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1 **The evolution of bite force and head morphology in scincid lizards: diet and habitat use as possible**  
2 **drivers.**

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13 **Abstract**

14 Diet and habitat use impose mechanical constraints that may impact head morphology and bite force.  
15 Skinks (Scincidae) comprise the largest family of lizards with ~1700 species currently described. They  
16 also show an important morphological and ecological diversity. Using phylogenetically informed  
17 analyses, we studied the interrelationships between ecology (diet, habitat use), head morphology, and  
18 bite force in these lizards. Our results show a strong link between body size, bite force, and diet, with  
19 herbivorous species being larger and biting harder than species from other dietary groups. Despite a  
20 lack of differences in body size and head morphology, omnivorous species bite harder than  
21 insectivorous species, likely to process the fibrous plant material that is part of their diet. Overall,  
22 lineages that evolved greater bite forces also showed an increased in relative head height allowing for  
23 more vertically oriented jaw muscles. Moreover, we find evidence for correlated evolution between  
24 bite force and head length: skinks that bite harder tend to have shorter jaws that likely provide a  
25 greater mechanical advantage when biting at the tip of the jaw. Surprisingly, habitat use does not  
26 appear to be correlated with morphological traits or bite force, but this needs to be explored further.

27 **Key words:** skinks - performance - diet - habitat use - head shape

## 28 **Introduction**

29 The vertebrate skull is a complex integrated system composed of numerous structural units (Herrel *et al.*, 2007a). These units are forged by different biotic and abiotic interactions and are critical to several  
30 functions including defense (e.g., Cooper *et al.*, 1999), locomotion (e.g., Teodecki *et al.*, 1998; Gans, 1975), male-male combat (e.g., Huyghe *et al.*, 2005; Lappin *et al.*, 2006), mating (e.g., Herrel *et al.*,  
31 1999b), drinking (e.g., Bels *et al.*, 1994; Cundall, 2000), and feeding (e.g., Wainwright and Richard, 1995; Cundall and Greene, 2000; Schwenk, 2000). As such the skull plays a key role in many different  
32 ecological and behavioral contexts (Hanken and Hall, 1993). Moreover, the skull houses and protects  
33 the brain and the main sensory organs (e.g., eyes, vomeronasal apparatus). As these organs take up  
34 space within this integrated system there may be competing demands for space (Barel, 1982) and  
35 function (Herrel *et al.*, 2001c) between these different structural units. Thus, the skull is the result of  
36 structural integration and functional compromises (Wainwright and Richard, 1995; Vanhooydonck *et al.*, 2011; Corbin *et al.*, 2015; Edwards *et al.*, 2016; Maestri *et al.*, 2016; Watanabe *et al.*, 2019), which  
37 renders our understanding of the factors driving variation in cranial morphology complex.  
38

42 The study of animal performance is important in this context as it allows variation in morphology to be  
43 linked to variation in ecology (Wainwright and Reilly, 1994; Irschick and Higham, 2016). Indeed,  
44 selection acts at the level of whole-organism performance rather than on the underlying structural  
45 components (Arnold, 1983; Careau and Garland, 2012; Lailvaux and Husak, 2014). Consequently,  
46 performance traits reflect both the behavior and the ecological context of a species (Irschick *et al.*,  
47 2005; Herrel *et al.*, 2007a; Huyghe *et al.*, 2007). One of the most relevant performance traits associated  
48 with the cranial system is bite force (Wainwright and Richard, 1995; Schluter, 2000; Anderson *et al.*,  
49 2008). This performance trait is important in the acquisition of resources, in fighting, and in defense  
50 (Herrel *et al.*, 1998; Erickson *et al.*, 2003). The use of novel resources and the conquest of new  
51 ecological niches by an animal are consequently often associated with morphological adaptations of  
52 the jaw system resulting in variation in bite force across species (Herrel *et al.*, 2004b; Cattau *et al.*,  
53 2018). Moreover, for some species, bite force has been demonstrated to be heritable (Zablocki-  
54 Thomas *et al.*, 2021) and to impact survival in the field (Herrel *et al.*, 2016), making it a key performance  
55 trait that is likely under selection.

56 Previous studies on lizards and other vertebrates have shown that the evolution towards higher bite  
57 force often goes hand in hand with the evolution of larger body size (Aguirre *et al.*, 2002; Herrel *et al.*,  
58 2004a, 2010; Chazeau *et al.*, 2013). However, irrespective of variation in body size, the evolution of a  
59 bigger head also promotes stronger bites due to the larger absolute jaw muscle volume that can be  
60 housed (Herrel *et al.*, 2001a, 2001b, 2006). Bite force has been suggested to determine diet in lizards

61 with an increase in bite force often leading to a greater trophic diversity (Wittorski *et al.*, 2016; Taverne  
62 *et al.*, 2021). Durophagy and herbivory, for example, are dietary specialisations that require high bite  
63 force due to the mechanical resistance of these hard and fibrous food items (Herrel *et al.*, 1999a;  
64 2004b; Schaerlaeken *et al.*, 2012). It has consequently been suggested that lizards eating such food  
65 items should have higher and wider heads with more massive cranial muscles than lizards that eat  
66 softer foods (Herrel and Holanova, 2008; Schaerlaeken *et al.*, 2012).

67 On the other hand, habitat use can also generate mechanical limitations affecting head size and shape  
68 and thus indirectly also drive bite force evolution. In fossorial lizards, for example, the time needed to  
69 burrow, and the energetic cost of burrowing correlate with bite force given that both are determined  
70 by head width (e.g., Navas *et al.*, 2004; Barros *et al.*, 2011; Vanhooydonck *et al.*, 2011; Le Guilloux *et al.*,  
71 2020). In addition, crevice dwellers or climbing lizards may show reduced head and body heights  
72 to be able to exploit crevices and to avoid toppling backwards during climbing (Herrel *et al.*, 2001b, c;  
73 Kohlsdorf *et al.*, 2008). Moreover, tree dwelling lizards typically have narrow heads allowing more  
74 stability when running on narrow branches (Herrel *et al.*, 2001d; Kohlsdorf *et al.*, 2008). Consequently,  
75 head size and shape may be the result of trade-offs between feeding, habitat use, and locomotion and,  
76 as such, affect bite force (Vanhooydonck *et al.*, 2011). Therefore, not only head size but also head  
77 shape is likely an important determinant of bite force (Herrel *et al.*, 2007b; Fabre *et al.*, 2014a, b).

