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Original Article

Drivers of variation in head shape and bite force in monitor lizards

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ABSTRACT

Monitor lizards (Varanidae) comprise 88 species exhibiting morphological and ecological diversity. Because diet and habitat impose functional constraints on cranial morphology and bite force, we investigated their evolutionary relationships using phylogenetically informed comparative methods. Body size strongly influenced cranial morphology, initially masking ecological signals. After correcting for size, clear patterns of size-independent cranial shape variation emerged. Insectivorous, arboreal, and saxicolous species exhibited proportionally more elongated heads, consistent with trade-offs favouring jaw closing speed over force, whereas durophagous species showed taller, more robust heads adapted for forceful biting. Comparative analyses indicated that habitat and diet primarily influence head shape rather than size, with habitat effects driven mainly by terrestrial–arboreal contrasts and dietary effects by divergence between durophagous and insectivorous species. Morphological disparity analyses revealed that habitat use structures head shape diversity once size effects are removed, whereas dietary categories show comparable variation. *Varanus komodoensis* consistently occupied an isolated position in morphospace. Terrestrial and carnivorous species exhibited higher bite forces than arboreal, saxicolous, and insectivorous species, but differences disappeared after accounting for body size. Lower jaw length was the strongest predictor of bite force. Finally, we estimated bite force in the extinct varanid *Megalania* (*Varanus priscus*) and compare it to data for other large predators.

Keywords: bite force; cranial morphology; diet; habitat; varanidae

INTRODUCTION

The vertebrate skull is a complex and integrated system composed of numerous structural elements (Herrel *et al.* 2007). It protects critical components such as the brain and major sensory organs (e.g. eyes, ears, nose, vomeronasal system) and is shaped by both biotic and abiotic selective pressures. Functionally, the skull plays a central role in a wide array of behaviours and ecological functions, including defence (e.g. Cooper *et al.* 1999, Herrel *et al.* 2001b), locomotion (e.g. Gans 1975, Teodecki *et al.* 1998), male–male combat (e.g. Huyghe *et al.* 2005, Lappin *et al.* 2006), reproduction (e.g. Herrel *et al.* 1999b, 2001b), drinking (e.g. Bels *et al.* 1994, Cundall 2000), and especially feeding (e.g. Wainwright and Richard 1995, Cundall and Greene 2000, Schwenk 2000). Since many vital organs occupy space within the skull, spatial and functional trade-offs inevitably arise among its different components (Barel 1982, Herrel *et al.* 2001a, 2001b). As a result, the vertebrate skull reflects the complex interplay between structural integration and functional compromise (Wainwright and Richard 1995, Vanhooydonck *et al.* 2011, Corbin *et al.* 2015, Edwards *et al.* 2016, Maestri *et al.* 2016, Watanabe *et al.* 2019). These interdependencies often complicate our ability to disentangle the evolutionary pressures and developmental constraints driving morphological variation of the cranium.

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Bite force is a key functional trait with implications for survival and plays a role in prey capture, intra- and interspecific combat, and defence (Erickson *et al.* 2003). As it is a heritable trait (Zablocki-Thomas *et al.* 2021), bite force is subject to natural selection. In lizards and other vertebrates, larger body size is generally associated with increased bite force (Aguirre *et al.* 2002, Herrel *et al.* 2004a, 2010, Chazeau *et al.* 2013). Nevertheless, irrespective of variation in body size, larger heads typically also allow for stronger bites due to the greater volume of jaw muscles they can house (Herrel *et al.* 2001a, 2001b, 2006). The exploitation of novel food resources and the occupation of new ecological niches are moreover often associated with morphological adaptations of the jaw apparatus, which in turn drive variation in bite force (Herrel *et al.* 2004b, 2008, Cattau *et al.* 2018). Durophagy and herbivory, for instance, are dietary strategies that require elevated bite force due to the mechanical demands of crushing or tearing hard and fibrous food items (Herrel *et al.* 1999a, 2004b, Schaerlaeken *et al.* 2012). Consequently, it has been suggested that lizards consuming such items tend to exhibit taller and wider heads with more robust cranial musculature than those feeding on softer prey (Herrel and Holanova 2008, Schaerlaeken *et al.* 2012).

Habitat use may also impose mechanical constraints on head morphology and thus indirectly affect bite force evolution (Kohlsdorf *et al.* 2008). In arboreal and saxicolous species, for instance, a reduction in head and body height may facilitate access to narrow crevices. This also enhances stability during climbing by lowering the centre of gravity, thus avoiding the generation of a backward moment causing the animal to topple backwards (Herrel *et al.* 2001b, 2001c, Kohlsdorf *et al.* 2008). Additionally, arboreal species often possess narrow heads, which may enhance balance when moving along slender branches (Herrel *et al.* 2001d, Kohlsdorf *et al.* 2008). Therefore, head size and shape are probably shaped by trade-offs among habitat use, locomotor demands, and feeding ecology, all of which influence bite force (Vanhooydonck *et al.* 2011).

The genus *Varanus* currently comprises 88 extant described species, exhibiting a remarkable diversity in body size and ecological adaptations. Among these living representatives, body size ranges from the diminutive *Varanus sparnus*, measuring only 23 cm in total length and weighing less than 17 g, to the iconic Komodo dragon (*Varanus komodoensis*), which may exceed 3 m in length and weigh up to 100 kg (Auliya and Koch 2020). Most species are predatory, yet distinct dietary specializations can be recognized. Carnivorous species feed primarily on vertebrates, whereas insectivorous species mainly consume arthropods. In addition, some species are described as durophagous, referring not to the taxonomic identity of their prey but to their ability to process hard or resistant items such as molluscs, crustaceans, or vertebrates (e.g. turtles). Importantly, durophagy reflects a functional feeding capability and does not necessarily imply that such prey constitute the majority of the diet. Finally, a small clade of species endemic to the Philippines has evolved predominantly frugivorous feeding habits (Auliya and Koch 2020). Monitor lizards display a wide array of habitat specializations. While most species are terrestrial, some are highly arboreal, possessing long, prehensile tails that aid in grasping branches. Others are semi-aquatic, with dorsally positioned nostrils enabling breathing while mostly submerged. Their laterally compressed tails further aid aquatic locomotion. Finally, many species are adapted to rocky environments (Auliya and Koch 2020).

In this study, we measure bite force in 14 species and cranial morphology in 19 species of monitor lizards (*Varanus*). Utilizing their morphological, ecological, and taxonomic diversity, we assess how variation in head morphology relates to bite force and whether this relationship differs across species with distinct diets and habitat preferences. We hypothesize that bite force differs among dietary groups, with durophagous species exhibiting relatively higher bite forces than insectivorous or carnivorous ones. Additionally, we predict that arboreal and saxicolous species will exhibit different head shapes and lower bite forces due to habitat-specific constraints on head morphology (Herrel *et al.* 2001d, Kohlsdorf *et al.* 2008, Vanhooydonck *et al.* 2011, Paluh and Bauer 2017).

MATERIALS AND METHODS

Specimens

Our dataset included measurements of head morphology, body size, and bite force for 14 species (Table 1; Supporting Information Tables S3 and S4) (Fig. 1). In addition to data collected from live specimens, we incorporated head measurements from preserved specimens to complete our morphological dataset. This approach allowed us to collect morphological data for a total of 19 distinct species (Table 1; Tables S3 and S4), representing almost a quarter of all currently recognized living monitor lizard species. Species names followed the binomial nomenclature provided by The Reptile Database (http://www.reptile-database.org/). The number of individuals sampled per species varied depending on specimen availability for morphological and *in vivo* measurements (Table 1).

Linear measurements

Seven head and body measurements were recorded for each individual (Table 1; Supporting Information Tables S3 and S4) (Fig. 2). Snout–vent length (SVL) was measured from the tip of the snout to the cloaca. Head length (Headl) was measured from the posterior margin of the parietal bone to the tip of the upper jaw; head width (Headw) was measured at the widest point of the head, typically at the level of the jugal bone; head height (Headh) at the tallest point of the skull, posterior to the orbit; and lower jaw length (Lower_jawl) from the posterior margin of the retroarticular process to the tip of the lower jaw. Additionally, we measured the distance from the snout to the quadrate bone (Tip-quadr) and to the coronoid bone (Tip-coron). All measurements were taken on the right side of each specimen using digital calipers (Mitutoyo CD-20DC, Kawasaki, Japan; accuracy: 0.01 mm). All measurements were taken on whole heads, including the skin, both for preserved and live specimens. The underlying bone morphology was easily identifiable either visually or by palpation, allowing accurate localization of measurements points. For *V. komodoensis*, measurements were obtained from pictures with a scale using ImageJ software (Schneider *et al.* 2012). Species-level values were obtained by retaining only adult specimens and calculating mean values for each variable. When adult individuals

Table 1. Mean morphological traits and bite force of the species included in our study.

