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► **To cite this version:**

Margot Le Guilloux, Aurélien Miralles, John Measey, Bieke Vanhooydonck, James O'reilly, et al.. Trade-offs between burrowing and biting force in fossorial scincid lizards?. *Biological Journal of the Linnean Society*, 2020, 130 (2), pp.310-319. 10.1093/biolinnean/blaa031 . hal-02990274

**HAL Id: hal-02990274**

**<https://hal.science/hal-02990274>**

Submitted on 7 Nov 2020

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1 **Trade-offs between burrowing and biting force in fossorial scincid lizards?**

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16

17 # pages: 12

18 # tables: 1

19 # figures: 3

20 **Abstract**

21 Trade-offs are thought to be important in constraining evolutionary divergence as they may limit  
22 phenotypic diversification. The cranial system plays a vital role in many functions including defensive,  
23 territorial, predatory, and feeding behaviors in addition to housing the brain and sensory systems.  
24 Consequently, the morphology of the cranial system is affected by a combination of selective  
25 pressures that may induce functional trade-offs. Limbless head-first burrowers are thought to be  
26 constrained in their cranial morphology as narrow heads may provide a functional advantage for  
27 burrowing. However, having a wide and large head is likely beneficial in terms of bite performance.  
28 We used 15 skink species to test for the existence of trade-offs between maximal push and bite  
29 forces, and explored the patterns of covariation between external head and body morphology and  
30 performance. Our data show that there is no evidence of a trade-off between bite and burrowing in  
31 terms of maximal force. Species that generate high push forces also generate high bite forces. Our  
32 data also show that overall head size covaries with both performance traits. However, future studies  
33 exploring trade-offs between force and speed or the energetic cost of burrowing may reveal other  
34 trade-offs.

35 **Keywords:** skink – morphology – covariation – divergence – cranial system – head-first burrowers.

## 36 Introduction

37 The phenotype of an organism reflects the selective pressures exerted by activities that are essential  
38 to its survival and its reproduction (Arnold, 1993). Sometimes, however, the functional demands  
39 exerted by different performance traits may result in trade-offs. Indeed, functional trade-offs arise  
40 when different functions exert conflicting pressures on the same anatomical structures (Arnold,  
41 1992; Van Damme *et al.*, 2002, 2003). Previous studies have further suggested that trade-offs may in  
42 some cases limit phenotypic variation by constraining evolutionary divergence (Vanhooydonck *et al.*,  
43 2001; Levinton & Allen, 2005; Konuma & Chiba, 2007; Herrel *et al.*, 2009). The cranial system plays a  
44 vital role in many activities including defensive, territorial, predatory and feeding behaviors in  
45 addition to housing and protecting the brain and major sensory organs (Andrews *et al.*, 1987; Cooper  
46 & Vitt, 1993; Herrel *et al.*, 2007; Kohlsdorf *et al.*, 2008; Dumont *et al.*, 2016). Consequently, the  
47 morphology of the cranial system is affected by these combined selective pressures which may  
48 potentially induce functional trade-offs.

49 The hypothetical trade-off between biting and burrowing performance is particularly interesting in  
50 limbless burrowing animals. These organisms are obligate head-first burrowers and the evolution of  
51 their morphology is thought to be constrained. Indeed, because the energy required for burrowing  
52 increases exponentially with body and head diameter (Navas *et al.*, 2004), having a thin body and a  
53 narrow head may provide a functional advantage for burrowing. Yet, this is likely detrimental in  
54 terms of bite performance (Verwaijen *et al.*, 2002; Navas *et al.*, 2004; Herrel & O'Reilly, 2006;  
55 Vanhooydonck *et al.*, 2011; Baeckens *et al.*, 2017; Hohl *et al.*, 2017). Maximum bite force has been  
56 suggested to limit the type and size of food an animal can eat (Herrel *et al.* 1999, 2001, 2008; Aguirre  
57 *et al.*, 2003; McBrayer & Corbin, 2007; Edwards *et al.*, 2013). Consequently, a cranial form optimized  
58 for soil penetration may compromise the types of food an animal can eat and *vice versa* (Andrews *et al.*  
59 *et al.*, 1987; Barros *et al.*, 2011; Baeckens *et al.*, 2017).

