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Divergent paths, convergent heads: morphological adaptation of head shape to habitat use and diet 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, posteriorly wider heads suited for burrowing; aquatic species show streamlined profiles for hydrodynamic efficiency; and arboreal snakes tend to possess elongated heads 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 plays a central role in shaping animal morphology by favoring traits that enhance survival and reproductive success. When species are exposed to similar ecological pressures, they often evolve similar phenotypes—an evolutionary pattern known as convergent evolution (Losos, 2011; Stayton, 2015). However, the extent to which traits respond to ecological selection can vary significantly across morphological systems (Wainwright, 2007; Deepak et al., 2022). Different factors can explain head shape variation including feeding behavior, sexual selection, and habitat use (Pough & Groves, 1983; 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 or 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 habitats may follow distinct evolutionary and morphological pathways (Losos et al., 1998). This is especially true for aquatic snakes facing similar environmental pressures, yet showing 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 habitat-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). Among the various selective pressures acting on snake morphology, diet is by far the most studied and influential driver of head shape evolution. Numerous studies have demonstrated that trophic specialization—whether

61 targeting elongate, bulky, hard-shelled, or elusive prey—has led to distinct and repeated
62 morphological adaptations in cranial morphology (Klaczko et al., 2016; Fabre et al., 2016;
63 Segall et al., 2020; Deepak et al., 2022). For example, feeding-related morphological
64 evolution is evident in sea snakes, where selective pressures related to foraging mode have
65 resulted in distinct head shapes (Sherratt et al., 2018). Similarly, homalopsid and xenodontine
66 snakes have evolved unique head shapes driven by the functional demands imposed by the
67 prey they eat (Klaczko et al., 2016; Fabre et al., 2016). Habitat-related selective pressures also
68 influence snake morphology. *Boidae* and *Pythonidae*, for instance, exhibit head shape
69 convergence driven primarily by habitat use (Esquerré & Keogh, 2016).

70 Previous studies on head shape convergence in snakes have focused on arboreal,
71 aquatic, fossorial and terrestrial snakes. For instance, aquatic species frequently develop
72 narrow heads with upward-facing eyes and nostrils, features that improve their ability to
73 capture prey, move efficiently through water and spot predators while remaining submerged
74 (Hibbitts and Fitzgerald, 2005; Vincent et al., 2009; Segall et al., 2016, 2020; Deepak et al.,
75 2022). Similarly, burrowing snakes possess robust heads adapted for digging and streamlined
76 bodies with reduced ventral scales, which help them burrow with minimal friction (Fabre et
77 al., 2016; Herrel et al., 2008). Meanwhile, microcephalic sea snakes exhibit distinct head
78 shapes linked to developmental changes, representing habitat specialization rather than direct
79 functional convergence (Sherratt et al., 2019). Terrestrial snakes from different lineages often
80 exhibit convergence in robust, broad head shapes associated with subduing large or ground-
81 dwelling prey, reflecting similar ecological demands despite phylogenetic differences
82 (Klaczko et al., 2016; da Silva et al., 2018; Carrasco et al., 2023; Pandelis et al., 2023).
83 Finally, arboreal snakes frequently converge on slender, elongate head shapes with enlarged
84 orbits—adaptations that enhance precision in prey capture and navigation in structurally
85 complex habitats (Carrasco et al., 2023; Pandelis et al., 2023; Seneci et al., 2025).

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 that facilitates substrate penetration and minimizes the energetic cost of burrowing (Navas et al., 2004). This prediction is supported by recent work showing that fossorial snakes display consistent cranial streamlining associated with head-first burrowing, including reduced head width and reinforced snouts (Deepak et al., 2022; Seneci et al., 2025). These morphological traits have evolved independently in multiple lineages of burrowing snakes, reflecting strong functional convergence related to locomotion in compact substrates. Head shape in fossorial snakes is expected to be primarily shaped by locomotor demands rather than feeding ecology, as these species typically consume small, soft-bodied soil invertebrates that do not require specialized cranial adaptations for prey capture or processing. Arboreal snakes are predicted to have slender heads, which enhance crypsis and maneuverability among branches and foliage—traits commonly observed in arboreal colubrids and vipers (Carrasco et al., 2023; Palci et al., 2024). However, mollusk specialists such as *Dipsas* and *Sibon* often exhibit more robust or blunt head shapes, which are associated with the biomechanical demands of molluscivory, including increased muscle mass and cranial rigidity for extracting soft-bodied prey from shells (Palci et al., 2024). Aquatic snakes are expected to exhibit high disparity in head shape, reflecting their exploitation of diverse prey types and the functional demands of navigating various aquatic environments (Deepak et al., 2022). This pattern has been documented in multiple aquatic snake lineages, where variation in prey capture strategies (e.g., gripping, constriction) and ecological specialization (e.g., fish, amphibians, crustaceans) correlates with significant cranial morphological diversity (Segall et al., 2016). Species that utilize multiple environments (e.g., semi-aquatic, semi-arboreal, semi-fossorial) are predicted to exhibit intermediate morphological features that reflect functional compromises between distinct

ecological demands. These semi-specialized species would occupy broader morphospaces due to the need to balance locomotion and foraging strategies across habitats (Ortiz-Medina et al., 2022; Pandelis et al., 2023).We also predict that greater morphological variation will be observed in snakes that live in transitional habitats and that have non-specialized diets.

Materials and Methods

Sample and ecological classification

We collected data from 281 species used for habitat use (521 specimens) and 197 species for diet (384 specimens). Animals were housed in three European Natural History Museums: the research collection of the last author (99 specimens), the Alexander Koenig Museum in Bonn (319 specimens), and the Museum of Natural Sciences in Brussels (103 specimens). Our measurements were taken from adult specimens whenever possible. However, in some cases, only young individuals were available. For some species, only subadults were measured because of a lack of availability of adults (Table S1). Our sampling aimed to encompass the phylogenetic and ecological diversity of snakes, while remaining limited by the availability of specimens in these collections.