78 In this study, we analyze the proximate determinants of bite force across 56 species of the family  
79 Scincidae. This group of lizards was chosen as it is the most species-rich lizard family characterized by  
80 an exceptional morphological and ecological diversity (Chapple *et al.*, 2021; Uetz *et al.*, 2022). Skinks  
81 show a great diversity in diet ranging from insectivorous to herbivorous and durophagous species.  
82 Moreover, they can be found on all continents except Antarctica and exploit a wide variety of habitats  
83 ranging from arboreal over fossorial to terrestrial and even semi-aquatic. In addition to this  
84 tremendous ecological diversity, scincid lizards are also morphologically diverse, yet remain relatively  
85 poorly studied (Greer, 1974; William and Peterson, 1982; Paluh and Bauer, 2017; Foster *et al.*, 2018).  
86 Capitalizing on the morphological, ecological, and taxonomic diversity of skinks, we examine here the  
87 relationship between head morphology and bite force in the sample of skinks and assess whether this  
88 differs among lizards with distinct ecologies (diet, habitat use). We specifically predict that bite force  
89 will differ between diet groups with herbivorous species biting harder than insectivorous species as  
90 shown previously for other lizard groups (Herrel *et al.*, 1999a; Vitt *et al.*, 2003; Herrel *et al.*, 2004b;  
91 Metzger and Herrel, 2005). We further predict that fossorial species, climbers, and saxicolous species  
92 will differ in head size and shape and will have lower bite forces given the constraints on head size and

93 shape in these habitats (Herrel *et al.*, 2001d; Kohlsdorf *et al.*, 2008; Barros *et al.*, 2011; Vanhooydonck  
94 *et al.*, 2011; Paluh and Bauer, 2017).

## 95 **Material and Methods**

### 96 *Specimens*

97 The sample consisted of data on head dimensions, body size, and bite force for 331 individuals across  
98 56 species of skinks. Seven of these belong to the Acontinae, 16 to the Scincinae and 33 to the  
99 Lygosominae. We use binomial nomenclature as provided by the Reptile Database (Uetz *et al.*, 2022).  
100 The number of individuals sampled per species (Table 1) varies according to the availability of  
101 specimens for morphological and *in vivo* measurements.

### 102 *Morphometrics*

103 Five morphological measurements were taken for all specimens (Fig. 1, Table 1). We used the same  
104 measurements as described in Herrel and Holanova (2008). Snout-vent length (SVL) was measured  
105 from the tip of the snout to the posterior edge of the anal scale, head length (headl) from the back of  
106 the parietal bone to the tip of the upper jaw, head height (headh) was measured at the highest part of  
107 the head and posterior to the orbit, head width (headw) at the widest part of the head and at the level  
108 of jugal bone, and lower jaw length (lj) was measured from the back of the retroarticular process to  
109 the tip of lower jaw. The bones used in these measurements were easily identified by palpation. All  
110 measurements were taken using digital calipers (Mitutoyo CD-20DC, Kawasaki, Japan; precision: 0.01  
111 mm), and were taken on the right side of the specimens.

### 112 *Bite force*

113 *In vivo* bite forces were taken in captivity or in the field. Only data for adults were used for this study  
114 and the number of individuals per species varied (Table 1). Bite force measurements were taken using  
115 an isometric Kistler force transducer (type 9203, range  $\pm 500$  N; Kistler, Zurich, Switzerland) mounted  
116 on a purpose-built holder and connected to a Kistler charge amplifier (Type 5995 A, Kistler; see Herrel  
117 *et al.*, 1999b). When the bite plates were placed between the jaws of the animals, prolonged and  
118 repeated biting typically resulted. The place of application of bite forces was standardized for all  
119 animals by metal stops that were mounted on the bite plates, thus assuring that animals always bit at  
120 the same position along the tooth row. Gape angle was standardized by moving the bite plates away  
121 from each other for larger animals resulting in animals biting at a gape angle of 30°. Surgical tape was  
122 wrapped around the bite plates to provide grip and to prevent damage to the teeth. Bite forces were  
123 measured five times for each animal and only the highest measurement was retained and considered

124 to be the maximal bite force. The maximal raw bite force recorded from the amplifier was multiplied  
125 by 0.67 to correct for the lever arms of the set-up.

#### 126 *Diet*

127 Species were classified into one of three dietary categories: herbivory (4 species), omnivory (7 species),  
128 and insectivory (45 species) (Table 2). Here, herbivorous species are considered to have a diet  
129 consisting of at least 70% fibrous plant material (i.e., all plant material except fruits and nectar),  
130 omnivorous species have a diet with 10% to 70% of plant material, and insectivorous species are those  
131 with less than 10% of plant material (Cooper and Vitt 2002). As our study included a broad diversity of  
132 species, dietary data were not always available for each species. In that case the diet of a sister taxon  
133 of the same genus for which data were available was used. *Sister taxa were used in only a few*  
134 *instances, and in all cases, diet did not show much variation within the genus. Moreover, we only*  
135 *extrapolated from other species in cases of insectivory to avoid inflating the number of independent*  
136 *origins of the less common diet types.*

#### 137 *Habitat use*

138 Skinks were classified into five habitat groups, *in part based on Meiri (2018)*: arboreal (2 species),  
139 fossorial (22 species), saxicolous (3 species), semi-aquatic (3 species), and terrestrial (26 species) (Table  
140 2). Arboreal species live in the vegetation and are rarely observed on the ground, unlike saxicolous  
141 species, which are as comfortable on the ground as in trees or rocks (Ribeiro *et al.*, 2008). Semi-aquatic  
142 species spend significant amounts of time in water and are excellent swimmers, contrary to fossorial  
143 species which spend most of their time buried in the substrate. All other species were classified as  
144 terrestrial.

#### 145 *Statistical analysis*

146 All statistical analyses were run in R (R Development Core Team, 2005). First, we calculated species  
147 means using only adults from the data set. Second, we pruned the time-calibrated phylogeny from  
148 Zheng and Wiens (2016) using the R packages ape (Paradis and Schliep, 2019) and Geiger (Pennet *et*  
149 *al.*, 2014) to include only the species in our data set (Fig. 2). To account for the non-independence of  
150 species due to shared ancestry (Felsenstein, 1985), all statistical analyses were performed in a strict  
151 phylogenetic comparative framework.