60 Burrowing is a complex behavior that remains rather poorly understood in limbless head-first  
61 burrowing vertebrates (but see Gaymer, 1971; Gans, 1973; O'Reilly *et al.*, 1997; Teodecki *et al.*, 1998;  
62 Navas *et al.*, 2004; De Schepper *et al.*, 2005). The maximal push force that an animal can generate is  
63 likely important as it may allow an animal to penetrate a greater variety of soil types, and thus  
64 expand its resource base in terms of potential habitat and food resources. As limbless species burrow  
65 by recruiting muscles along the long axis of the body (Rieppel, 1981; Navas *et al.*, 2004;  
66 Vanhooydonck *et al.*, 2011; Hohl *et al.*, 2017), the diameter and size of the body should be related to  
67 the maximal push force it can generate. However, to facilitate soil penetration the width of the head  
68 should rather be narrow as this optimizes the pressure for a given force (e.g. Measey & Herrel, 2006;

69 Herrel & Measey, 2010; Barros *et al.*, 2011). Moreover, the speed by which it can penetrate the soil  
70 (and not only the force generated) is also likely a factor significantly contributing to the burrowing  
71 performance (Ducey *et al.*, 1993; Teodecki *et al.*, 1998; Vanhooydonck *et al.*, 2011). Although few  
72 quantitative data exist, a previous study suggested the presence of a trade-off between bite force  
73 and burrowing speed in a limbless skink, *Acontias percevali*, mediated by the conflicting demands on  
74 head dimensions (Vanhooydonck *et al.*, 2011). Whether this is more generally the case and whether  
75 trade-offs also exist between bite force and push force remains unknown, however. As burrowing  
76 force is dependent on the axial musculature different anatomical traits are responsible for the  
77 generation of bite force versus burrowing force. Consequently, trade-offs between these two  
78 performance traits, if present, are not mediated by direct functional conflict for the optimization of  
79 single functional trait. Rather, burrowers can be expected to have narrow heads for efficient soil  
80 penetration which may come at a cost of bite force.

81 Here, we test for the presence of a trade-off between maximal bite force and the maximal push force  
82 in a range of burrowing and leaf-litter dwelling skinks. Scincid lizards represent an ideal study system  
83 as this family includes a variety of ecologies and morphologies with quadrupedal surface-dwelling  
84 species, epigeal serpentiform species with partially reduced front- and/or hindlimbs, and burrowing  
85 completely limbless species, and a plethora of intermediate forms (Pianka & Vitt, 2003; Miralles *et al.*  
86 2015; Wagner *et al.*, 2018; Bergmann & Morinaga, 2019). At least 15 independent evolutions of a  
87 serpentiform body form have taken place within the group (Benesh & Withers, 2002; Miralles *et al.*,  
88 2012) allowing for a robust framework to test for associations between life-style, performance, and  
89 morphology. Consequently, we also explore the patterns of covariation between head and body  
90 morphology and the two performance traits studied here (bite force and push force).

## 91 **Materials and methods**

### 92 ***Animals***

93 Morphological measurements were performed on 197 individuals and performance measurements  
94 were obtained for 176 individuals across 14 different species of skinks (Table 1). Animals were  
95 sampled between 2000 and 2017. The specimens were adults of often unknown sex. Data were  
96 collected *in situ* in the field or in the lab for species that were obtained through the pet trade. An  
97 additional 20 individuals from the collections of the National Museum of Natural History in Paris  
98 were used for morphological measurements.

### 99 ***Morphometrics***

100 Each individual was weighed using an electronic balance (Ohaus,  $\pm 0.1\text{g}$ ). Head length, head width,  
101 head depth and lower jaw length were measured using a digital caliper (Mitutoyo,  $\pm 0.01\text{ mm}$ ) as  
102 described previously (Herrel and Holanova, 2008). The snout-vent length measured by stretching the  
103 animals along a ruler ( $\pm 1\text{ mm}$ ).