Based on the literature, eight habitat use categories were determined (Spawls et al., 2002; Whitaker & Captain, 2004; Campbell & Lamar, 2004; Marais, 2004; O'Shea, 2005; Vogel, 2006; Glaw & Vences, 2007; Bartlett & Bartlett, 2009; Das, 2010; O'Shea, 2018; Allen, 2019; Chippaux, 2019; Pietersen et al., 2021; Egan, 2022; Das, 2023). We classified the species into 102 terrestrial, 34 arboreal, 19 aquatic, 7 fossorial, 43 semi-arboreal, 33 semi-aquatic, and 29 semi-fossorial species. We based our ecological categorization on the biomechanical constraints imposed by the environment (Table S2). For instance, similar

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

135 We used the time-calibrated phylogeny and dietary data from the supplementary
136 material of the paper by Title et al. (2024). This paper contain a recent time-calibrated
137 phylogeny of 6,885 species and a complete dataset of diet proportions of more than 68,547
138 species of squamates. Categories were modified and regrouped based on the functional
139 constraints imposed by the prey. We define a total of ten dietary groups, including 19
140 generalists, 3 hard egg feeders, 76 hard prey feeders, 16 invertebrate feeders, 2 mollusk
141 specialists, 2 soft egg specialists, and 79 soft prey eaters (Table S3). In creating these
142 categories, we grouped salamanders, lizards, and fish together as they have cylindrical and
143 flexible bodies and as such should impose similar functional constraints.

144 *Geometric morphometric data*

145 For each individual a photo of the head in dorsal view was taken with a Nikon ©
146 D3100 camera. We omitted photos from a lateral view because of sample quality (head
147 deformed & specimens with mouth partially open). Snakes were placed on a grid paper for
148 calibration and scale (1 x 1cm squares; Figure S1A). To perform the geometric morphometric
149 analysis, 25 landmarks and 10 semi-landmarks were selected (Figure S1B) and defined (Table
150 S4). These landmarks and semi-landmarks were based on the literature (Manier, 2004;
151 Mangiacotti et al., 2014; Ruane, 2015; Roth-Monzón et al., 2021). They capture the general
152 head shape of the animals and are easy to identify. This approach was applied to quantify
153 interspecific variation in head shape in a standardized way, while minimizing noise due to
154 orientation or placement error.

As we based our analysis on landmarks placed on cephalic scales, only species from the Alethinophidia, including Colubridae, Elapidae, Lamprophiidae, Homalopsidae, Pareidae, Psammophiidae, and Pseudoxyrhophiidae were used. We excluded Scolecophidean snakes due to incompatible landmark patterns. 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 with the *geomorph* package (Adams et al., 2025), using the function *gpagen*. Generalized Procrustes Analysis (GPA) superimposes configurations by translating, scaling, and rotating landmark coordinates to remove non-shape variation, thereby allowing comparisons of pure shape (Rohlf & Slice, 1990; Figure S1C). Species means were then computed from Procrustes-aligned coordinates and used in subsequent analyses. Semi-landmarks were slid along their tangent directions, minimizing bending energy to optimize their positions. Statistical robustness of landmarking was assessed through repeatability tests and visual inspection of variation across replicates.

Phylogenetic signal

The phylogenetic tree was pruned to match our species in the morphometric data. To evaluate the extent to which shape variation is structured by phylogeny we used the *physignal* function in R from the *geomorph* package. The *physignal* function quantifies the strength of phylogenetic signal using a generalized K-statistic, comparing observed similarity with expectations under Brownian motion. We applied this method to test whether head shape variation was structured by shared ancestry. Significance was assessed with 1000

179 permutations of tip labels, generating a null distribution against which the observed signal
180 was compared. A value close to 1 would indicate a strong phylogenetic signal, meaning
181 closely related species exhibit more similar shapes than would be expected by random chance.
182 On the other hand, values significantly less than 1 suggest a weaker phylogenetic signal,
183 indicating that the variation in shape is less influenced by the evolutionary history of the
184 species.

185 *Allometry*

186 Allometry was quantified using a phylogenetic generalized least squares (PGLS)
187 model, with shape coordinates as the dependent variable and centroid size as the predictor.
188 This test was used to evaluate whether differences in head shape could be explained by
189 differences in body size. Phylogenetic generalized least squares (PGLS) models fit a
190 regression that accounts for shared ancestry by incorporating the expected covariance
191 structure among species (Grafen, 1989). We implemented this in R using the function
192 *procD.pgls* from *geomorph*, and statistical significance was assessed via permutation tests on
193 residual sums of squares.

194 *Phylogenetic principal components analysis*

195 A phylogenetically-informed principal component analysis (PCA) was performed
196 using the *phytools* package (Revell, 2012) to explore shape variation in relation to habitat and
197 diet categories. This method was applied to reduce the dimensionality of morphometric data
198 and visualize axes of greatest variation while accounting for phylogenetic structure.
199 Eigenvalues were calculated to assess the variance explained by the principal components,
200 and the first two principal components (PC1 & PC2) were visualized. The phylomorphospace
201 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). Phylogenetic PCA modifies classical PCA by incorporating a phylogenetic covariance matrix, ensuring that loadings reflect evolutionary relationships. Implementation was done with the *phyl.pca* function in the *phytools* package, and significance of phylogenetic structure in ordination was assessed by comparing eigenvalues with those expected under Brownian motion simulations.

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. Phylogenetic MANOVA extends multivariate ANOVA by accounting for phylogenetic covariance, testing for mean shape differences among groups. Implementation was performed with *procD.pgls* function from *geomorph* package, which computes sums of squares and generates P-values by permutation (1000 iterations) of residuals, thereby providing a non-parametric assessment of significance.