152 *To explore the effect of diet and habitat on overall body size (SVL), we performed a two-way*  
153 *phylogenetic analysis of variance (PhyANOVA) using a Brownian motion model followed by*

154 phylogenetic post-hoc tests using the `aov.phylo` function of `geiger` (Pennell *et al.*, 2014) and the  
155 `PhyANOVA` function of the `phytools` package (Revell and Revell, 2014).

156 To explore morphological differences according to diet and habitat, we performed multivariate  
157 phylogenetic analysis of covariance (phylogenetic MANOVA) using residual head dimensions. To do so  
158 all morphological variables were logarithmically transformed ( $\log_{10}$ ) to fulfil assumptions of normality  
159 and homoscedasticity (Kachigan, 1991; Sokal and Rohlf, 1995). Subsequently, the  $\log_{10}$ -transformed  
160 head dimensions were regressed on  $\log_{10}$ -transformed SVL using generalized least squares regressions  
161 with phylogenetic size correction (PGLS; Mao *et al.*, 2015) and unstandardized residuals were  
162 extracted. These were then used as input for a phylogenetic MANOVA to test the effects of diet and  
163 habitat irrespective of variation in head size. Subsequently phylogenetic ANOVAs and post-hoc tests  
164 with `phylolm` function from `phylolm` package (Ho *et al.*, 2016) were run to better understand which  
165 variables drove the results and which groups differed from one another.

166 To determine which morphological traits explained variation in bite force, all morphological and bite  
167 force measures were  $\log_{10}$ -transformed and used as input for a phylogenetic stepwise multiple  
168 regression analysis with bite force as the dependent variable and the morphological traits as the  
169 independent variables. To do this, the `phylostep` function of `phylolm` package (Ho *et al.*, 2016) was  
170 used with Brownian Motion as the evolutionary model. This evolutionary model was selected by  
171 running the `fitContinuous` function from `Geiger` package (Pennell *et al.*, 2014). The best regression  
172 model was selected based on the minimal AIC and variables in the model were selected using both  
173 forward and backward procedures. A phylogenetic regression was then using the `phylolm` function  
174 from the `phylolm` package (Ho *et al.*, 2016) to estimate the relationship between bite force and the  
175 morphological traits.

176 To investigate the effect of diet and habitat on bite force, we performed a two-way phylogenetic  
177 analysis of variance (PhyANOVA) with a Brownian motion model and followed by phylogenetic post-  
178 hoc tests using the `aov.phylo` function of `geiger` (Pennell *et al.*, 2014) and the `PhyANOVA` function of  
179 the `phytools` package (Revell and Revell, 2014). The post-hoc pairwise comparison tests taking  
180 phylogeny into account were performed using the Bonferroni method. As bite force is correlated with  
181 overall body size, we analyzed differences in bite force between diet and habitat groups using  
182 phylogenetic analysis of covariance (PhyANCOVA) with SVL as our co-variate. As no post-hoc pairwise  
183 comparisons are possible using this approach we extracted the unstandardized residuals from a bite  
184 force - SVL phylogenetic regression. These residuals (further referred to as residual bite force in the  
185 manuscript) were used as input for a PhyANOVA coupled to phylogenetic post-hoc pairwise



186 comparison tests to test for differences between diet and habitat groups. Analyses were run separately  
187 for each diet and habitat use as our a priori predictions were different.

## 188 Results

189 The two-way PhylANOVA testing for differences in snout-vent length between species consuming  
190 different prey and utilizing different habitats showed significant differences between diet groups ( $F_{2, 49} = 20.14$ ;  $P = 0.002$ ), but not between species occupying different habitats ( $F_{4, 49} = 1.47$ ;  $P = 0.58$ ). The  
191 interaction between habitat and diet was also significant ( $F_{2, 47} = 7.11$ ;  $P = 0.003$ ). Phylogenetic post-  
192 hoc tests indicated that herbivorous species were larger than omnivorous ( $P = 0.015$ ) and insectivorous  
193 species ( $P = 0.003$ ).  
194

195 A phylogenetic MANOVA detected significant differences in head shape between diet groups (Wilks'  
196 Lambda = 0.36;  $F_{8, 100} = 8.23$ ;  $P < 0.001$ ). Subsequent univariate PhylANOVAs indicated that species  
197 were different for most variables with herbivorous species having relatively wider heads than  
198 insectivorous species. A second phylogenetic MANOVA further indicated significant differences in head  
199 shape among species from different habitats (Wilks' Lambda = 0.26;  $F_{16, 147.28} = 5.05$ ;  $P = 0.018$ ).  
200 However, the univariate PhylANOVAs indicated no differences after Bonferroni correction. An  
201 inspection of the means suggests that fossorial skinks differ the most from skinks occupying other  
202 habitats and had the smallest morphological traits suggesting they have small heads for their body  
203 size.

204 A phylogenetic regression of bite force on snout-vent length was significant ( $P < 0.001$ ; Fig 3) suggesting  
205 that larger species have higher bite forces. The phylogenetic stepwise multiple regression analysis with  
206 head dimensions as predictors of bite force retained a significant model explaining 78% of the variation  
207 of bite force ( $R^2 = 0.78$ ;  $AIC_{(k=2)} = 485$ ). Head height ( $\beta = 9.68$ ) was the best predictor and positively  
208 impacted bite force while head length ( $\beta = -3.02$ ) negatively impacted bite force.

209 A two-way phylogenetic analysis of variance indicated absolute bite force differences between dietary  
210 groups ( $F_{2, 49} = 36.7$ ;  $P < 0.001$ ) but not habitat groups ( $F_{4, 49} = 2.20$ ;  $P = 0.43$ ). The interaction between  
211 diet and habitat was significant ( $F_{2, 47} = 9.37$ ;  $P = 0.002$ ). Bonferroni phylogenetic post-hoc tests  
212 indicated that herbivorous species were different from omnivorous and insectivorous species (all  $P <$   
213  $0.01$ ). Omnivorous species were also different from insectivorous species ( $P = 0.021$ ). An inspection of  
214 the means showed that herbivorous species are characterized by higher bite forces followed by  
215 omnivorous, and insectivorous species (Figure 4).