Species	*N*	Origin	SVL (mm)	Head length (mm)	Head width (mm)	Head height (mm)	Lower jaw length (mm)	Tip quadrate length (mm)	Tip coronoid length (mm)	Bite force (N)
Varanus acanthurus	1	Bebesaurus	135.44 (juvenile)	24.34	12.95	10.59	24.67	22.23	16.72	9.31
Varanus albigularis	1	–	260.00 (juvenile)	56.28	37.10	31.05	65.84	58.63	43.27	–
Varanus beccarii	2	Planet Exotica	274.00 ± 9.90	48.67 ± 1.90	24.27 ± 3.04	18.22 ± 0.17	52.06 ± 2.92	45.59 ± 1.02	35.78 ± 2.32	31.16 ± 6.16
Varanus bengalensis	1	–	304.44 (sub-adult)	61.48	34.50	29.81	68.12	61.22	46.77	–
Varanus exanthematicus	2	La Ferme Tropicale	385.00 ± 21.21	59.44 ± 4.32	42.41 ± 0.09	35.49 ± 3.80	72.43 ± 4.77	61.68 ± 4.56	42.55 ± 3.77	95.27 ± 15.35
Varanus glauerti	2	La Ferme Tropicale	214.00 ± 8.49	38.98 ± 1.99	17.54 ± 1.82	12.25 ± 0.64	39.95 ± 0.06	34.54 ± 0.64	25.32 ± 0.38	27.75 ± 12.89
Varanus gouldii	1	–	250.00 (juvenile)	47.28	24.74	19.44	48.32	43.04	32.74	–
Varanus komodoensis	1	Touroparc	1110.75	302.46	203.53	115.64	237.39	232.86	168.72	195.20
Varanus macraei	5	Planet Exotica and Touroparc	277.00 ± 48.80	47.28 ± 4.59	24.10 ± 4.19	19.65 ± 2.73	51.97 ± 5.42	45.89 ± 5.30	34.22 ± 5.58	39.66 ± 14
Varanus melinus	1	Touroparc	700.00	75.64	40.91	32.22	84.62	75.82	54.68	74.38
Varanus mertensi	2	–	462.50 ± 45.96	62.50 ± 3.54	45.50 ± 0.71	31.25 ± 1.77	72.50 ± 3.54	64.50 ± 6.36	45.50 ± 3.54	–
Varanus niloticus	3	La Ferme aux Crocodiles	326.67 ± 27.54 (juvenile)	51.53 ± 1.04	25.45 ± 1.96	20.14 ± 0.30	57.73 ± 2.18	49.70 ± 1.38	38.09 ± 2.84	37.99 ± 2.89
Varanus panoptes	1	La Ferme Tropicale	780.00	92.02	48.15	39.29	100.72	87.34	69.28	78.56
Varanus pilbarensis	1	Bebesaurus	127.45 (juvenile)	26.11	13.87	9.17	29.52	25.29	18.61	–
Varanus prasinus	2	Planet Exotica	252.50 ± 21.92	44.49 ± 4.36	23.64 ± 6.95	18.84 ± 3.53	53.07 ± 8.53	44.01 ± 4.62	32.18 ± 1.58	37.19 ± 18.48
Varanus reisingeri	2	Bebesaurus	262.50 ± 17.68	45.89 ± 2.52	20.12 ± 1.08	17.55 ± 0.97	49.19 ± 2.52	42.30 ± 2.23	30.84 ± 1.13	29.35 ± 6.44
Varanus salvator	1	La Ferme aux Crocodiles	780.00	118.79	75.00	49.00	140.58	126.38	89.64	103.18
Varanus timorensis	2	Bebesaurus	134.03 ± 4.17 (juvenile)	24.60 ± 0.99	11.35 ± 0.51	9.49 ± 0.49	26.15 ± 0.57	22.96 ± 0.37	17.18 ± 0.91	4.39 ± 0.52
Varanus varius	2	La Ferme Tropicale	505.00 ± 21.21	80.15 ± 1.05	40.79 ± 0.42	29.02 ± 0.10	89.96 ± 1.60	78.51 ± 0.88	59.73 ± 1.61	40.47 ± 1.04

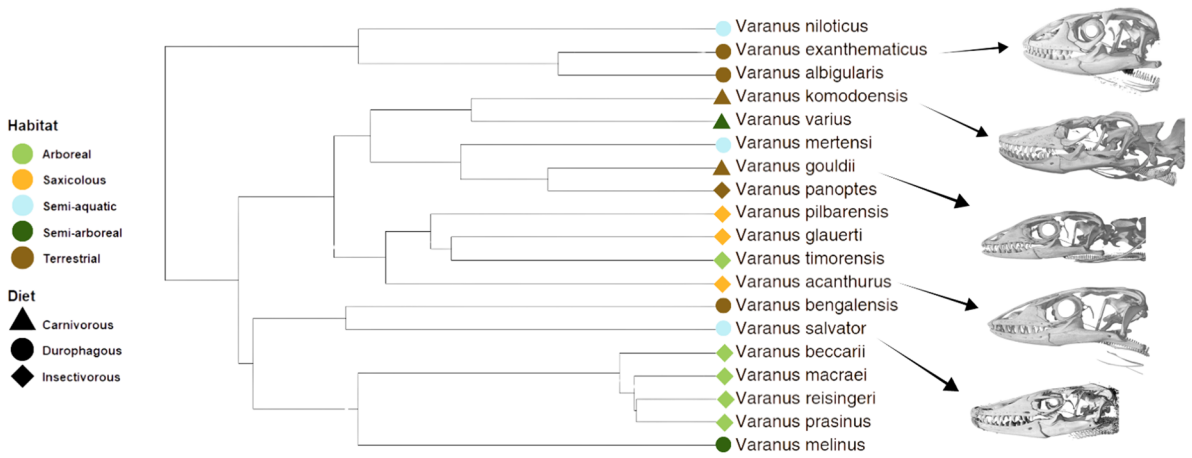

Figure 1. Phylogenetic tree of the monitor lizard species examined in this study, annotated with their respective ecological traits, representative skulls of selected species, and based on the phylogeny of Title *et al.* (2024). Representative skulls of selected species are shown alongside the tree to illustrate cranial morphological diversity within the genus *Varanus*; cranial models were obtained from previously published datasets and digital repositories (DigiMorph.org).

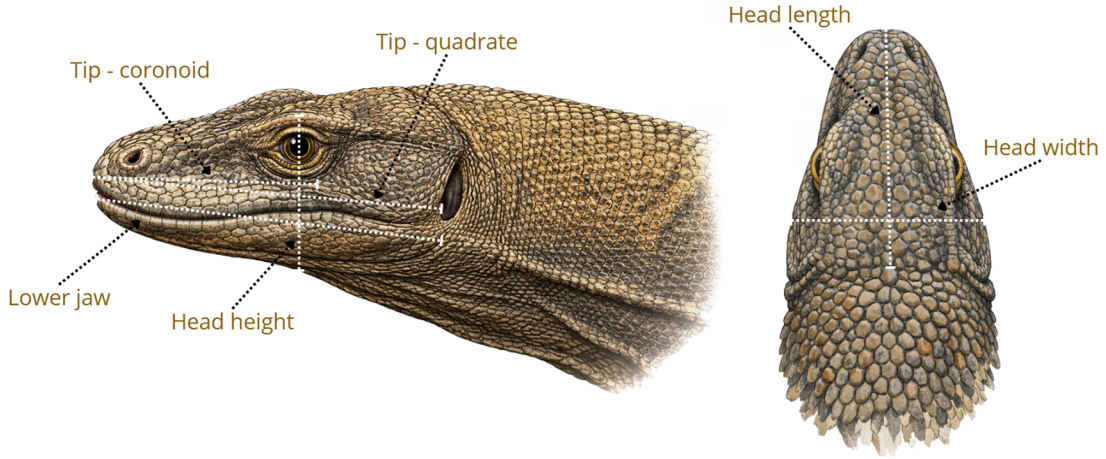

Figure 2. Schematic representation of the morphological measurements used in the analyses. The illustration of the head of *Varanus komodoensis* was generated using artificial intelligence.

were unavailable, the largest subadult or juvenile specimens were included to represent the species (Table 1).

