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Original Article

Variable yet ubiquitous: hierarchical scaling of head functional morphology in lizards

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Abstract

Understanding how form–function relationships scale across levels of biological organization is essential for uncovering the mechanisms driving morphological and performance diversity. We examined the association between head shape and bite force in lacertid lizards across three hierarchical levels: individuals within species, species within the genus *Podarcis*, and species across the family Lacertidae. Using geometric morphometrics of dorsal and lateral head shape combined with bite force measurements, we tested whether the strength and direction of the form–function relationship is conserved across scales and whether body size mediates these patterns. Our analyses revealed significant associations between head shape and bite force at all levels, with body size exerting a strong but not exclusive influence. Importantly, while the form–function link persisted after removing allometric effects, the evolutionary trajectories of this relationship were not aligned across scales: regression vectors differed randomly rather than following consistent directions. These results indicate that performance consistently constrains head morphology, yet the evolutionary pathways linking form and function vary across scales, reflecting a flexible interplay between selective pressures, developmental constraints, and phylogenetic history.

Keywords: geometrics morphometrics, bite force, scalation patterns, phylogenetic comparative methods, form–function, microevolution, macroevolution

Introduction

Understanding the organization of phenotypic variation across hierarchical levels of biological complexity is crucial for comprehending the evolutionary mechanisms that shape patterns of biodiversity (Hallgrimsson & Hall, 2005; Hansen & Martins, 1996; Kaliontzopoulou et al., 2018; Simon et al., 2025a). Ecological pressures experienced by individuals at the population level can be strong enough to drive phenotypic divergence, leading to the emergence of macroevolutionary patterns that persist across higher biological levels, from individuals to populations, up to species, indicating that the mechanisms driving diversification may be uniform across these levels (Hansen & Martins, 1996; Kaliontzopoulou et al., 2018; Taverne et al., 2021; Woodgate et al., 2025). Individuals harbor genetic and phenotypic variation that is selected through survival and reproduction (Lande, 1976). Selective pressures and other evolutionary processes such as drift cause variation among individuals and give rise to variation in populations, which, if reinforced through divergence mechanisms (e.g., reproductive isolation), may gradually translate into phenotypic variation among different species (Turelli et al., 2001). This process often follows genetic and phenotypic lines of least resistance (McGlothlin et al., 2018; Rhoda et al., 2023; Schluter, 1996; Tejero-Cicuéndez et al., 2023), where selection acts preferentially on traits that exhibit the greatest variation within populations, shaping long-term evolutionary trajectories. However, the selective landscape is rarely uniform, and organisms are exposed to a wide range of ecological pressures that vary across spatial and temporal scales (Arnold et al., 2001). These pressures interact with intrinsic constraints—such as developmental limitations or biomechanical tradeoffs—which can restrict the range of possible phenotypic outcomes (Collar et al., 2009; Vermeij, 1973). As a result, variation may be highly specific to each biological level, with microevolutionary trends at the population level not always translating predictably into macroevolutionary patterns (Simon et al., 2025b).

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Across biological levels, the study of the interplay between organismal structure and function is fundamental to understanding evolutionary processes that drive phenotypic variation (Arnold, 1992; Herrel et al., 2001b; Kaliontzopoulou et al., 2012, 2018; Taverne et al., 2021; Wainwright, 2007). Performance, often recognized as a primary target of natural selection, plays a crucial role in shaping fitness outcomes (Arnold, 1983; Huey & Stevenson, 1979; Thompson et al., 2017). Because selection acts directly on performance-related traits, a strong relationship between size, form, and function is expected, particularly for morphological traits that contribute to variation in performance (Arnold, 1983; Cruz et al., 2021; Irschick et al., 2008; Taylor & Thomas, 2014; Wainwright, 2007). However, while this relationship is often expected to follow a one-to-one correspondence based on biomechanical principles, such as for the vertebrate lower jaw (Wainwright & Shaw, 1999), it also exhibits high levels of variability, not only within species but also across hierarchical levels of organization. Additionally, body size has a direct impact on performance and shape (Gould, 1966; Herrel et al., 2008; Tseng, 2013), thus it is also expected to constitute a critical factor influencing the form–function relationship. Size, although an integral part of the phenotype and can influence the form–function relationship in non-proportional ways (Mitchell et al., 2024, 2025). Therefore, accounting for size effects may be necessary to disentangle other form-specific functional adaptations from allometric constraints. Different and sometimes conflicting selective pressures act on these phenotypic systems, leading to redundancy, where different morphological trait combinations can result in similar functional outcomes (Mitchell et al., 2024). This phenomenon, known as many-to-one mapping (Wainwright et al., 2005), occurs when function depends on nonlinear form–function relationships or arises as a response to multivariate morphological systems (Thompson et al., 2017; Wainwright et al., 2005).

For example, biologists have widely used the relationship between head shape and biting performance in lizards to address numerous ecomorphological questions. (Cruz et al., 2021; De Meyer et al., 2019; Herrel et al., 2001b; Kaliontzopoulou et al., 2012; Verwaijen et al., 2002). Bite force plays a critical role in a wide range of biological and ecological functions, including mating, territory defense, male–male interactions (Huyghe et al., 2005) and feeding (Taverne et al., 2021), often reflecting the combined influence of natural and sexual selection (Kaliontzopoulou et al., 2012). As such, several selective pressures have been shown to influence the evolution of bite force through morphological adaptations of the head (Gomes et al., 2018; Husak, 2008; Kaliontzopoulou et al., 2012) (e.g., habitat occupation, refuge use). Additionally, selective pressures may operate differently across hierarchical biological levels. For example, sexual selection typically acts at the individual level within species through processes such as male–male competition and mating success (Huyghe et al., 2005; Lappin & Husak, 2005; Lappin et al., 2006), whereas ecological pressures related to habitat occupation and refuge use tend to structure phenotypic variation at broader population or species levels, reflecting differences among habitats and ecological niches (Kaliontzopoulou et al., 2012; Vicent-Castelló et al., 2025).

The biomechanical relationship between head dimensions and bite force has been repeatedly investigated, showing that a simple linear relation is not the rule for this form–function system (Cruz et al., 2021; De Meyer et al., 2019; Herrel et al., 2001b; Verwaijen et al., 2002). Indeed, head height and width have been shown to be strong, but not unique or universal, predictors of bite force, due to their influence on jaw adductor muscle size and orientation (Herrel et al., 2001b; Kaliontzopoulou et al., 2012). Moreover, it has been demonstrated that body size also plays a fundamental role in mediating these relationships, as both head shape and bite force scale with size (Isip et al., 2022; Kaliontzopoulou et al., 2008). Thus, despite the fact different morphological features of the head may be influenced by different selective pressures, both overall head size and specific shape components (e.g., head height, head width, and jaw length) have been shown to directly affect biting performance (Kaliontzopoulou et al., 2008; Villalobos-Chaves & Santana, 2022; Wittorski et al., 2016). Indeed, other anatomical elements can be also modified to produce similar bite force outcomes, for instance, musculature orientation and size, fiber diameter, etc. (Herrel et al., 2007a, 2008; Wittorski et al., 2016). This suggests that this complex head shape-bite force system is influenced by multiple selective pressures, leading to evolutionary modifications that enhance fitness by improving the functional outcome thought many-to-one morphological combinations.