216 A phylogenetic ANCOVA performed on the bite force indicated significant differences ( $F_{2, 52} = 11.23$ ;  $P$   
217 = 0.003) between diet, but not habitats groups ( $F_{4, 50} = 6.77$ ;  $P = 0.078$ ) when taking into account  
218 differences in snout-vent length. The phylogenetic ANOVA using residual bite forces indicated  
219 significant differences between diet groups ( $F_{2, 49} = 6.78$ ;  $P = 0.499$ ). The same PhylANOVA on habitat  
220 groups indicated, however, no significant differences ( $F_{4, 49} = 5.32$ ;  $P = 0.12$ ). Phylogenetic post-hoc  
221 tests showed that herbivorous species were different from omnivorous species ( $P = 0.036$ ) and  
222 insectivorous species ( $P = 0.003$ ) in residual bite force. Insectivorous species were also different from  
223 omnivorous species ( $P = 0.039$ ). An inspection of the means showed that herbivorous species have the  
224 highest and insectivorous species the lowest relative bite forces.

## 225 **Discussion**

226 As the lizard cranial system is implicated in many functions (e.g., Baeckens *et al.*, 2017) that may  
227 require conflicting head morphologies (e.g., Paluh and Bauer, 2017), trade-offs can occur that constrain  
228 its evolution (Vanhooydonck *et al.*, 2011). Based on data on head morphology and bite force for 56  
229 species of ecologically diverse skinks, we examined the interrelationships between head morphology,  
230 bite force, and ecology to assess the ecological correlates of cranial design and performance.  
231 Phylogenetic comparative analyses showed that cranial morphology and performance were  
232 determined by dietary specialisation but not habitat use.

233 Our results show that bite force is dependent on size with larger animals showing greater bite forces  
234 as expected based on scaling relationships. Herbivorous species stand out as being larger than  
235 insectivorous and omnivorous species, thus providing them with a functional advantage and allowing  
236 them to generate larger absolute bite forces (Herrel *et al.*, 2001b; 2006; 2014). The evolution towards  
237 a larger body size in herbivorous species could also be facilitated by reduced selection on agility which  
238 is essential for lizards hunting active prey like insects or small vertebrates (Van Damme, 1999).  
239 Moreover, the ubiquitous nature of plants in the environment and a presumably low foraging cost may  
240 provide additional advantages promoting large body size in herbivorous lizards (Pough, 1973). Large  
241 body size provides several other advantages including a longer intestinal tract, higher thermal inertia,  
242 and a lower surface to volume ratio, and may thus allow herbivorous lizards to meet their energetic  
243 demands (Pough, 1973; Van Damme, 1999). Interestingly, no size difference was observed between  
244 omnivorous and insectivorous species. Omnivorous species are considered opportunistically  
245 herbivorous with much of their diet being based on arthropods. This may constrain their body size if  
246 agility is an important constraint during prey capture (Schwenk, 2000; Herrel, 2007; Hoppe *et al.*,  
247 2021).

248 Our data further highlight that herbivorous species have relatively wider heads than insectivorous  
249 species. A wider head positively affects the maximum allowable muscle volume, and thus the cross-  
250 sectional area of the jaw adductors (Bowman, 1961; Herrel *et al.*, 2005). It is tempting to interpret this  
251 difference in head morphology as the result of natural selection. Indeed, fibrous plant material  
252 requires greater bite forces to be reduced before swallowing and thus a wider head may provide a  
253 solution to these physical constraints (Herrel and De Vree, 1999; Herrel *et al.*, 1999c; 2004b). Although  
254 omnivorous species did not differ from insectivorous species in overall head shape, they did show a  
255 greater bite force. This difference might be explained by the inclusion of fibrous plant material into the  
256 diet, as highlighted for other taxa (Herrel *et al.*, 1999b; 2001a; Metzger and Herrel, 2005). Indeed, it  
257 can be expected that the most demanding food item is the one driving the upper limit of bite force  
258 and as such omnivorous species can be expected to evolve a high enough force to allow them to reduce  
259 fibrous and tough plant matter. However, the generalist morphology in omnivorous species may be  
260 driven by conflicting demands imposed by dietary diversity (Herrel *et al.*, 2004b). Thus, an increase in  
261 bite force but not head size could allow a non-specialist to switch to an omnivorous diet by allowing  
262 the inclusion of harder or tougher food items. We might have expected insectivorous species to differ  
263 morphologically from omnivorous species with a smaller head and longer snout (Toyama, 2016). This  
264 lack of morphological differences suggests that omnivorous species have retained the ancestral  
265 morphology of insectivorous species. In a second step, a specialization towards herbivory or a  
266 durophagous diet may be allowed by developing a wider, taller head (Herrel and Holanova, 2008;  
267 Schaerlaeken *et al.*, 2012; Meyers *et al.*, 2018).

268 Interestingly, and unlike what has been observed for other taxa (e.g., Barros *et al.*, 2011; Openshaw  
269 and Keogh, 2014), no differences in overall body size were observed between species occupying  
270 different habitats. This suggests that habitat use may not impose strong constraints on size in skinks.  
271 Surprisingly, our results also indicated no differences in head shape and bite force between habitat  
272 groups other than a tendency for burrowers to have narrower heads. The tendency for burrowing  
273 species to differ in head morphology is not unexpected as a fossorial lifestyle may impose significant  
274 energetic constraints on head size (Teodecki *et al.*, 1998; Navas *et al.*, 2004). The lack of strong  
275 common morphological and functional specializations in species occupying different habitats is  
276 probably the result of functional compromises (e.g., fossorial and durophagous trade-offs; Baeckens  
277 *et al.*, 2017) or of independent evolutionary trajectories of different habitat specialists and needs to  
278 be investigated further. More, since habitat can impact the width or height of the body as well as limb  
279 morphology, further analyzes of body shape are needed to better understand the constraints imposed  
280 by different habitat types on morphology in skinks (e.g., Pounds, 1988; Goodman *et al.*, 2008; Herrel  
281 *et al.*, 2008; Meiri, 2008; Pafilis and Kotsakiozi, 2008).