Bite force

Bite force was measured in captivity using individuals housed in zoos and pet shops. Measurements were taken using Kistler isometric force transducers connected to charge amplifiers. Most individuals were measured using a type 9203 transducer (±500 N; Kistler, Zurich, Switzerland) and a type 5995A amplifier, mounted on a custom-built holder (see Herrel *et al.* 1999b). For larger species, a type 9311B piezoelectric transducer (±5000 N; Kistler Inc.) was used (see Herrel *et al.* 2002, Brassard *et al.* 2020) and the transducer was fixed to a wooden handle. The bite plates were wrapped in surgical tape to protect the teeth and ensure grip. To standardize measurements across species, bite force was recorded at two positions when possible, at the tip of the snout and at the corner of the mouth. For smaller specimens, the mouth opening was too narrow to position the bite force transducer at the posterior site, so only anterior measurements could be obtained. For individuals with both measurements, we calculated the ratio of posterior to anterior bite force. The mean ratio across these species was then used to estimate posterior bite force for species where only anterior bite data were available. Only posterior bite force values (measured or estimated) were retained for comparative analyses (Table 1). Each individual performed five bite trials, and the highest value was considered as the maximal bite force. Raw values were corrected for the mechanical advantage of the setup. Bite force was summarized at the species level by averaging measurements from adult individuals whenever possible. In cases where adults were unavailable, values from the largest subadult or juvenile specimens were used (Table 1).

Ecological groups

Species were categorized into five groups based on habitat preferences: arboreal, terrestrial, semi-arboreal, saxicolous, and semi-aquatic. Arboreal species primarily inhabit vegetation and rarely descend to the ground, whereas terrestrial species spend most of their time on the ground. Semi-arboreal species use both

Table 2. Ecological traits and literature references of each species measured.

Species	Diet	Habitat	References
Varanus acanthurus	Insectivorous	Saxicolous	Losos and Greene 1988, Greer 1989.
Varanus albigularis	Durophagous	Terrestrial	Dalhuijsen *et al.* 2014, Horn and Visser 1989, Pianka *et al.* 2004.
Varanus beccarii	Insectivorous	Arboreal	Losos and Greene 1988, Eidenmüller 2021.
Varanus bengalensis	Durophagous	Terrestrial	Losos and Greene 1988, Auliya and Koch 2020.
Varanus exanthematicus	Durophagous	Terrestrial	Losos and Greene 1988, Auliya and Koch 2020.
Varanus glauerti	Insectivorous	Saxicolous	James *et al.* 1992, Losos and Greene 1988, Greer 1989.
Varanus gouldii	Carnivorous	Terrestrial	Shine 1986, Losos and Greene 1988, Greer 1989, Pianka 1994.
Varanus komodoensis	Carnivorous	Terrestrial	Losos and Greene 1988.
Varanus macraei	Insectivorous	Arboreal	Auliya and Koch 2020, Eidenmüller 2021.
Varanus melinus	Durophagous [data inferred from closely related species (*Varanus douarrha* and *V. indicus*)]	Semi-arboreal	Auliya and Koch 2020.
Varanus mertensi	Durophagous	Semi-aquatic	Shine 1986, Greer 1989.
Varanus niloticus	Durophagous	Semi-aquatic	Losos and Greene 1988, Pianka *et al.* 2004.
Varanus panoptes	Insectivorous	Terrestrial	Shine 1986, Greer 1989.
Varanus pilbarensis	Insectivorous	Saxicolous	Greer 1989, James *et al.* 1992.
Varanus prasinus	Insectivorous	Arboreal	Losos and Greene 1988, Greer 1989, Eidenmüller 2021.
Varanus reisingeri	Insectivorous	Arboreal	Eidenmüller 2021.
Varanus salvator	Durophagous	Semi-aquatic	Rusli *et al.* 2020, Yu *et al.* 2021.
Varanus timorensis	Insectivorous	Arboreal	Greer 1989, Auliya and Koch 2020, Eidenmüller 2021.
Varanus varius	Carnivorous	Semi-arboreal	Weavers 1989, Jessop *et al.* 2010, Eidenmüller 2021.

arboreal and terrestrial environments. Saxicolous species are specialized for life on rocky substrates, while semi-aquatic species spend a considerable amount of time in water and are proficient swimmers (Table 2). Species were further assigned to one of three dietary categories: insectivory, durophagy, or carnivory. Insectivorous and carnivorous species were classified based on the dominant prey items found in their stomach contents (Table 2). Durophagous species were identified by their ability to consume hard prey such as crabs, molluscs, or tortoises, regardless of the proportion of these items in their overall diet. For *Varanus melinus*, for which direct dietary data were unavailable, information was inferred from the most closely related species—*Varanus douarrha* and *Varanus indicus*—because their ecological and dietary traits are expected to be most similar.

Statistical analyses

All statistical analyses were conducted in R v.4.4.0 (R Core Team 2025). Phylogenetic non-independence was accounted for in all comparative analyses using a Brownian motion correlation structure and was based on the phylogeny of Title *et al.* (2024).

Our dataset includes specimens spanning a wide range of body sizes, with SVL ranging from 127.45 to 1110.75 mm (Table 1; Supporting Information Tables S3 and S4). To test whether species living in different habitats or consuming different diets differed in overall size, univariate phylogenetic ANOVAs were performed, with post-hoc pairwise comparisons. To compare morphology among species it is necessary to separate the effects of size and shape. SVL is commonly used as a proxy for body size in lizards. This is particularly relevant for museum specimens, in which preservation in ethanol or formaldehyde causes substantial mass loss but has comparatively minor effects on linear dimensions (Kristoffersen and Salvanes 1998). To correct for size, we used the log-shape ratio method (Mosimann 1970, Klingenberg 2016). This method consists of scaling each morphological variable by a measure of size and then log-transforming the resulting ratios. The log-shape ratio method preserves shape variation associated with evolutionary allometry, that is, shape changes that covary predictably with size (Klingenberg 2016, Price *et al.* 2019). We applied this approach using two alternative proxies of size, each addressing a distinct biological question. First, we calculated log-shape ratios using SVL as our size variable (Tables S1, S5 and S6). In this case, each morphological trait was divided by the SVL of the corresponding specimen and log-transformed. This correction removes the effect of overall body size. Second, we calculated log-shape ratios using a cranial size estimate defined as the geometric mean of head length, head width, and head height (Tables S2, S7 and S8). Each trait was divided by this geometric mean and log-transformed. This approach treats size as a composite measure of the three principal cranial dimensions, avoiding reliance on a single variable and providing a more integrative estimate of head size (Price *et al.* 2019).

Patterns of morphological variation were explored using phylogenetic principal component analysis (pPCA) under a Brownian motion model, implemented with the phyl.pca function in 'phytools' (Revell 2024). Analyses were conducted on three datasets: (i) raw cranial measurements, (ii) log-shape ratios using SVL as a size proxy, and (iii) log-shape ratios using the geometric mean of head length, head width, and head height. The pPCA was performed on covariance matrices for raw measurements and on correlation matrices for size-corrected datasets.

The effects of habitat use and dietary specialization on cranial morphology were tested using phylogenetic multivariate analysis of variance (MANOVA) implemented in the mvgls function of

the 'mvMORPH' package (Clavel *et al.* 2015). For raw cranial measurements, models included the six cranial variables. For size-corrected datasets, MANOVAs were conducted on principal component scores derived from the pPCA, using the first two components for SVL-based log-shape ratios and the first three components for head-size-based log-shape ratios (Supporting Information Table S9). When significant multivariate effects were detected, univariate phylogenetic ANOVAs were performed on individual cranial variables or principal component axes using the 'phytools' package, with post-hoc pairwise comparisons conducted when significant. Morphological disparity among ecological groups was quantified using the distance-to-centroid metric implemented in the 'dispRity' package (Guillerme 2018). Disparity analyses were performed separately for raw cranial measurements, SVL-based log-shape ratios, and cranial-size-based log-shape ratios.

Differences in bite force among habitat categories and dietary groups were tested using phylogenetic ANOVAs implemented in the phylANOVA function of the 'phytools' package (Revell 2024) and post-hoc pairwise comparisons were performed when overall effects were significant. Because bite force scales strongly with body size, we further assessed ecological effects using phylogenetic analysis of covariance (PGLS-ANCOVA), in order to separate the effects of body size and ecology. Log-transformed bite force was modelled as a function of log-transformed SVL, ecological category (habitat or diet), and their interaction using generalized least squares (GLS) models implemented in the 'nlme' package (Pinheiro *et al.* 2025). Model significance was evaluated using Type II ANOVAs, and Tukey-adjusted post-hoc comparisons were conducted using the 'multcomp' package (Hothorn *et al.* 2008). To identify the best morphological predictors of bite force, a series of phylogenetic generalized least squares (PGLS) regressions were fitted. Log-transformed bite force was modelled separately as a function of log-transformed SVL and individual log-transformed head measurements. Model support was compared using Akaike's Information Criterion (AIC), and the variable associated with the lowest AIC value was considered the best predictor of bite force.