Analyses of covariation

A phylogenetic Two-Block PLS (Partial Least Squares) analysis was carried out using the *phylo.integration* function from the *geomorph* package, to test for covariation between head shape and diet composition. This method identifies axes of maximal covariation between two data blocks while correcting for non-independence among species due to shared ancestry (Rohlf & Corti, 2000). Implementation was performed with the *phylo.integration* function in *geomorph*, and significance was assessed through permutation tests (1000 iterations) comparing observed singular values with those from randomized datasets. We used continuous proportions of prey items (e.g., hard prey, soft prey, invertebrates, etc.), allowing

225 for a finer representation of dietary gradients across species. This matrix was aligned with
226 shape data from Procrustes-aligned landmarks, and phylogenetic relationships were accounted
227 for.

228 *Convergence*

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

242 *Disparity analysis*

243 We performed a morphological disparity analysis to assess the relationship between
244 shape variation and habitats or diet groups while accounting for phylogenetic relationships,
245 using the *morphol.disparity* function from the *geomorph* package. We used Procrustes-
246 aligned shape coordinates (GPA) and tested for differences in morphological disparity across
247 habitats and diet categories. A 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 = 0.096), indicating a weak phylogenetic signal. Furthermore, the result was not statistically significant (P = 0.91), 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 (Df = 1; SS = 4.12; Rsq = 0.027; F = 6.82; Z = 2.63; $P < 0.05$). Despite a relatively low proportion of variance explained, the allometric signal in head shape variation was significant.

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; Figure 2). Although most of the variance is explained by PC1 and PC2, we also visualized the morphospaces defined by PC1 vs PC3 (Figure S3; Figure S5) and PC2 vs PC3 (Figure S4; Figure S6) to capture additional axes of shape variation and to ensure that our interpretations were not restricted to a single projection. 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 head (Figure 1). Arboreal and semi-arboreal snakes, by contrast, tend to occupy higher PC1 values and display slender, elongated heads. Aquatic and semi-aquatic species are more dispersed along PC1, with heads often appearing streamlined. Terrestrial snakes are widely spread across the morphospace and semi-fossorial and semi-arboreal species tend to fall in intermediate regions of the morphospace.

In terms of diet, species consuming soft-bodied prey (e.g., snakes, lizards) generally exhibit higher PC1 values, associated with elongated and narrower heads (Figure 2; Figure 3). Conversely, species feeding on harder prey (e.g., rodents, birds, mollusks) are found in the lower range of PC1 and often exhibit broader, more robust heads. Mollusk specialists and other durophagous feeders show this trend most strongly. PC2 variation also reflects dietary adaptations: species with lower PC2 values, such as soft-prey specialists and generalists, tend to have narrower heads, while invertebrate feeders cluster around broader and more robust head shapes. Deformation grids show that many species exhibit a combination of longer, narrower snouts with posterior heads widening—contributing to the shared V-shaped morphology in fossorial, semi-aquatic, and some hard-prey specialists (Figure 1). Overall, generalist feeders and species with diverse prey types occupy wide, overlapping regions of the morphospace, indicating that head shape in snakes is shaped by a complex interplay between habitat use and dietary specialization.

Differences between habitat groups

The MANOVA indicates significant differences between habitat groups in head shape (Table 1). When adding Log_{10}-transformed centroid size as a covariate, we found significant effects of habitat, centroid size and the interaction between the two. The interaction between habitat and centroid size was also significant. Moreover, post-hoc pairwise comparisons

294 further revealed that fossorial snakes, as well as semi-fossorial, differ significantly from all
295 ecological groups (Table 2). Additionally, semi-aquatic and semi-arboreal differ from
296 terrestrial snakes in head shape.

297 *Differences between diet groups*

298 There was a trend toward head shape differentiation among diet groups, based on
299 dominant dietary regimes, as revealed by the phylogenetic MANOVA (Table 3). When
300 adding Log_{10}-transformed centroid size as a covariate, this tendency remained. Centroid size
301 did differ between dietary groups, while interactions were not significant (Table 3). Post-hoc
302 pairwise comparisons indicated a significant difference in head shape between species
303 consuming hard prey and those consuming soft prey ($P < 0.05$; Table 4). There were trends
304 observed between hard prey and soft eggs feeders ($P = 0.090$), as well as between
305 invertebrates and soft eggs feeders ($P = 0.092$).

306 *Analyses of covariance*

307 Our results revealed a significant covariation between head shape and habitat use (r-
308 PLS = 0.38, Z = 2.67, $P < 0.01$), as well as between head shape and diet (r-PLS = 0.59, Z =
309 3.82, $P < 0.05$). This indicates that species occupying different habitat types or relying on
310 different dietary resources differ in head shape. Specifically, the distribution of species along
311 the first PLS axis suggests that morphological variation is aligned with ecological gradients
312 (Figure 4). Aquatic and fossorial species appear to cluster separately from arboreal or
313 terrestrial taxa, reflecting adaptive morphological specializations for swimming, burrowing,
314 or climbing. In the case of diet, species that consume hard prey tend to separate from those
315 feeding primarily on soft-bodied prey or eggs, suggesting that cranial shape variation may be
316 driven by biomechanical demands related to prey processing (Figure 5).

Convergence

The convergence test results revealed contrasting patterns of morphological evolution depending on whether species were grouped by habitat use or diet (Table 5). Among habitat groups, strong evidence for morphological convergence was found within aquatic and fossorial species. These two groups showed significantly lower mean angles of phenotypic distance (ang.state = 58.46 and 11.29, respectively; $P < 0.01$ for both). These results were also supported by the timing-based convergence metric, indicating that the convergent traits evolved synchronously within these clades (ang.state.time = 331.51 and 98.38, respectively; $P < 0.01$ for both groups). In contrast, no significant convergence was detected within the other habitat groups, such as terrestrial, arboreal, semi-arboreal, semi-aquatic, or semi-fossorial species (Table 5). While some of these groups (e.g., arboreal or semi-aquatic) showed moderately low angles of phenotypic distance, the results were not statistically significant.