282 Head height and head length were the primary determinants of bite force in the species of skinks  
283 included in our study. A taller head, just like a wider head, likely increases the space available for jaw  
284 adductors which may drive the observed increase in bite force (Bowman, 1961; Herrel *et al.*, 2001b;  
285 2006). Moreover, a taller head may also allow for more vertically placed jaw adductors providing them  
286 with a greater moment arm and a more efficient conversion ratio of muscle force into bite force (Herrel  
287 *et al.*, 2001b). Conversely, head length had a negative effect on bite force (see also Westneat, 2004).  
288 An increase in head length involves an increase in the jaw outlever and given that animals were made  
289 to bite at the tips of the jaws this can be expected to negatively impact bite force (Herrel *et al.*, 2001b;  
290 2007a). Indeed, the jaws of lizards are in the form of a third-order lever, with the lower jaw being the  
291 lever arm (Kerr, 2010; Cox, 2017). Thus, the variation in the length of the head will influence the  
292 distance between the input force and the output force of the lever (Wainwright and Richard, 1995;  
293 Fabre *et al.*, 2014a). However, to better understand how head length may impact bite force a more in-  
294 depth analysis of the jaw in- and outlevers in relation to bite force is needed.

## 295 **Conclusion**

296 Our data demonstrate a strong link between body size, bite force, and diet with herbivorous species  
297 being larger and biting harder in absolute terms. Moreover, in Scincidae the evolution towards more  
298 powerful bites goes hand in hand with an increase in head height but a decrease and head length.  
299 Habitat use did not appear to be an important driver of head shape or bite force in the species included  
300 in our data set, yet this remains to be explored further using a broader and more comprehensive  
301 sample of species.

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## 310 **Data availability**

311 All data are available in table one of the manuscript.

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572 **Figure legends**

573 **Figure 1:** Illustration of the measurements taken on the heads of the lizards, illustrated on a picture  
574 of the head of *Eumeces schneideri*.

575 **Figure 2:** Time-calibrated phylogeny representing the relationships between the species included in  
576 this study modified from Zheng and Wiens (2016). The family, diet, habitat, and body form of each  
577 species are indicated.

578 **Figure 3:** Scatter plot of species mean bite force against species mean snout-vent length. The diet  
579 and the habitat of species are indicated. The species depicted on the graph are: *Corucia zebrata*,  
580 *Tiliqua occipitalis*, *Acontias meleagris*, *Typhlosaurus vermis*, *Scincus mitranus*, *Trachylepis*  
581 *quinquetaeniata* and *Ablepharus kitaibelii*. The shaded area represents 95% confidence intervals.  
582 Note that x- and y-axes are on a logarithmic scale.

583 **Figure 4:** Plot of bite force against snout-vent length. The regression lines for each diet group are  
584 represented. Red dots: insectivorous species; blue dots: omnivorous species; green dots: herbivorous  
585 species. The shaded areas represent 95% confidence intervals. Note the log-axes.

586 **Table 1:** Morphological traits and bite force of the species included in our study.

Species	n	svl (mm)	Head length (mm)	Head width (mm)	Head height (mm)	lower jaw length (mm)	Bite force (N)
<i>Ablepharus kitaibelii</i>	13	40.94 ± 2.43	6.44 ± 0.45	3.62 ± 0.28	2.55 ± 0.22	5.85 ± 0.57	0.3 ± 0.14
<i>Acontias kgalagadi</i>	5	116.12 ± 12.1	7.27 ± 0.49	3.6 ± 0.2	3.23 ± 0.86	5.7 ± 0.34	1.16 ± 0.4
<i>Acontias litoralis</i>	42	116.62 ± 11.72	6.22 ± 0.86	3.13 ± 0.24	2.66 ± 0.18	5.41 ± 0.62	0.77 ± 0.19
<i>Acontias meleagris</i>	6	194.24 ± 16.34	10.43 ± 1.08	5.81 ± 0.9	4.56 ± 0.55	7.67 ± 1.16	9 ± 1.77
<i>Acontias percivali</i>	13	224.3 ± 10.04	14.26 ± 0.15	8 ± 0.06	6.98 ± 0.08	13.25 ± 0.44	10.08 ± 2.62
<i>Bellatorias frerei</i>	1	188.36	31.56	22.48	17.9	35.7	81.47
<i>Chalcides ocellatus</i>	13	96.11 ± 24.98	13.46 ± 2.84	9.03 ± 2.24	7.7 ± 2	14.71 ± 3.18	8.51 ± 4.19
<i>Chalcides sepsoides</i>	17	83.41 ± 5.73	9.9 ± 0.48	5.93 ± 0.33	5.05 ± 0.24	9.97 ± 0.71	4.12 ± 0.75
<i>Chalcides sphenopsiformis</i>	1	83	7.99	4.97	4.25	7.51	3.16
<i>Cophoscincopus greeri</i>	4	65.73 ± 2.09	12.93 ± 0.55	8.19 ± 0.66	6.98 ± 0.56	12.14 ± 1	7.49 ± 0.79
<i>Corucia zebrata</i>	2	275 ± 7.07	50.6 ± 4.53	48.88 ± 2.37	36.03 ± 3.01	57.1 ± 1.63	206.85 ± 94.36
<i>Ctenotus uber</i>	3	86.26 ± 23.66	15.08 ± 3.61	9.99 ± 2.41	8.81 ± 2.54	17.5 ± 4.19	7.86 ± 4.19
<i>Cyclodomorphus gerrardii</i>	1	70.92	14.9	10.15	7.34	17.15	16.683
<i>Cyclodomorphus michaeli</i>	2	122.69 ± 14.11	15.49 ± 2.12	9.41 ± 1.07	9.12 ± 0.04	19.49 ± 2.7	9.74 ± 1.15
<i>Eulamprus heatwolei</i>	5	109.17 ± 23.2	21.37 ± 3.6	13.7 ± 2.9	11.24 ± 2.26	25.96 ± 5.23	16.66 ± 7.24
<i>Eumeces schneiderii</i>	3	122.01 ± 22.8	24.61 ± 1.57	16.16 ± 2.98	13.97 ± 2.53	27.48 ± 3.02	53.27 ± 6.25
<i>Isopachys gyldenstolpei</i>	1	180	10.54	6.6	5.82	8.77	5.89
<i>Leptosiphos kilimensis</i>	5	69.81 ± 14.29	10.26 ± 1.14	5.63 ± 0.84	4.18 ± 0.61	10.5 ± 1.55	2.36 ± 1.87
<i>Lerista edwardsae</i>	16	81.03 ± 7.34	7.99 ± 0.45	4.91 ± 0.35	4.18 ± 0.34	7.4 ± 0.87	2.51 ± 0.63
<i>Mochlus fernandi</i>	2	124.75 ± 11.92	22.09 ± 1.94	15.96 ± 2.21	12.19 ± 2.04	25.36 ± 3.46	41.07 ± 0.95
<i>Mochlus sundevallii</i>	15	87.31 ± 29.36	12.73 ± 2.84	7.87 ± 1.87	6.37 ± 1.73	12.95 ± 3.08	8.84 ± 5.06
<i>Morethia butleri</i>	1	45.92	8.34	4.99	3.98	8.92	1.07
<i>Panaspis togoensis</i>	1	35.59	6.89	3.4	2.2	6.95	0.33
<i>Panaspis wahlbergii</i>	1	35.59	6.89	3.4	2.2	6.95	0.33
<i>Plestiodon fasciatus</i>	4	67.72 ± 1.68	13.8 ± 1.32	9.31 ± 0.95	6.33 ± 0.76	15.72 ± 1.04	6.58 ± 1.51
<i>Plestiodon gilberti</i>	1	89.92	16.77	11.32	8.39	18.86	10.19
<i>Plestiodon laticeps</i>	17	99.87 ± 11.14	19.59 ± 2.56	15.09 ± 2.84	9.75 ± 1.77	22.43 ± 3.01	17.86 ± 4.26
<i>Plestiodon tetragrammus</i>	2	58.72 ± 3.23	9.42 ± 0.25	6.38 ± 0.06	5.33 ± 0.31	11.36 ± 0.99	1.61 ± 0.33
<i>Pygomeles braconnieri</i>	1	165	13.31	8.17	6.65	12.33	9.36
<i>Scelotes bipes</i>	9	75.47 ± 11.8	6.2 ± 0.62	3.18 ± 0.61	2.7 ± 0.32	5.53 ± 0.62	1.38 ± 0.71
<i>Scelotes limpopoensis</i>	1	61.07	7.3	3.81	2.81	7.32	0.51