Bite force in the extinct giant monitor lizard *Varanus priscus* (Megalania) was estimated using a PGLS regression describing the relationship between log-transformed bite force and log-transformed SVL across extant species. Predictions were generated by extrapolating the regression to estimated SVL values for *V. priscus* (Conrad *et al.* 2012). SVL was used for this estimation because detailed cranial measurements are unavailable for this extinct taxon, whereas SVL has been reliably estimated in the literature and remains a strong predictor of bite force, even if it is not the most powerful morphological predictor identified in extant species. Predicted bite force values were back-transformed to newtons, and prediction intervals were calculated to quantify uncertainty associated with extrapolation beyond the extant size range.

RESULTS

Body size differences

Phylogenetic ANOVAs revealed significant differences in SVL among habitat categories in the bite force dataset ($F = 4.04$, $P = .035$). Post-hoc comparisons indicated that terrestrial species were significantly larger than arboreal ($P = .027$) and saxicolous taxa ($P = .020$). Similarly, SVL differed significantly among dietary groups ($F = 4.30$, $P = .020$), with carnivorous species exhibiting greater body size than insectivorous species ($P = .027$). In contrast, no significant differences in SVL were detected among habitat ($P = .105$) or dietary categories ($P = .113$) in the morphological dataset. Together, these results indicate that ecological structuring of body size is detectable in the functional (bite force) dataset but disappeared when a larger taxonomic sample is considered.

Table 3. Results of univariate phylogenetic ANOVAs testing the effect of habitat on each raw head dimension.

Variable	Degrees of freedom	*F*	*P*
Head length	4,14	1.07	.43
Head width	4,14	1.15	.39
Head height	4,14	1.88	.15
Lower jaw length	4,14	1.79	.18
Tip quadrate length	4,14	1.57	.25
Tip coronoid length	4,14	1.61	.25

Head size

Analyses based on raw cranial measurements showed that PC1 captured most of the variance and primarily reflected overall body size (Supporting Information Fig. S1). This axis clearly separated large-bodied species (e.g. *V. komodoensis*, *V. melinus*, *V. panoptes*) from smaller species such as *V. acanthurus* and *V. pilbarensis*. In contrast, PC2 described size-independent variation in cranial shape, indicating that species of comparable body size can nevertheless differ markedly in skull proportions. Along this axis, *V. komodoensis* was clearly distinct from other large-bodied species, including *V. salvator*, *V. melinus*, and *V. panoptes*, highlighting its unique cranial morphology.

Phylogenetic MANOVA detected no significant effect of habitat on cranial morphology when using raw data ($F_{24,32} = 1.18$, $P = .32$), and univariate phylogenetic ANOVAs similarly revealed no habitat-related differences for individual cranial variables (Table 4). Dietary effects were slightly more pronounced: although the phylogenetic MANOVA only approached significance ($F_{12,22} = 2.12$, $P = .06$), univariate analyses showed that carnivorous species possessed significantly larger head dimensions than insectivorous species (Table 5).

Disparity analyses based on raw cranial measurements revealed no significant differences among habitat or dietary categories (all $P > .05$). However, several pairwise comparisons exhibited marginal *P*-values: terrestrial versus arboreal ($P = .085$), terrestrial versus saxicolous ($P = .075$), and terrestrial versus semi-arboreal species ($P = .064$) for habitat; and carnivorous versus durophagous ($P = .087$) and carnivorous versus insectivorous species ($P = .084$) for dietary regime. Durophagous and insectivorous taxa showed no notable differences ($P = .674$). Overall, these results indicate that variation in cranial morphology is largely dominated by body size, which may mask potential ecological signals.

Table 4. Results of univariate phylogenetic ANOVAs on each raw head variable and comparison between diets; significant results are in bold.

Variable	Degrees of freedom	*F*	*T*	*P*
Head length	2,14	**3.99**	–	**.032**
Carnivorous vs. Insectivorous	–	–	**2.82**	**.024**
Carnivorous vs. Durophagous	–	–	−1.99	.16
Insectivorous vs. Durophagous	–	–	1.02	.28
Head width	2,14	**3.87**	–	**.038**
Carnivorous vs. Insectivorous	–	–	**2.77**	**.045**
Carnivorous vs. Durophagous	–	–	−1.78	.24
Insectivorous vs. Durophagous	–	–	1.22	.24
Head height	2,14	**4.13**	–	**.03**
Carnivorous vs. Insectivorous	–	–	**2.77**	**.036**
Carnivorous vs. Durophagous	–	–	−1.47	.185
Insectivorous vs. Durophagous	–	–	1.65	.184
Lower jaw length	2,14	**4.14**	–	**.031**
Carnivorous vs. Insectivorous	–	–	**2.78**	**.042**
Carnivorous vs. Durophagous	–	–	−1.49	.19
Insectivorous vs. Durophagous	–	–	1.63	.17
Tip quadrate length	2,14	**4.14**	–	**.035**
Carnivorous vs. Insectivorous	–	–	**2.81**	**.024**
Carnivorous vs. Durophagous	–	–	−1.60	.25
Insectivorous vs. Durophagous	–	–	1.53	.25
Tip coronoid length	2,14	**4.12**	–	**.035**
Carnivorous vs. Insectivorous	–	–	**2.82**	**.042**
Carnivorous vs. Durophagous	–	–	−1.68	.25
Insectivorous vs. Durophagous	–	–	1.43	.25

Table 5. Comparison of raw cranial traits as predictors of bite force.

Variable	AIC
Tip coronoid	−3.70
SVL	−4.03
Head width	−4.30
Head height	−4.73
Tip quadrate	−5.22
Head length	−5.42
Lower jaw length	−6.45

Log-shape ratios relative to SVL

After correcting cranial variables for body size using log-shape ratios relative to SVL, PC1 represented relative cranial size (Supporting Information Fig. S2). Species such as *V. melinus*, *V. panoptes*, and *V. salvator* exhibit proportionally larger heads, whereas *V. albigularis* and *V. bengalensis* showed relatively smaller cranial dimensions. PC2 captured finer-scale variation in cranial shape, particularly involving head height and width. Along this axis, *V. komodoensis*, *V. exanthematicus*, and *V. mertensi* were clearly separated, reflecting proportionally taller and wider skulls. Durophagous species generally displayed higher PC2 scores than insectivorous species, and terrestrial and semi-aquatic taxa tended to score higher than arboreal and saxicolous species.

Multivariate analyses revealed no significant effect of habitat on size-corrected cranial morphology (phylogenetic MANOVA: $F_{8,26} = 1.60$, $P = .17$). However, univariate tests showed that habitat significantly affected PC2 ($F_{4,14} = 3.63$, $P = .036$) but not PC1, indicating that habitat use influences cranial shape rather than relative size. Post-hoc comparisons identified a significant difference between terrestrial and arboreal species. Dietary category did not significantly affect cranial morphology in multivariate analyses ($F_{4,30} = 1.76$, $P = .16$) or PC1, but was significant for PC2 ($F_{2,16} = 5.16$, $P = .02$). This is driven by differences between durophagous and insectivorous species. Carnivorous species did not differ significantly from either group.

Disparity analyses of SVL-corrected data revealed clearer ecological patterns than raw measurements. Cranial disparity differed significantly among several habitat categories. Specifically, arboreal species exhibited lower disparity than terrestrial species ($P = .034$), saxicolous species ($P = .023$), and semi-arboreal species ($P < .001$). Other habitat comparisons were not significant (all $P > .05$). In contrast, no significant differences in disparity were detected among dietary groups (carnivorous vs. durophagous: $P = .692$; carnivorous vs. insectivorous: $P = .319$; durophagous vs. insectivorous: $P = .264$), indicating that diet does not strongly structure overall size-independent cranial shape variability.

Log-shape ratios based on the geometric mean of cranial dimensions

When cranial variables were expressed as log-shape ratios relative to the geometric mean of cranial dimensions, PC1 primarily described variation in the relative development of jaw elements, including the lower jaw, quadrate, and coronoid process (Supporting Information Fig. S3). High scores along this axis characterized species with proportionally elongated cranial elements, predominantly insectivorous and arboreal or saxicolous taxa. PC2 reflected variation in head height relative to skull length and width, highlighting a trade-off between elongation and robustness. Durophagous species exhibited proportionally taller skulls than insectivorous species, and terrestrial and semi-aquatic taxa showed more robust head profiles. *Varanus komodoensis* remained an outlier in morphospace. The loadings of PC1–PC3, reflecting the contribution of each cranial variable to overall shape variation, are detailed in Table S9.