#### 104 ***Maximal push force***

105 Maximal push forces were measured in the field or in the lab following the protocol described in  
106 Vanhooydonck *et al.* (2011). Measurements of peak push forces during burrowing were made using a  
107 custom piezoelectric force platform (Kistler Squirrel force plate,  $\pm 0.1\text{ N}$ ). The force platform was  
108 positioned on a custom-designed metal base and connected to a charge amplifier (Kistler Charge  
109 Amplifier type 9865). A Perspex block with 1 cm deep holes of different diameters was mounted on  
110 the force plate, level with the front edge. One of the holes was loosely filled with soil from the  
111 container of the animal that was tested. A Perspex tunnel with a diameter similar to the maximal  
112 body diameter of the test animal was mounted on the metal base in front of (but not touching) the  
113 force plate, and aligned with the soil-filled hole in the Perspex block. First, a skink was introduced  
114 into the tunnel and allowed to move through it until reaching the soil-filled chamber. Next, the  
115 animal was stimulated to burrow into the soil by tapping the end of the tail sticking out of the tunnel,  
116 or by prodding the animal inside the tunnel with the blunt end of a thin wooden stick. Forces were  
117 recorded during a 60 s recording session at 500 Hz, and three trials were performed for each  
118 individual, with at least 1 h between trials. Forces were recorded in three dimensions using the  
119 Bioware software (Kistler). For each individual we then extracted the highest peak resultant force  
120 across all trials as an indicator of that animal's maximal push force.

#### 121 ***Maximal bite force***

122 Maximal bite forces were measured in the field or the lab following Herrel *et al* (1999). In brief, *in*  
123 *vivo* bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler Inc.,  
124 Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type  
125 5058 A, Kistler Inc.). Biting causes the upper plate to pivot around the fulcrum, and thus pull is  
126 exerted on the transducer. Capture of the animals typically resulted in a characteristic threat  
127 response where the jaws are opened maximally. The free end of the holder was then placed between  
128 the jaws of the animal, which immediately resulted in fierce and prolonged biting. The gape angle ( $\pm$   
129  $30^\circ$ ) and the place of application of the bite force was standardized with animals always biting at the  
130 tips of the jaws. Measurements were repeated five times for each animal and the maximum value  
131 recorded was considered to be the maximal bite force for that animal.

## 132 **Analyses**

133 Morphometric and force data were  $\text{Log}_{10}$ -transformed before analysis to ensure normality and  
134 homoscedasticity.

135 All analyses were performed in R (version 3.4.0) while taking into account the phylogenetic  
136 relationships among species. The phylogenetic framework used was obtained from the molecular  
137 data set of Pyron *et al.* (2013; Fig. 1). This required the reconstruction of a phylogeny by pruning the  
138 tree to include only species for which we had performance and morphological data. First, a  
139 phylogenetic generalized least squares (PGLS) regression was run in R (function `gls` with `corBrownian`  
140 in `Phytools`; Revell, 2012) with the mean maximal push force per species against mean maximal bite  
141 forces to test for the presence of a trade-off between bite and push force. To test for co-variation  
142 between morphology and performance we ran a phylogenetic two-block partial least squares  
143 analysis ( $\phi$ 2bPLS) using the function 'phylo.integration' implemented in 'geomorph' in R (Adams,  
144 Otárola-Castillo & Paradis, 2013). This method quantifies the degree of association between two data  
145 matrices. It is a descriptive multivariate analysis robust to multicollinearity between variables and  
146 therefore suitable for the use of morphometric and performance variables. The analysis generates  
147 axes that explain the covariance between the two data matrices.