<i>Scelotes montispectus</i>	1	61.58	6.81	3.32	2.83	6.4	1.27
<i>Scelotes sexlineatus</i>	5	80.25 ± 18.98	7.51 ± 1.18	3.81 ± 0.66	3.16 ± 0.54	6.61 ± 1.34	0.54 ± 0.23
<i>Scincella cherriei</i>	1	33.08	7.57	4.26	3.15	7.84	0.37
<i>Scincopus fasciatus</i>	1	154.16	35.71	24.09	18.54	36	29.212
<i>Scincus mitranus</i>	9	90.72 ± 12.14	17.93 ± 2.29	9.99 ± 1.25	9.12 ± 1.13	15.53 ± 2.01	24.87 ± 9.37
<i>Scincus scincus</i>	5	91.02 ± 3.04	18.78 ± 3.96	10.72 ± 0.72	9.82 ± 0.88	17.74 ± 1.47	18.97 ± 3.59
<i>Tiliqua multifasciata</i>	4	181.85 ± 41.77	29.14 ± 4.28	31.8 ± 6.19	21.41 ± 3.06	35.68 ± 7.09	67.23 ± 2.47
<i>Tiliqua occipitalis</i>	1	292.42	58.91	42.32	30.4	49.77	58.89
<i>Tiliqua rugosa</i>	15	281.56 ± 27.79	45.84 ± 4.81	51.41 ± 5.34	32.89 ± 3.61	56.83 ± 7.11	157.11 ± 41.84
<i>Tiliqua scincoides</i>	14	262.09 ± 67.45	48.68 ± 9.63	38.49 ± 8.97	29.57 ± 6.8	52.93 ± 9.18	158.49 ± 38.08
<i>Trachylepis capensis</i>	2	85.72 ± 10.43	15.68 ± 1.07	10.63 ± 0.5	8.78 ± 0.1	17.26 ± 0.34	15.81 ± 1.23
<i>Trachylepis homalocephala</i>	2	62.86 ± 8.22	11.66 ± 0.91	8.02 ± 0.47	5.72 ± 0.93	12.36 ± 0.83	9.97 ± 0.58
<i>Trachylepis punctatissima</i>	1	67.4	13.21	8.3	5.79	13.47	8.07
<i>Trachylepis quinquetaeniata</i>	1	107.9	19.4	10	5.6	17.8	1.05
<i>Trachylepis spilogaster</i>	2	63.68 ± 23.03	13.53 ± 3.26	8.92 ± 3.01	5.78 ± 1.86	13.22 ± 3.15	5.94 ± 4.77
<i>Trachylepis striata</i>	4	89.4 ± 18.96	18.6 ± 4.9	11.31 ± 4.12	7.8 ± 2.73	20.34 ± 6.64	19.7 ± 24.25
<i>Trachylepis sulcata</i>	5	69.82 ± 4.65	14.92 ± 1.07	9.78 ± 0.64	6.3 ± 0.22	16.29 ± 1.06	6.76 ± 2.39
<i>Trachylepis varia</i>	3	72.7 ± 23.48	17.15 ± 5.83	10.53 ± 3.85	5.85 ± 1.34	16.74 ± 5.66	9.04 ± 3.78
<i>Trachylepis variegata</i>	3	48.48 ± 2.73	10.46 ± 0.72	6.24 ± 0.24	4.42 ± 0.31	10.68 ± 0.35	1.37 ± 0.32
<i>Tribolonotus gracilis</i>	3	96.96 ± 9.91	31.1 ± 3.81	23.42 ± 2.49	15.64 ± 1.08	31.29 ± 2.94	55.88 ± 8.15
<i>Tribolonotus novaeguineae</i>	2	90.15 ± 2.69	25.52 ± 1.47	17.51 ± 1.54	12.23 ± 2.37	25.06 ± 0.1	42.41 ± 3.13
<i>Tropidophorus baconi</i>	1	126.17	29.48	20.07	15.41	31.17	43.99
<i>Typhlosaurus caecus</i>	25	186.08 ± 34.42	6.96 ± 0.8	3.59 ± 0.54	2.06 ± 0.27	4.88 ± 0.77	3.53 ± 1.6
<i>Typhlosaurus lomiae</i>	8	109.13 ± 6.75	5.57 ± 0.25	2.63 ± 0.06	2.15 ± 0.05	4.08 ± 0.45	0.45 ± 0.12
<i>Typhlosaurus vermis</i>	5	214.2 ± 48.57	6.93 ± 0.99	3.33 ± 0.37	2.79 ± 0.33	5.46 ± 0.86	1.02 ± 0.25

587 Table entries are means ± standard deviations. Morphological measurements are in mm, bite forces  
588 in Newton. n: number of specimens measured.