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

Disparity analysis

Our findings indicate that semi-fossorial species exhibit the highest morphological disparity (0.0122; Figure 6). Aquatic species displayed the second highest score in morphological disparity (0.0116). Moderate levels of disparity were observed in terrestrial

species (0.0112) and semi-arboreal species (0.0111). Conversely, 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.

Our findings further indicated that species consuming soft prey exhibit the highest morphological disparity (0.018; Figure 6). Species consuming hard prey and mollusks 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 S6). 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.

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

364 adaptations across lineages. Similar patterns have been observed by da Silva et al. (2018),
365 who reported convergent heads shapes in aquatic and fossorial snakes regardless of
366 phylogenetic affiliation, emphasizing the influence of habitat-driven functional demands.
367 Likewise, da Silva et al. (2018) found that trophic specialization drove significant cranial
368 divergence among Neotropical snakes with limited phylogenetic signal, suggesting that diet,
369 like habitat, can supersede phylogenetic inertia. On the other hand, Esquerré and Keogh
370 (2016) found a moderate phylogenetic influence on head shape in Australian pythons and
371 boas, though ecological divergence still played a key role—highlighting potential clade-
372 specific variation in the balance between constraint and adaptation. Although our allometric
373 test revealed a statistically significant relationship between centroid size and shape, the effect
374 was small ($R^2 = 0.025$). This decoupling indicates that selection acts more directly on cranial
375 morphology than on body size (da Silva et al., 2018).

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

386 The phylogenetic MANOVA confirmed significant overall differences in head shape
387 among habitat groups, with fossorial and semi-fossorial species showing distinct

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

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

410 Dietary specialization also contributes meaningfully to head shape variation. Species
411 feeding on soft-bodied prey such as snakes, amphibians, or fish often display elongated,

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

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

437 constraints that shape divergent cranial solutions to similar dietary challenges (Segall et al.,
438 2020; Pandelis et al., 2023). The exclusion of underrepresented groups, such as mollusk
439 feeders or egg specialists, from our convergence analyses may also limit our ability to detect
440 certain trends.

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

450 While these results provide valuable insights, it is important to consider potential
451 methodological limitations. In particular, we acknowledge the limitations of using a 2D dorsal
452 view to represent head shape. The omission of the third dimension means that important
453 aspects of morphology, such as underslung jaws in burrowing taxa or relatively tall heads in
454 arboreal species, may not be adequately captured. Prior studies have shown that 2D methods
455 can underestimate morphological variance (Buser et al., 2018) and in some cases introduce
456 errors comparable to interspecific differences (Liu et al., 2014). The reliability of 2D analyses
457 is particularly limited for highly three-dimensional structures. While our 2D dataset provides
458 valuable comparative information, we note that complementary data from lateral views or full
459 3D reconstructions (e.g., CT scans) would enhance the robustness of functional and
460 evolutionary inferences.

461 Beyond analytical methods, a number of biological and data-driven limitations should
462 be acknowledged. First, the categorization of habitats remains somewhat coarse and
463 potentially subjective. For example, semi-fossorial species may share more ecological traits
464 with terrestrial than fully fossorial snakes, and semi-aquatic species vary widely in their
465 dependence on aquatic environments (Esquerré & Keogh, 2016; Silva et al., 2017).
466 Incorporating quantitative ecological data—such as habitat features (e.g., branch density, soil
467 compaction, water salinity) or substrate use (e.g., frequency of use of forest soil, mud, or tree
468 species)—could refine these categories and better capture the ecological continuum
469 (Manjarrez et al., 2017b; Title et al., 2024). Second, although our dietary classifications are
470 grounded in empirical data, they could be enhanced by integrating quantitative prey traits—
471 such as size and hardness—that more accurately represent the functional challenges faced by
472 predators, rather than relying solely on prey shape (Vincent et al., 2009; da Silva et al., 2018).
473 For instance, both birds and frogs may be categorized as soft prey, yet their ecologies and
474 physical properties differ markedly, potentially requiring distinct feeding adaptations (Segall
475 et al., 2020; Deepak et al., 2022). Understanding the functional properties of prey would thus
476 provide more nuanced insights into head shape evolution. Furthermore, the inclusion of
477 behavioral variables—such as foraging strategy or strike kinematics—would significantly
478 strengthen the link between morphology and ecological function (Herrel et al., 2008; Segall et
479 al., 2016; Moon et al., 2019). These traits are likely to interact with head shape in complex
480 ways that are not fully captured by static ecological or dietary categories alone. Additionally,
481 focusing on taxonomically or ecologically specialized clades (e.g., snail-eaters, egg
482 specialists) could shed light on extreme morphological adaptations that illustrate more clearly
483 how head shape evolves under strong selective pressure (Pandelis et al., 2023; Palci et al.,
484 2024). Finally, subadult specimens can change our biological interpretation because of
485 ontogenetic changes in shape where the adult form can be very different in head shape pattern

compared to juveniles or even subadult individuals, due to different habitat use or diet (Patterson et al., 2022).