148 As body size simultaneously impacts head and body dimensions and forces, we ran PGLS analyses  
149 with snout-vent length (SVL) or body mass as our predictor and morphometric and performance  
150 traits as our independent variables and extracted the unstandardized residuals. Next, we used a  
151 regression to explore the existence of a trade-off between our two residual performance traits  
152 independent of variation in overall body size. Finally, we ran a two-block partial least squares  
153 analyses (2BPLS) on the residual data to explore patterns of covariation between morphology and  
154 performance independent of variation in overall size using.

## 155 **Results**

### 156 *Trade-offs between bite force and push force*

157 The linear regression taking into account phylogeny shows that maximum push force is positively  
158 correlated with maximal bite force (PGLS:  $r = 1.36$ ,  $P < 0.001$ ), suggesting that species that produce  
159 strong push forces are also those who produce strong bite forces and that are generally larger (Fig.  
160 2A). Analyses performed on the snout-vent length corrected data show a similar result (PGLS:  $r =$   
161  $0.89$ ,  $P < 0.001$ ) with animals that bite harder for a given snout-vent length also being better pushers

162 (Fig. 2B). However, when correcting force measurements for body mass, residual bite force was no  
163 longer correlated with residual push force ( $r = -0.63$ ,  $P = 0.053$ ; Fig. 2C). An inspection of the plot (Fig.  
164 2C) suggests that more elongate and smaller species like *Typhlosaurus vermis* and *T. lomiae* as well as  
165 *Acontias litoralis* and *A. kgalagadi* tend to have relatively higher push forces whereas the stockier,  
166 larger species like *Scincus scincus*, *A. meleagris*, and *Mochlus sundevalli* appear to have relatively  
167 large bite forces but low push forces.

#### 168 *Covariation between morphology and performance*

169 The Phylogenetic two-blocks PLS analysis was significant ( $rPLS = 0.983$ ,  $P = 0.001$ ). Heavier, larger and  
170 wider animals with longer, taller and wider heads produce larger push and also bite forces (Fig. 3A).  
171 The two-block PLS analysis run on the size-corrected data with snout-vent length as a covariate was  
172 also significant ( $rPLS = 0.969$ ,  $P < 0.001$ ; Fig. 3B). This analysis indicates that the maximal push force  
173 and the maximal bite force co-vary both principally with overall body and head robustness with  
174 animals that are more elongate producing relatively lower push and bite forces. An analysis on the  
175 size corrected data using body mass was also significant ( $rPLS = 0.73$ ,  $P = 0.012$ ), yet showed a  
176 different pattern. This analysis shows that more elongate animals produce relatively higher push  
177 forces whereas the more robust limbed species with wide heads and bodies produce low push but  
178 high bite forces for their body mass (Fig. 3C).

#### 179 **Discussion**

180 Our results based on a broad range of burrowing and leaf-litter dwelling skinks show that there is no  
181 direct trade-off between bite force and burrowing force in this group. Species that produce strong  
182 push forces are also those which produce strong bite forces in both absolute and relative terms.  
183 These results suggest that whereas bite force may trade-off with burrowing speed (Teodecki *et al.*,  
184 1998; Vanhooydonck *et al.*, 2011) this may not be the case for push force. Indeed, the same traits  
185 that favor increased bite force (large, robust heads and wide bodies) also appear to favor high push  
186 forces, at least in absolute terms. This makes intuitive sense as the muscles used to generate both  
187 bite and push force are positioned to the lateral side of the body in scincid lizards (Huyghe *et al.*,  
188 2009; Vanhooydonck *et al.*, 2011). For example, the external adductor muscle is one of the largest  
189 contributors to overall bite force generation and lies external to the mandible (Vanhooydonck *et al.*,  
190 2011). Similarly, the iliocostalis and longissimus muscles that generate the push forces are also  
191 positioned laterally to the vertebral column. Consequently, wider heads and wider bodies should  
192 induce an increase in both absolute bite and push force. However, whereas these traits may favor  
193 absolute force, the speed by which animals can penetrate the soil may be negatively impacted by the



194 presence of wider heads and bodies (Teodecki *et al.*, 1998; Vanhooydonck *et al.*, 2011). Moreover,  
195 the energetic cost of burrowing may also be negatively impacted by these traits (Navas *et al.*, 2004).