589 **Table 2:** Ecological traits for each species included in the study and references.

Species	Family	Diet	Habitat	References
<i>Ablepharus kitaibelii</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Acontias kgalagadi</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Acontias litoralis</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Acontias meleagris</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Acontias percivali</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Bellatorias frerei</i>	Lygosominae	Omnivorous	Terrestrial	Meiri, 2018
<i>Chalcides ocellatus</i>	Scincinae	Insectivorous	Fossorial	Andrews <i>et al.</i> , 1987; Carretero <i>et al.</i> , 2010
<i>Chalcides sepsoides</i>	Scincinae	Omnivorous	Fossorial	Meiri, 2018
<i>Chalcides sphenopsiformis</i>	Scincinae	Insectivorous	Fossorial	Andrews and Kenney, 1990; Attum <i>et al.</i> , 2004; Meiri, 2018
<i>Cophoscincopus greeri</i>	Lygosominae	Insectivorous	Semi-aquatic	Meiri, 2018
<i>Corucia zebrata</i>	Lygosominae	Herbivorous	Arboreal	Meiri, 2018
<i>Ctenotus uber</i>	Lygosominae	Omnivorous	Terrestrial	Meiri, 2018
<i>Cyclodomorphus gerrardii</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Cyclodomorphus michaeli</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Eulamprus heatwolei</i>	Lygosominae	Insectivorous	Semi-aquatic	Meiri, 2018
<i>Eumeces schneiderii</i>	Scincinae	Omnivorous	Terrestrial	Meiri, 2018
<i>Isopachys gyldenstolpei</i>	Lygosominae	Insectivorous	Fossorial	Das, 2010; Chan-ard <i>et al.</i> , 2015; Camaiti <i>et al.</i> , 2022
<i>Leptosiphos kilimensis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Lerista edwardsae</i>	Lygosominae	Insectivorous	Fossorial	Meiri, 2018
<i>Mochlus fernandi</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Mochlus sundevallii</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Morethia butleri</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Panaspis togoensis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Panaspis wahlbergii</i>	Lygosominae	Insectivorous	Terrestrial	Razzetti and Msuya, 2002; Ceriaco <i>et al.</i> , 2018
<i>Plestiodon fasciatus</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Plestiodon gilberti</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Plestiodon laticeps</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Plestiodon tetragrammus</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Pygomeles braconnieri</i>	Scincinae	Insectivorous	Fossorial	Glaw and Vences, 2007; Meiri, 2018
<i>Scelotes bipes</i>	Scincinae	Insectivorous	Fossorial	Meiri, 2018
<i>Scelotes limpopoensis</i>	Scincinae	Insectivorous	Fossorial	Meiri, 2018
<i>Scelotes montispectus</i>	Scincinae	Insectivorous	Fossorial	Fitzsimons, 1943; Branch and Braack, 1987; Bates <i>et al.</i> , 2014
<i>Scelotes sexlineatus</i>	Scincinae	Insectivorous	Fossorial	Fitzsimons, 1943; Branch and Braack, 1987; Bates <i>et al.</i> , 2014
<i>Scincella cherriei</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Scincopus fasciatus</i>	Scincinae	Insectivorous	Fossorial	Meiri, 2018
<i>Scincus mitranus</i>	Scincinae	Omnivorous	Fossorial	Meiri, 2018

<i>Scincus scincus</i>	Scincinae	Omnivorous	Fossorial	Meiri, 2018
<i>Tiliqua multifasciata</i>	Lygosominae	Herbivorous	Terrestrial	Meiri, 2018
<i>Tiliqua occipitalis</i>	Lygosominae	Herbivorous	Terrestrial	Shea, 2006; Swan <i>et al.</i> , 2017
<i>Tiliqua rugosa</i>	Lygosominae	Herbivorous	Terrestrial	Meiri, 2018
<i>Tiliqua scincoides</i>	Lygosominae	Omnivorous	Terrestrial	Meiri, 2018
<i>Trachylepis capensis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis homalocephala</i>	Lygosominae	Insectivorous	Saxicolous	Meiri, 2018
<i>Trachylepis punctatissima</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis quinquetaeniata</i>	Lygosominae	Insectivorous	Saxicolous	Spawls <i>et al.</i> , 2001; Meiri, 2018; Dendi <i>et al.</i> , 2019
<i>Trachylepis spilogaster</i>	Lygosominae	Insectivorous	Arboreal	Meiri, 2018
<i>Trachylepis striata</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis sulcata</i>	Lygosominae	Insectivorous	Saxicolous	Meiri, 2018
<i>Trachylepis varia</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis variegata</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Tribolonotus gracilis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Tribolonotus novaeguineae</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Tropidophorus baconi</i>	Lygosominae	Insectivorous	Semi-aquatic	Hikida <i>et al.</i> , 2003; Chuaynkern <i>et al.</i> , 2014
<i>Typhlosaurus caecus</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Typhlosaurus lomiae</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Typhlosaurus vermis</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018

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592 **Table 3:** Results of the phylogenetical ANOVAs.

<b>Variable</b>	<b>Df</b>	<b>F</b>	<b>P<sub>phylo</sub></b>
Snout-vent length			
Diet	2, 49	<b>20.14</b>	<b>0.002</b>
Habitat	4, 49	1.47	0.58
Bite force			
Diet	2, 49	<b>36.7</b>	<b>&lt; 0.001</b>
Habitat	4, 49	2.20	0.43
Relative bite force			
Diet	2, 49	<b>6.78</b>	<b>0.0499</b>
Habitat	4, 49	5.32	0.12
Factor: diet			
Head length	2, 53	<b>6.22</b>	<b>0.062</b>
Head height	2, 53	<b>9.39</b>	<b>0.015</b>
Head width	2, 53	<b>8.31</b>	<b>0.02</b>
Lower jaw length	2, 53	4.85	0.102
Factor: habitat			
Head length	4, 51	<b>9.44</b>	<b>0.033</b>
Head height	4, 51	7.11	0.063
Head width	4, 51	<b>10.44</b>	<b>0.028</b>
Lower jaw length	4, 51	<b>11.88</b>	<b>0.014</b>

593 Significant results are in bold.

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595 **Table 4:** Bonferroni post-hoc results testing for differences between for diet categories.