In this study, we use lizards from the Old-World family Lacertidae to examine how form–function relationships emerge at the macroscale based on patterns observed at lower biological levels. We investigate how the relationship between head shape and bite force scales from individuals to species within the genus *Podarcis*, and ultimately to broader family-level patterns across the Lacertidae. We focus on *Podarcis* as a well-studied, ecologically diverse but also relatively cohesive group of lizards of moderate size variation and with generally similar life-histories and biological traits. Moreover, this group has been widely used to address ecomorphological and evolutionary questions (Edwards et al., 2013; Gomes et al., 2018; Herrel et al., 2001a; Kaliontzopoulou et al., 2012; McBrayer, 2004; Verwaijen et al., 2002), revealing complex interactions among selective pressures (e.g., sexual dimorphism, foraging mode, diet, male–male competition) that influence head morphology and whole-organism performance (Gomes et al., 2018; Verwaijen et al., 2002) at the intra- and inter-specific levels (Verwaijen et al., 2002). To explore whether these form–function relationships are consistent across biological scales, we analyze individuals from species in the genus *Podarcis* to characterize intraspecific patterns; then we assess whether these patterns scale up across species within the genus; and finally, we integrate data from 71 lacertid species. We hypothesize that (1) body size significantly influences the relationship between head shape and bite force, but that aspects of this relationship persist even after accounting for allometric effects, (2) the covariation between head shape and bite force is detectable both at microevolutionary (within-species) and macroevolutionary (among-species) scales, and (3) this shape–function relationship is consistently maintained across hierarchical levels of biological organization. To address these hypotheses, we employed geometric morphometrics to describe the dorsal and lateral view, which were accompanied by bite force measurements. Different parts of head shape (dorsal and lateral) may be influenced by distinct selective pressures (e.g., sexual selection, habitat occupation, refuge use, and size), potentially leading to different evolutionary patterns. However, we also expect the head to evolve as a single functional unit, accommodating diverse morphological configurations while producing similar functional outputs—consistent with the many-to-one mapping paradigm (Wainwright et al., 2005). Given the strong relationship between head shape and bite force, we expect this pattern to be mirrored across biological levels (Emerson & Arnold, 1989). Moreover, when the effect of the size is not removed from the data, we expect the form–function pattern to be more straightforward, since the allometric effect should make this relationship to be less variable.

Material and methods

Data collection

Morphological and performance data from lacertid lizard individuals were obtained from different field campaigns and museum collections by the authors (Table S1). Morphological data included records for 875 individuals for dorsal and 883 for lateral shape; and performance data for 1,151 individuals. Individuals obtained from fieldwork were captured by noose and then released at the site of collection. From those individuals, morphological measurements, dorsal and lateral high-resolution pictures were taken, and bite force was measured. From museum collections, only morphological measurements and high-resolution pictures were taken. Only adult males were utilized to remove any variation due to ontogeny and sexual dimorphism.

As linear morphological measurements, snout–vent length (SVL), pileus length and mouth length were measured to the closest 0.01 mm from each individual using electronic calipers (Table S1). SVL serves as the standard measure of body size for reptiles. Pileus length, defined as the distance from the tip of the snout to the posterior border of the parietal scales, and mouth length, measured from the tip of the snout to the posterior border of the last supralabial scale, were used to calibrate images for downstream geometric morphometric analysis.

To quantify head shape, we employed geometric morphometric (Adams et al., 2004, 2013; James Rohlf & Marcus, 1993) based on high-resolution photographs of the dorsal and the right lateral side of the head. Pictures were taken for all individuals (both field-caught and from museum collections) using an Olympus Tough TG-5 digital camera. The lens of the camera was always parallel to the head surface. Head shape was characterized using two-dimensional landmark-based geometric morphometrics (Adams et al., 2004, 2013; James Rohlf & Marcus, 1993). We digitized nine landmarks and three semilandmarks for the lateral shape and 10 landmarks and four semilandmarks for the dorsal shape (Figure 1) using the function *digitizeImages* available in the package StereoMorph (Olsen & Westneat, 2015) and the software TPSdig2-32 (Rohlf, 2006) and TPSutil32 (Rohlf, 2015). Semilandmarks were used to quantify the shape of curved regions of the head, including the posterior margin of the dorsal view and the jaw and supraocular curvature in the lateral view (Figure 1). Landmarks were placed to capture the overall geometry of both lateral and dorsal head shape, ensuring that both internal and external structures were represented, following the approach described in previous studies (Kaliontzopoulou et al., 2007, 2010).

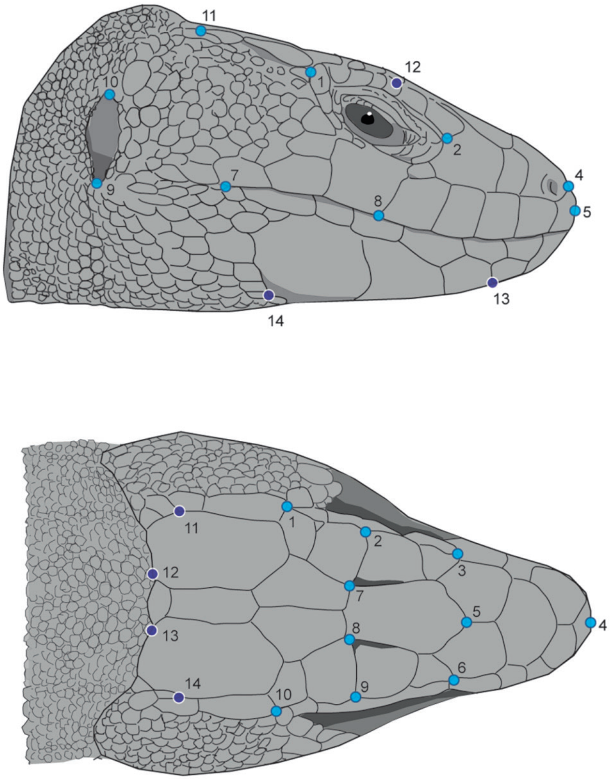

Figure 1. Landmarks (dark dots with black outlines) and semilandmarks (light dots with white outlines) are used to quantify the shape of the head in lateral (top) and dorsal (bottom) views.

For those specimens where one or two landmarks were missing due to bad resolution of sections of images or missing scales, we reconstructed the positions of the missing landmarks using the thin plate spline (TPS) method to estimate the missing landmark positions based on the corresponding location in complete specimens (Gunz et al., 2009). We employed the function *estimate.missing* in the geomorph package (Adams et al., 2025; Baken et al., 2021). This procedure was implemented separately for individuals from each species so as not to confound variation across hierarchical levels. In addition, for lateral head shape, the position of missing landmarks was estimated separately for the skull and lower jaw, as the angle of opening of the jaws in each photograph would affect the missing landmark estimation in the complete landmark configuration. After estimation, both subsets were centered on the articulation point, combined back together, and reordered to match the original landmark order. We then used *fixed.angle* function in geomorph (Adams et al., 2025; Baken et al., 2021) to remove variation in the position of the lower jaw related to the skull by fixing the angle between them to a common angle see (Adams, 1999). For dorsal head shape, we removed the asymmetric component of shape variation, and retained only the symmetric portion of head shape using the *bilat.* symmetry function in geomorph (Adams et al., 2025; Baken et al., 2021). Once all data were collected, corrected, and estimated, a Generalized Procrustes Analysis (GPA) was performed to