196 However, whereas the limbed species are the best biters in absolute terms and when corrected for  
197 body mass the more elongate specialized burrowers (e.g. *Acontias*, *Scelotes*, *Typhlosaurus*) actually  
198 produce greater push forces. Indeed, the specialized head-first limbless burrowers like *Acontias* or  
199 *Typhlosaurus* have higher push forces for their mass despite being more elongate and less robust.  
200 Moreover, individuals of these species were usually captured at deeper soil depths and in less sandy  
201 soils (A. Herrel & J. Measey, personal observations) suggesting that they are overall better at  
202 burrowing. Thus, rather than absolute push force relative push force may be the principal driver of  
203 burrowing specialization. However, given the paucity of quantitative data on soil hardness and  
204 burrow depth in fossorial animals a quantitative analysis of these patterns is not possible.  
205 Additionally, it would be of interest to gather similar data on other groups of fossorial skinks from  
206 different radiations (Australia, Madagascar, Philippines, see Wagner *et al.*, 2018; Morinaga &  
207 Bergmann, 2020) as the data in the present study are strongly biased towards African skinks,  
208 especially the Acontinae.

#### 209 ***Traits affecting bite and burrow performance***

210 Despite the absence of trade-offs, we hypothesized that morphological traits that co-vary with each  
211 type of performance trait might be different. In contrast to our prediction, the phylogenetic two-  
212 block PLS analysis showed that all traits covaried with both forces, especially body mass. Heavier,  
213 larger and wider animals with long, tall and wide heads produced greater forces in absolute terms.  
214 However, analyses performed on the size corrected data showed different results. Indeed, whereas  
215 the relative mass and the diameter of the body and head relative to the length of the animal appear  
216 to drive both variation in bite force and push force, as with absolute data, when correcting for body  
217 mass this was no longer the case. More robust and less elongate limbed species with wide and deep  
218 heads like *Chalcides ocellatus*, *Scincus scincus* or *Mochlus sundevalli* produce relatively high bite, yet  
219 low push forces (see Fig. 3C). This is expected as it had been shown that the maximal bite force  
220 generated by an individual is determined by its head dimensions (Verwaijen *et al.*, 2002; Navas *et al.*,  
221 2004; Herrel & O'Reilly, 2006; Vanhooydonck *et al.*, 2011; Baeckens *et al.*, 2017; Hohl *et al.*, 2017).  
222 Maximum push force has, however, been suggested to be determined by the total length of the body  
223 (Rieppel, 1981; Navas *et al.*, 2004; Measey & Herrel, 2006; Barros *et al.*, 2011; Vanhooydonck *et al.*,  
224 2011; Hohl *et al.*, 2017) as also suggested by our data. Indeed, more elongate species of the genera  
225 *Typhlosaurus* as well as the more elongate *Acontias* species (*A. litoralis*, *A. kgalagadi*) showed high  
226 push forces yet low bite forces (Fig. 3C). It would, however, be of interest to perform finer scale

227 analyses of head shape or skull shape using geometric morphometric approaches. This may also  
228 allow teasing apart of differences between the back and the front of the skull likely impacted by  
229 constraints on biting versus burrowing (Cornette *et al.*, 2015).

230 In conclusion, we were unable to demonstrate a trade-off between bite and push force. Whereas  
231 both forces were positively correlated in both absolute and relative terms, the traits driving variation  
232 in force differed when body size was taken into account. For a given body mass the more elongate  
233 forms produced higher push forces, possibly due to the fact that to create push forces the axial  
234 muscles along the entire body are used. Ecological as well as detailed anatomical studies are clearly  
235 needed to better understand the relationships between morphology, performance and ecology as  
236 well as the anatomical drivers of variation in performance.