Our study underscores the complex and multifactorial nature of head shape evolution in snakes, driven more by ecological function than phylogenetic history or allometry. Moon et al. (2019) emphasized the remarkable adaptability of the snake feeding system, noting that head morphology reflects not only dietary and ecological demands, but also performance constraints like gape limitation, strike kinematics, and prey handling strategies. They highlight how head shape plays a central role in functional performance—such as strike accuracy, hydrodynamics, and force generation—yet also caution that our understanding remains limited by the narrow taxonomic and ecological scope of most studies. To address this, future research should aim for a more integrative approach—linking head morphology with detailed data on strike mechanics, bite force, and prey-handling behaviors across ecological contexts. For instance, striking behaviors vary between aquatic and terrestrial environments, and bite performance has only been measured in a few species, 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 habitats to different prey items (Crotty & Jayne, 2015). Furthermore, intraspecific variation in feeding plasticity (Manjarrez et al., 2017a; Bonnet et al., 2021; Ortiz-Medina et al., 2022), as well as ontogenetic (López 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

510 snake evolution. In doing so, we can build a more mechanistic understanding of how
511 morphology translates into ecological success.

512 **Conclusion**

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

526 Our use of cephalic scale-based morphometrics offers a pragmatic and ecologically relevant
527 proxy for head shape in large comparative datasets, but we recognize its limitations. Internal
528 cranial architecture, muscle arrangement, and soft tissue all contribute to ecological
529 performance and remain largely unexplored in this context. Moving forward, a more
530 integrative approach—incorporating performance data (e.g., bite force, strike dynamics),
531 behavioral traits (e.g., foraging strategy, prey handling), and finer-scale ecological metrics—
532 will be essential for linking form to function. Investigating intraspecific variation, ontogeny,
533 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.

Author Contribution

David Hudry: conceptualization, investigation, writing – original draft, writing – review and editing

Anthony Herrel: conceptualization, investigation supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available on Github at https://github.com/DavidHudry/Supplementary-Geomorphometric-Data .

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721 **Figures**

722 **Figure 1:** Phylomorphospace illustrating head shape variation across 281 species of snakes.
723 The phylogeny is plotted in the morphospace described by the first two axes (PC1 vs. PC2).
724 Nodes are colored based on species habitat classification.

725 **Figure 2:** Phylomorphospace illustrating head shape variation across 197 species of snakes.
726 The phylogeny is plotted in the morphospace described by the first two axes (PC1 vs. PC2).
727 Nodes are colored based on species diet classification.

728 **Figure 3**: Phylogenetic PCA illustrating proportions of prey items of the 197 species of
729 snakes included in the analyses as described by the first two axes (PC1 vs. PC2).

730 **Figure 4:** Two-block phylogenetic PLS plot illustrating covariation between head shape and
731 ecological niches in snakes. Species are plotted along the first PLS axis of head shape (x-axis)
732 and ecological niche (y-axis). Points are colored by habitat category, with selected species
733 labeled.

734 **Figure 5:** Two-block phylogenetic PLS plot illustrating covariation between head shape and
735 diet in snakes. Species are plotted along the first PLS axis of head shape (x-axis) and diet (y-
736 axis). Points are colored by diet category, with selected species labeled.

737 **Figure 6:** Barplot of the morphological disparity analysis across habitats and diets. The plot
738 presents Procrustes variances for each habitat and diet, indicating the level of morphological
739 variation within groups.
740

741 **Tables**

742 Table 1: Results of the phylogenetic MANCOVA and MANOVA testing the effect of habitat
743 use on shape with and without accounting for allometry. The table presents the degrees of
744 freedom (Df), sum of squares (SS), mean squares (MS), proportion of explained variance
745 (R^2), F-statistic (F), and p-value.

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

746

747 Table 2: Results of the Tukey post-hoc test for pairwise comparisons of morphological

748 disparity across habitat groups. The table presents the effect size (d), upper confidence limit at

749 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	$P < 0.05$

750

751 Table 3: Results of the phylogenetic MANCOVA and MANOVA testing the effect of diet on

752 head shape. The table presents the degrees of freedom (Df), sum of squares (SS), mean

753 squares (MS), proportion of explained variance (R^2), F-statistic (F), and p-value.

	Df	SS	MS	R^2	*F*	*P*
MANCOVA						
Centroid size	1	5.85	5.85	0.04	8.59	$P < 0.05$
Diet	5	6.78	1.36	0.04	1.99	0.083
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

754

755 Table 4: Results of the Tukey post-hoc test for pairwise comparisons of morphological

756 disparity across diet groups. The table presents the effect size (d), upper confidence limit at

757 95% (UCL 95%), Z-score (Z), and p-value (p.value) for each comparison.