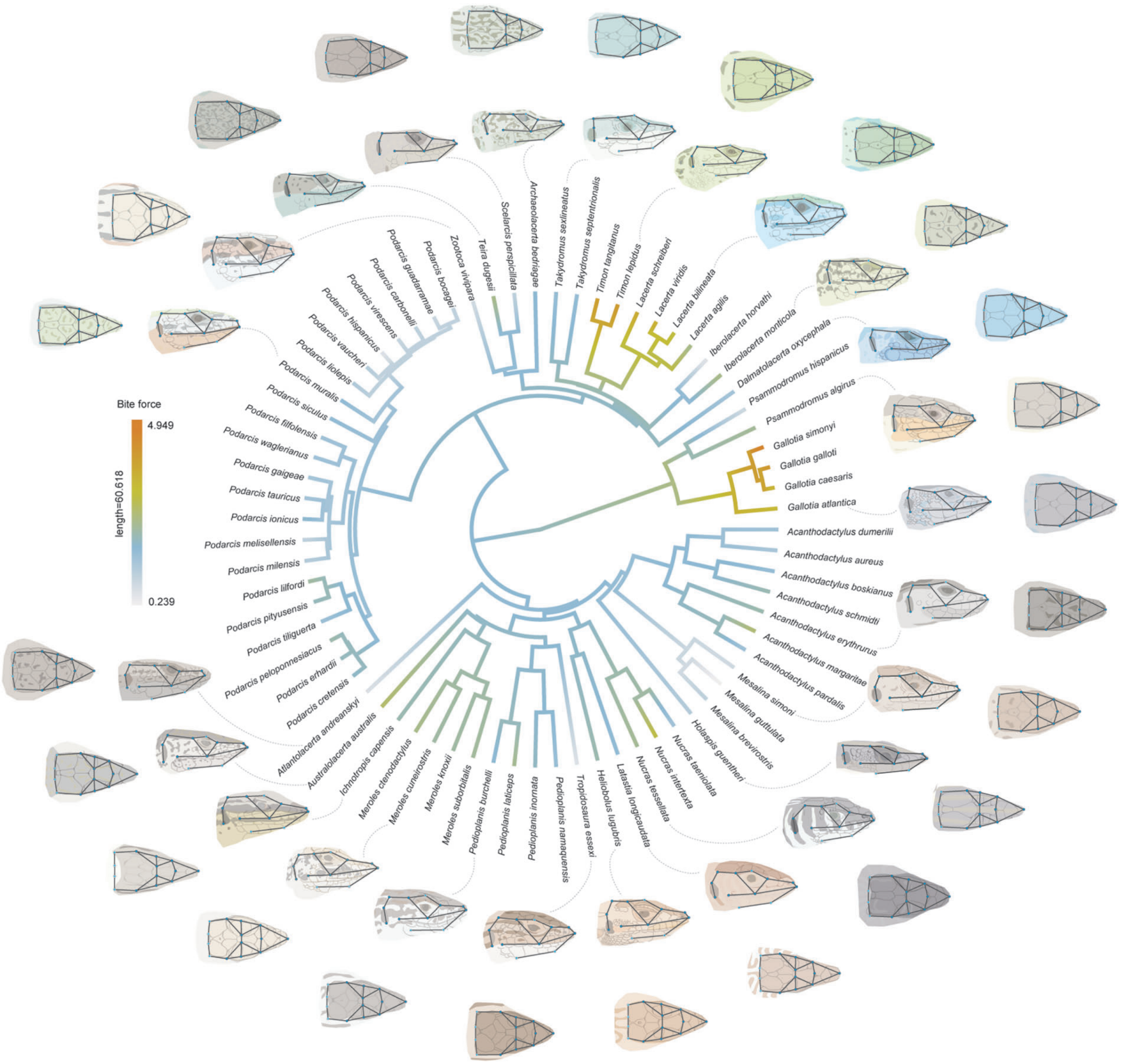

Figure 2. Phylogenetic tree showing raw bite force values across lacertid lizards. Branch colors represent relative bite force residuals after correcting for body size. At each tip, a representative species is shown for each genus, depicted with a stylized illustration of the dorsal and lateral head view and its corresponding mean shape outline derived from geometric morphometric data.

align all specimens to a common coordinate system and standardize components of non-shape variation (position, orientation, and size) using the function *gpagen* in geomorph (Adams et al., 2025; Baken et al., 2021).

Bite force was measured employing an isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland), mounted on a vertical holder made of stainless steel and connected to a Kistler charge amplifier (type 5995A, Kistler Inc., Winterthur, Switzerland). Bite force measurements were obtained by provoking lizards to bite on two parallel thin stainless steel plates connected to the force transducer (see Herrel et al., 1999, 2001a for further information). The tip of the plates was delimited using a marker to ensure the bite was standardized at the point of force exertion for all specimens (Gomes et al., 2020). Each lizard was tested five times to ensure we obtained the maximal individual bite force, which was retained and log-transformed for further analyses.

Comparative analyses

To examine the evolution of head shape and bite force, we applied phylogenetic comparative methods using the most comprehensive time-calibrated phylogeny available for Lacertidae (Garcia-Porta et al., 2019), which includes 246 species, pruned to match the species included at each biological level of analysis (intraspecific, genus, and family levels; Figure 2), using the function *drop.tip* implemented in ape package (Paradis et al., 2004).

Phylogenetic signal of form and function

We applied two complementary approaches to evaluate phylogenetic signal in univariate traits (e.g., bite force and SVL), using Blomberg's K statistic (Blomberg et al., 2003), and in high-dimensional morphological traits (dorsal and lateral head shape), using its multivariate extension, K_{mult} (Adams, 2014). First, we assessed whether trait values were more similar among closely related species than expected by chance by testing against a random association of data to the tips of the phylogeny ($K = 0$) (Adams, 2014; Blomberg et al., 2003). This was accomplished using the *physignal* and *physignal.z* functions implemented in geomorph. Second, we tested whether observed values deviated from expectations under Brownian Motion (BM) ($K = 1$) model of evolution, by comparing empirical statistics to null distributions generated through phylogenetic simulations (Enríquez-Urzelai et al., 2022). To test if K was significantly different from 1, we employed the code available at http://blog.phytools.org/2011/12/testingfor-phylogenetic-signal-k.html for univariate data and an expansion of this method for multivariate data (Bellvert et al., 2023). Finally, for the multivariate datasets (dorsal and lateral shape), we evaluated whether the phylogenetic signal was distributed equally across shape dimensions or was concentrated in specific directions in shape space. To accomplish this, we employed the approach of Mitteroecker et al., 2025, which decomposes the phylogenetic signal into its constituent dimensions. We implemented the procedure using the function *physignal.eigen* in geomorph (Adams et al., 2024, 2025; Baken et al., 2021; Mitteroecker et al., 2025).

Phylogenetic regression of form and function

To characterize the relationship between form and function across hierarchical levels of biological organization and the effect of size on this relationship, we conducted phylogenetic regressions at three hierarchical levels: (1) individuals within species, (2) species means within the genus *Podarcis*, and (3) species means across the family Lacertidae. These analyses were performed using both the raw shape data and the residuals from a multivariate regression of shape on size. we conducted phylogenetic regressions at three hierarchical levels: (1) individuals within species, (2) species means within the genus *Podarcis*, and (3) species means across the family Lacertidae. These analyses were performed using both the raw shape data and the residuals from a multivariate regression of shape on size.