The phylogenetic MANOVA did not detect a significant multivariate effect of habitat on the first three PC axes ($F_{12,32} = 1.36$, $P = .23$). Nonetheless, univariate phylogenetic ANOVAs revealed a significant effect of habitat on PC1 ($F_{4,14} = 3.88$, $P = .032$) and a marginal effect on PC3 ($F_{4,14} = 2.44$, $P = .102$), driven mainly by arboreal species. Pairwise habitat comparisons for PC1 indicated that arboreal species exhibited significantly lower PC1 scores compared to terrestrial species ($P = .050$). Marginal differences were observed between arboreal and semi-aquatic species on PC3 ($P = .060$). Other habitat comparisons were non-significant (all $P > .2$). Diet exhibited a marginally non-significant multivariate effect ($F_{6,28} = 2.02$, $P = .096$), but univariate ANOVAs revealed significant effects on all three PCs. Pairwise comparisons indicated that durophagous species differed significantly from insectivorous species along PC1–PC3 (all $P < .05$) and from carnivorous species along PC2 ($P < .05$). Comparisons between carnivorous and insectivorous species were non-significant (PC1: $P = .084$; PC2: $P = .319$; PC3: $P = .096$), as were comparisons between durophagous and insectivorous species on PC2 and PC3 (PC2: $P = .692$; PC3: $P = .264$). Overall, these results indicate that while

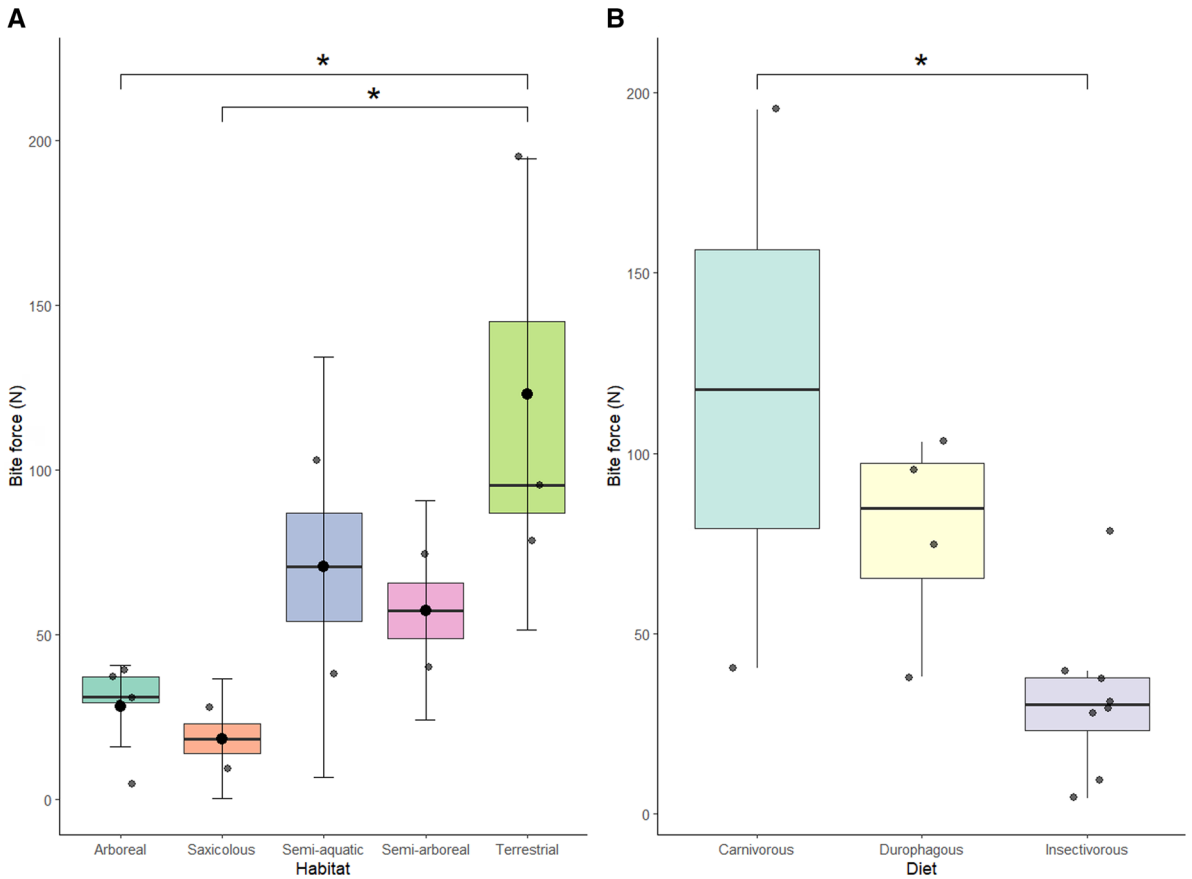

Figure 3. Boxplots of bite force as a function of habitat (A) or diet (B).

multivariate cranial shape variation is not strongly structured by habitat or diet, specific axes reveal subtle patterns. Habitat effects are concentrated primarily on PC1 and PC3, whereas dietary effects distinguish durophagous species across multiple axes.

Disparity analyses based on geometric means broadly mirrored the results obtained with SVL-corrected data, but revealed slightly stronger habitat-related differences. Pairwise comparisons indicated that terrestrial and arboreal species differed significantly in cranial disparity ($P = .023$), as did terrestrial versus semi-arboreal species ($P = .043$), arboreal versus semi-arboreal species ($P = .036$), and arboreal versus semi-aquatic species ($P = .016$). Other habitat comparisons were non-significant ($P \geq .079$). In contrast, dietary categories showed no significant differences, with pairwise *P*-values ranging from 0.158 to 0.221, indicating that diet does not strongly influence cranial disparity once size is accounted for.

Bite force

A phylogenetic ANOVA revealed significant variation in absolute bite force among habitat groups ($F_{4,9} = 3.97$, $P = .025$), with post-hoc tests indicating that terrestrial species bit significantly harder than both arboreal ($P = .010$) and saxicolous species ($P = .018$; Fig. 3A). No other pairwise differences were detected. Similarly, raw bite force differed significantly among dietary groups ($F_{2,11} = 4.27$, $P = .01$), with carnivorous species exhibiting higher values than insectivorous species ($P = .009$; Fig. 3B). After accounting for body size, phylogenetic ANCOVAs showed no significant effect of either habitat ($P = .41$) or diet ($P = .97$) on bite force, although body size itself remained a strong predictor (respectively $P = .0021$ and $P = .0003$). Pairwise comparisons of size-corrected bite force revealed no significant differences among habitats or dietary categories. Although durophagous species tended to exhibit higher bite force values, these differences were not statistically supported.

Model comparison based on AIC values revealed that lower jaw length was the best univariate predictor of log-transformed bite force, outperforming body size (SVL) and other cranial dimensions (Table 3). Quadrate length and head height also showed substantial support. Based on the regression model relating bite force to body size in extant species, we estimated the bite force of the extinct giant monitor lizard *V. priscus* (Megalania), for which SVL has been estimated at 1725 mm for an average adult and up to 3000 mm for the largest individuals (Conrad *et al.* 2012). The predicted bite forces for *V. priscus* are 386.5 N for an average-sized individual and 852.4 N for the largest estimated specimen (Fig. 4).

DISCUSSION

The lizard cranial system is involved in multiple functions (Herrel *et al.* 2007, Baeckens *et al.* 2017), some of which may result in trade-offs that constrain cranial evolution (Toro *et al.* 2004, Herrel *et al.* 2009, Vanhooydonck *et al.* 2011, 2014, Herrel and Bonneaud 2012). Using data on head morphology and bite

