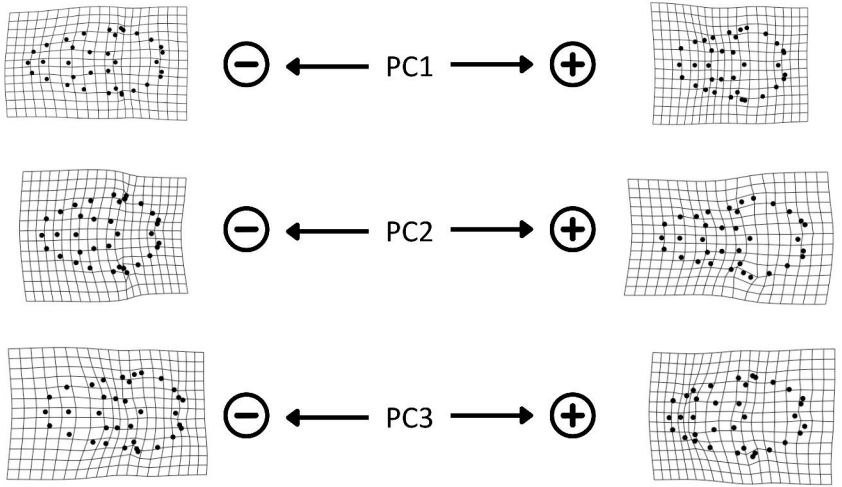
Table 9: Results of the morphological disparity analysis across ecological niches and diets. The table presents Procrustes variances for each niche and diet, indicating the level of morphological variation within groups.

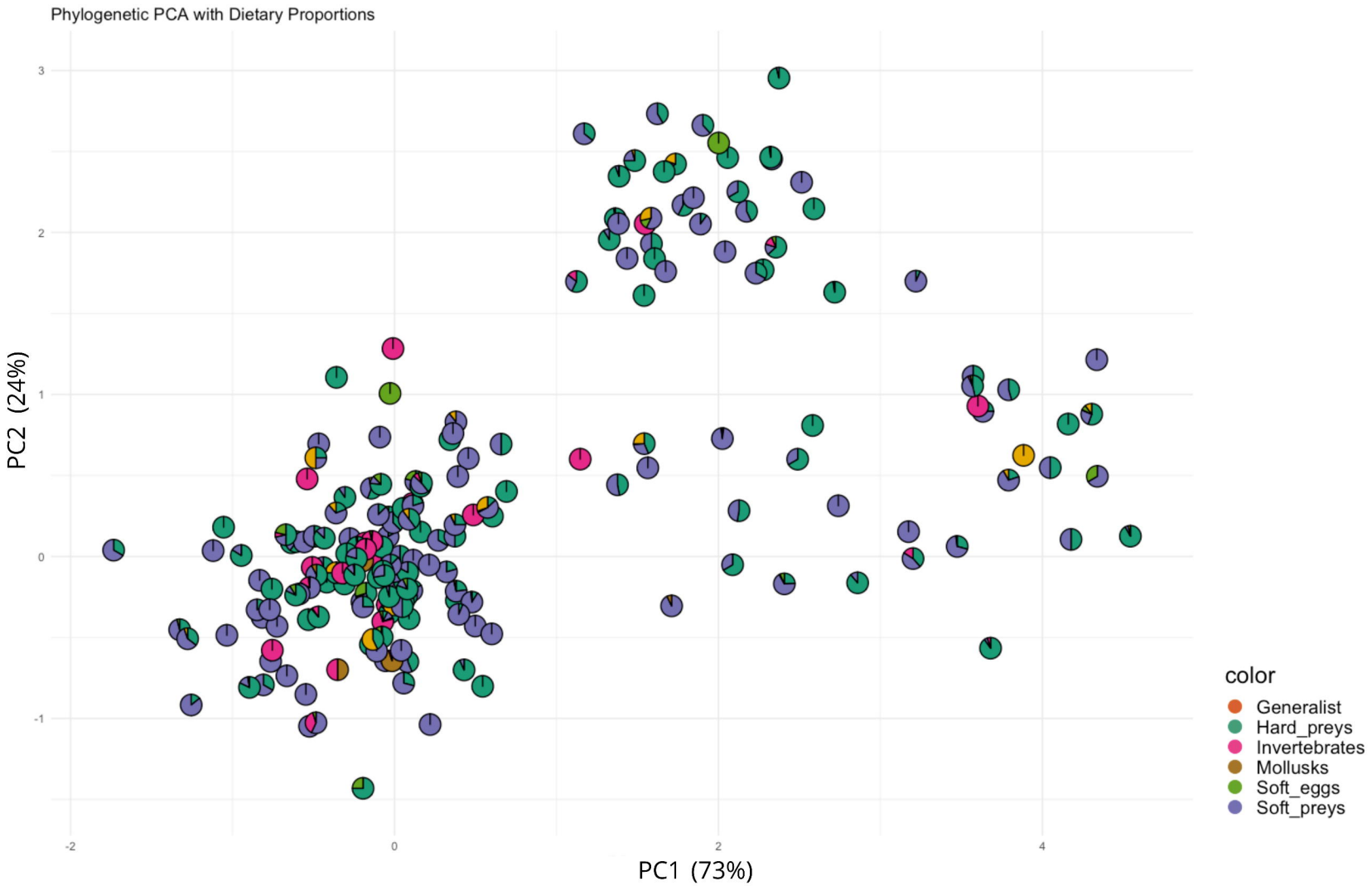
| Comparison | Procrustes variance |
|---|---|
| Habitat type | |
| Aquatic | 0.011605613 |
| Arboreal | 0.008724903 |
| Fossorial | 0.010839093 |
| Semi-aquatic | 0.010766939 |
| Semi-arboreal | 0.011107773 |
| Semi-fossorial | 0.012223323 |
| Terrestrial | 0.011249285 |
| Diet | |
| Generalist | 0.007111103 |
| Hard eggs | 0.008578330 |
| Hard prey | 0.010988433 |
| Invertebrates | 0.008819887 |
| Mollusks | 0.008497849 |
| Soft eggs | 0.002473988 |
| Soft prey | 0.017594851 |