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

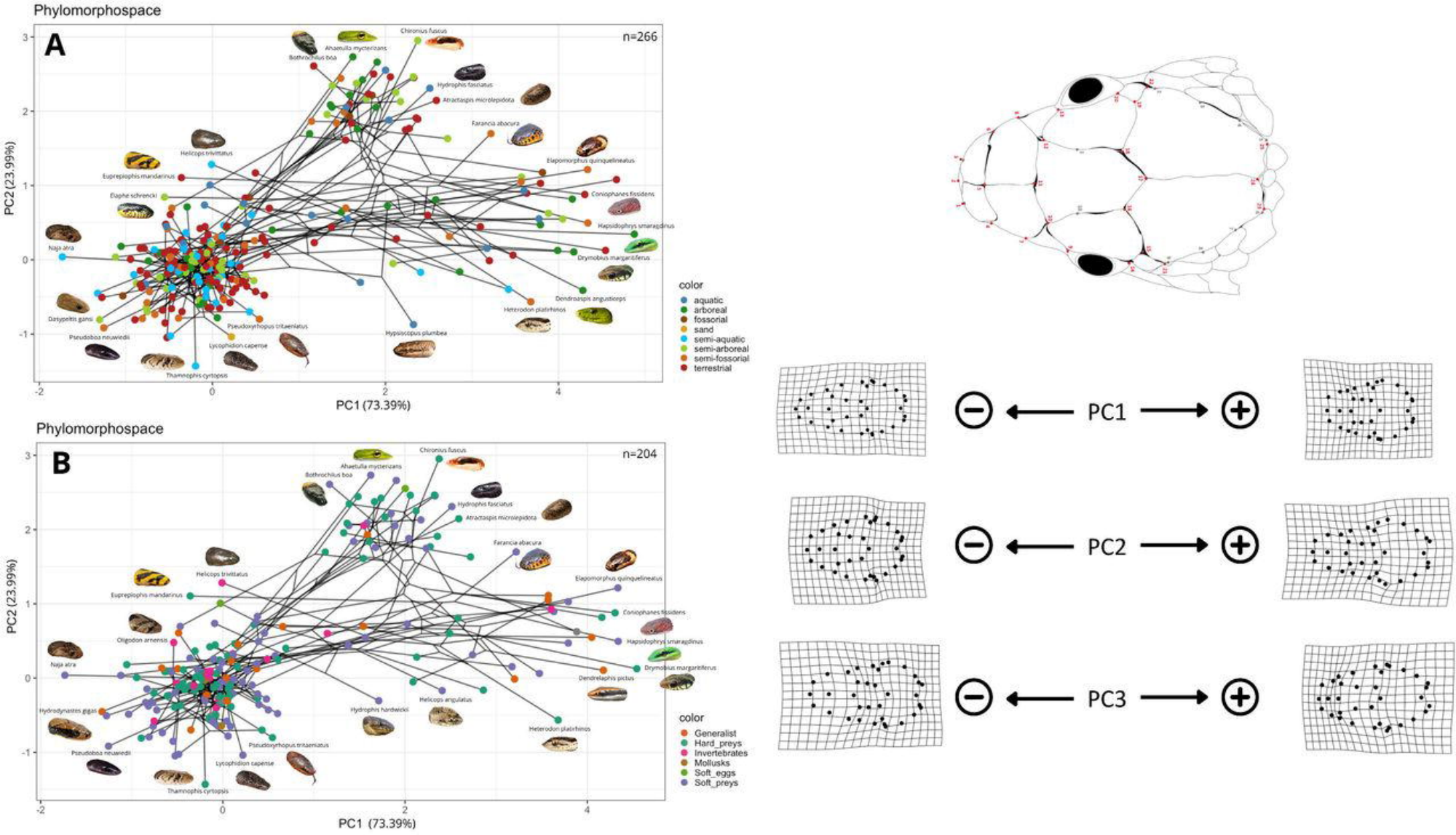
758

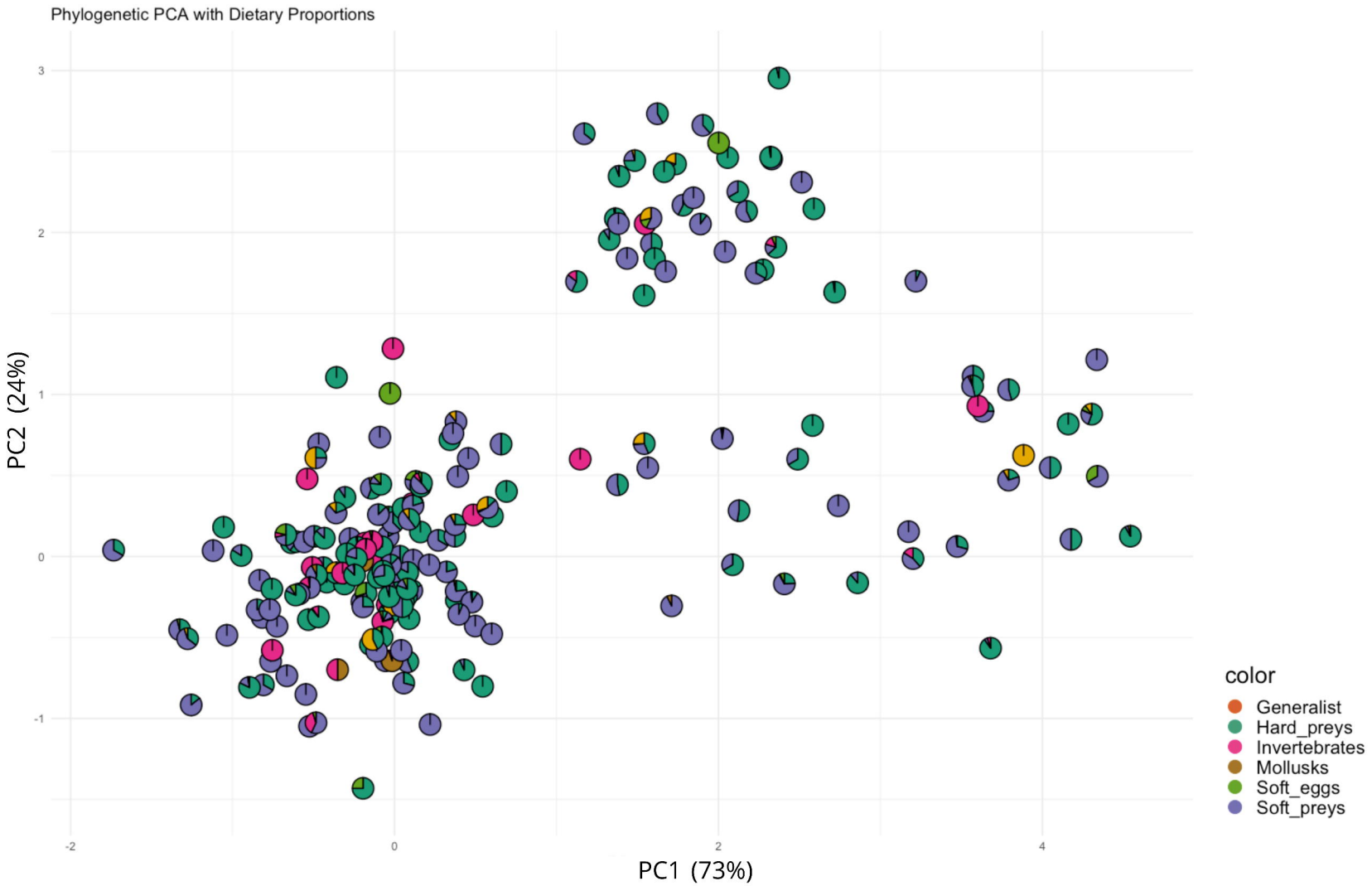
759 Table 5: Results of the convergence test. State1 and state2 correspond to pair of ecological
760 groups being compared. The mean angles of phenotypic distance are reported using ang.state
761 (state) and the test of convergence with timing of diversification using ang.state.time (time),
762 with the corresponding p-values.