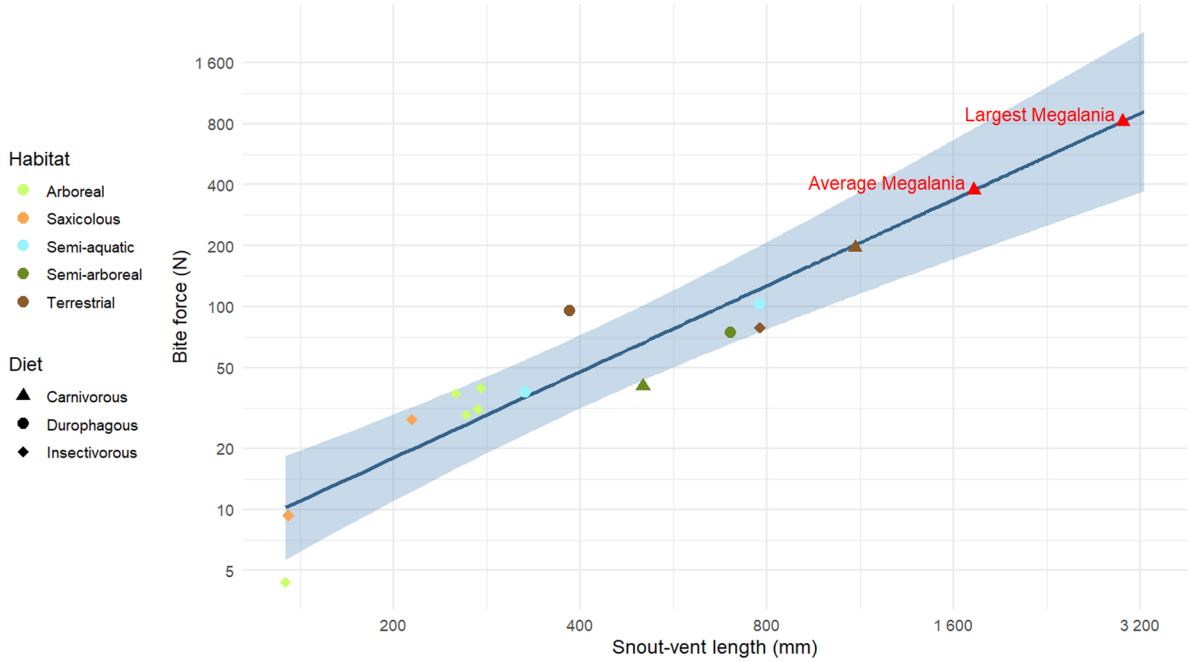

Figure 4. Regression of bite force as a function of snout–vent length, with species ecological traits indicated, including a 95% confidence interval around the regression line and extrapolation of bite force for *Megalania* (*Varanus priscus*).

force from 14 ecologically diverse monitor lizard species, we examined the relationships between cranial shape, bite force, and ecology to identify ecological correlates of cranial form and function.

As expected, variation in head morphology and bite force was predominantly driven by body size, with larger individuals producing higher absolute bite forces. This pattern probably confers an advantage to terrestrial and carnivorous species, which tend to reach larger body sizes than arboreal, saxicolous, and insectivorous species, thereby enhancing their ability to subdue and process larger prey. More broadly, the evolution of increased body size itself may differ in different habitats, particularly in terrestrial environments where mechanical constraints are reduced compared to arboreal and saxicolous settings. Freed from the structural limitations associated with climbing and balance, terrestrial species can attain larger sizes, which in turn drive cranial modifications that enhance bite force and provide access to a wider range of trophic resources. In contrast, species that target smaller and more agile prey, such as insects, may be subject to selective pressures favouring agility or speed instead. These findings support the hypothesis that body size can function as an adaptive pathway linking habitat, trophic ecology, and feeding performance. Although our results overall suggest that body size plays a predominant role in ecological diversification within Varanidae, the lack of significant effects in the morphological dataset—contrasting with the bite force dataset—cautions against overinterpreting these findings. Indeed, our dataset includes juveniles and relatively few specimens per species, particularly among carnivores. This may introduce biases contributing to these unexpected patterns. Further studies incorporating a broader range of species, larger numbers of adult specimens, and more balanced representation across habitats and diets are needed to robustly test and consolidate these findings.

However, once size effects were removed analyses consistently revealed that insectivorous species, as well as arboreal and saxicolous ones, tend to possess proportionally more elongated heads and jaws. This pattern is well aligned with established functional and biomechanical models of prey capture in lizards. Elongation of the jaws is known to enhance jaw closing speed rather than force production, reflecting a fundamental trade-off between bite force and jaw velocity (Herrel *et al.* 2001c, 2004b). For example, a relatively shorter mandible can increase the mechanical advantage for force production at the tip of the jaw (Herrel *et al.* 2001a, Herrel and Holanova 2008). Conversely, elongated head length tends to increase the jaw out lever relative to the in lever during biting, which can mechanically reduce bite force at the jaw tips but provides a higher jaw closing velocity. This negative association between head length and bite force has been documented in squamate studies where the geometry of lever arms imposes a trade-off between force and jaw length (Herrel *et al.* 2001b, Westneat 2004). Species with long and slender jaws probably experience reduced rotational inertia and mechanical resistance during jaw closure, allowing faster strikes that are advantageous for capturing elusive or rapidly moving prey such as insects (Herrel *et al.* 2002). Consequently, elongated cranial morphologies are commonly associated with insectivorous feeding strategies and have been repeatedly documented in lizards exploiting prey types that require rapid jaw movements rather than high bite forces (Herrel *et al.* 2004b, Herrel and O'Reilly 2006).

Importantly, habitat use may further shape these functional trends by imposing additional biomechanical constraints. Arboreal and saxicolous species not only share elongated cranial morphologies but also tend to exhibit reduced head height and overall cranial robustness. Such morphologies may facilitate access to narrow crevices and improve climbing performance by lowering the centre of gravity, thereby reducing the risk of backward

toppling during vertical or inclined locomotion (Herrel *et al.* 2001b, 2001d, Kohlsdorf *et al.* 2008). Narrower and flatter heads may also enhance balance when moving along slender branches, a recurring constraint in arboreal environments (Herrel *et al.* 2001d, Kohlsdorf *et al.* 2008).

In contrast, durophagous species were consistently characterized by proportionally taller and wider heads, particularly evident along shape axes describing variation in head height and robustness. A similar pattern was observed for habitat use, with terrestrial and semi-aquatic species exhibiting taller heads than arboreal or saxicolous species. These morphologies are widely interpreted as adaptations for forceful biting and the processing of hard or resistant prey (Herrel and Holanova 2008, Schaerlaeken *et al.* 2012). Independent of overall body size, increases in head height and width expand the available space for jaw adductor musculature, allowing greater muscle volume and a larger physiological cross-sectional area, both of which directly enhance bite force capacity (Herrel *et al.* 2001a, 2001b, 2006). Additionally, a taller head may permit a more vertical orientation of the adductor muscles, increasing their moment arms and improving the mechanical efficiency of force transmission at the bite point (Herrel *et al.* 2001b, 2006). Hard prey such as molluscs and crustaceans are typically rare or absent in arboreal environments, making the evolution of durophagy unlikely. In addition, the morphological demands of durophagy—particularly taller, wider, and more robust heads capable of generating high bite forces—are mechanically conflicting with the constraints of arboreal locomotion, which tend to favour elongated, shallower heads with reduced mass that facilitate balance. Consequently, in arboreal species, habitat-driven selective pressures appear to predominate, canalizing cranial morphology in ways that limit both the functional and the ecological opportunity for the evolution of durophagous feeding strategies.

Arboreal and saxicolous lifestyles are associated with cranial morphologies that balance mechanical efficiency in capturing small, agile prey with the functional demands of balance and stable locomotion in structurally complex environments. In contrast, terrestrial and semi-aquatic habitats, as well as durophagous diets, are linked to proportionally taller and wider heads that accommodate greater jaw adductor volume and improve leverage, thereby enhancing bite force capacity for the processing of hard or resistant prey. These observations suggest that habitat and dietary specialization may interact as joint selective pressures in shaping cranial evolution. Overall, these results indicate that cranial shape in these taxa reflects a compromise between the constraints imposed by habitat and those imposed by diet, with indirect consequences for the evolution of bite force (Vanhooydonck *et al.* 2011).

Disparity analyses support the interpretation that habitat use plays a major role in shaping cranial shape diversity once size effects are removed. Significant differences in cranial disparity among habitat categories indicate that distinct locomotor and structural constraints influence the range of viable cranial morphologies. In contrast, dietary categories exhibited relatively similar levels of cranial shape dispersion, suggesting that diet primarily drives directional changes in cranial proportions rather than constraining overall morphological variability. This pattern implies that habitat-related mechanical and spatial constraints may exert a stronger influence on cranial shape evolution than diet alone, at least in varanid lizards.

Finally, *V. komodoensis* remained isolated from all other monitor lizards across all morphospaces, reflecting its proportionally broader and more robust skull. This distinctive cranial morphology probably arises from a combination of extreme body size, unique feeding ecology, and biomechanical constraints associated with subduing relatively large prey. Its consistent separation underscores the extent to which *V. komodoensis* represents an evolutionary outlier within the genus, rather than an extrapolation of trends observed in smaller-bodied species. Although our results highlight the exceptional cranial morphology of *V. komodoensis*, further research will be necessary to identify the processes underlying its divergence from other varanid species. In particular, integrative approaches combining biomechanics, ecology, and evolutionary history will be essential to clarify the mechanisms driving this pronounced cranial specialization within the genus.