### 237 **Acknowledgments**

238 We would like to thank Günter Wagner and an anonymous reviewer for helpful and constructive  
239 comments on a previous version of this manuscript. We would also like to thank Anne-Claire Fabre  
240 for extensive help with the analyses and without whom this paper would not have been possible.  
241 South African field-work was conducted in under provincial research permits in the Western Cape  
242 (AAA007-00035-0035), Limpopo (333-00015) and Northern Cape (FAUNA 1243/2008). AH and JM  
243 thank Krystal Tolley and the National Research Foundation (NRF) of South Africa (South African  
244 Biosystematics Initiative-SABI, Key International Science Collaboration-KISC), and ethics clearance  
245 from SANBI (0010/08).

### 246 **Funding**

247 This work was supported by a grant from Agence Nationale de la Recherche under the LabEx ANR-10-  
248 LABX-0003-BCDiv, in the program 'Investissements d'avenir' n\u0001 ANR-11-IDEX-0004-02.

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## 362 **Figure legends**

363 **Figure 1:** phylogeny used in the analyses modified from Pyron et al. (2013).

364 **Figure 2:** Phylogenetic regressions of species averages of maximal bite force against maximal push  
365 force. (A) Absolute push force is significantly correlated with absolute bite force. (B) Residual bite  
366 force is significantly and positively correlated with residual push force when correcting for overall  
367 snout-vent length. (C) Residual bite force is no longer related to variation in residual push force when  
368 corrected for variation in body mass.

369 **Figure 3:** Covariance between morphological and performance data. (A) Phylogenetic two-block  
370 partial least square analysis between morphology and performance illustrating that more robust  
371 species (i.e. with greater body mass and bigger heads) produce greater push and bite forces. (B) Two-  
372 block partial least square analysis on the force and morphological data corrected for variation in  
373 snout-vent length. Species with relatively higher mass, heads size and body diameter produce greater  
374 bite and push forces. (C) Two-block partial least square analysis on the force and morphological data  
375 corrected for variation in body mass showing that species that are relatively more elongate (higher  
376 snout-vent length for their mass) show relatively higher push forces. In contrast, species that are  
377 stockier, less elongate and with bigger heads produce relatively higher bite forces.

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379 Table 1. Mean and standard deviation of morphological and functional data for the 14 species included in this study.