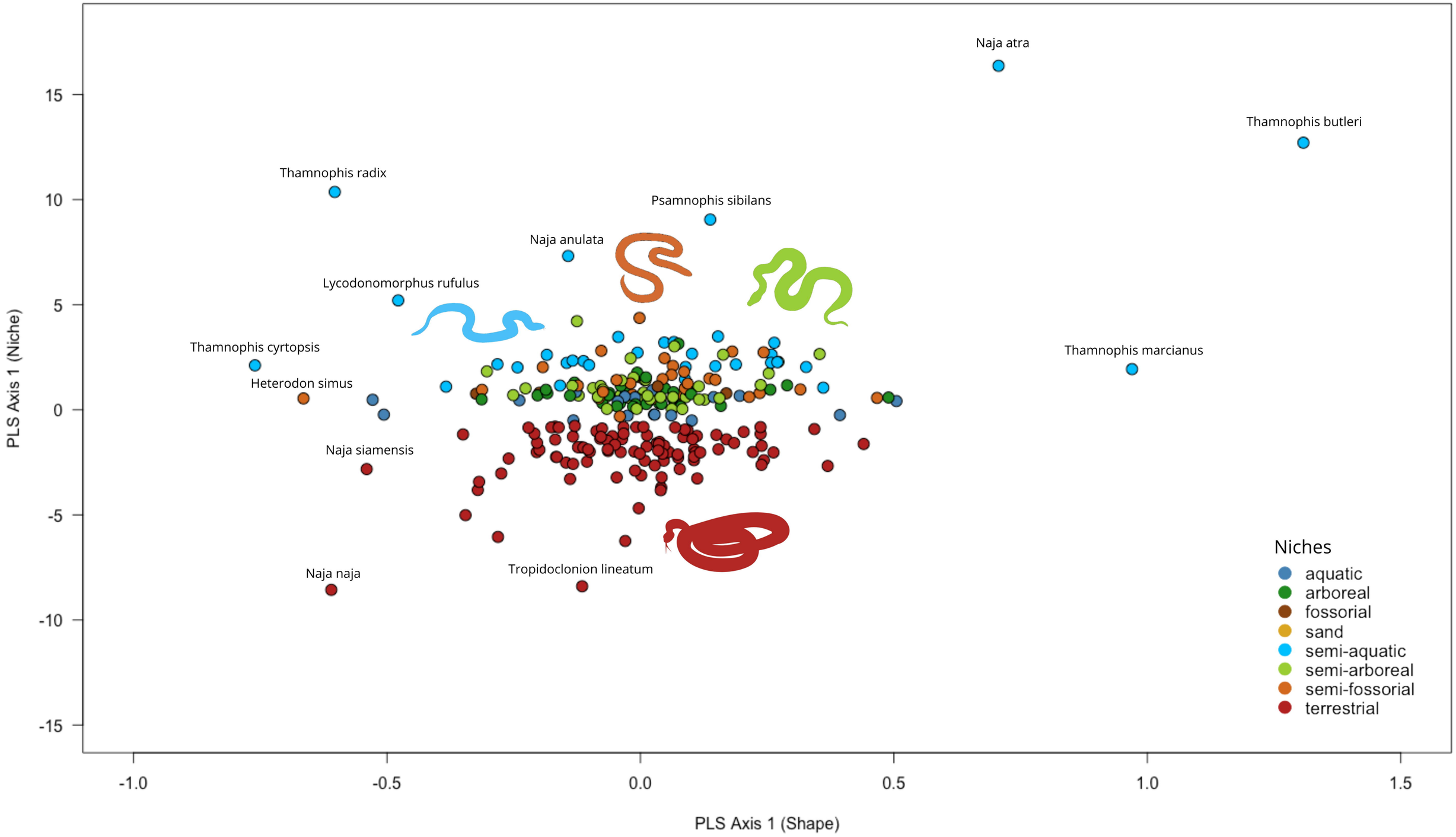
763

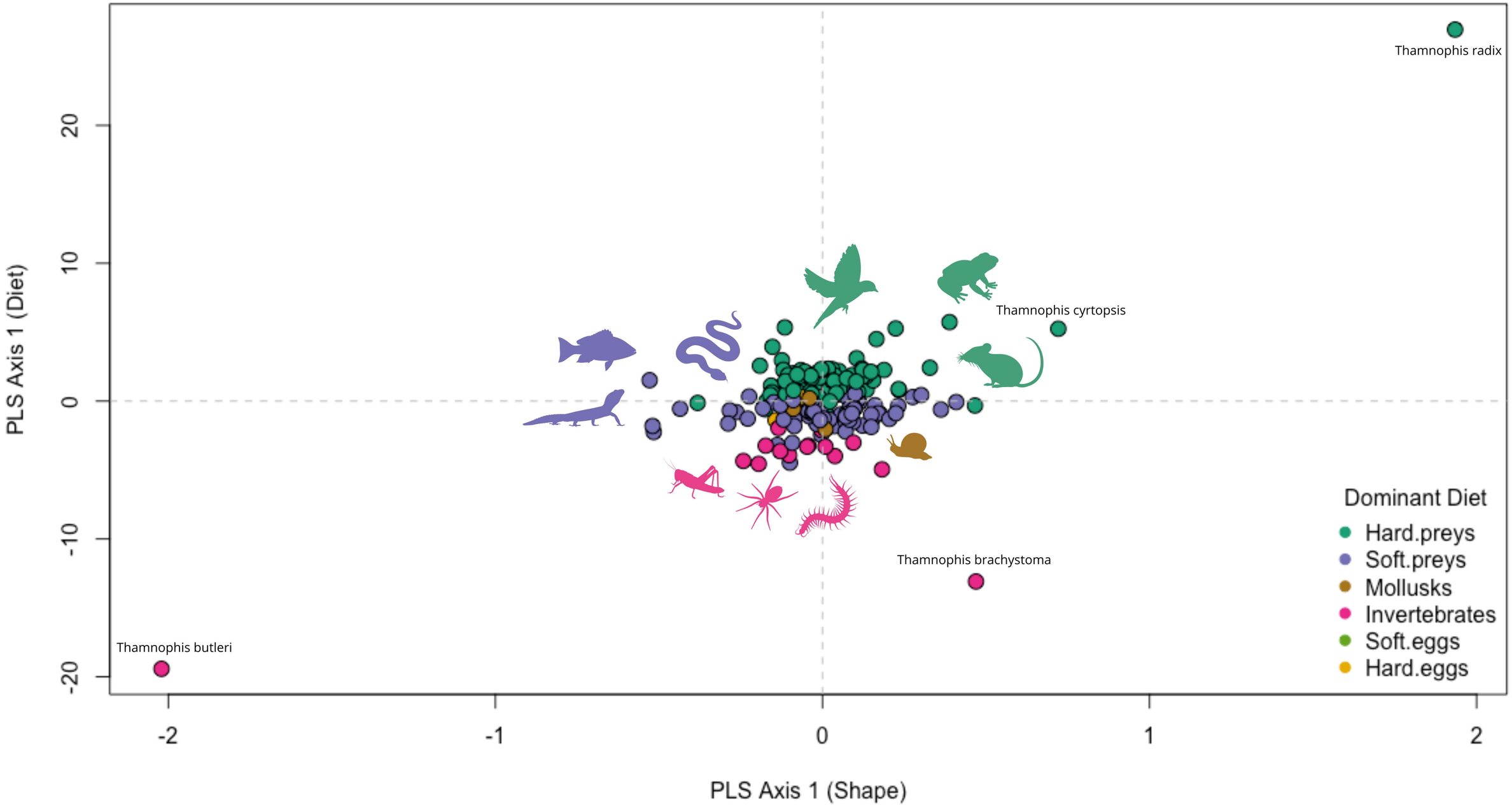
	State	*P*	Time	*P*
Habitat				
terrestrial	90.31	0.736	518.63	0.984
arboreal	85.40	0.087	478.54	0.271
semi-arboreal	91.41	0.886	507.65	0.715
aquatic	58.46	$P < 0.01$	331.51	$P < 0.01$
semi-aquatic	85.42	0.078	538.57	0.937
fossorial	11.29	$P < 0.01$	98.38	$P < 0.01$
semi-fossorial	90.73	0.563	525.32	0.850
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

764


Phylomorphospace
A
n=266
PC2 (23.99%)
PC1 (73.39%)
Chironius fuscus
Ahaetulla mycterizans
Bothrochilus boa
Hydrophis fasciatus
Atractaspis microlepidota
Farancia abacura
Helicops trivittatus
Elapomorphus quinquelineatus
Eupreplophis mandarinus
Elaphe schrenckii
Coniophanes fissidens
Hapsidophrys smaragdinus
Naja atra
Drymobius margaritiferus
Dendroaspis angusticeps
Heterodon platirhinos
Dasypeltis gansi
Pseudoxyrhopus tritaeniatus
Pseudoboa neuwiedii
Hypsiscopus plumbea
Lycophidion capense
Thamnophis cyrtopsis
color
aquatic
arboreal
fossorial
sand
semi-aquatic
semi-arboreal
semi-fossorial
terrestrial
Phylomorphospace
B
n=204
PC2 (23.99%)
PC1 (73.39%)