Removing the effects of allometric scaling was achieved by extracting residuals from regressions of bite force and shape against SVL. To ensure continuity across the combined datasets used in our multi-scale analyses, we standardized all size corrections using SVL, as this was the only size metric shared by all individuals across bite force and shape datasets, whereas centroid size (cs) was not always available. This approach allowed us to remove the effect of size, effectively eliminating the allometric component from the shape data (Klingenberg, 2016). We consider this distinction important in the context of geometric morphometrics. While Procrustes analysis standardizes for size and scale by superimposing landmarks (i.e., performing a size correction), residuals from the shape-size regression enable us to further isolate specific form–function patterns by removing the influence of allometry, which is a procedure commonly applied in geometric morphometric studies (Ivanović & Kalezić, 2010; Klingenberg, 2016; Klingenberg & Marugán-Lobón, 2013; Klingenberg et al., 2003).

At each level, we analyzed both dorsal and lateral head shape in relation to bite force. First, at the intraspecific level, we used extended phylogenetic generalized least squares (E-PGLS) (Adams & Collyer, 2024) to regress bite force on dorsal and lateral head shape in individuals from 21 *Podarcis* species, including species as an interaction term. We employed this method because it allows us to investigate intraspecific variability while also accounting for the evolutionary relationships between species (i.e., phylogenetic nonindependence). We used the function *lm.rrpp.ws* implemented in the RRPP package (Collyer & Adams, 2018, 2024). Then, at the genus level, we calculated species means for bite force and both head shape views and performed phylogenetic regressions using a tree pruned to include only *Podarcis* species. Finally, at the family level, we repeated the regressions with species means for all lacertid species and the full phylogeny. For genus and family level analyses, we employed the function *lm.rrpp* implemented in the RRPP package (Collyer & Adams, 2018, 2024).

In order to visualize the data, first, to biologically interpret shape variation, we generated TPS deformation grids using the function *plotRefToTarget* from the geomorph package (Adams et al., 2025; Baken et al., 2021). Predicted shapes for the minimum and maximum bite forces were obtained using the *shape.predictor* function implemented in geomorph (Adams et al., 2025; Baken et al., 2021). The mean shape of all species was used as a reference, and the grids were magnified threefold (3×) to enhance the visualization of landmark displacements (Figures 3, 4). To describe the association between head shape and bite force and visualize its variation across species and hierarchical levels, we utilized scatter plots where the multivariate shape data were reduced into a univariate vector employing the predicted line method (reg.type = "PredLine") (Adams & Nistri, 2010).

Slope comparisons across biological levels

To determine whether from-function trends were consistent across biological levels of organization (individual, genus, and family), we compared the angular differences between the individual-level *Podarcis* species regressions and the macroevolutionary trends observed at the *Podarcis* genus and *Lacertidae* family levels, based on a modification of the procedure from Tejero-Cicuéndez et al., 2023. First, using the regressions described above, we obtained residuals from the genus- and family-level models. We then applied a permutation procedure, in which these residuals were randomly permuted (999 iterations), and model statistics were recalculated to generate an empirical null distribution for evaluating the observed test statistics (Collyer & Adams, 2007; Collyer et al., 2015; Freedman & Lane, 1983). We then compared the individual regressions for each *Podarcis* species to the vector representing the genus slope and family slope, by calculating pairwise differences in their angular direction in morphospace and evaluating these relative to empirical sampling distributions obtained through RRPP (Adams & Collyer, 2009; Collyer & Adams, 2013). We also calculated the mean angle observed from the pairwise comparison among *Podarcis* species using shape residuals and raw shape data, in order to observe the difference in mean angles between raw and size-corrected data.

Results

Phylogenetic signal

Phylogenetic signal was significantly greater than expected by chance for all traits, as indicated by large effect sizes