Our results also indicate that a medium-sized *Megalania* could produce a maximum bite force of approximately 386.5 N, whereas the largest specimens—potentially exceeding 575 kg in body mass (Fry *et al.* 2009)—could bite with a force of nearly 852.4 N. Due to its exceptional size, the extinct megalania (*V. priscus*) would have exhibited a bite force far exceeding that of any extant monitor lizard, including *V. komodoensis*, which is itself capable of taking down relatively large prey. It is therefore not unlikely that *Megalania* exploited a trophic niche centered on the Australian Pleistocene megafauna, capturing and consuming large vertebrate prey. For comparison, in extant crocodilians bite force ranges from the small *Paleosuchus palpebrosus* (∼10 kg; ∼1 m), capable of generating around 900 N, to *Crocodylus porosus* (∼300–1000 kg; 3.9–6 m), which can produce approximately 8900 N, with a recorded maximum of 16414 N (Webb *et al.* 1978, Campos *et al.* 2010, 2015, Erickson *et al.* 2012, Seymour *et al.* 2013). Moreover, several extant mammals develop substantially higher bite forces for equivalent or lower body masses: *Canis lupus* (∼40 kg) ≈1262 N; *Panthera pardus* (30–90 kg) ≈1377 N; *Crocuta crocuta* (45–80 kg) ≈1422 N; *Panthera tigris* (80–300 kg) ≈3007 N; *Panthera leo* (∼150 kg) ≈3405 N; and *Ursus maritimus* (∼300 kg) ≈2404 N (Smuts *et al.* 1980, Derocher and Wiig 2002, Christiansen and Adolfssen 2005, Hayward 2006, Hilderbrand and Golden 2013, Stein and Hayssen 2013). However, the data for mammals must be interpreted cautiously as they are based on modelling studies only that have never been validated with *in vivo* data. Thus, when scaled to body mass, the maximum bite force of *Megalania* appears relatively modest. However, this is consistent with the functional strategy observed in extant varanids, particularly *V. komodoensis*. This species is not optimized for crushing or resisting torsional loads but rather for traction through a grip-and-rip strategy, using compressed and serrated teeth to inflict deep lacerations, with substantial postcranial involvement during prey dismemberment (Fry *et al.* 2009). By analogy, *Megalania* may have combined biting and traction rather than relying on compressive forces comparable to those of crocodilians. Moreover, piscivorous crocodilians with slender teeth have been shown to generate very high tooth pressures despite having lower absolute bite forces (Erickson *et al.* 2012). Following this principle, *Megalania* may likewise have generated high tooth pressures

despite moderate bite force values, due to its laterally compressed and blade-like teeth. Taken together, these considerations help explain how *Megalania* could subdue and consume large prey without possessing an exceptionally high maximum bite force relative to its body size.

To finish, one potential limitation of this study lies in the relatively small sample sizes, whether by species, habitat type, or diet, which may introduce bias. Additionally, the origin of the specimens represents another constraint. Indeed, most measurements were taken on individuals born in captivity, for which the exact age and precise provenance remain unknown. The diet provided and the environments in which these animals were raised may differ from those encountered in the wild. All these factors may introduce biases that could affect the results. Consequently, we remain cautious about extrapolating our findings to wild populations.

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SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

FUNDING

None declared.

DATA AVAILABILITY

All data are available in Tables 1, S1 and S2.

REFERENCES

Aguirre LF, Herrel A, Van Damme R *et al.* An ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. *Proceedings of the Royal Society of London* 2002;**269**:1271–8.

Auliya M, Koch A. *Visual Identification Guide to the Monitor Lizard Species of the World (Genus Varanus)*. Germany: Bundesamt für Naturschutz, 2020.

Baeckens S, García-Roa R, Martín J *et al.* Fossorial and durophagous: implications of molluscivory for head size and bite capacity in a burrowing worm lizard. *Journal of Zoology* 2017;**301**:193–205.

Barel CDN. Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Netherlands Journal of Zoology* 1982;**33**:357–424.

Bels VL, Chardon M, Vandewalle P *et al. Biomechanics of Feeding in Vertebrates*. Berlin: Springer, 1994.

Brassard C, Merlin M, Guintard C *et al.* Bite force and its relation to jaw shape in domestic dogs. *Journal of Experimental Biology* 2020;**223**: jeb224352.

Campos Z, Sanaiotti T, Magnusson W. Maximum size of dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807), in the Amazon and habitats surrounding the Pantanal, Brazil. *Amphibia-Reptilia* 2010;**31**:439–42.

Campos Z, Sanaiotti T, Marques V *et al.* Geographic variation in clutch size and reproductive season of the dwarf caiman, *Paleosuchus palpebrosus*, in Brazil. *Journal of Herpetology* 2015;**49**:95–8.

Cattau CE, Fletcher , RJJr, Kimball RT *et al.* Rapid morphological change of a top predator with the invasion of a novel prey. *Nature Ecology & Evolution* 2018;**2**:108–15.

Chazeau C, Marchal J, Hackert R *et al.* Proximate determinants of bite force capacity in the mouse lemur. *Journal of Zoology* 2013;**290**:42–8.

Christiansen P, Adolfssen JS. Bite forces, canine strength and skull allometry in carnivores (Mammalia, Carnivora). *Journal of Zoology* 2005;**266**:133–51.

Clavel J, Escarguel G, Merceron G. mvMORPH: an R package for fitting multivariate evolutionary models to morphometric data. *Methods in Ecology and Evolution* 2015;**6**:1311–9.

Conrad JL, Balcarcel AM, Mehling CM. Earliest example of a giant monitor lizard (*Varanus*, Varanidae, Squamata). *PLoS One* 2012;**7**:e41767.

Cooper , WEJr, Van Wyk JH, Le F P *et al.* Incompletely protective refuges: selection and associated defences by a lizard, *Cordylus cordylus* (Squamata: Cordylidae). *Ethology* 1999;**105**:687–700.

Corbin CE, Lowenberger LK, Gray BL. Linkage and trade-off in trophic morphology and behavioural performance of birds. *Functional Ecology* 2015;**29**:808–15.

Cundall D. Drinking in snakes: kinematic cycling and water transport. *The Journal of Experimental Biology* 2000;**203**:2171–85.

Cundall D, Greene HW. Feeding in snakes. In: Schwenk K (ed.), *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates*. San Diego: Academic Press, 2000, 293–333.

Dalhuijsen K, Alexander G, Branch W. A comparative analysis of the diets of *Varanus albigularis* and *Varanus niloticus* in South Africa. *African Zoology* 2014;**49**:83–93.

Derocher AE, Wiig Ø. Postnatal growth in body length and mass of polar bears (*Ursus maritimus*) at Svalbard. *Journal of Zoology* 2002;**256**: 343–9.

Edwards S, Herrel A, Vanhooydonck B *et al.* Diving in head first: trade-offs between phenotypic traits and sand-diving predator escape strategy in *Meroles* desert lizards. *Biological Journal of the Linnean Society* 2016;**119**:919–31.

Eidenmüller B. *The Book of Monitor Lizards*. Frankfurt am Main: Edition Chimaira, 2021.

Erickson GM, Lappin AK, Vliet KA. The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *Journal of Zoology* 2003;**260**:317–27.

Erickson GM, Gignac PM, Steppan SJ *et al.* Insights into the ecology and evolutionary success of crocodilians revealed through bite-force and tooth-pressure experimentation. *PloS One* 2012;**7**:e31781.

Fry BG, Wroe S, Teeuwisse W *et al.* A central role for venom in predation by *Varanus komodoensis* (Komodo Dragon) and the extinct giant *Varanus* (*Megalania*) *priscus*. *Proceedings of the National Academy of Sciences* 2009;**106**:8969–74.

Gans C. Tetrapod limblessness: evolution and functional corollaries. *American Zoologist* 1975;**15**:455–67.

Greer A. *The Biology and Evolution of Australian Lizards*. Chipping Norton, NSW: Surrey Beatty, 1989.

Gauthier JA, Kearney M, Maisano JA *et al.* Assembling the squamate Tree of Life: perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History* 2012;**53**:3–308.

Guillerme T. DispRity: a modular R package for measuring disparity. *Methods in Ecology and Evolution* 2018;**9**:1755–63.

Hayward MW. Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology* 2006;**270**:606–14.

Herrel A, Aerts P, Fret J *et al.* Morphology of the feeding system in agamid lizards: ecological correlates. *The Anatomical Record* 1999a;**254**: 496–507.