	Herbivorous	Insectivorous	Omnivorous
<i>Snout-vent length</i>			
Herbivorous		<b>0.003</b>	<b>0.015</b>
Insectivorous	<b>0.003</b>		0.534
Omnivorous	<b>0.015</b>	0.534	
<i>Bite force</i>			
Herbivorous		<b>0.003</b>	<b>0.003</b>
Insectivorous	<b>0.003</b>		<b>0.021</b>
Omnivorous	<b>0.003</b>	<b>0.021</b>	
<i>Realtive bite force</i>			
Herbivorous		0.594	1
Insectivorous	0.594		0.15
Omnivorous	1	0.15	
<i>Head length</i>			
Herbivorous		0.222	1
Insectivorous	0.222		0.282
Omnivorous	1	0.282	
<i>Head height</i>			
Herbivorous		0.075	1
Insectivorous	0.075		0.126
Omnivorous	1	0.126	
<i>Head width</i>			
Herbivorous		<b>0.048</b>	0.528
Insectivorous	<b>0.048</b>		0.396
Omnivorous	0.528	0.396	
<i>Lower jaw length</i>			
Herbivorous		0.33	1
Insectivorous	0.33		0.477
Omnivorous	1	0.477	

596 Significant results are in bold.

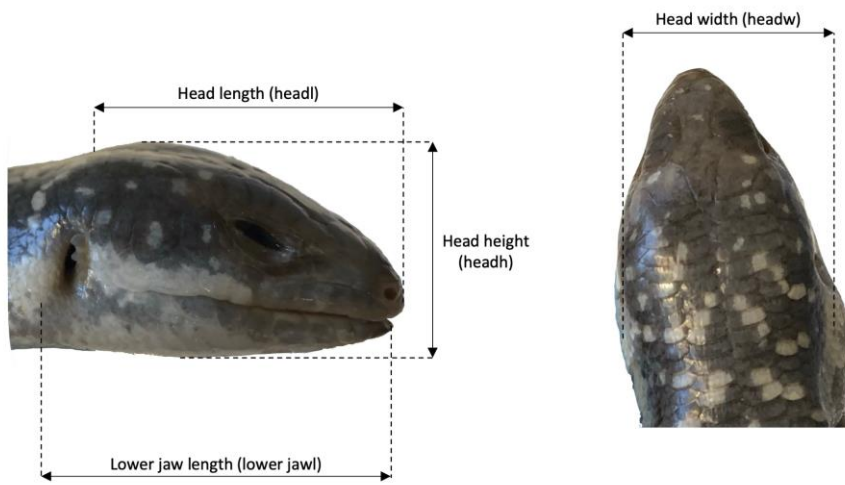
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598 **Table 5:** Results of linear regressions.

<b>Variable</b>	<b>Coefficient</b>	<b>SE</b>	<b>R<sup>2</sup></b>	<b>P</b>
Phylogenetic regression on bite force				
Snout-vent length	<b>1.73</b>	<b>0.217</b>	<b>0.54</b>	<b>&lt; 0.001</b>
Phylogenetic stepwise multiple regression with bite force as factor				
Head height	<b>9.68</b>	<b>0.45</b>	<b>0.7</b>	<b>&lt; 0.001</b>
Head length	<b>-3.02</b>	<b>0.37</b>	<b>0.46</b>	<b>&lt; 0.001</b>

599 Significant results are in bold. SE; Standard Errors

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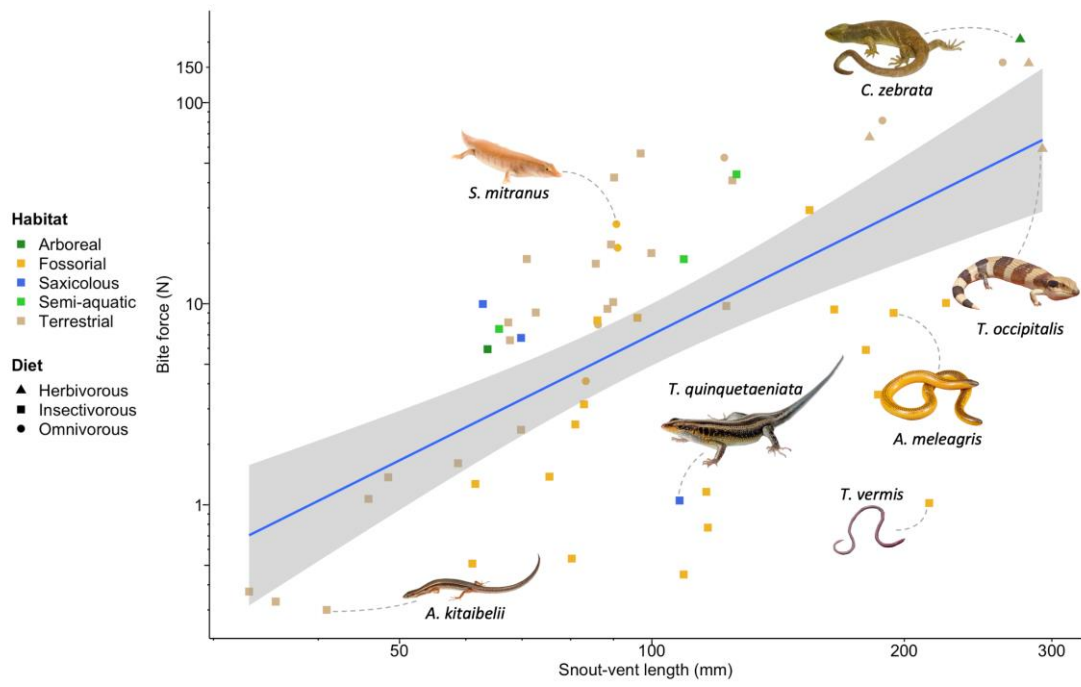


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