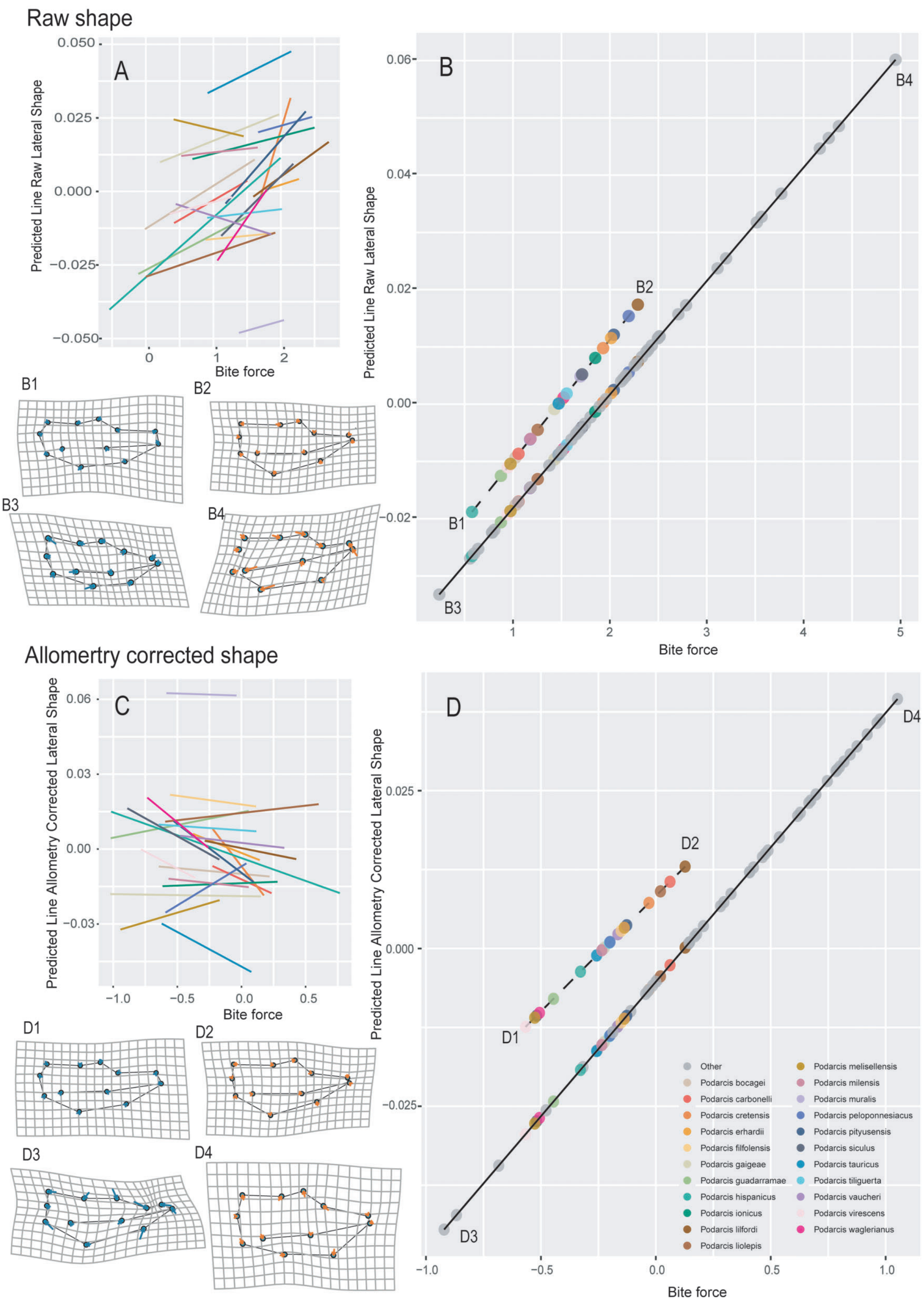

Figure 3. Visualization of the relationship between dorsal head shape and bite force using regression scores. Multivariate dorsal head shape was reduced to a univariate regression score by projecting individual shapes onto the shape–bite force regression vector (regression score method). Panels A and B show analyses using raw data for *Podarcis* individuals (A) and Lacertidae species (B). Panels C and D show the corresponding analyses after removal of the allometric component. In all panels, points represent individual specimens or species means, and lines depict species-specific regression trends in regression score space, illustrating the direction and relative strength of multivariate shape–bite force associations. Regression lines do not represent direct fits to raw multivariate shape data but are graphical summaries of multivariate relationships. In panel A, dots which correspond to individuals are not shown to avoid noise in the interpretation. Deformation grids (3× magnification) illustrate head shape associated with maximum (right) and minimum bite force (left) at the genus and family levels and correspond to the predicted shapes along each fitted regression.

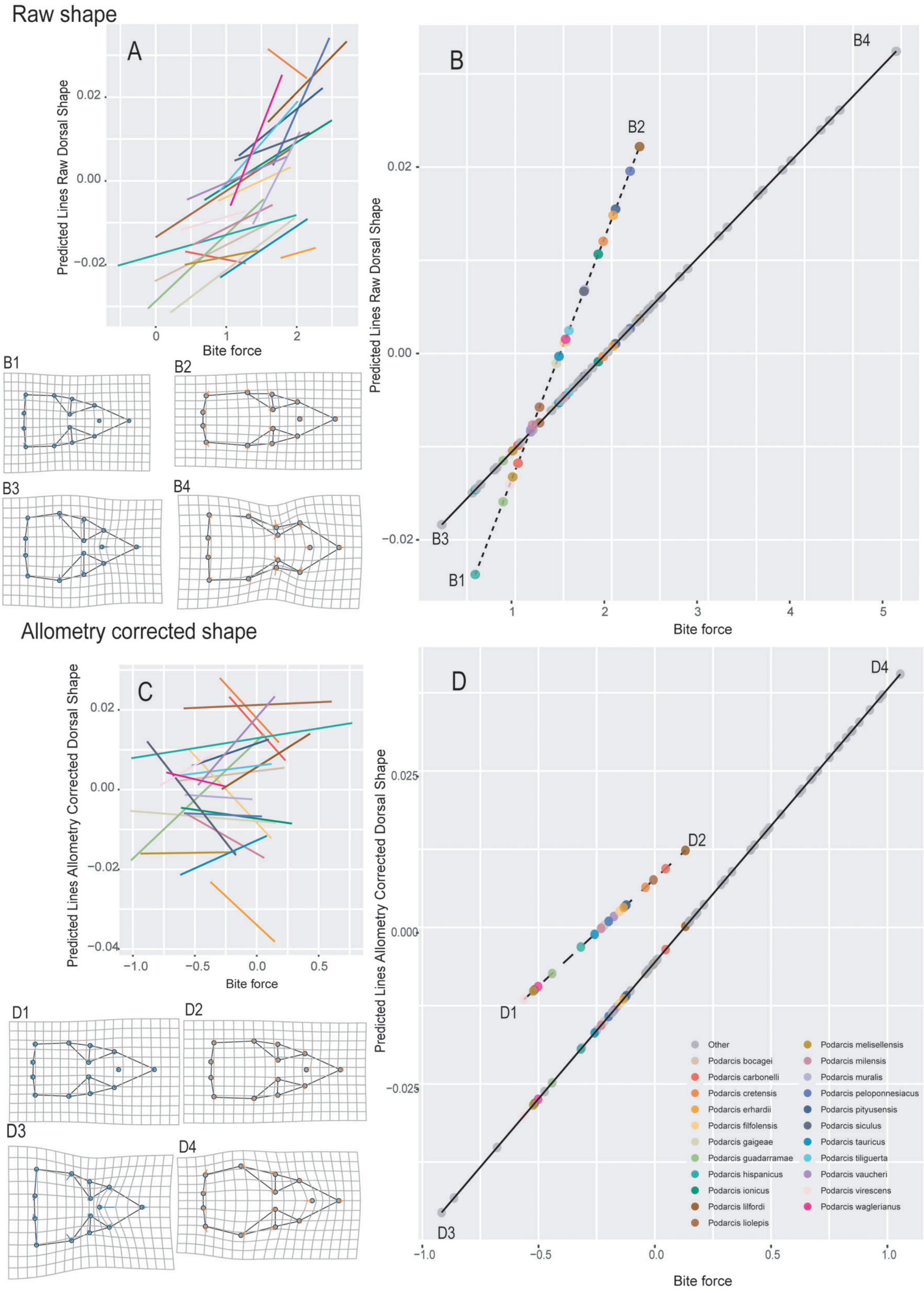

Figure 4. Visualization of the relationship between latera head shape and bite force using regression scores. Multivariate lateral head shape was reduced to a univariate regression score by projecting individual shapes onto the shape–bite force regression vector (regression score method). Panels A and B show analyses using raw data for *Podarcis* individuals (A) and Lacertidae species (B). Panels C and D show the corresponding analyses after removal of the allometric component. In all panels, points represent individual specimens or species means, and lines depict species-specific regression trends in regression score space, illustrating the direction and relative strength of multivariate shape–bite force associations. Regression lines do not represent direct fits to raw multivariate shape data but are graphical summaries of multivariate relationships. In panel A, dots which correspond to individuals are not shown to avoid noise in the interpretation. Deformation grids (3× magnification) illustrate head shape associated with maximum and minimum bite force at the genus and family levels and correspond to the predicted shapes along each fitted regression.

Table 1. Results of phylogenetic regressions conducted to test for differences in raw dorsal and lateral shape and bite force relationship at different biological levels: using *Podarcis* individuals, *Podarcis* species, and all Lacertidae species in this study.

Dorsal shape ***Podarcis* individuals** **Dorsal shape ∼ Bite force ∗ species I *Podarcis* phylogeny**				**Lateral shape** ***Podarcis* individuals** **Lateral shape ∼ Bite force ∗ species I *Podarcis* phylogeny**			
bite	1	5.752	**0.001**	bite	1	6.569	**0.001**
Sp	21	20.513	**0.001**	sp	21	22.298	**0.001**
bite:sp	21	6.260	**0.001**	bite:sp	21	4.278	**0.001**
Residuals	626			Residuals	619		
Total	669			Total	662		
Podarcis species				*Podarcis* species			
Dorsal shape ∼ Bite force I *Podarcis* phylogeny				Lateral shape ∼ Bite force I *Podarcis* phylogeny			
bite	1	1.946	**0.026**	bite	1	-0.372	0.628
Residuals	20			Residuals	20		
Total	21			Total	21		
Lacertidae species				Lacertidae species			
Dorsal shape ∼ Bite force I Lacertidae phylogeny				Lateral shape ∼ Bite force I Lacertidae phylogeny			
bite	1	0.624	0.281	bite	1	2.422	**0.009**
Residuals	69			Residuals	69		
Total	70			Total	70		

Note. d.f. = degrees of freedom; Z = Z-score. *P*-values are based on 1,000 residual permutations and significant *p*-values (at $\alpha = 0.05$) are highlighted in bold.