Chironius fuscus
Ahaetulla mycterizans
Bothrochilus boa
Hydrophis fasciatus
Atractaspis microlepidota
Farancia abacura
Helicops trivittatus
Elapomorphus quinquelineatus
Eupreplophis mandarinus
Coniophanes fissidens
Oligodon arnensis
Hapsidophrys smaragdinus
Naja atra
Drymobius margaritiferus
Dendrelaphis pictus
Helicops angulatus
Hydrodynastes gigas
Hydrophis hardwickii
Heterodon platirhinos
Pseudoxyrhopus tritaeniatus
Pseudoboa neuwiedii
Lycophidion capense
Thamnophis cyrtopsis
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


Naja atra
Thamnophis butleri
Thamnophis radix
Psamnophis sibilans
Naja anulata
Lycodonomorphus rufulus
Thamnophis cyrtopsis
Heterodon simus
Thamnophis marcianus
Naja siamensis
Naja naja
Tropidoclonion lineatum
Niches
aquatic
arboreal
fossorial
sand
semi-aquatic
semi-arboreal
semi-fossorial
terrestrial
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


Thamnophis radix
Thamnophis cyrtopsis
Thamnophis brachystoma
Thamnophis butleri
Dominant Diet
Hard.preys
Soft.preys
Mollusks
Invertebrates
Soft.eggs
Hard.eggs
PLS Axis 1 (Diet)
PLS Axis 1 (Shape)
20
10
0
-10
-20
-2
-1
0
1
2