Species	SVL (mm)	Head length (mm)	Head width (mm)	Head depth (mm)	Lower jaw length (mm)	Mass (g)	Body diameter (mm)	Push force (N)	Bite force (N)
<i>Acontias kgalagadi</i>	116.12 ± 12.10 (N = 5)	7.27 ± 0.49 (N = 5)	3.60 ± 0.20 (N = 5)	3.23 ± 0.86 (N = 5)	5.70 ± 0.34 (N = 5)	1.95 ± 0.64 (N = 5)	4.28 ± 0.37 (N = 5)	0.56 ± 0.20 (N = 5)	1.16 ± 0.40 (N = 5)
<i>Acontias litoralis</i>	108.34 ± 16.64 (N = 47)	5.95 ± 0.91 (N = 47)	3.01 ± 0.29 (N = 47)	2.54 ± 0.26 (N = 47)	5.09 ± 0.76 (N = 47)	1.39 ± 0.45 (N = 47)	3.38 ± 0.48 (N = 47)	0.51 ± 0.25 (N = 41)	0.73 ± 0.19 (N = 42)
<i>Acontias meleagris</i>	194.24 ± 16.34 (N = 6)	10.43 ± 1.08 (N = 6)	5.81 ± 0.90 (N = 6)	4.56 ± 0.55 (N = 6)	7.67 ± 1.16 (N = 6)	9.74 ± 2.85 (N = 6)	7.26 ± 1.30 (N = 6)	3.13 ± 0.47 (N = 3)	8.99 ± 1.77 (N = 6)
<i>Acontias percivali</i>	246.83 ± 12.48 (N = 12)	13.88 ± 1.34 (N = 12)	8.00 ± 0.75 (N = 12)	6.98 ± 0.70 (N = 12)	13.25 ± 0.76 (N = 7)	16.87 ± 5.07 (N = 12)	9.28 ± 0.99 (N = 12)	5.32 ± 0.85 (N = 12)	10.08 ± 3.06 (N = 12)
<i>Chalcides ocellatus</i>	80.88 ± 24.41 (N = 16)	11.85 ± 2.76 (N = 16)	7.76 ± 2.18 (N = 16)	6.53 ± 1.95 (N = 16)	12.96 ± 3.04 (N = 16)	10.28 ± 6.88 (N = 16)	10.77 ± 3.26 (N = 16)	4.56 ± 1.39 (N = 14)	6.82 ± 4.19 (N = 13)
<i>Chalcides sepsoides</i>	83.41 ± 5.73 (N = 17)	9.90 ± 0.48 (N = 17)	5.93 ± 0.33 (N = 17)	5.05 ± 0.24 (N = 17)	9.97 ± 0.71 (N = 17)	4.66 ± 1.02 (N = 17)	7.45 ± 0.65 (N = 17)	2.46 ± 0.75 (N = 17)	4.12 ± 0.75 (N = 17)
<i>Mochlus sundevallii</i>	83.64 ± 18.88 (N = 10)	12.40 ± 2.40 (N = 10)	7.68 ± 1.55 (N = 10)	6.20 ± 1.19 (N = 10)	12.64 ± 2.29 (N = 10)	9.83 ± 6.55 (N = 10)	6.97 ± 1.32 (N = 7)	1.56 ± 1.25 (N = 7)	12.33 ± 6.45 (N = 10)
<i>Pygomeles braconnieri</i>	109.67 ± 37.11 (N = 6)	10.61 ± 1.72 (N = 6)	6.25 ± 1.44 (N = 6)	5.06 ± 0.99 (N = 6)	9.40 ± 1.98 (N = 6)	12.78 ± 7.34 (N = 6)	7.99 ± 3.85 (N = 6)	7.50 (N = 1)	9.36 (N = 1)
<i>Scelotes bipes</i>	74.56 ± 10.67 (N = 12)	6.18 ± 0.57 (N = 12)	3.22 ± 0.58 (N = 12)	2.62 ± 0.42 (N = 12)	5.46 ± 0.58 (N = 12)	1.56 ± 0.73 (N = 11)	3.84 ± 0.66 (N = 12)	0.36 ± 0.16 (N = 8)	1.33 ± 0.70 (N = 11)
<i>Scelotes montispectus</i>	61.58 (N = 1)	6.81 (N = 1)	3.32 (N = 1)	2.83 (N = 1)	6.40 (N = 1)	1.00 (N = 1)	3.55 (N = 1)	0.55 (N = 1)	1.27 (N = 1)