($K \approx 0.5$ for dorsal and lateral head shape, $Z \approx 12$–31; $K \approx 0.3$ for bite force, $Z \approx 3$; Table S2). Moreover, comparisons against the expected value under Brownian motion revealed that K values for shape and bite force were significantly lower than 1, indicating less phylogenetic signal than predicted by a pure BM model. The exploratory analysis of the phylogenetic signal across multivariate dimensions revealed that, in both dorsal and lateral head shape, the signal was not evenly distributed but appears to be concentrated in the first K-components. (Table S2, Figure S1). This implied that the degree of phylogenetic signal was not "weak" but rather was restricted to certain directions of shape space (see Mitteroecker et al., 2025 and Adams & Collyer, 2019 for discussion). Finally, SVL exhibited a K value not significantly different from 1, suggesting that its distribution across the phylogeny closely follows Brownian expectations.

Allometric patterns

Across all hierarchical levels, head shape showed significant associations with body size (SVL) in both dorsal and lateral configurations, except for the genus-level lateral analysis. At the individual level, SVL explained 9.9% of dorsal shape variation and 4.8% of lateral shape variation. This size–shape relationship persisted at broader evolutionary scales. At the genus level, SVL accounted for 24.7% of dorsal shape variation across species, whereas the association between SVL and lateral shape was not statistically significant, despite explaining 9.9% of the variation. At the family level, SVL explained 13.4% of dorsal shape variation and 6.0% of lateral shape variation (Tables S3, S4). Bite force showed a strong allometric relationship with body size, with SVL explaining 75.9% of the variation in bite force (Table S5). Overall, allometric effects were detected across traits, head orientations, and hierarchical levels, although their statistical support and deformation magnitude varied among analyses.

Allometric deformation grids indicated that size-related shape variation was spatially structured and differed in magnitude between hierarchical levels (Figures S2, S3). In the dorsal view, increasing size was associated with lateral displacement of posterior cranial landmarks, resulting in broader posterior head outlines, whereas smaller sizes exhibited narrower posterior configurations. These deformation patterns were observed at both genus and family levels, with greater landmark displacement and grid warping at the family level (Figure S2). In the lateral view, allometric variation was expressed as changes in head depth and anteroposterior proportions, with larger sizes showing increased mid-cranial depth and reduced snout elongation, and smaller sizes displaying shallower and more elongate head profiles. Consistent with the statistical results, lateral allometric deformation at the genus level was comparatively limited, whereas family-level lateral deformation was more pronounced (Figure S3).

Form–function associations

Focusing on the relationships between form and function when using raw data, we found a significant association between shape and bite force at the *Podarcis* individual level in both dorsal and lateral views, with this relationship differing across species, as indicated by a significant bite force × species interaction (Tables 1, S6, S7). At the genus and family level, contrasting patterns were found between dorsal and lateral shape. Dorsal shape exhibited a significant relationship with bite force at the genus, but not the family level. Instead, for lateral shape this pattern was reversed: there was no significant relationship between shape and bite force at the genus level, but there was at the family level (Tables 1, S6, S7).

When removing the allometric effect through regression of shape and bite force data against SVL, we observed that form–function relationships were largely retained across the different biological levels. We found that, at the individual level, shape and bite force remained significantly associated considering both the dorsal and lateral head views, with species-specific differences maintained (Tables 2, S8, S9). Across *Podarcis* species, we found that in dorsal shape, the relationship between form and function was marginally

Table 2. Results of phylogenetic regressions conducted to test for differences in allometric-corrected dorsal and lateral shape and bite force relationship at different biological levels: using *Podarcis* individuals, *Podarcis* species, and all Lacertidae species in this study.

Dorsal shape ***Podarcis* individuals**				**Lateral shape** ***Podarcis* individuals**			
Dorsal shape ~ Bite force ∗ species I *Podarcis* phylogeny				Dorsal shape ~ Bite force ∗ species I *Podarcis* phylogeny			
bite	1	2.704	**0.005**	bite	1	3.857	**0.001**
Sp	21	17.473	**0.001**	Sp	21	21.347	**0.001**
bite:sp	21	8.193	**0.001**	bite:sp	21	5.475	**0.001**
Residuals	626			Residuals	619		
Total	669			Total	662		
Podarcis species				*Podarcis* species			
Dorsal shape ~ Bite force I *Podarcis* phylogeny				Dorsal shape ~ Bite force I *Podarcis* phylogeny			
bite	1	1.647	0.055	bite	1		
Residuals	20			Residuals	20		
Total	21			Total	21	0.505	0.316
Lacertidae species				Lacertidae species			
Dorsal shape ~ Bite force I Lacertidae phylogeny				Dorsal shape ~ Bite force I Lacertidae phylogeny			
bite	1	2.729	**0.003**	bite	1	2.925	**0.001**
Residuals	69			Residuals	69		
Total	70			Total	70		

Note. d.f.: degrees of freedom; Z: Z-score. *P*-values are based on 1,000 residual permutations and significant *p*-values (at $\alpha = 0.05$) are highlighted in bold.

significant (Tables 2, S8, S9), while in lateral shape this relationship was not significant (Tables 2, S8, S9). Finally, at the family level, both dorsal and lateral shape exhibited a positive association with bite force (Tables 2, S8, S9).

With respect to shape changes associated with maximum and minimum bite force, analyses using both raw and allometric-corrected data revealed relatively subtle variation at the genus level (*Podarcis*) in both dorsal and lateral views (Figures 3, 4). In contrast, at the family level, shape variation was more pronounced, with specific cranial regions showing stronger and more spatially differentiated responses to bite force variation. At the family level, when using raw data, in the dorsal view, bite-force variation was primarily expressed through changes in the mid-cranial region, where strong-biting individuals exhibited medial displacement of landmarks toward the midline, whereas weaker-biting individuals showed comparatively broader configurations (Figure 3). Across both views, posterior head landmarks remained comparatively stable, indicating that most bite-force-related variation was concentrated in the anterior and mid-cranial regions. In the lateral view, maximum bite force was associated with deformation patterns characterized by expansion of the anteroposterior region of the head, along with shortening and deepening of the snout (Figure 3). Individuals with lower bite force showed the opposite pattern, displaying a more elongate and slenderer configuration of the snout and jaw region.

After removal of the allometric component, bite-force-related shape variation was still detected in both head views at the family level (Figure 3). In the dorsal view, size-corrected shape variation associated with bite force was mainly expressed in the posterior cranial region. Individuals with lower bite force showed greater displacement of posterior landmarks, resulting in relatively expanded posterior head configurations, whereas individuals with higher bite force displayed more constrained posterior regions (Figure 3). Displacement of mid-cranial landmarks was comparatively limited, indicating that bite-force-related shape variation when the allometric effect is removed is concentrated toward the posterior portion of the cranial vault. In the lateral view, higher bite force was associated with localized deformation patterns involving subtle expansion of the mid-cranial region and moderate changes in snout depth. Individuals with lower bite force exhibited a more elongate and slender snout configuration, with shape differences primarily restricted to the anterior portion of the head (Figure 4).