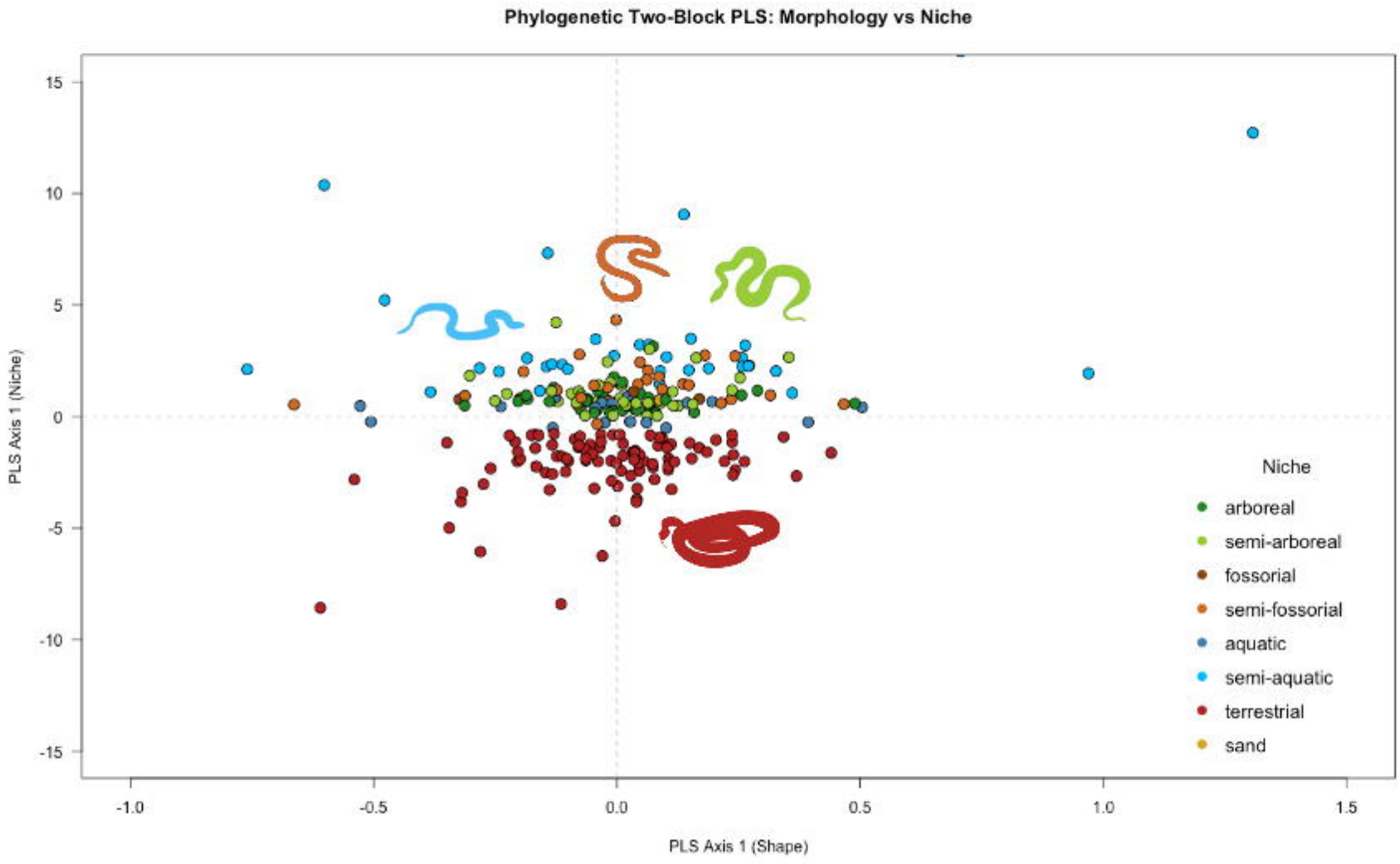

Phylomorphospace
A
n=266
Chironius fuscus
Ahaetulla mycterizans
Bothrochilus boa
Hydrophis fasciatus
Atractaspis microlepidota
Farancia abacura
Helicops trivittatus
Elapomorphus quinquelineatus
Eupreplophis mandarinus
Coniophanes fissidens
Elaphe schrencki
Hapsidophrys smaragdinus
Naja atra
Drymobius margaritiferus
Dendroaspis angusticeps
Heterodon platirhinos
Dasypeltis gansi
Pseudoxyrhopus tritaeniatus
Pseudoboa neuwiedii
Hypsiscopus plumbea
Lycophidion capense
Thamnophis cyrtopsis
PC2 (23.99%)
PC1 (73.39%)
color
aquatic
arboreal
fossorial
sand
semi-aquatic
semi-arboreal
semi-fossorial
terrestrial