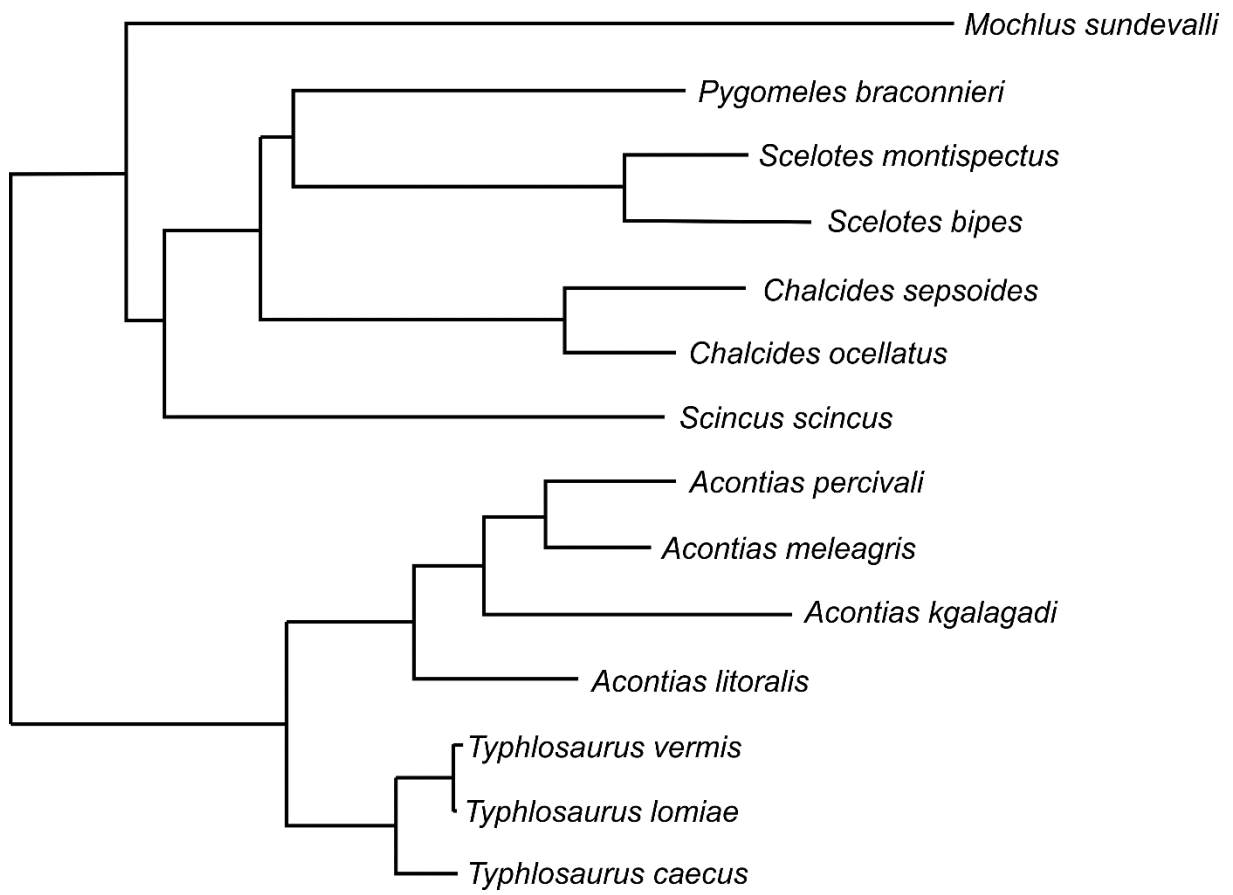


<i>Scincus scincus</i>	92.20 ± 3.04 (N = 5)	18.76 ± 0.72 (N = 5)	10.65 ± 0.75 (N = 5)	9.92 ± 0.88 (N = 5)	18.44 ± 1.47 (N = 5)	18.75 ± 3.96 (N = 5)	14.76 ± 1.35 (N = 5)	7.72 ± 2.04 (N = 5)	18.39 ± 3.59 (N = 5)
<i>Typhlosaurus caecus</i>	171.30 ± 34.42 (N = 32)	6.70 ± 0.80 (N = 32)	3.39 ± 0.54 (N = 32)	1.98 ± 0.27 (N = 32)	4.67 ± 0.77 (N = 32)	3.42 ± 1.48 (N = 32)	4.27 ± 0.72 (N = 32)	2.11 ± 1.02 (N = 32)	3.01 ± 1.60 (N = 32)
<i>Typhlosaurus lomiae</i>	106.33 ± 10.49 (N = 9)	5.52 ± 0.29 (N = 9)	2.60 ± 0.09 (N = 9)	2.13 ± 0.07 (N = 9)	3.99 ± 0.50 (N = 9)	0.92 ± 0.19 (N = 9)	2.91 ± 0.17 (N = 9)	0.32 ± 0.08 (N = 8)	0.45 ± 0.12 (N = 9)
<i>Typhlosaurus vermis</i>	195.33 ± 48.57 (N = 6)	6.76 ± 0.99 (N = 6)	3.18 ± 0.37 (N = 6)	2.67 ± 0.33 (N = 6)	5.40 ± 0.86 (N = 6)	2.68 ± 1.09 (N = 6)	3.56 ± 0.39 (N = 6)	1.58 ± 0.33 (N = 5)	0.93 ± 0.25 (N = 6)

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