Slope variation across levels

Slope comparisons across all phylogenetic levels (individual, genus, and family) revealed that patterns were not significantly more similar or more different than expected. This suggests that vector angles describing differences in the form–function relationship across biological levels are not different from what is expected for a random collection of vectors (Tables S10, S11; Figure S2). Importantly, this pattern was maintained regardless of whether the effect of body size was included or not (Tables S10–S13; Figure S2). The only exception was *Podarcis melisellensis*, which was more different than expected from the family trend of association between raw lateral shape and bite force (Table S11, Figure S2), and *Podarcis milensis* which did not follow the genus-level trend in size-corrected lateral shape (Table S13, Figure S2).

Discussion

Understanding how form–function relationships scale across levels of biological organization is essential for uncovering the mechanisms driving morphological and performance diversity (Calsbeek et al., 2006; Hansen & Martins, 1996; Kaliontzopoulou et al., 2018; Taverne et al., 2021; Woodgate et al., 2025). Our evidence from lacertid lizards suggests that the association between bite force and head shape is mostly evident at each evolutionary scale; however, the relationship between these traits is not consistent across levels of biological organization.

We found that body size is one of the elements driving the relationship between form and function within species and across the entire lacertid family, as it was expected due to the strong allometric effects on both morphology and performance (Gould, 1966; Kaliontzopoulou et al., 2008, 2012). However, this phenotypic association remained significant even after removing the allometric effect, suggesting that, in lacertids, head shape itself carries functionally relevant variation beyond allometric-related scaling, pointing to an intrinsic link between form and function (Figures 3, 4). At the intraspecific level, clear and significant relationships between morphology and performance were identified, with variation among *Podarcis* species suggesting that species-specific selective pressures influence this association. Interestingly, while this relationship was also evident at the macroscale, it was less present at the genus level. Both head views (dorsal and lateral) seem to be contributing similarly to these trends, which implies that the head operates as a functional unit responding to external pressures, despite previous suggestions that its components may evolve under different regimes (Herrel et al., 2001b; Lappin et al., 2006). However, while the form–function association was consistently present, its direction was not conserved across the within-species, genus, and family levels. Instead, form–function vectors were no more similar or different than expected by chance. This may suggest that different evolutionary pressures operate at each level, or that the selective pressures that act on each level are the same, but organisms respond differently, due to developmental constraints or phylogenetic history, thus producing variable form–function outcomes.

Despite this variability, the presence of a significant relationship across levels supports the idea that performance outcomes constrain head morphology, even when evolutionary pathways differ. Therefore, we interpret that in lacertid lizards, the head shape–bite force relationship is a general functional relationship that persists even after removing the allometric effect and remains present across multiple evolutionary scales. However, this relationship does not follow a common evolutionary trajectory across levels, which is congruent with many-to-one mapping scenario (Thompson et al., 2017; Wainwright et al., 2005), where different phenotypic configurations can result in similar functional outcomes. Nevertheless, other scenarios are possible, such as the absence of multi-level selection or the influence of non-selective and potentially random processes, which could account for the absence of congruence across levels.

The role of size and head shape in bite force variation

Body size plays a central role in influencing several biological traits (Bergmann, 1847; Christiansen & Adolfssen, 2005; Lindstedt & Hoppeler, 2023), where allometry frequently dominates the evolution of morphology and performance (Arnold, 1983; Gould, 1966; Mitchell et al., 2024; Tejero-Cicuéndez et al., 2023; Wainwright, 1994). As predicted, we found that both shape and performance present aa strong allometric trend, which is partially mediating the form–function relationship in lacertid species (Kaliontzopoulou et al., 2012; Taverne et al., 2023). Increasing in size, implies an increase in the space available for accommodating musculature (Deeming, 2022), which therefore produces an increase in bite force, that is presented in our results with the highest variation of bite force explained by size (Aguirre et al., 2002; Isip et al., 2022; Verwaijen et al., 2002). Moreover, the unit under selection is expected to involve size-related elements, as there is no strict division between size and shape in nature. However, to address the questions in this study, we consider it crucial to examine performance and shape both before and after removing the effect of allometry, as size may obscure latent patterns in the form–function relationship.

Accordingly, our results indicate that size is not the sole driver of the form–function relationship. After accounting for allometric variation in both bite force and morphology, bite-force-shape associations were maintained at both the intraspecific and family levels, and additional patterns emerged, such as a clear relationship between bite force and dorsal head shape at the family level that was not detected in the raw data (Tables S10–S13). This suggests that, although size plays a major role, form–function relationships are also shaped by intrinsic, size-independent factors beyond allometry alone (Figures 3, 4), although the variation explained by the form–function models is limited (Tables 1, 2, S6–S9). For example, elements such as the internal architecture of the jaw musculature (e.g., muscle fiber orientation, insertion sites, and physiology) and the proportions between jaw in-levers and out-levers, play a critical role in determining bite force (Herrel et al., 1997, 1998; Kaliontzopoulou et al., 2012). These biomechanical and anatomical features can influence performance independently of overall body size and may help explain the persistence of form–function relationships beyond allometric scaling.

Once the allometric effect has been removed, a clear relationship between bite force and head shape is maintained at both the intraspecific and family levels (Figures 3, 4). At the intraspecific level, however, this relationship varies among *Podarcis* species, as reflected by differences in the strength and direction of species-specific associations. This variation suggests that distinct selective pressures modulate how head shape translates into bite performance across species and how not a single morphological solution underline bite force responses across *Podarcis* species, suggesting a many-to-one mapping scenario (Mitchell et al., 2024). Previous work has shown that dietary specialization, sexual selection, and habitat use can each shape the form–function relationship in *Podarcis*, often in different and sometimes opposing ways (Gomes et al., 2018; Kaliontzopoulou et al., 2012; Taverne et al., 2023; Woodgate et al., 2025).

For example, species consuming harder prey may evolve broader, more robust heads associated with increased bite force, yet the specific morphological traits underlying performance differ among species such as *P. siculus* and *P. melisellensis*, indicating that no single form–function solution is shared across the genus (Taverne et al., 2020). In contrast, in *P. erhardii*, bite force variation is linked primarily to male–male competition rather than diet, highlighting the role of sexual selection in shaping performance (Donihue et al., 2016; Gomes et al., 2018; Woodgate et al., 2025). Habitat structure can further modify this relationship by imposing spatial constraints on head shape, particularly in climbing species, although such morphological changes do not always translate into performance differences (Kaliontzopoulou et al., 2012; Vicent-Castelló et al., 2025). Together, these findings indicate that allometry-independent form–function relationships provide a flexible framework upon which multiple ecological and social pressures act, producing divergent evolutionary trajectories despite shared functional demands.

In agreement with our expectations, both the dorsal and lateral view of the head present a clear link with bite force at intraspecific and family level. This suggests that although different head dimensions are probably under the effect of different selective pressures (Cruz et al., 2021; Herrel et al., 2001b; Vicent-Castelló et al., 2025; Woodgate et al., 2025), it seems that the entire structure acts as a single evolutionary unit in lacertid lizards. Therefore, the head may be navigating along the adaptive landscape to accommodate variation which is always responding to performance requirements, which goes accordingly with the many-to-one mapping scenario (Simon et al., 2025b; Wainwright et al., 2005). Nevertheless, we observed that each part of the head accommodates different morphological adaptations to explain bite force variation at different levels. For example, comparing how head varies at genus level vs. family level, we observed that the head shape of *Podarcis* is much more conserved that at family level, probably due to phylogenetic relatedness and ecological similarities (Figures 3, 4).