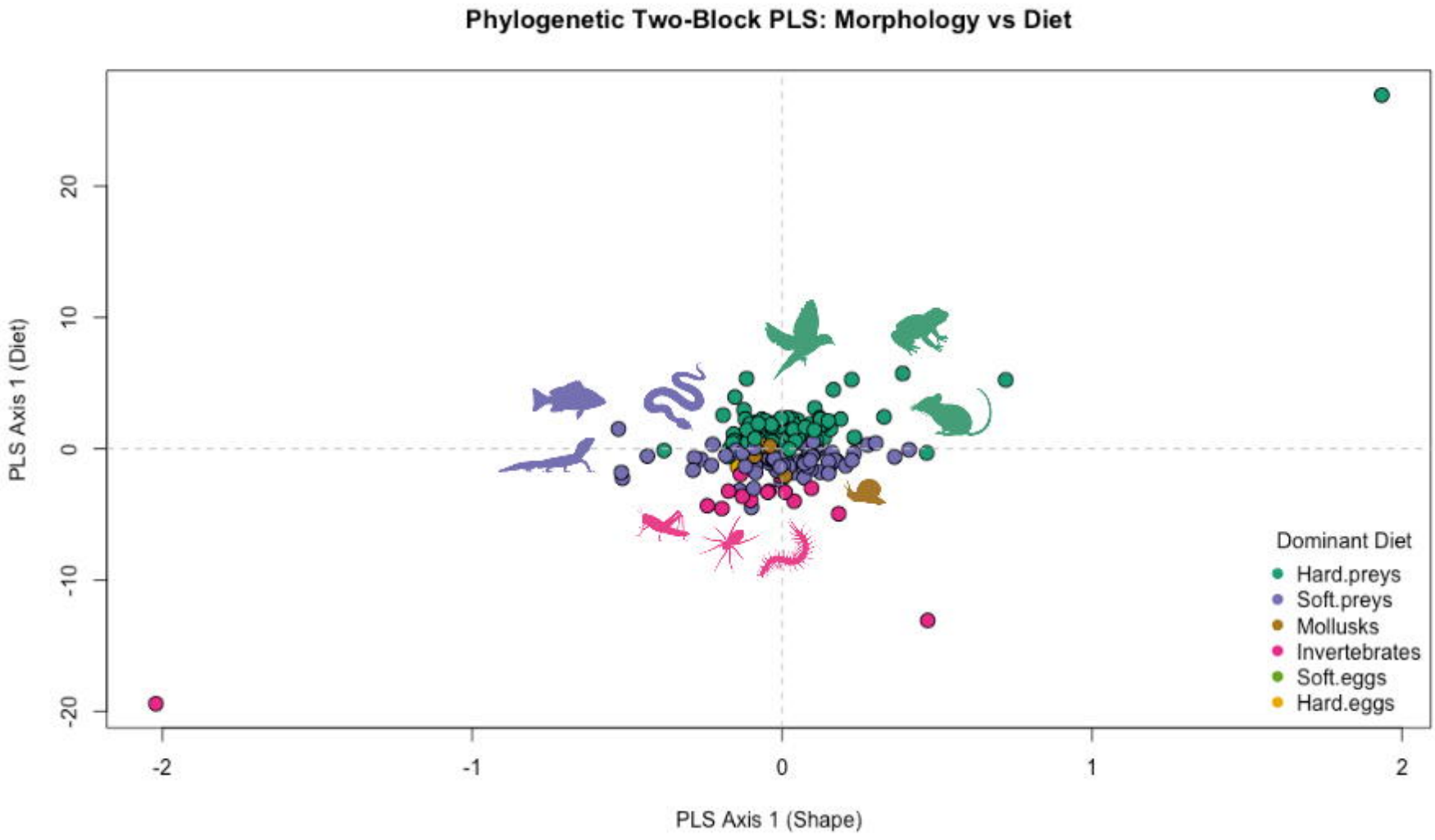

Phylomorphospace
B
n=204
Chironius fuscus
Ahaetulla mycterizans
Bothrochilus boa
Hydrophis fasciatus
Atractaspis microlepidota
Farancia abacura
Helicops trivittatus
Elapomorphus quinquelineatus
Eupreplophis mandarinus
Coniophanes fissidens
Oligodon annensis
Hapsidophrys smaragdinus
Naja atra
Drymobius margaritiferus
Dendrelaphis pictus
Helicops angulatus
Hydrodynastes gigas
Hydrophis hardwickii
Heterodon platirhinos
Pseudoxyrhopus tritaeniatus
Pseudoboa neuwiedii
Lycophidion capense
Thamnophis cyrtopsis
PC2 (23.99%)
PC1 (73.39%)
color
Generalist
Hard_preys
Invertebrates
Mollusks
Soft_eggs
Soft_preys




PC1
PC2
PC3


Phylogenetic PCA with Dietary Proportions
PC2 (24%)
PC1 (73%)
3
2
1
0
-1
-2
0
2
4
color
Generalist
Hard_preys
Invertebrates
Mollusks
Soft_eggs
Soft_preys


Phylogenetic Two-Block PLS: Morphology vs Niche
PLS Axis 1 (Niche)
PLS Axis 1 (Shape)
15
10
5
0
-5
-10
-15
-1.0
-0.5
0.0
0.5
1.0
1.5
Niche
arboreal
semi-arboreal
fossorial
semi-fossorial
aquatic
semi-aquatic
terrestrial
sand


Phylogenetic Two-Block PLS: Morphology vs Diet
PLS Axis 1 (Diet)
20
10
0
-10
-20
-2
-1
0
1
2
PLS Axis 1 (Shape)
Dominant Diet
Hard.preys
Soft.preys
Mollusks
Invertebrates
Soft.eggs
Hard.eggs