Herrel A, Spithoven L, Van Damme R *et al.* Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology* 1999b;**13**:289–97.
Herrel A, Van Damme RV, Vanhooydonck B *et al.* The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* 2001a;**79**:662–70.
Herrel A, De Grauw ED, Lemos-Espinal JA. Head shape and bite performance in xenosaurid lizards. *The Journal of Experimental Zoology* 2001b;**290**:101–7.
Herrel A, Meyers JJ, Nishikawa KC *et al.* The evolution of feeding motor patterns in lizards: modulatory complexity and possible constraints. *American Zoologist* 2001c;**41**:1311–20.
Herrel A, Meyers JJ, Vanhooydonck B. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*). *Biological Journal of the Linnean Society* 2001d;**74**:305–14.
Herrel A, O'Reilly JC, Richmond AM. Evolution of bite performance in turtles. *Journal of Evolutionary Biology* 2002;**15**:1083–94.
Herrel A, Vanhooydonck B, Joachim R *et al.* Frugivory in polychrotid lizards: effects of body size. *Oecologia* 2004a;**140**:160–8.
Herrel A, Vanhooydonck B, Van Damme R. Omnivory in lacertid lizards: adaptive evolution or constraint? *Journal of Evolutionary Biology* 2004b;**17**:974–84.
Herrel A, Joachim R, Vanhooydonck B *et al.* Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal of the Linnean Society* 2006;**89**:443–54.
Herrel A, O'Reilly JC. Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology: PBZ* 2006;**79**:31–42.
Herrel A, Schaerlaeken V, Meyers JJ *et al.* The evolution of cranial design and performance in squamates. *Integrative and Comparative Biology* 2007;**47**:107–17.
Herrel A, Holanova V. Cranial morphology and bite force in *Chamaeleolis* lizards: adaptations to molluscivory? *Zoology (Jena, Germany)* 2008;**111**:467–75.
Herrel A, Huyghe K, Vanhooydonck B *et al.* Rapid large scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proceedings of the National Academy of Sciences* 2008;**105**:4792–5.
Herrel A, Podos J, Vanhooydonck B, Hendry AP Force–velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation?. *Functional Ecology* 2009;**23**:119–125.
Herrel A, Moore JA, Bredeweg EM *et al.* Sexual dimorphism, body size, bite force and male mating success in tuatara. *Biological Journal of the Linnean Society* 2010;**100**:287–92.
Herrel A, Bonneaud C. Trade-offs between burst performance and maximal exertion capacity in a wild amphibian, *Xenopus tropicalis*. *Journal of Experimental Biology* 2012;**215**:3106–11.
Hilderbrand GV, Golden HN. Body composition of free-ranging wolves (*Canis lupus*). *Canadian Journal of Zoology* 2013;**91**:1–6.
Horn H, Visser G. Review of reproduction of monitor lizards (*Varanus* spp.) in captivity. *International Zoo Yearbook* 1989;**28**:140–50.
Hothorn T, Bretz F, Westfall P. Simultaneous inference in general parametric models. *Biometrical Journal. Biometrische Zeitschrift* 2008;**50**:346–63.
Huyghe K, Vanhooydonck B, Scheers H *et al.* Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology* 2005;**19**:800–7.
James CD, Losos JB, King DR. Reproductive biology and diets of goannas (Reptilia: Varanidae) from Australia. *Journal of Herpetology* 1992;**26**:128–36.
Jessop TS, Urlus JAKE, Lockwood T *et al.* Preying possum: assessment of the diet of lace monitors (*Varanus varius*). *Biawak* 2010;**4**:59–63.
Klingenberg CP. Size, shape, and form: concepts of allometry in geometric morphometrics. *Development Genes and Evolution* 2016;**226**:113–37.
Kohlsdorf T, Grizante MB, Navas CA *et al.* Head shape evolution in Tropidurinae lizards: does locomotion constrain diet? *Journal of Evolutionary Biology* 2008;**21**:781–90.
Kristoffersen JB, Salvanes A. Effects of formaldehyde and ethanol preservation on body and otoliths. *Sarsia* 1998;**83**:95–102.
Lappin AK, Brandt Y, Husak JF *et al.* Gaping displays reveal and amplify a mechanically based index of weapon performance. *The American Naturalist* 2006;**168**:100–13.
Losos J, Greene H. Ecological and evolutionary implications of diet in monitor lizards. *Biological Journal of the Linnean Society* 1988;**35**:379–407.
Maestri R, Patterson BD, Fornel R *et al.* Diet, bite force and skull morphology in the generalist rodent morphotype. *Journal of Evolutionary Biology* 2016;**29**:2191–204.
Maisano JA, Laduc TJ, Bell CJ *et al.* The cephalic osteoderms of *Varanus komodoensis*. *The Anatomical Record* 2019;**302**:1675–80.
Mosimann JE. Size allometry: size and shape variables. *Journal of the American Statistical Association* 1970;**65**:930–45.
Paluh DJ, Bauer AM. Comparative skull anatomy of *Trachylepis* skinks. *PLoS ONE* 2017;**12**:e0184414.
Pianka ER. Comparative ecology of *Varanus* in the Great Victoria Desert. *Australian Journal of Ecology* 1994;**19**:395–408.
Pianka ER, King DR, King RA. *Varanoid Lizards of the World*. Bloomington: Indiana University Press, 2004.
Pinheiro J, Bates D, R Core Team. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-168, 2025.
Price SA, Friedman ST, Corn KA *et al.* Building a body shape morphospace of teleostean fishes. *Integrative and Comparative Biology* 2019;**59**:716–730.
Revell LJ. phytools 2.0: an updated R ecosystem for phylogenetic comparative methods. *PeerJ* 2024;**12**:e16505.
Rusli MU, Chen G, Booth D *et al.* Diet preference and activity of Asian water monitor. *Journal of Sustainability Science and Management* 2020;**15**:61–7.
R Core Team R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 2025. https://www.R-project.org/
Schaerlaeken V, Holanova V, Boistel R *et al.* Built to bite: feeding kinematics and bite forces of a specialized durophagous lizard. *Journal of Experimental Zoology Part A* 2012;**317**:371–81.
Schneider CA, Rasband WS, Eliceiri KW. NIH Image to ImageJ. *Nature Methods* 2012;**9**:671–5.
Schwenk K (ed.), *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. San Diego: Academic Press, 2000.
Seymour RS, Gienger CM, Brien ML *et al.* Scaling of standard metabolic rate in estuarine crocodiles *Crocodylus porosus*. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* 2013;**183**:491–500.
Shine R. Food habits, habitats and reproductive biology of four sympatric species of varanid lizards. *Herpetologica* 1986;**42**:346–60.
Smuts GL, Robinson GA, Whyte IJ. Comparative growth of wild male and female lions (*Panthera leo*). *Journal of Zoology* 1980;**190**:365–73.
Stein AB, Hayssen V. *Panthera pardus* (Carnivora: Felidae). *Mammalian Species* 2013;**45**:30–48.
Teodecki EE, Brodie EDJr, Formanowicz , DRJr, *et al.* Head dimorphism and burrowing speed in the African caecilian *Schistometopum thomense* (Amphibia: Gymnophiona). *Herpetologica* 1998;**54**:154–60.
Title PO, Singhal S, Grundler MC *et al.* The macroevolutionary singularity of snakes. *Science (New York, N.Y.)* 2024;**383**:918–23.
Toro E, Herrel A, Irschick D. The evolution of jumping performance in Caribbean *Anolis* lizards. *The American Naturalist* 2004;**163**:844–56.
Vanhooydonck B, Boistel R, Fernandez V *et al.* Push and bite: trade-offs between burrowing and biting. *Biological Journal of the Linnean Society* 2011;**102**:91–9.
Wainwright PC, Richard BA. Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* 1995;**44**:97–113.
Watanabe A, Fabre AC, Felice RN *et al.* Ecomorphological diversification in squamates. *Proceedings of the National Academy of Sciences* 2019;**116**:14688–97.
Weavers B. Diet of the lace monitor lizard (*Varanus varius*). *Australian Zoologist* 1989;**25**:83–5.

Webb GJW, Messel H, Crawford J *et al.* Growth rates of *Crocodylus porosus* (Reptilia: Crocodilia) from Arnhem Land, northern Australia. *Wildlife Research* 1978;**5**:385–99.
Westneat MW. Evolution of levers and linkages in the feeding mechanisms of fishes. *Integrative and Comparative Biology* 2004;**44**:378–89.
Yu X, Mohd Zanudin AB, Rusli MU *et al.* Diet reflects opportunistic feeding habit of the Asian water monitor. *Animal Biology* 2021;**72**:27–37.
Zablocki-Thomas P, Lailvaux S, Aujard F *et al.* Maternal and genetic correlations between morphology and performance traits. *Biological Journal of the Linnean Society* 2021;**134**:28–39.

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