At the family level, however, we observe much more variation, since very different species in terms of ecology and phylogenetically distance are included in the analysis. In the dorsal view, bite force variation is primarily expressed through changes in the mid-cranial region involving the frontal and parietal bones (Figures 3, S2). In raw data, strong-biting taxa shows medial compression with landmarks displaced toward the midline, a pattern partially overlapping with size-related dorsal shape change. After accounting for allometry, this medial compression persists but becomes spatially restricted, indicating a size-independent association between dorsal cranial alignment and bite force. This mid-cranial compression may allow for an expansion of the jaw adductors thus producing stronger bites through cranial rigidity (Herrel et al., 2007b; Dutel et al., 2021; Reilly et al., 2007). In contrast, we observe that the posterior part of the cranial region remains relatively stable across analyses, with more variation in species with lower bite force. Although this may seem incongruent at first, the shortening of the head observed in the lower bite-force deformation grids (Figure 3) could produce a subtle expansion of the posterior cranium to compensate for bite-force output. At the family level, however, we observe much more variation, since very different species in terms of ecology and phylogenetically distant are included in the analysis.

In the lateral view, deformation grids show that maximum bite force is associated with expansion of the posterior region of the head and increased dorsoventral depth, patterns that closely resemble the size-related shape change (Figures 4, S3). These changes suggest an enlargement of the jaw adductor region, increasing the space available for muscle mass and thereby enhancing force production (Gröning et al., 2013; Taverne et al., 2021). In addition, strong bite force is associated with shortening and deepening of the snout, a configuration that may improve mechanical advantage by optimizing jaw levers and resistance to reaction forces during biting lever (Herrel et al., 2007a). This could be associated to diet changes, such as herbivory, which make animals bigger and therefore strong biters like the big *Gallotia* species that are positioned to the right part of the scatter plot (Figure 3) (Barahona et al., 2000; Lopez-Darias et al., 2015). Conversely, weaker bite force corresponds to a more elongate and slender lateral profile, particularly in the snout and jaw region. This morphology is consistent with flatter head configurations observed in taxa facing spatial constraints, such as climbing species (Vicent-Castelló et al., 2025). Species that we found that present similar morphologies associated with weak bite force are for example *Iberolacerta* and *Holaspis* which happen to be both small animals adapted to climbing.

Importantly, comparisons between raw and allometry-adjusted deformation grids indicate that much of the lateral shape variation associated with bite force is mediated by allometry (Figure S3). Once size effects are removed, although bite force–related shape differences persist, it is reduced in magnitude and becomes more localized, primarily involving subtle increases in head depth and curvature in the mid-to-posterior cranial region. This suggests that, aside from overall scaling, bite force can be modulated through finer scale adjustments of cranial geometry rather than wholesale reorganization of the head.

Lack of coherence of the form–function relationship across hierarchical levels

We originally hypothesized that the link between head shape and bite force would be maintained across hierarchical levels of biological organization. This expectation was based on the assumption that similar biomechanical principles should govern the mapping of form to function across scales (Emerson & Arnold, 1989). Therefore, if the form–function association were shaped by consistent selective pressures and constraints, we would expect that the direction of the multivariate regression vector to remain more similar than expected across levels, from individuals to genus up to family.

However, our results do not support this prediction. While the form–function relationship was present at some levels, the directions of the regression vectors were neither significantly more similar nor more divergent than expected by chance when compared across levels (Table S9–10, Figure S4). In other words, the scaling of the form–function relationship in lacertid lizards seems to follow a random pattern in multivariate space. One interpretation of these patterns is that changes in form–function dynamics at lower levels may lead to shifts in performance and potentially alter the adaptive landscape over evolutionary time (Martin & Wainwright, 2013; Simon et al., 2025b). One possible explanation, is that selective pressures shaping head shape–bite force relationship differ between species, producing species-specific responses that do not translate into consistent macroevolutionary trends, a pattern also observed in other taxa (Simon et al., 2025b). Alternatively, the same or similar selective pressures may act across species, but individual species might respond differently, yielding different form–function outcomes, due to genetic constraints or phylogenetic limitations (Simon & Moen, 2023). For example, in this specific case, we observed that there are specific shape dimensions that are more phylogenetically constrained than others (Figure S1), therefore, the response to species-specific selective pressures would be mirrored in certain axis of the multivariate space (Mitteroecker et al., 2025).

Both head shape and bite force are known to be influenced by a variety of selective pressures. Whether trends are conserved across levels may therefore depend on how much each of these pressures contributes to fitness within and between species (Simon et al., 2025b; Woodgate et al., 2025). These divergent selective contexts can shape head morphology in different ways, ultimately modifying the head shape–performance relationship. In addition to ecological and behavioral factors, variation in form–function trajectories may also reflect functional constraints, such as the degree to which traits are integrated and must coordinate to perform biomechanical tasks (Ghalambor et al., 2003; Wainwright, 2007; Walker, 2007). Likewise, trade-offs between competing performance demands may constrain the directions in which morphology can evolve (Le Guilloux et al., 2020). For example, trade-offs between bite magnitude and endurance have been found in lacertid lizards (Gomes et al., 2020). Other trade-offs between bite force features, such as strength and velocity has been found in other groups (Herrel et al., 2009; Sansalone et al., 2024), as well as specific trade-offs between different performance categories, such as locomotion and bite force (Cameron et al., 2013), which may be present also in lacertid lizards. Depending on which functions are most critical in each context, selection may favor different morphological solutions, thereby altering the shape–performance link across species (Garland et al., 2022). As a result, even though form–function integration remains present, the evolutionary pathways it follows may vary substantially depending on the ecological and behavioral pressures acting on each species. In *Podarcis*, it is likely that all these factors are at play, but their relative influence or the species' responses to them, may differ, leading to randomly-divergent form–function patterns that fail to align with those observed at higher levels of organization, as it was shown for specific *Podarcis* species (Woodgate et al., 2025).

Conclusion

Taken together, the results of this study highlight a central paradox: The form–function relationship between head shape and bite force is present and statistically strong across multiple levels of organization, yet the evolutionary trajectories that it follows differ across these scales. Despite the apparent randomness in vector orientation, the functional link is robust. This suggests a flexible system in which both selective pressures and other potential evolutionary constraints may shift or produce different responses, but performance remains consistently influenced by morphology (Ghalambor et al., 2003). This underscores a key evolutionary insight: strong form–function integration can persist even in the absence of a single, conserved evolutionary path which reflects the combination between constraints and evolvability in this comprehensive phenotypic evolution.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data and code are available on Dryad at DOI: 10.5061/dryad.x0k6djhzg.

Author contributions

P.V-C. collected a portion of the data, processed it, and conducted all analyses. C.A.S-C. contributed to data collection. P.V-C., A.K., and D.A. established the theoretical framework. D.A. and P.V-C. designed the statistical analysis framework. All authors contributed to the conceptualization, overall study design, and interpretation of the results. P.V-C. prepared the manuscript with input from all authors

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Conflict of interest

Editorial processing of the manuscript was conducted independently of A.K., who is an Associate Editor of *Evolution*. The other authors declare no conflict of interest.

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